Behaviour and conservation of whale sharks on the Belize Barrier Reef

by

Rachel T. Graham

Thesis submitted for the degree of PhD
in
Environmental Science

Environment Department
University of York
September 2003

Abstract

Populations of large pelagic migratory fish have declined steeply in the past two decades due to overexploitation. Efforts to manage or protect these species have been constrained by their cryptic nature and a paucity of knowledge of their biology and behaviour. Conservation of migratory animals requires understanding of the movements of individual animals, populations and species. Whale sharks (*Rhincodon typus*), the main subject of this thesis, are large, planktivorous, highly mobile and pantropical, and their life history traits of late maturity, longevity and low fecundity make them vulnerable to overexploitation but little is known of their behaviour.

A five-year study of their behaviour in an unexploited population was undertaken on the Belize Barrier Reef between 1998 and 2003, in relation to a spatio-temporally predictable food source, in order to improve management and conservation. Whale sharks displayed strong diel, intra- and inter-seasonal fidelity to Gladden Spit, a particular site that hosts large seasonal aggregations of spawning snappers. The population of whale sharks at Gladden Spit is transient and composed primarily of juvenile males. Individuals measured a mean total length of 6.3 m ± SD 1.7 m (range: 3.0 m to 12.7 m; error of ± 0.50 m). Satellite pop-off tags revealed that the whale sharks were physiologically robust, being able to dive over 1000 m and withstand temperatures under 5^0C possibly for orientation or to locate abundant sources of food. Diving behaviour displayed a strong circadian and circalunar component.

After feeding on cubera and dog snapper (*Lutjanus cyanopterus* and *L. jocu*) spawn at Gladden, sharks dispersed throughout the Belize Barrier Reef with directed movements of over 550 km recorded to the tip of the Yucatan Peninsula and east of the Bay Islands in Honduras. Whale sharks did not appear to aggregate at any of seven other documented fish spawning aggregation sites on the Belize Barrier Reef.

The mutton snapper (*L. analis*) fishery based at Gladden Spit experienced significant declines in catch per unit effort and size of fish caught between 2000 and 2002. Declines occured despite a drop in the number of fishers fishing the spawning aggregation since the inception of the fishery. Whale sharks did not appear to prey on mutton snapper spawn and were unlikely contributors to the mutton snappers' decline. In 2002, whale shark encounter tourism brought US$ 1.35 million to the Gladden Spit and Silk Cayes Marine

Reserve communities, offering an economic alternative to the mutton snapper fishery. Patterns of whale shark movement and feeding behaviour indicated that the marine reserve boundaries encompassed the main spawning aggregation and whale shark feeding zones. Increased visitor and boat numbers to the marine reserve coincided with alterations in the spawning behaviour of aggregating snappers and consequently the visitation of whale sharks at Gladden Spit. Strong management directives and enforcement are needed at the marine reserve to check unregulated growth of tourism and thus minimize its impacts on the fish spawning aggregations and visiting whale sharks.

Table of Contents

List of Tables

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

Acknowledgements

This research was funded by the UK Darwin Initiative (Grant no.162/9/005), the Natural Environment Research Council (NERC)(Grant no.025R00522), The Oak Foundation, the PADI Aware Foundation, and the Royal Geographical Society's Dax-Copp Travelling Fellowship. In addition, the research benefited from in-kind support from the Belize Fisheries Department, Wildlife Computers, the NGOs GreenReef, the Friends of Nature, the Toledo Institute for Development and Environment, the Belize Audubon Society, The Wildlife Conservation Society, The Nature Conservancy, Lighthawk and the Smithsonian Institution. Discover Scuba and MARES donated SCUBA equipment and Princeton Tech donated dive lights. For all of this support I am most grateful.

First and foremost I would like to thank my supervisor Professor Callum M. Roberts who offered unwavering support, encouragement and wise guidance throughout the doctoral process. His enthusiasm, scientific curiosity and positive outlook made working with him a pleasure.

In Belize, I am very grateful for the support of many individuals whose participation and enthusiasm in this project made the research and results a reality. I would specifically like to thank Eloy Cuevas, Dan Castellanos Jr., Shayne Pech, Daniel Castellanos Sr., Alfred and Jason Williams for boat and dive support. My heartfelt thanks go out to many of the local fishermen who depend on Gladden Spit for their livelihood and who shared much valuable information and insights with me on the aggregation fisheries, primarily Lennox "CocoPlum" Leslie, Elvis "Waga" Leslie, Lawrence Leslie, Edlin Leslie, Percy "Chamon" Leslie, Mr. Villa, Carlton "Mr. Jack" Young Sr. Thanks to many local tourguides including Julie Berry, Hank "Ocean S." Rhamdas, and Ellie Dial for their constant support and good humour. Thanks to Friends of Nature, especially Lindsay Garbutt, Shalini Cawich, Tamba (aka Matthew Nicholas) and the office staff for their support of this research. I would also thanks to Karl Kohlbecker for providing us with companionship and housing on Little Water Caye and to Alison and Bill Moore on Hatchett Caye for their support and hospitality. Thanks to the Smithsonian's Mike Carpenter and Dan Miller on Carrie Bow Caye for always finding a spot for us during our long treks up and down the reef. In Punta Gorda, many thanks go to Jeanelle Borlan for her good cheer and food during the fieldwork and to Stacy Noel whose common sense advice was always much appreciated. Thanks to

Will Heyman for his enthusiasm, unwavering love of fish and promotion of spawning aggregation conservation. Carol and Richard Foster have been true friends throughout. The fieldwork would not have been nearly as enjoyable or as productive without them.

While working with the Belize Department of Fisheries I would especially like to thank Beverly Wade, James Azueta, Isaiah Majil, Ramon Carcamo and Athen Marin. The breadth of data collection would not have been possible without the help of volunteers from the University of Belize including Alicia Eck, Betty Garbutt, Shirley Mae Parham, Vanessa Garcia, Zeeta Huehue, Rosa Mes, Felicia Mes, Ian Anderson, and Marsha Vargas, and our volunteer from the University of York, Nia Cherrett. Thanks to Wil Maheia from the Toledo Institute for Environment and Development and Ed Boles of University of Belize for helping to identify UB volunteers in the first place! Many thanks to GreenReef's Mito Paz and to Jill Hepp – a superb field hand, seconded from her Peace Corps placement and GreenReef every spring to work with us at Gladden. Additionally, to the staff at Belize Audubon Society and the Bacalar Chico Marine Reserve thanks for helping set down and retrieve acoustic receivers. A hearty thanks goes to Raymond Mossiah with the Belize Tourist Board, who provided the Belize-related tourism statistics. Many thanks to the Enric Sala and Rick Starr (working with the Wildlife Conservation Society and The Scripps Oceanographic Institute) for setting up a frequency-compatible array of acoustic receivers around Glover's Reef Atoll and sharing data on the presence versus absence of whale sharks that I had acoustically tagged.

In the University of York's Environment Department I wish to thank the dynamic duo Nola Barker and Gerry Newton-Cross for their constant good humour and prodigious supplies of croissants. Many thanks to Dave Rafaelli, Ricardo Scarpa and Mark Bulling for timely feedback and to Colin McClean, Fiona Gell, Chris Schelten, Lynda Rodwell, Vanessa Perez-Cirera and Andrea de Saenz whose discussions and suggestions made the path enjoyable and that much smoother. Thanks to Dave Hay, Jenny Turner, Maroula Hill and Julie Hawkins for their support.

Many thanks to Emma Hickerson, GP Schmall and the office staff from the Texas Flower Gardens National Marine Sanctuary who graciously received and transferred so many boxes of gear. Emma provided superb logistical support throughout the project and is a much-appreciated friend and colleague. Thanks to Simon Jennings of CEFAS who kindly analysed the stable isotope content of a variety of tissues and eggs from Gladden Spit. The field work benefited from good suggestions made by Chuck Farwell at the Monterey Bay

Aquarium, Heidi Dewar (Census for Marine Life) and Andre Boustany (Tag-A-Tuna and Stanford University), Tim Clark (University of Hawaii), and John Stevens (CSIRO). This thesis benefited from discussions with a range of fish-o-files and elasmo-files including Sarah Fowler, Rachel Cavanaugh, Peter Klimley, Chris Lowe, Kevin Rhodes and Kim Warren-Rhodes.

Last but far from least I want to thank two very important people in my life: Dan Castellanos, my lovely and very talented partner, who has been tremendously supportive and helpful, always with the right words at the right time, helping me to navigate obstacles and always seeing the good in everything. And my mother, Christine MacCallum whose support and encouragement have never wavered. Her spirit of adventure, hard work, love of life, resilience in the face of seemingly insurmountable obstacles and the belief that *nothing* is impossible makes her my role model.

Declaration

The collection of the mutton snapper landings and catch per unit effort data (Chapter 6) was undertaken jointly with the Belize Department of Fisheries, with University of Belize students and Belizean project participants further assisting me in data collection. I administered the pilot tourism surveys with the assistance of project participants including several student volunteers from the University of Belize (Chapter 7).

During the tagging (Chapters 2,3,4,5), I was assisted by Belizean project participants, notably Eloy Cuevas and Alfred Williams. For the photo identifications, I took the majority of images used but benefited from several identification images provided by Richard Foster, Dan Castellanos and Andy Stockbridge. Jim Smart developed the Fast Fourier Transform analysis and graphs used in Chapter 5 and Simon Jennings analysed whale shark and mutton snapper tissue samples for stable isotope contents (Chapter 3).

Although several project participants assisted me in the underwater fish census work over the years, the data used in this thesis (Chapter 6) represents that which I gathered. I collected all other data and interpreted it, and the writing of the thesis is solely my own work. Prof. Callum Roberts and Dr. Mark Bulling kindly made editorial comments on chapters.

"Sapadilli Tam"

You want to hear of w'at I know,
About de fish day tark of so,
De one dat people use to see,
Outside o' Sapadilli Caye?

Now list'n don't y'u be supprise;-
I seen dat shark wid my own eyes;
Not only once but time a score,
W'en I was tradin' to Omoa.

De fust time dat I seen dat shark,
De evenin jus was getting dark;
De sea was smude, de win' was low:
De schooner "Jane" was driftin' slow.

Jus' den dere came in sight a sail,
(we t'ought t'was one) an' so we hail;
but it was goin' fas', it seem
as if it was p'opell wid steam.

But w'en it get to us quite near.
We all was full wid awful fear,
For now we could plainly see,
It was a monster of de sea.

He check his speed den round us swim;
But we did not quite care fo' him.
We t'ink how we could mek him go,
So overboa'd some pork we t'row.

He start at once de food to eat,
An' den we try to mek retreat.
For now de win' commence to blow,
We put de boat to' near de sho'.

An' so it was we get away,
As bes' respec' to him we pay;
An' pray ne'ermo' to have a calm,
W'en nearin' Sapadilli Tam.

Dere's some strange story dat I hear,
De trut' of dem I cannot swear.
But I am stric'ly now compel,
To give to you as how dey tell-

A dorey once was coming o'er,
Wid Waika from Masquiter Shore-.
Dey saw a caye (Dey t'ought 'twas one)
An' so dey went to it to lan'.

So we'n dey went asho' an' look,
Dey mek a fire an' start to cook;
But w'en de pot was bubblin' free,
De shark sink undeneat' de sea.

'Tis also tol' dat coc'nut tree,
upon his back some people see,
but dere is some mistake I fear,
for I had never seen it dere.

But many a time about dat sea,
W'en nearin' Sapadilli Caye,
De sailor heart would beat fo' fear,
Dat Sapadilli Tam is near.

By James S. Martinez, Belize 1920

From "Caribbean Jingles – Dialect and other poems of British Honduras

Chapter 1. Introduction

1.1 Conservation of migratory animals

Conservation of migratory animals requires a range of strategies to be effective. Although recent conservation practices have highlighted the need to conserve functional habitats and ecosystems, many species of animals and insects are highly mobile and move throughout several habitats and ecosystems. In light of socio-economic and political constraints, conservation of highly mobile animals is increasingly focussing on characterising the nature and connectivity of a species' spatio-temporal predictability such as feeding, reproduction, and development. It is therefore necessary to understand the movement behaviour of individual animals to understand migration or movement patterns of populations and species. This must also be coupled with an understanding of factors influencing migratory animals throughout their life-cycle such as the state of breeding or feeding habitats (Vistnes *et al.*, 2001; Webster *et al.*, 2002). This knowledge can then provide the basis for the management and conservation of mobile populations in relation to changing patterns of resource availability, and the condition of habitats used as breeding and nursery sites.

Migratory behaviour has been broadly documented across taxa (Dingle, 1996). Migrations encompass "a regular seasonal movement of animals from one place to another, often from a breeding site to a non-breeding site" (Webster *et al.*, 2002). This reflects the back and forth movements and north-south migrations of songbirds and the eastern population of monarch butterflies (*Danaus plexippus*) from their springtime residence in North America to overwintering sites in Mexico (Dingle, 1996). However, migration may also include several sites used in a cyclical manner as seen with the seasonal movements of wildebeest (*Chonnochaetes taurinus*) throughout different areas of the Serengeti Park in Tanzania based on rainfall patterns and resource availability (Dingle, 1996). This behaviour suggests an organised process of movement whereby migrating animals use the same sensory cues.

Migrations or large-scale movements display spatio-temporal plasticity in response to changes in environmental conditions (Thouless, 1995), habitat change and disturbance (de Boer *et al.*, 2000), resource depletion (Ferguson *et al.*, 2001), and predator avoidance (Rettie & Messier, 2001). Additionally, the same species can display differences in migratory patterns between different populations, as revealed by the movements of two humpback whale populations. One overwinters in Hawaii and feeds in Artic waters and the other overwinters off the Mexican coast and feeds both in the Artic and near the Farallon Islands of California (Baker *et al.*, 1986).

Several methodologies have been recently developed to assess the broad movements of individuals and populations across variable time-scales. Conventional tagging can provide information on point-to-point distance covered by a migrating animal, dispersal from specific areas and distribution data on a species. Yet, mark-release-recapture methods are reliant on the recapture of tagged individuals. Acoustic and satellite telemetry tracking technology (see Chapter 4) can provide researcher-independent data on movement behaviour and habitat preferences but can only be used with animals large enough to carry the equipment without impacting their survival. Population-specific genetic markers are increasingly used to help "assign" individual animals such as birds caught in overwintering grounds to specific breeding sites, and variations of stable isotopes of carbon, hydrogen, deuterium, strontium and nitrogen accumulated in animal tissues and their prey can occur systematically over different geographic ranges to reveal prey preferences, trophic levels and sites utilised during an animal's life-cycle (Webster *et al.*, 2002).

Consequently, results from studies on migratory behaviour have led to the development of a range of conservation measures, from ones that are site-specific, such as terrestrial and marine protected areas and corridors that link these sites, to temporally-specific measures such as seasonal bans on hunting or fishing, and species-specific extraction bans driven by assessments such as the IUCN Red List of Threatened Species of Fauna and Flora (IUCN, 2000).

1.2 Impact of human-wildlife interactions on conservation

Migratory behaviour almost invariably brings wildlife into contact with humans. Resulting interactions can aid or thwart conservation efforts of the species encountered. Interactions may range from the non-consumptive ones with little or no impact on a species' life-cycle and behaviour, to exploitation and mortality through consumptive use by humans. Additionally, there exist the perceived impacts of migratory animals on humans. In East Caprivi, Namibia, African elephants (*Loxodonta africana*) and lions (*Panthera leo*) compete with local farming communities for the same resources, complicating management and undermining conservation efforts (O'Connell Rodwell *et al.*, 2000). This has led Eltringham (1994) to suggest that wildlife shoulder costs of resource conflicts and "pay its way". Ecotourism represents one way that wildlife can produce benefits for impacted communities. Ecotourism, and its subsets of nature and wildlife tourism, provide non-consumptive encounters with wildlife that have proved lucrative and sustainable. These have often generated public and private support for the target species and helped to conserve other associated species and key habitats necessary for the survival of migrating species (Burger, 2000).

Community-based ecotourism programs can foster local support for migratory species based on viewing wildlife and provide significant revenues that can offset conservation costs, many of which are often born by local people (Young, 1999). Yet, ecotourism can also impact the animals it aims to conserve through direct effects on the target species (Richardson, 1998; Orams, 2000; Farrell & Marion, 2001; Orams, 2002), development of infrastructure to accommodate tourists, pollution, alterations of their habitats (Richardson, 1998; Farrell & Marion, 2001), or lack of political and local interest (Songorwa, 1999). Whales are part of a family of charismatic species (Cetaceans) sought after by nature tourists who fuel a rapidly growing global whale-watching industry. In 2000, this form of ecotourism was valued at over US$ 1 billion distributed among 87 countries, which has provided widespread support against whaling efforts (Hoyt, 2000).

Consumptive exploitation of wildlife is widespread. In the marine realm stocks of large migratory fish species such as billfish, tuna, swordfish and sharks, have declined globally due to over-fishing (UNFAO, 1995). Quotas and species-specific laws used to protect many of these species have failed to stem their over-exploitation, due to the open-access nature of many coastal and pelagic ecosystems, the frequent difficulty in assessing species stock sizes (Lauck *et al.*, 1998; Roberts, 1998; Safina, 1999), and a lack of knowledge of their reproductive and migratory behaviour. Additionally, massive bycatch from the long-line fishery and tuna-purse seine fisheries (de Silva *et al.*, 2001; Francis *et al.*, 2001; Romanov, 2002) has contributed to a substantial decline in many migratory species' populations, undermining fisheries management practices such as catch quotas. In fact, Baum *et al.* (2003) recently exposed a dramatic decrease of 75% in many shark species in the NW Atlantic over the past 15 years. Myers and Worm (2003) further show that 10% or less of large predatory fish, including sharks, remain since industrialised fishing began in the 1960s.

To stem fisheries declines, marine reserves are garnering increasing support worldwide as a cost-effective tool for ecosystem and habitat protection (Roberts, 1994, 1997), biodiversity conservation (Bohnsack, 1990; Bohnsack & Ault, 1996), and the enhancement of fish stocks (Roberts, 1995; Lauck *et al.*, 1998; Gell & Roberts, 2003). However, marine protected areas are designed to meet many objectives (Jones, 1994), often compromising the ability to effectively protect fish stocks (Allison *et al.*, 1998), including those species that migrate beyond the boundaries of designated areas. It is possible to enhance migratory species' protection by focusing on protection at vulnerable life-stages or areas of repeated or high use (Roberts & Sargant, 2002; Norse *et al.*, in press) and even venturing away from coastal areas to declare reserves in open-ocean habitats located in international waters (Mills & Carlton, 1997; Hyrenbach *et al.*, 2000). Yet, protection of large migratory fish species continues to be undermined by a glaring lack of information on their ecology and behaviour (IUCN, 1996; Lutcavage *et al.*, 1999), which effectively excludes them from the marine reserve design process.

1.3 The whale shark as an example

Compared to other large-sized animals such as the African elephant (*Loxodonta africana*) and a range of marine mammal species species such as humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*) little is known about the life history and biology of the world's largest fish, the whale shark (*Rhincodon typus*) (Figure 1.1), primarily due to its relative elusiveness. This same lack of information on population abundance and patterns of movement throughout its life-cycle has led to difficulties in assessing the vulnerability of this species, further constraining conservation efforts for this species.

The whale shark was first described by Smith in 1828 after an encounter with an individual off the coast of South Africa (Smith, 1828). First named *Rhiniodon typus* (rhinio=file; don= tooth) – the name was later changed to *Rhincodon typus* – the whale shark is the only member of its family Rhincodontidae. This species is most closely related to other orectolobiforms or carpet sharks such as the nurse shark (*Ginglymostoma cirratum*) of the family Ginglimostomatidae, and the zebra shark (*Stegostoma fasciatum*) of the family Stegostomatidae (Compagno, 2001). The whale shark is also known in different parts of the world as pez dama, damero, domino, chagrin, sapodilla tom, jimbay-zamay, and butanding. Gudger (1915; 1941) provided some of the first studies on the biology of whale sharks with updated compilations and reviews provided by Last and Stevens (1994), Colman (1997), Fowler (2000) and Compagno (2001).

Sharks are thought to have evolved in the Early Devonian over 400 million years ago (Zangrl, 1981) and whale sharks may have evolved in the Middle Cretaceous

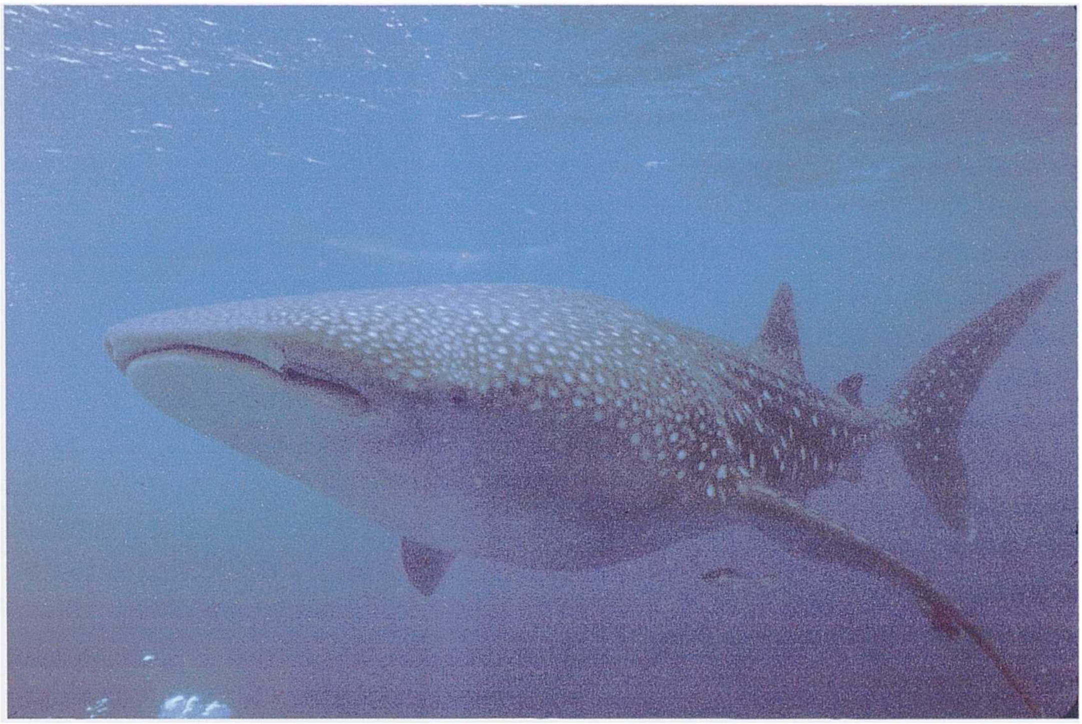


Figure 1.1: A whale shark, *Rhincodon typus*. Circumtropical and planktivorous, the whale shark reaches lengths of 18 m and weights of 34 t.

around 90-125 million years ago with many other species of modern sharks (deCarvalho, 1996; Compagno, 1999). Whale sharks inhabit both coasts and open-oceans and are distributed throughout the world's tropical and warm temperate seas (Gudger, 1915; Wolfson, 1986; Colman, 1997b) with occasional forays into cooler temperate waters e.g. near New York (Gudger, 1936). Planktivorous in their feeding habits, they have evolved several mechanisms such as ram filter-feeding and stationary suction-feeding that enable them to successfully target and filter high-density food sources such as thick "soups" of plankton or "bait balls" of small fish. Whale sharks feed on a variety of prey including plankton (copepod spp., e.g. *Acartia clausi*, myctophid spp., euphausiid spp. e.g., *Pseudeuphausia latfrons*), baitfish, jellyfish and squid (Gudger, 1915; Colman, 1997b), and fish spawn (Heyman *et al.*, 2001). Whale sharks are low tertiary consumers with a trophic level of 3.6 (Cortes, 1999) feeding opportunistically by switching to different food types depending on availability (Colman, 1997b; Stevens *et al.*, 1998) (Graham, unpublished data).

Although whale sharks may be primarily solitary animals (Colman, 1997b), they occasionally aggregate in loose groups, often segregated by sex and size (Norman, 1999) (see Chapter 2). Predictable seasonal aggregations are rare, yet have been identified in sites such as the Philippines, Western Australia, India, Seychelles, Baja California and Yucatan Peninsula (Mexico), Thailand's Andaman Sea, South Africa, Bay Islands of Honduras, and Belize. Whale shark patterns of movement and seasonal site fidelity are slowly being elucidated by researchers, work often fuelled by the increasing number of divers and snorkelers seeking whale sharks in the hopes of an encounter. They exhibit periods of intra- and inter-annual site fidelity associated with seasonal increases in prey abundance. In Baja California, whale shark sightings increase in the spring when copepod abundances are high (Clark & Nelson, 1997), and in Ningaloo Reef, Western Australia, congregations are loosely timed with the advent of the coral spawning and associated increase in krill abundance (Taylor, 1994; 1996). In Belize, whale sharks are observed to feed on the eggs of snappers (Lutjanidae) that aggregate seasonally to spawn (Heyman *et al.*, 2001). These aggregations may be further enhanced by the presence of oceanographic features such as ocean fronts (Colman 1997; Taylor 1996), physical features such as reef passages that concentrate zooplankton (Wolanski & Hamner, 1988), seamounts that promote a number of physical processes that locally enhance productivity and concentrate prey (Trasvina-Castro *et al.*, 2003), conditions that may also occur at reef promontories.

Whale sharks move readily beyond political boundaries and have been recorded in the territorial waters of at least 120 countries (COP12, 2002), with most sightings recorded in tropical waters of the shark's preferred temperature range of 21^0-25^0 C (Iwasaki, 1970; Last & Stevens, 1994). They are now known to undertake large-scale transoceanic migrations with a 13,000 km journey recorded from Baja California to Tonga (Eckert & Stewart, 2001), two individuals moving from the Seychelles to Somalia and to the Andaman Sea/Thailand respectively (Graham, unpublished data), and in the Western Caribbean, from Belize to the north coast of Yucatan and beyond the Bay Islands of Honduras (see Chapter 4). These movements are very possibly in search of, or targeting, dense patches of food. Whale sharks may therefore serve as indicators for their ability to target highly productive sites, widely dispersed across ocean basins, as recorded with basking sharks in temperate seas of the coast of Britain (Sims & Quayle, 1998). Their large size and docile nature may therefore make them flagship species for ocean health and charismatic advocates for marine conservation.

Whale sharks have been documented to attain at least 18 m long (Eckert & Stewart, 2001), although a maximum length of 20 m and an estimated 34 t was recorded by Chen *et al.* (1996) in 1987. Length at maturity is controversial with females reaching maturity at an estimated 4.4 m to 5.6 m (Grove & Lavenberg, 1997) to over 9.0 m for males in South Africa (Wintner, 2000) and 9.0-10.0 m for both sexes in Australia (Taylor, 1994; Colman, 1997b), both of which are greater than length at maturity calculated by Fishbase life history parameters for this species[1]. As females of the nurse shark, the closest relative to the whale shark, reach maturity at 86% of their maximum size (Castro, 2000), whale shark size at maturity is more likely to be over 9.0 m. This further represents a possible age at maturity of 25-30+ years of age (Taylor, 1994; Colman, 1997b). Male sharks observed in Belize did not appear to be mature with fully developed claspers when smaller than 8.5m long (Graham, pers. obs., see Chapter 2).

Using von Bertalanffy growth curves, Pauly (2002) calculated two K values for an asymptotic length of 14 m and weight of 20 t based on parameters derived from basking sharks and gill size respectively. Resulting values of K = 0.031 year^{-1} and K = 0.051 year^{-1}, suggested that whale sharks may live to 60 or 100 years old respectively, with a generation time ranging between 24 and 63 years (Pauly, 2002). Whale shark mortality rates worldwide and regionally are unknown. Human-induced juvenile and adult mortality may be higher in the Indo-Pacific as compared to the Atlantic and Caribbean due to known fisheries for this species. Targeted whale shark fisheries are documented

[1] Estimated life history parameters for the whale shark: www.fishbase.org.

for India (Hanfee, 2001) and Taiwan (Chen *et al.*, 1996) with anecdotal reports of catches from Mozambique (S. Sutton, pers. comm. 2002). No documented mortality of whale sharks has occurred in Belize or along the Mesoamerican Barrier Reef. A small fishery is known to have existed in Cuba, and was banned by the Government in 1991 (F. Pina, pers. comm. 2000). Incidental catches of whale sharks occur (Gudger & Hoffman, 1930), occasionally during tuna purse seine net sets, where fishers specifically set nets around whale sharks as tuna aggregate to feed around them (Romanov, 2002). Sharks are usually released as they can damage fishing nets, but some occasionally die through mishandling during release (Fisheries observer Seychelles, pers. comm. 2001). Mortality through ship strikes provided Gudger with numerous publications and distributional reports of whale sharks throughout the world (Gudger, 1937b, 1937a, 1937c, 1938, 1939). Predation of whale sharks has also been documented by orcas (*Orcinus orca*) attacking and feeding on a ~6.0 m total length (TL) shark in the Gulf of California (O'Sullivan & Mitchell, 2000). A neonate whale shark was recovered from the stomach of an Indo-Pacific blue marlin (*Makaira mazara*) in Mauritius (Colman, 1997b) and from a blue shark (*Prionace glauca*) in the mid–Atlantic (Kukuyev, 1995). Pauly (2002) conservatively estimates that 9% of adults die each year based on the calculated *K*-value of 0.051 year^{-1} and a mortality of 0.088 year^{-1}.

Whale sharks are ovoviviparous, bearing live young that developed in egg cases inside the uterus (Last & Stevens, 1994). Relatively prolific compared to all other documented species of shark, a single 10.6 m female whale shark was found carrying 300 young (Joung *et al.*, 1996). Courtship and mating behaviour are undocumented as yet. The gestation period is unknown but may emulate the nurse shark's period of 5-6 months followed by a 2 year reproductive pause (Castro, 2000). Growth in the wild appears slow during the post-3 m juvenile stage (see Chapter 2) as compared to individuals held and fed in aquaria (Uchida *et al.*, 2000). Neonate whale sharks may grow rapidly from a birth size of about 55 cm to counter predation by species such as blue sharks (Kukuyev, 1995). A lack of sightings or landings of whale sharks smaller than 3 m further support probable early rapid growth. It is not known where the majority of the 55 cm to 3 m individuals are located, although several free-swimming neonates were caught in nets off the pacific coast of Central America, off the Western coast of Africa in the Atlantic Ocean (Wolfson, 1983), off Taiwan (Chang *et al.*, 1997) and a miscarried egg case was retrieved from a trawler net in the Gulf of Mexico (Baughman, 1955), indicating that these may be four of the whale shark's reproductive grounds.

The global whale shark population is unknown. Through photo-identification programs, at least 106 individuals were identified in Belize over the course of 5 years (Chapter 2) and over 100 recorded in Ningaloo Reef, Western Australia (Norman, pers. comm. 2000).

1.4 Threats and conservation

Whale sharks are commercially important to the fisheries and tourism industries and are listed as "Vulnerable" to extinction in the World Conservation Union's Red List of Threatened Species (IUCN, 2000). Although apparently not subject to a targeted fishery in the Atlantic, the whale shark is heavily exploited for its meat, liver oil, cartilage, skin and fins in the Indian and Pacific Oceans (Chen *et al.*, 1996; Hanfee, 2001; Alava *et al.*, 2002), leading to serious sightings declines in areas where visitations are considered predictable (Stevens, pers. comm. 2000) (COP12, 2002). In fisheries, the whale shark has non-consumptive value as an aggregator and key indicator of other commercially important fish species (Gudger, 1941; Colman, 1997b) including several species of tuna (Iwasaki, 1970; Arnborm & Papastavrou, 1988). Tuna fisheries worldwide often target whale sharks when setting nets (Romanov, 2002), an activity which occasionally leads to whale shark mortalities (Graham, unpublished data). Initially valuable dead, with a set of fins recently valued on a Chinese market at US$15,000, whale sharks are highly vulnerable to exploitation based on their life history traits. This is not a productive fishery species and targeted efforts are not sustainable even in the short-term, with rapid stock collapses and declines in predictable sightings documented in the space of a few years where targeted fisheries take place (COP12, 2002).

Although still fished in Pakistan, Taiwan, Indonesia and China (Chen *et al.*, 1996; Hanfee, 2001), most countries are slowly realising that whale sharks are worth more alive through the tourist trade, than dead. Consequently, several countries, such as the Maldives, Honduras, India and the Philippines, Australia, and specific states in the United States have passed laws protecting whale sharks (COP12, 2002). Greater global protection is potentially conferred by international agreements. Whale sharks are listed on the United Nations Convention for Migratory Species and Straddling Stocks. In November 2002, they were listed on the Appendix II of the Convention on International Trade in Endangered Species of Fauna and Flora (CITES) that monitors and regulates the global trade in whale shark products. However, the highly lucrative Asian shark fin trade and demand for "tofu shark", as whale shark meat is known, will test the recently established listing. CITES cannot monitor domestic trade and highly mobile fishing vessels are able to capture individuals and take them back to their home port, thus avoiding CITES monitoring. Additional national and regional accords that protect whale sharks in their territorial waters, coupled with education about the species and the benefits of promoting non-consumptive and lucrative economic alternatives such as encounter-tourism, will be needed to reduce trade in whale shark products.

1.5 Whale shark tourism

An increase in the numbers of snorkelers and divers taking to the tropical seas has fuelled shark diving worldwide. In this niche tourism, whale sharks represent the jewel in the diver's or snorkeler's crown of marine experiences due to their curious nature that often enables very close encounters. Well-managed and non-invasive tourism bolsters a whale shark's non-consumptive value and can further protect whale sharks through education and the lasting impression that an encounter can make on the visitor. Dedicated whale shark tourism is currently offered in several countries including Mexico, Belize, Honduras, Galapagos (Ecuador), South Africa, Mozambique, Kenya, Seychelles, Maldives, Thailand, the Philippines, and Australia. Ningaloo Reef in Western Australia is the longest established and possibly most lucrative of whale shark tourism sites, having started in the late 1980s (Taylor, 1994) and commercially developed since 1993 (Davis *et al.*, 1997; Davis, 1998). Whale shark-human interactions there generated over US$ 3.1 million for a 2-month season in 1995, with benefits distributed between 15 tour operators (Davis *et al.*, 1997) and this figure has risen steadily since (Norman, pers. comm. 2003). At that time, whale shark tourists spent an average of US$ 1,540 per trip (Davis *et al.*, 1997) similar to the average whale shark tourist expenditures recorded in Belize (see Chapter 7 on whale shark tourism).

Tourist impacts on whale sharks are difficult to assess. However, touching, grabbing and riding sharks often produces an immediate negative response whereby the shark dives down or moves away rapidly and deprives others of the encounter (Norman, pers. comm. 2000, Graham, unpublished data). Consequently, several sites that host predictable whale shark sightings have established an "etiquette" that regulates whale shark encounters. The basic rules forbid touching or harassing whale sharks and establishing distance guidelines between tourists or boats and the sharks, and a maximum number of people allowed in the water at any time. In Australia, only snorkelers are allowed to interact with whale sharks and a minimum distance of 3 m from the head and body and 4 m from the tail must be respected. A maximum of 10 snorkelers are allowed per whale shark, operators may not cut off the path of the shark and no flash photography is allowed (Colman, 1997a). Some tour operators in Belize, Mozambique and Mexico have recently adopted several of these regulations in order to better manage their whale shark tourism.

1.6 Study site

The Belize Barrier Reef and the Mesoamerican Reef Barrier System

The Belize Barrier Reef Complex (BBRC) covers an area about 22,800km^2 (Kramer *et al.*, 2000), approximately 10-35 km wide and 250 km in length (Figure 1.2). Encompassing fringing reefs to the north, the near-unbroken barrier reef becomes a network of patch reefs, seagrass beds, and mangrove cayes south of Ambergris Caye (Rutzler & Macintyre, 1982). The BBRC also encompasses three atolls located 7 to 45 km from the main reef and separated by waters over 1,000 m deep. In 1998, the BBRC was subjected to a coral bleaching event that led to massive coral mortalities following elevated sea-temperatures precipitated by an El-Niño event (Aronson *et al.*, 2002). Surface currents are driven south by the prevailing north-easterly winds (McField, 2001).

The Belize Barrier Reef encompasses a network of 12 marine protected areas (MPAs), seven of which are declared World Heritage Sites by the United Nations' Educational, Cultural and Scientific Organisation (UNESCO) (Figure 1.2). The Belize Department of Fisheries manages five of the MPAs, and five local non-governmental organisations manage seven remaining MPAs under co-management agreements with the Department of Fisheries. McField conducted an evaluation of Belize MPA management effectiveness and found that these were managed "moderately satisfactory" (McField, 2000).

The BBRC forms an important subset of the Mesoamerican Barrier Reef System (MBRS) that extends from the tip of Mexico's Yucatan Peninsula near Isla Contoy to the Bay Islands off the north coast of Honduras (~950 km) (Figure 1.3). This reef system is comprised of patch, fringing, and barrier reefs, and four atolls, and forms the western flank of the Caribbean basin large marine ecosystem. The MBRS was identified as a reef entity in 1997 when the Ministers of Environment from Mexico, Belize, Guatemala and Honduras determined that a regional agreement was needed to help conserve this natural seascape. The resulting Tulúm declaration of 1997 formally described this regional reef system and the mechanisms to manage it. The MBRS was recently named a hot-spot for biological diversity and in pressing need of conservation

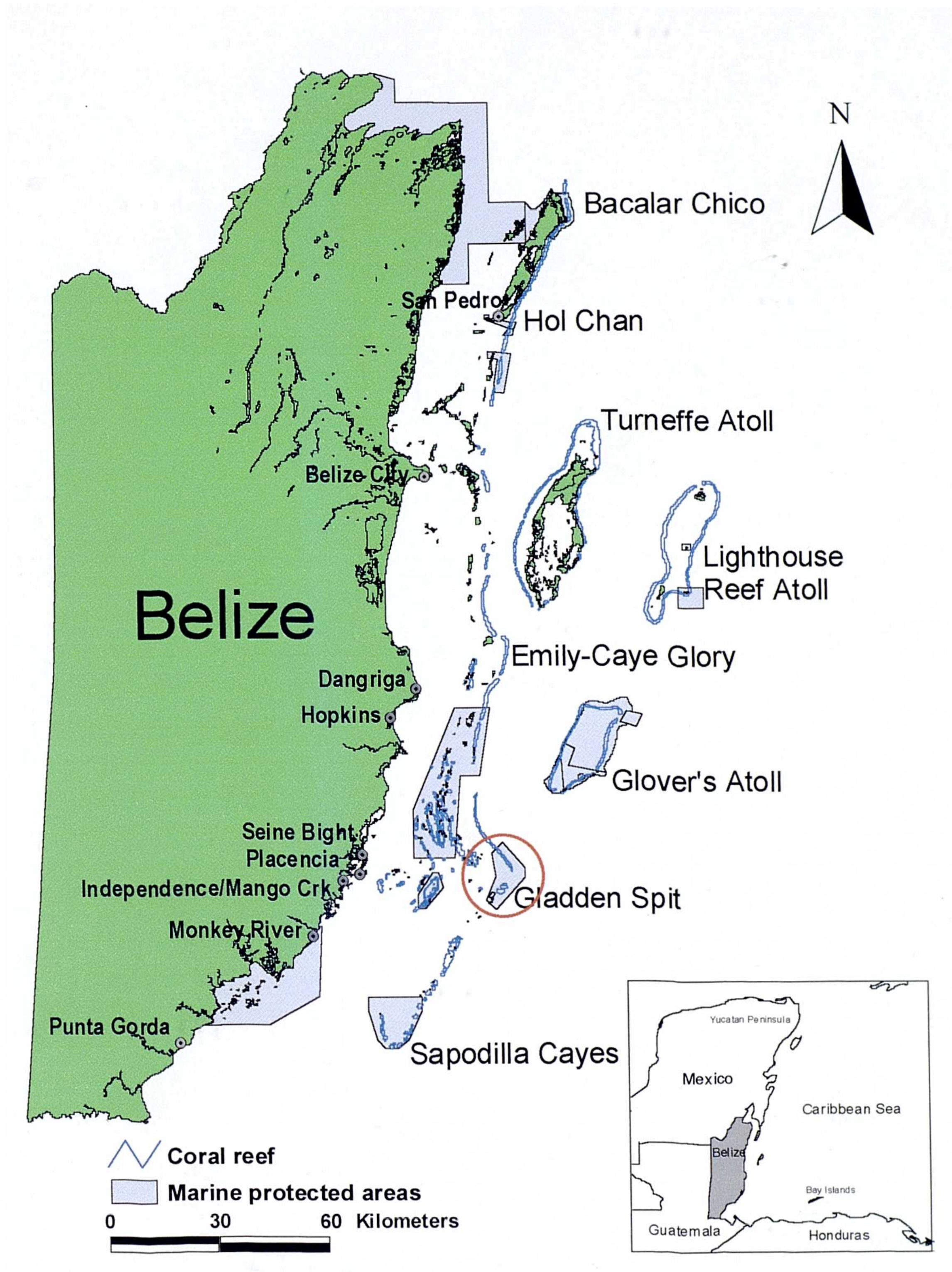


Figure 1.2: Belize Barrier Reef and marine reserves with locator map (Base map of Belize courtesy of Coastal Zone Management Authority).

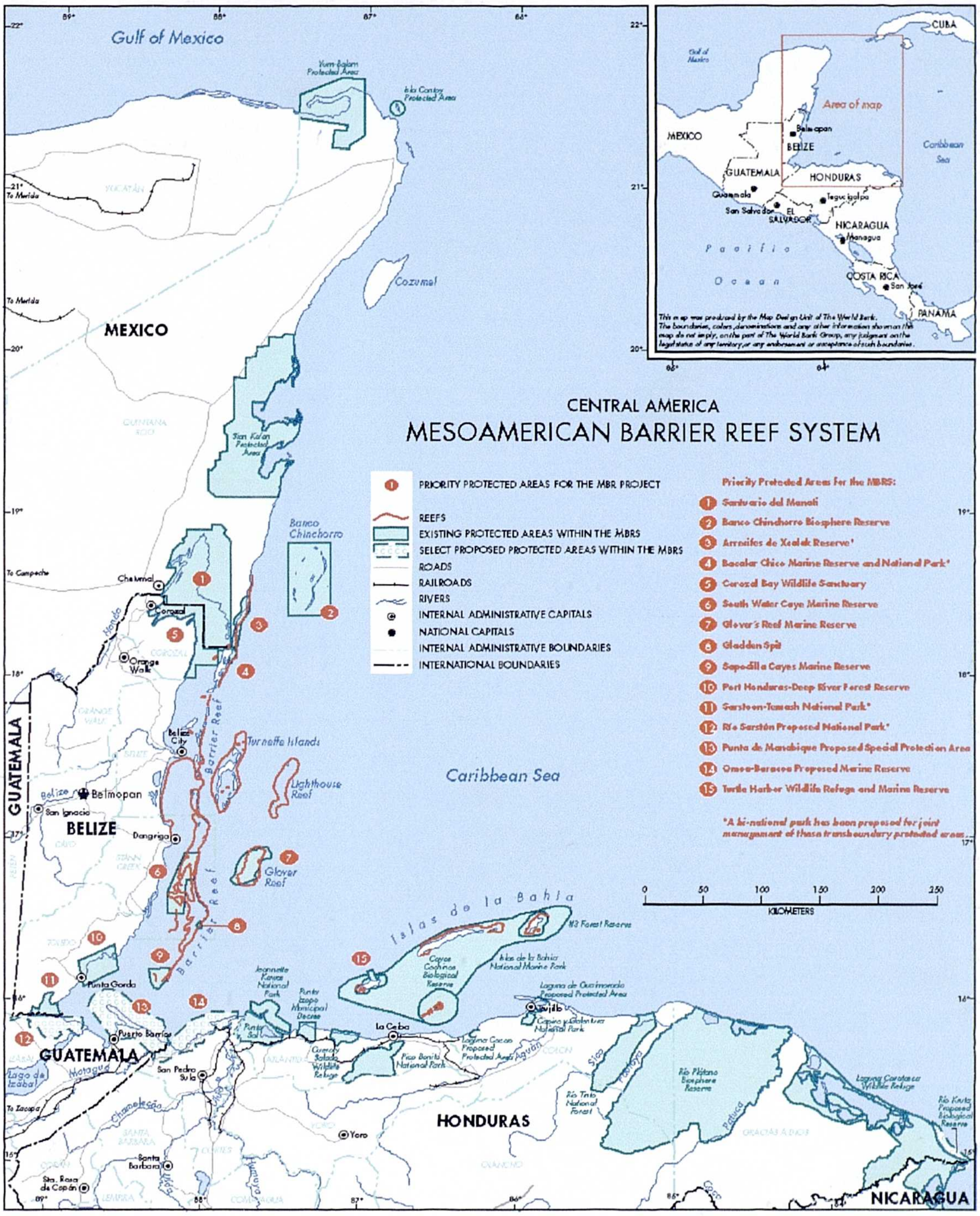


Figure 1.3: The Mesoamerican Barrier Reef Systems (MBRS) and its network of marine reserves (map courtesy of the MBRS project).

based on anthropogenic threats (Roberts *et al.*, 2002). As such, four international non-governmental organisations, the World Wildlife Fund, Wildlife Conservation Society, Conservation International and The Nature Conservancy, as well as a World Bank-funded multilateral project have focused conservation efforts and funding on this region.

Gladden Spit

The primary study site where all tagging of whale sharks undertaken for this thesis took place is located at Gladden Spit, a promontory located two-thirds of the way south on the Belize Barrier Reef at 16°35'N, 88°00'W, and about 46 km from the mainland (Figure 1.4). A channel located immediately south of the bend in the reef transects Gladden Spit. The northern half of the point slopes away gently from the reef crest for 2.5 km and reaches 45 m depth before steeply dropping off to over 2000 m into the southern finger of the Cayman Trench. On the southern end of the point beyond the channel, the narrow shelf drops off rapidly reaching over 1000 m within 3 km of the reef crest. Slope topography at the promontory is characterized by poorly developed spur and groove, low relief with small patches of coral, predominantly *Montastrea* spp. and several species of gorgonians and soft corals interspersed with sand and rubble.

Gladden Spit hosts at least 30 species of reef fish that show indications of aggregating to spawn, 11 of which have been observed to spawn (see Chapter 6). The oceanographic and physical features of reef promontories appear to provide spawning fish with a means for enhancing reproductive success (Johannes, 1978; Claro, 1991; Domeier & Colin, 1997), and geographically-distinct areas where whale sharks can be sighted on a predictable basis. In fact, thousands of cubera and dog snapper (*L. cyanopterus* and *L. jocu*) spawn at the site from March through June and attract a rare yet seasonal aggregation of feeding whale sharks (Heyman *et al.* 2001). Additionally, focal fishermen traditionally fish Gladden's seasonal mutton snapper spawning aggregation, the last commercially viable spawning aggregation fishery left in Belize.

Due to the importance of Gladden Spit's multi-species spawning aggregations and visiting whale sharks, Gladden Spit and the Silk Cayes were declared a marine reserve on 18 May 2000 (Statutory Instrument no. 68 of 2000), established under a co-management structure between the Department of Fisheries and the local conservation non-governmental organisation Friends of Nature (FON; formerly known as Friends of Laughing Bird Caye) on 29 April 2002. The marine reserve was primarily designed to encompass the main spawning aggregation fishing site along the fore-reef edge, the spawning aggregation area and the three Silk Cayes. As a result it covers 10,523

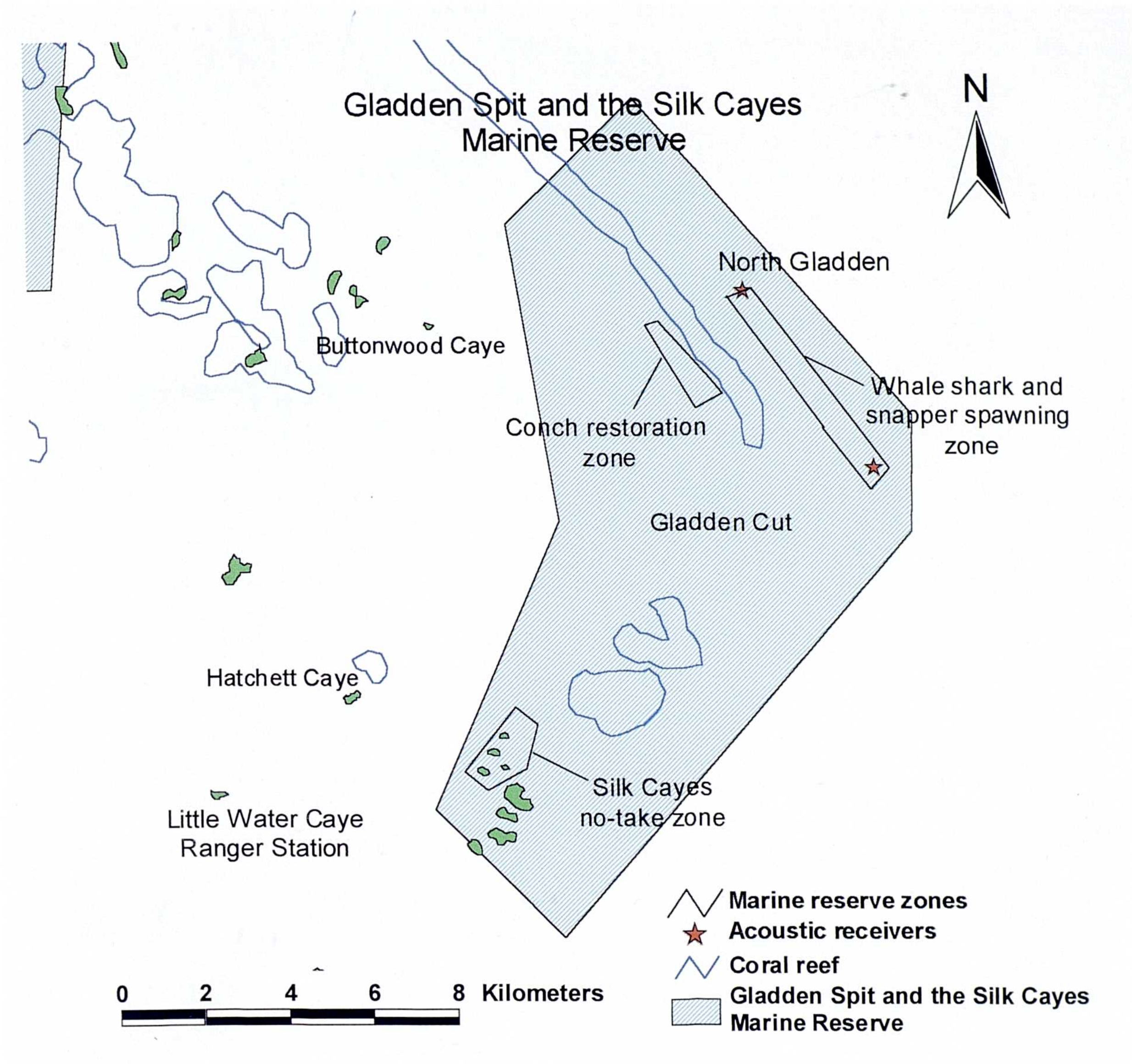


Figure 1.4: The Gladden Spit and the Silk Cayes Marine Reserve (GSSCMR). Zone boundaries defined by GPS points provided in the GSSCMR management plan (base map courtesy of Coastal Zone Management Authority).

hectares, and encompasses a no-take zone around the three Silk Cayes, a restoration zone for conch in the back reef / lagoon and a reef fish spawning aggregation and whale shark conservation zone located at the edge of the fore-reef slope. The marine reserve will soon be expanded along its western edge to encompass Little Water Caye, a small island recently purchased by FON to site the marine reserve's ranger station. FON recently redrafted whale shark tourism regulations originally drafted in 2000, submitted these to local consultations with the stakeholder communities (Appendix 7.A) and included them in the marine reserve's first management plan (FON, 2003). These are set to become law in the near future. Although fishing on the spawning aggregation is not regulated, based on the extirpation of most of Belize's spawning aggregations (Paz & Grimshaw, 2001), FON is seeking a compromise between traditional fishing and protection of spawning aggregations. Consequently, it is looking to enforce seasonal species bans on fishing grouper spp. and limit the number of boats and fishers at the site and is looking at extending licenses to a maximum of ten traditional fishers (FON, 2003).

1.7 Duration of study

Field visits to Gladden Spit began in May 1998 and took place over 9-14 days following the full moon every April and May from 1999-2002. I monitored whale shark presence and reef fish spawning activity at Gladden Spit in May and August 1998, January 1999, April-July and September 1999, March–June 2000, August-October 2000, December 2000, January 2001, March-June 2001, October and December 2001, January-July 2002, and March-April 2003. All field visits bracketed the full moon and varied in length from 3-14 days, 2-3 days before the full moon up to 14 days after the full moon. Fieldwork consisted of 274 trips to the reef and 932 hours of diving. This study's focus is primarily on fieldwork undertaken between April 2000 and July 2002.

1.8 Thesis aims

This thesis addressed the issue of conserving migratory species, focussing on the whale shark. It used the site at Gladden Spit, Belize, as a focus for research efforts. The primary aim was to enhance our knowledge of the movement behaviour of whale sharks, especially in relation to food sources, and the implications of this for management strategies such as the design of marine reserves. The thesis also examined the economic aspects of whale shark behaviour and ecology by focusing on the case study of the mutton snapper fishery at Gladden Spit and by seeking to quantify the actual and potential contribution of whale sharks to ecotourism revenues in Belize.

The status of the seasonal spawning aggregation fishery at Gladden Spit was assessed as a potential source of competition for feeding whale sharks through the removal of mutton snapper roe. Ever since whale sharks were discovered to feed on the spawn of aggregating cubera and dog snapper eggs (Heyman *et al.*, 2001), local fishermen perceived that whale sharks impacted mutton snapper abundance and were responsible for an alleged decline in fish catches. Whale shark tourism was also investigated as an economic alternative to the small-scale snapper fishery. In addition to research on whale shark behaviour and tourism, this study originally set out to assess if whale sharks predated mutton snapper eggs, and hence the potential future recruits to the spawning aggregation at Gladden Spit. This would have been compared to the fishery impact of removing spawning stock biomass (see Chapter 6). Two years of research were conducted on the Barrier Reef between 1998 and 1999 on the whale sharks and spawning snappers prior to the start of this work.

This study specifically focused on a newly reported population of whale sharks for the Atlantic (Heyman *et al.* 2001), at six reef promontories located along the 250 km Belize Barrier Reef and the offshore atolls (see Figure 1.2 map). These sites harbour large spawning aggregations of several species of reef fish or did so before overexploitation.

This research has been timely; tourism recently supplanted agriculture and fisheries and became Belize's primary source of income (CSO, 2002). The network of 12 marine reserves and burgeoning whale shark tourism is forming a lucrative cornerstone in Belize's new tourism strategy to specifically promote adventure eco-tourism. However, the creation of additional marine reserves and the unregulated whale shark tourism threatens to further displace traditional fishers. As a result, the socio-economic tradeoffs between both tourism and fisheries needed to be assessed to optimise marine reserve design and promote local support for, distribution of, and ownership of benefits. One of the immediate aims of this study was to transform results into resource conservation and management guidelines.

The aims of the research presented in this thesis were specifically to:

1. Assess the size and structure of the seasonal visiting population of whale sharks at Gladden Spit.
2. Assess whale shark site fidelity to Gladden Spit

3. Investigate whale shark patterns of movements along and beyond the Belize Barrier Reef in relation to seasonal prey abundance.
4. Characterise the mutton snapper spawning aggregation fishery at Gladden Spit
5. Investigate the growing whale shark tourism in Belize with a focus on Gladden Spit.

1.9 Thesis outline

In Chapter 2 the visiting whale shark population at Gladden Spit is described in terms of structure between 1999 and 2003. Two methods used to estimate abundance of the visiting population are discussed.

In Chapter 3 whale shark site fidelity to Gladden Spit both intra- and inter-annually is described using data collected from remote acoustic telemetry. Foraging behaviour is described in the context of food availability and physical and biological cues.

Chapter 4 addresses large-scale movement patterns of whale sharks along the Mesoamerican Barrier Reef and between different acoustic monitoring sites on the Belize Barrier Reef located in protected and non-protected areas. Use of three different tagging methodologies to examine movement is discussed. The degree of site fidelity to each of the study sites is estimated in comparison to Gladden Spit.

Chapter 5 assesses whale shark diving behaviour for four satellite-tagged sharks in relation to a predictable food source and the lunar phase. Comparisons with other species of marine animals are discussed.

Chapter 6 provides a detailed account of the snapper spawning aggregation fishery at Gladden Spit between 2000 and 2002 as this may compete with whale sharks for food. Seasonal landings data, fishery values and catch per unit effort data are presented for Gladden Spit. Conflicts with other site users including whale sharks and tour-operators are discussed.

In Chapter 7 the growing whale shark tourism at Gladden Spit and greater Belize is described in relation to the snapper spawning aggregation fishery at Gladden Spit and other Belize spawning aggregation sites. The results of a tourism survey conducted in 2001 and 2002 that focused on the Gladden Spit and Silk Cayes Marine Reserve and its seasonal aggregation of whale sharks are presented in the context of tourism growth in Belize. Carrying capacity, management of whale shark tourism and the socio-economic tradeoffs with the competing artisanal fisheries are discussed.

1.10 References

Alava M. N. R., Dolumbalo E. R. Z., Yaptinchay A. A. & Trono R. B. 2002. Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In: *Elasmobranch Biodiversity Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997.* (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 132-147. Sabah, Malaysia. IUCN, Gland, Switzerland.

Allison G. W., Lubchenco J. & Carr M. H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications.* **8** (1): S79-S92.

Arnborm T. & Papastavrou V. 1988. Fish in association with whale sharks *Rhiniodon typus* near the Galapagos Islands *Noticias de Galapagos*, pp 13-15.

Aronson R. B., Precht W. F., Toscano M. A. & Koltes K. H. 2002. The 1998 bleaching event and its aftermath on a coral reef in Belize. *Marine Biology.* **141**: 435-447.

Baker C. S., Herman L. M., Perry A., Lawton W. S., Straley J. M., Wolman A. A., Kaufman G. D., Winn H. E., Hall J. D., Reinke J. M. & Ostman J. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Marine Ecology Progress Series.* **31**: 105-119.

Baughman J. L. 1955. The oviparity of the whale shark, *Rhiniodon typus*, with records of this and other fishes in Texas waters. *Copeia.* **1**: 54-55.

Baum J. K., Myers R. A., Kehler D. G., Worm B., Harley S. J. & Doherty P. A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science.* **299** (5605): 389-392.

Bohnsack J. A. 1990. The potential of marine fishery reserves for reef fish management in the US southern Atlantic. NOAA Technical Memo. NMFS-SEFC 261. 40 pp.

Bohnsack J. A. & Ault J. S. 1996. Management strategies to conserve marine biodiversity. *Oceanography.* **9** (1): 73-82.

Burger J. 2000. Landscapes, tourism, and conservation. *The Science of The Total Environment.* **249** (1-3): 39-49.

Castro J. I. 2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahamas Islands. *Environmental Biology of Fishes.* **58** (1): 1-22.

Chang W. B., Leu M. Y. & Fang L. S. 1997. Embryos of the whale shark, *Rhincodon typus*: Early growth and size distribution. *Copeia* (2): 444-446.

Chen C.-T., Liu K.-M. & Joung S.-J. 1996. Preliminary report on Taiwan's whale shark fishery. In: Fowler S. L., Reed T. M. & Dipper F. A. (eds) *Elasmobranch Biodiversity, Conservation and Management.* The IUCN Species Survival Commission, Sabah, Malaysia, July 1997, pp 162-167.

Clark E. & Nelson D. R. 1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes.* **50**: 63-73.

Claro R. 1991. Changes in fish assemblage structure by the effects of intense fisheries activities. *Tropical Ecology.* **32** (1): 36-46.

Colman J. 1997a. Whale shark interaction management, with particular reference to Ningaloo Marine Park. Western Australia Department of Conservation and Land Management, Marine Conservation Branch 27. Freemantle, Western Australia. 61 pp.

Colman J. G. 1997b. A review of the biology and ecology of the whale shark. *Journal of Fish Biology.* **51** (6): 1219-1234.

Compagno L. J. V. 1999. Systematics and body form. In: *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes.* (Hamlett W. C. ed.), pp 1-42. Baltimore, Maryland. The Johns Hopkins University Press.

Compagno L. J. V. 2001. Sharks of the World: An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, Mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). *FAO Species Catalogue for Fishery Purposes.* **2** (1): 269.

COP12. 2002. Proposal for inclusion of whale sharks on Appendix II - Proponents India and Philippines. CITES. 24 pp.

Cortes E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science.* **56** (5): 707-717.

CSO. 2002. Abstract of statistics: 2001. Central Statistical Office. Bclmopan, Belize.

Davis D. 1998. Whale shark tourism in Ningaloo Marine Park, Australia. *Anthrozoos.* **11** (1): 5-11.

Davis D., Banks S., Birtles A., Valentine P. & Cuthill M. 1997. Whale sharks in Ningaloo Marine Park: managing tourism in an Australian marine protected area. *Tourism Management.* **18** (5): 259-271.

de Boer W. F., Ntumi C. P., Correia A. U. & Mafuca J. M. 2000. Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology.* **38** (3): 188-201.

de Silva J. A., Condrey R. E. & Thompson B. A. 2001. Profile of shark bycatch in the US Gulf of Mexico menhaden fishery. *North American Journal of Fisheries Management*. **21** (1): 111-124.

deCarvalho M. R. 1996. Higher-level elasmobranch phylogeny, basal squaleans, and paraphyly. In: *Interrelationships of Fishes*. (Stiassny M. L. J., Parenti L. R. & Johnson G. D. eds.), pp 35-62. Academic Press.

Dingle H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, New York. 474 pp.

Domeier M. L. & Colin P. L. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science*. **60** (3): 698-726.

Eckert S. A. & Stewart B. S. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environmental Biology of Fishes*. **60** (1-3): 299-308.

Eltringham S. K. 1994. Can wildlife pay its way? *Oryx*. **28** (3): 163-168.

Farrell T. A. & Marion J. L. 2001. Identifying and assessing ecotourism visitor impacts at eight protected areas in Costa Rica and Belize. *Environmental Conservation*. **28** (3): 215-225.

Ferguson M. A. D., Gauthier L. & Messier F. 2001. Range shift and winter foraging ecology of a population of Arctic tundra caribou. *Canadian Journal of Zoology*. **79** (5): 746-758.

FON. 2003. Gladden Spit and Silk Cayes Marine Reserve Management Plan. Friends of Nature. Placencia, Belize. 72 pp.

Fowler S. L. 2000. Whale sharks *Rhincodon typus* policy research and scoping study. The Nature Conservation Bureau. UK. 27 pp.

Francis M. P., Griggs L. H. & Baird S. J. 2001. Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine Freshwater Research*. **52**: 165-178.

Gell F. R. & Roberts C. M. 2003. The Fishery Effects of Marine Reserves and Fishery Closures. WWF-US. 1250 24th Street, NW, Washington, DC 20037, USA. 90 pp.

Grove J. S. & Lavenberg R. J. 1997. *The fishes of the Galápagos Islands*. Stanford University Press, Stanford. 863 pp.

Gudger E. W. 1915. Natural history of the whale shark, *Rhineodon typus* Smith. *Zoologica*. **1** (19): 345-389.

Gudger E. W. 1936. Rhineodon at New York's front door. *Nat Hist*. **37**: 159-166.

Gudger E. W. 1937a. A whale shark impaled on the bow of a steamer near the Tuamotus, South Seas. *Science*. **85** (2204): 314.

Gudger E. W. 1937b. A whale shark rammed by a steamer off Colombo, Ceylon. *Nature*. **139**: 549.

Gudger E. W. 1937c. A whale shark speared on the bow of a steamer in the Caribbean Sea. *Copeia*. **1937** (1): 60.

Gudger E. W. 1938. A whale shark rammed by a vessel off the Pacific coast of western Panama. *Nature*. **141**: 516.

Gudger E. W. 1939. Four whale sharks rammed by steamers in the Red Sea region. *Copeia*. **1938** (4): 170-175.

Gudger E. W. 1941. The food and feeding habits of the whale shark, *Rhineodon typus*. **57** (1): 57-72.

Gudger E. W. & Hoffman W. H. 1930. The second capture of the whale shark, *Rhineodon typus*, near Havana Harbor, Cuba. *Science*. **71** (1851): 639-640.

Hanfee F. 2001. Gentle Giants of the Sea: A report on trade in whale shark off the Gujarat coast. TRAFFIC-India/WWF-India. 38 pp.

Heyman W. D., Graham R. T., Kjerfve B. & Johannes R. E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology-Progress Series*. **215**: 275-282.

Hoyt E. 2000. Whale Watching 2000: Worldwide Tourism Numbers, Expenditures, and Expanding Socioeconomic Benefits. International Fund for Animal Welfare. Crowborough. 157 pp.

Hyrenbach K. D., Forney K. A. & Dayton P. K. 2000. Marine protected areas and ocean basin management. *Aquatic Conservation-Marine and Freshwater Ecosystems*. **10** (6): 437-458.

IUCN. 1996. *1996 IUCN Red List of Threatened Animals*. World Conservation Union, Gland, Switzerland. 341 pp.

IUCN. 2000. *2000 IUCN Red List of Threatened Species*. World Conservation Union, Gland, Switzerland.

Iwasaki Y. 1970. On the distribution and environment of the whale shark, *Rhincodon typus*, in skipjack fishing grounds in western Pacific ocean. University of Tokai A-40. 37-51 pp.

Johannes R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes*. **3** (1): 65-84.

Jones P. J. S. 1994. A review and analysis of the objectives of marine nature reserves. *Ocean & Coastal Management.* **24** (3): 149-178.

Joung S. J., Chen C. T., Clark E., Uchida S. & Huang W. Y. P. 1996. The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma' supreme. *Environmental Biology of Fishes.* **46** (3): 219-223.

Kramer P., Kramer P. R., Arias-Gonzalez E. & McField M. 2000. Status of coral reefs of Northern Central America: Mexico, Belize, Guatemala, Honduras, Nicaragua and El Salvador. In: *Status of Coral Reefs of the World: 2000.* (Wilkinson C. ed.), pp 287-313.

Kukuyev E. I. 1995. The new finds in recently born individuals of the whale shark Rhiniodon typus (Rhiniodontidae) in the Atlantic Ocean. **36** (2): 203-205.

Last P. R. & Stevens J. D. 1994. *Sharks and Rays of Australia.* CSIRO Division of Fisheries, Australia. 507 pp.

Lauck T., Clark C. W., Mangel M. & Munro G. R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications.* **8** (1): S72-S78.

Lutcavage M. E., Brill R. W., Skomal G. B., Chase B. C. & Howey P. W. 1999. Results of pop-up satellite tagging of spawning size class fish in the gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries Aquatic Science.* **56**: 173-177.

McField M. 2000. Evaluation of Management Effectiveness: Belize Marine Protected Areas System. Coastal Zone Management Authority institute. Belize City, Belize. 53 pp.

McField M. 2001. The Influence of Disturbance and Management on Coral Reef Community Structure in Belize. PhD. College of Marine Sciences, Florida. 155 pp.

Mills C. E. & Carlton J. T. 1997. Rationale for a system of international reserves for the open ocean. *Conservation Biology.* **12** (1): 244-247.

Myers R. A. & Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature.* **423**: 280-281.

Norman B. M. 1999. Aspects of the biology and ecotourism industry of the whale shark *Rhincodon typus* in north-western Australia. M.Phil., Western Australia.

Norse E. A., Roberts C. M., Soule M. E., Crowder L. B. & Safina C. in press. Marine reserves for large pelagic species.

O'Connell-Rodwell C. E., Rodwell T., Rice M. & Hart L. A. 2000. Living with the modern conservation paradigm: can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia. *Biological Conservation.* **93** (3): 381-391.

Orams M. B. 2000. Tourists getting close to whales, is it what whale-watching is all about? *Tourism Management.* **21** (6): 561-569.

Orams M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management.* **23** (3): 281-293.

O'Sullivan J. B. & Mitchell T. 2000. A fatal attack on a whale shark *Rhincodon typus*, by killer whales *Orcinus orca* off Bahia de los Angeles, Baja Califonia. *American Elasmobranch Society Annual Meeting, La Paz, Mexico.*

Paz M. & Grimshaw T. 2001. Working towards the sustainable management of Nassau groupers in Belize. Workshop report. GreenReef. Belize City. 93 pp.

Pauly D. 2002. Growth and mortality of the basking shark *Cetorhinus maximus* and their implications for management of whale sharks *Rhincodon typus*. In: *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Worjkshop, Sabah, Malaysia, July 1997.* (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 199-208. Gland, Switerland and Cambridge, UK. IUCN SSC Shark Specialist Group.

Rettie W. J. & Messier F. 2001. Range use and movement rates of woodland caribou in Saskatchewan. *Canadian Journal of Zoology.* **79** (11): 1933-1940.

Richardson J. A. 1998. Wildlife utilization and biodiversity conservation in Namibia: conflicting or complementary objectives? *Biodiversity and Conservation.* **7** (4): 549-559.

Roberts C. M. 1994. Marine reserves: a brief guide for decision makers and users *Workshop on Coastal and Ocean Resources Management. NGO Islands Forum. UN Global Conference on the Sustainable Development of small Island Developing States.*, Barbados April 25- May 6, 1994.

Roberts C. M. 1995. Rapid buildup of fish biomass in a Caribbean marine reserve. *Conservation Biology.* **9** (4): 815-826.

Roberts C. M. 1997. No-take marine reserves: unlocking the potential for fisheries. In: *Marine Environmental Management: Review of Events in 1997 and Future Trends.* (Earl R. C. ed.), pp 127-132. Gloucester. Kempley.

Roberts C. M. 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries.* **23** (7): 16-19.

Roberts C. M., McClean C. J., Vernon J. E. N., Hawkins J. P., Allen G., McAllister D. E., Mittermeier C. G., Schueler F. W., Spalding M., Wells F., Vynne C. & Werner T. B. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*. **295**: 1280-1284.

Roberts C. M. & Sargant H. 2002. Fishery benefits of fully protected marine reserves: why habitat and behaviour are important. *Natural Resource Modeling*. **15** (4): 487-507.

Romanov E. V. 2002. Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. *Fishery Bulletin*. **100** (1): 90-105.

Rutzler K. & Macintyre I. G. 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. In: *The Atlantic Barrier Reef Ecosystem at Carrie Boy Cay, Belise, I: Structure and Communities*. (Rutzler K. & Macintyre I. G. eds.), pp 9-47. Washington D.C. Smithsonian Institution Press.

Safina C. 1999. *Song for the Blue Ocean*. Owl Books. 384 pp.

Sims D. W. & Quayle V. A. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature*. **393**: 460-464.

Smith A. 1828. Description of new, or imperfectly known objects of the animal kingdom, found in the south of Africa. *S. Afr. Commercial Advertiser*. **3** (145): 2.

Songorwa A. N. 1999. Community-based wildlife management (CWM) in Tanzania: are the communities interested? *World Development*. **27** (12): 2061-2079.

Stevens J. D., Norman B. M., Gunn J. S. & Davis T. L. O. 1998. Movement and behavioural patterns of whale sharks at Ningaloo Reef: the implications for tourism. National Ecotourism Final Report: Application Ref. No. 30051. CSIRO Marine Research. 35 pp.

Taylor J. G. 1994. *Whale Sharks, the Giants of Ningaloo Reef.* Angus & Robertson, Sydney.

Taylor J. G. 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*. **47** (4): 637-642.

Thouless C. R. 1995. Long distance movements of elephants in northern Kenya. *African Journal of Ecology*. **33** (4): 321-334.

Trasvina-Castro A., de Velasco G. G., Valle-Levinson A., Gonzalez-Armas R., Muhlia A. & Cosio M. A. 2003. Hydrographic observations of the flow in the vicinity of a shallow seamount top in the Gulf of California. *Estuarine, Coastal and Shelf Science.* **57** (1-2): 149-162.

Uchida S., Toda M., Kamei Y. & Teruya H. 2000. The husbandry of 16 whale sharks, *Rhincodon typus,* from 1980 to 1998 at Okinawa Expo Aquarium. *American Elasmobranch Society Annual Meeting, La Paz, Mexico.*:

UNFAO. 1995. The state of the world fisheries and aquaculture. United Nations Food and Agriculture Organization. Rome, Italy.

Vistnes I., Nellemann C., Jordhoy P. & Strand O. 2001. Wild reindeer: impacts of progressive infrastructure development on distribution and range use. *Polar Biology.* **24** (7): 531-537.

Webster M. S., Marra P. P., Haig S. M., Bensch S. & Holmes R. T. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution.* **17** (2): 76-83.

Wintner S. P. 2000. Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa. *Environmental Biology of Fishes.* **59** (4): 441-451.

Wolanski E. & Hamner W. M. 1988. Topographically controlled fronts in the ocean and their biological influence. *Science.* **241**: 177-181.

Wolfson F. H. 1983. Records of seven juveniles of the Whale Shark, *Rhiniodon typus. Journal of Fish Biology.* **22** (6): 647-655.

Wolfson F. H. 1986. Occurrences of the whale shark, *Rhincodon typus*, Smith. In: Uyeno T. & et. al. (eds) *Indo -Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes.* Ichthyological Society of Japan, Tokyo, pp 208-226.

Young E. 1999. Local people and conservation in Mexico's El Vizcaino Biosphere Reserve. *Geographical Review.* **89** (3): 364-390.

Zangrl R. 1981. Chondrichthyes I: Paleozoic Elasmobranchii. In: *Handbook of Paleoichthyology.* (Schultze H. P. & Kuhn O. eds.), pp 114. G.V. Verlag.

Chapter 2. Abundance and structure of the visiting population of whale sharks at Gladden Spit, Belize

Abstract

A lack of reliable data on whale shark (*Rhincodon typus*) abundance and its migratory patterns has constrained understanding of this species' ecology and hampered efforts to manage it. Using a combination of data on encounters, photo identification and conventional marker tagging, 106 individual whale sharks were identified as transient visitors to Gladden Spit between 1998 and 2003. Located on the Belize Barrier Reef, Gladden Spit hosts a predictable aggregation of whale sharks that feeds on the spawn of seasonally reproducing snappers. A minimum of 521 encounters with whale sharks was recorded. Results indicate that the fish spawning site is a preferred feeding area for juvenile male whale sharks. The majority of sharks encountered (60.3%, n = 314) had a mean total length (TL) of 6.3 m ± 1.7 m SD (range: 3.0 m to 12.7 m; error of ± 0.50 m). Thirty one percent of encountered sharks were sexed, 86% were juvenile males. Seventy sharks were tagged with conventional marker tags between 1999 and 2002. Mean length of measured and tagged sharks (n = 63) was 6.0 m ± 1.6 m SD (range 3.0 m to 9.7 m). Of these, 41% of tagged individuals were sexed with 83% recorded as juvenile males. Only 14 mature males, and eight females (two mature and six juveniles) were sighted from 1998 to 2003. Nine sharks were recorded with a total length over 9 m, which qualifies them as mature. Monitoring whale shark visiting population abundance, structure and rates of revisitation at Gladden Spit is key to their conservation in the region and underpins local tourism focused on whale shark interactions with people. Patterns of movement and low abundances of the visiting whale shark population recorded in this study support this species' recent Appendix II listing for Convention on the International Trade of Endangered Species of Fauna and Flora (CITES). These observations further provide the basis for establishing a regional law among range states to protect this species in their territorial waters.

2.1 Introduction

Management and conservation of vulnerable species is underpinned by reliable assessments of population abundance. The decline of sharks worldwide (FAO, 1994; Camhi *et al.*, 1997; Fowler *et al.*, 2002) and specifically in the NW Atlantic (Baum *et* *al.*, 2003) together with worldwide depletion of predatory fish stocks including sharks has prompted stronger conservation measures for affected species (Myers & Worm, 2003). Yet, estimating population abundance in cryptic and elusive animals is costly and challenging (Karanth, 1995; Karanth & Nichols, 1998; Schwarz & Seber, 1999; Carbone *et al.*, 2001; Wilson & Delahay, 2001; Silver *et al.*, in press). Assessing population abundance in highly migratory marine species is even more difficult due the uncertainties related to their patterns and range of movement and to the difficulties of conducting research in relatively inhospitable marine environments. Yet, a key step in the management and conservation of any threatened species is defining a population which Begon *et al.* (1996) states as:

> "A group of individuals of one species in an area, though the size and nature of the area is defined, often arbitrarily, for the purposes of the study being undertaken."

Therefore a spatial component needs to be quantified to define the parameters of a population, which might include the known home ranges or extent of movement of a species. The World Conservation Union (IUCN) does not focus on the spatial aspect (whilst it seeks to monitor population levels for reductions in numbers) to determine if a species is endangered. It states that a functional population consists of the number of mature individuals (IUCN, 2000). However, for marine fishes, IUCN has recently expanded its definition to reductions in biomass to account for sex-changing fish or species, or biased breeding sex ratios. It further notes that the species' ecology and behaviour such as site fidelity are key factors determining the vulnerability of a population. Site attachment infers a temporal factor, another criterion that could be used to define a population. In this study, the population of whale sharks was defined as the group of individuals that visits Gladden Spit every snapper spawning-season.

The development of new technologies such as infra-red triggered remote cameras have facilitated terrestrially-based population estimates of elusive species (Karanth & Nichols, 1998; Carbone *et al.*, 2001; York *et al.*, 2001; Silver *et al.*, in press), yet prove useless in the marine environment. Although non-catch dependent population estimates of marine mammals are widespread and facilitated by the species' need to surface and breathe (Best, 1990; Cerchio, 1998; Cerchio *et al.*, 1998), most estimates of population abundance in specific species of large migratory fish, particularly sharks, remain based on fisheries-dependent data (Branstetter, 1987; Bonfil, 1997; Fairfax, 1998; Punt *et al.*, 2000; Anislado-Tolentino & Robinson-Mendoza, 2001; Baum *et al.*, 2003; Myers &

Worm, 2003) or bycatch data (de Silva *et al.*, 2001; Francis *et al.*, 2001; Romanov, 2002). These surveys are therefore linked to fishing areas or zones as opposed to the species activity spaces or areas of occupation and therefore do not adequately represent the studied populations.

Fisheries-independent studies on shark populations and movement are increasing (Cliff *et al.*, 1996; Ferreira & Ferreira, 1996; Strong *et al.*, 1996; Simpfendorfer *et al.*, 2002), with a range of methods developed to study the population biology of sharks, all of which have their opportunities and drawbacks (Cailliet, 1996). Since 1962 the National Oceanographic and Atmospheric Administration's National Marine Fisheries Service Laboratory (NOAA-NMFS) implemented a cooperative shark tagging program with recreational anglers and commercial fishers leading to the tagging of over 87,000 sharks (Kohler *et al.*, 1998). However tag shedding appears common in a range of shark species (Davies & Joubert, 1967; Gruber, 1982; Carrier, 1985; Heupel & Bennett, 1997), undermining viable population estimates. Photo identification is a non-invasive method of identifying individuals that relies on cataloguing distinctive scars or markings originally developed to identify terrestrial animals and marine mammals (Katona *et al.*, 1979; Arnbom, 1987). Successfully used by organisations such as the International Fund for Animal Welfare in its North Atlantic & Mediterranean Sperm Whale Catalogue (NAMSC), photo-identification has been adapted to identify basking sharks (*Cetorhinus maximus*) in Britain[1] (Sims *et al.*, 2000b), white sharks (*Carcharodon carcharias*) at California's Farallon Islands (Klimley, 1996) and whale sharks in Ningaloo Reef, Australia and Belize (B. Norman, pers. comm., and this chapter). However, photo ID is not always error-proof as individuals may have similar scars or patterns of markings (Cailliet, 1996) or the entire animal can not be encompassed in one photograph leading to multiple identifications of the same animal (Graham, pers. obs.).

One of the most popular methodologies that holds the greatest promise for assessing population abundance is based on using mark-release and recapture or resightings (MRR) methods. These can be based on either a Lincoln-Petersen demographically closed-population estimation model used by Cliff *et al.* (1996) with white sharks in South Africa, or a demographically open-population model such as the Jolly-Seber (Schwarz & Seber, 1999; Seber, 2001) that Strong *et al.* (1996) used with white sharks at Dangerous Reef off the south coast of Australia. MRRs are burdened by

[1] A basking shark identification program has been set up at the UK-based Shark Trust and can be found at: http://www.sharktrust.org/

caveats despite their widespread use and apparent success in estimating the abundance of many animal species (Rabinowitz, 1993; Strong *et al.*, 1996; Tuyttens *et al.*, 1999; Carbone *et al.*, 2001; Chao, 2001). Assumptions may include whether a population is closed or open to immigration and emigration, whether it reflects birth and mortality rates, and resulting population estimates are prone to error if samples sizes are small (Schwarz & Seber, 1999; Schwarz, 2001; Seber, 2001). Additionally, field-based failures can further undermine the effectiveness of population estimation models, e.g., resightings of tags may be prone to error (Graham, pers. obs.) and tags can be readily shed based on tag type and response of the animal to tagging (Carrier, 1985; Heupel & Bennett, 1997; Heupel *et al.*, 1998; Sundstrom & Gruber, 2002). Basic knowledge of the species' behaviour is required to assess which model will provide the best estimate of population size. Both demographically closed and open-population models often yield very large confidence limits (at 95%) with small population samples, which may undermine the effectiveness of the methods and subsequent population management. Additionally, if the species investigated displays differences in habitat or dietary preferences based on sex or size common to many shark species (Springer, 1967; Klimley, 1987), then sampling and subsequent population estimates will not represent the true population.

The whale shark is a species vulnerable to any exploitation based on its life history characteristics (COP12, 2002; Pauly, 2002) (Chapter 1) and whose demographic status is unknown throughout its pan-tropical distributional range. A lack of reliable data on population densities and abundance (Fowler, 2000; COP12, 2002) coupled with the species' ability for large-scale movement (Eckert & Stewart, 2001; Eckert *et al.*, 2002) (Chapter 4) has constrained understanding of this species' ecology and undermined its effective conservation.

The available data on whale shark populations worldwide are based on fisheries-dependent data collected in Taiwan (Chen *et al.*, 1996), India (Hanfee, 2001) and the Philippines (Alava *et al.*, 2002), and catch-independent data in Belize (this chapter), Seychelles (Graham, unpublished data) and Ningaloo Reef, Western Australia (Taylor, 1996; Colman, 1997). Fisheries data have provided a snapshot of abundance in Taiwan, India and the Philippines, confirming that populations are relatively low with catches measured in the tens and hundreds of animals. Fished populations appear to be made up of highly mobile individuals that, according to recent data, demonstrate large-scale patterns of movement across ocean basins and between regions where targeted fisheries for whale sharks exist (Eckert & Stewart, 2001; Eckert *et al.*, 2002) (http://www.marine.csiro.au/research/tagging/hopetraveller/index.html) (Graham, unpublished data). The decline in whale shark sightings at several sites worldwide, often within the same ocean basin where targeted fishing takes place, further substantiates the existence of a small population (COP12, 2002). It is worth noting that changes in population abundance may also be due to the impacts of global climate change. Changes in prey density and abundance potentially due to rises in sea-surface temperature may have caused the high gray whale (*Eschrichtius robustus*) mortality witnessed in the Eastern Pacific in 1999 (Le Boeuf *et al.*, 2001). Zonal displacements of warm bodies of water triggered by the El Niño Southern Oscillation led to spatial shifts in the populations of skipjack tuna (*Katsuwonus pelamis*), and comparable temperature regime changes linked to changes in current patterns appear to have altered whale shark abundances recorded in Ningaloo Reef, Western Australia (Wilson *et al.*, 2001). Sims and Reid (2002) similarly recorded a downward trend in basking shark (*Cetorhinus maximus*) catches off the coast of Ireland from 1949 to 1975 that are correlated with a 27-year decline in copepod abundance over the same period.

This chapter examines three methods of assessing the abundance of a transient population of the usually elusive whale shark at Gladden Spit on the Belize Barrier Reef, a site chosen to maximize encounter rates. This population aggregates seasonally to feed on the spawn of reproducing snappers (see Chapter 3) and is not subject to fishing pressure in the region. Encounters, photo identification and conventional marker tagging of individuals were used as methods of generating fisheries-independent population abundance and structure data on whale sharks aggregating at Gladden Spit between 1998 and 2003. Management implications of results are discussed in the context of threats and opportunities to conserve whale sharks.

2.2 Materials and methods

2.2.1 Study site

A full site description and map is provided in Chapter 1.

2.2.2 Whale shark encounters and photo identification

Individual whale sharks encountered at Gladden Spit were sexed, measured and identified when possible during three two-week peak snapper spawning moons of May 1998, March through June from 1999 and 2002 and March through April 2003. A whale shark encounter took place if a boat, snorkeler or diver was ~10 m or less from the shark. Divers sexed sharks by diving under them and noting the presence and state of claspers. Sharks were classified into four categories: mature male, juvenile male, mature female and juvenile female. Fully developed and calcified claspers indicated that the shark was an adult male, small claspers that did not protrude or barely protruded from the pelvic fins indicated that the shark was still a juvenile. Lack of claspers indicated female sharks and maturity was based on an estimated total length of over 9 m which represents a known size at which female whale sharks are sexually mature (Joung *et al.*, 1996). To estimate shark total length, a diver (about 2 m in length with fins) swam underwater next to the whale shark while another diver estimated the number of diver lengths the shark represented. Research snorkelers and divers were also tested on land for whale shark length accuracy by using measured lengths of rope or prone divers with fins next to tape measures. Sharks swimming on the surface were measured by driving a boat (7.5 m) alongside the sharks, matching the tip of the tail with the stern of the boat, and estimating total length relative to the bow. Identification images were taken with underwater stills camera (Nikonos V with Fuji 400 slide film), digital cameras and videos with housings (Olympus 4040, Sony PC 110 and Light and Motion housings) to generate individual identifications of dorsal and caudal fin spot patterns and inalterable scars (total or partial fin loss and patterns of fin notches, as opposed to small scrapes and readily healed superficial wounds) (Figure 2.1). The unique pattern of spots behind the gills was also recorded to cross reference identifications made in Australia's Ningaloo Reef (Stevens *et al.*, 1998) (B. Norman, pers.comm. 2000). All data on whale sharks, including their tagging and resighting history were recorded in log-books and in an MS Excel spreadsheet and MS-Access database to create a permanent log of all individuals.

Once scanned or entered into the computer, images were catalogued using imagery software (ACDSee 5.0). A printable catalogue of all image identifications recorded was generated using photo organisational software (ACDSee Fotoslate) (see Apeendix 2.A). The file nomenclature that helped to retrieve records rapidly while providing the maximum of information on each individual image included the following criteria (separated by underscores for easy importation into MS Excel spreadsheets):

1. Unique identifying number (often one given by the digital camera if the image was taken digitally)
2. Side and body part of the shark: r = right, l = left (as viewed from above the shark); g = gills, d = dorsal fin, c = caudal fin.
3. Location the image was taken
4. Date image was taken

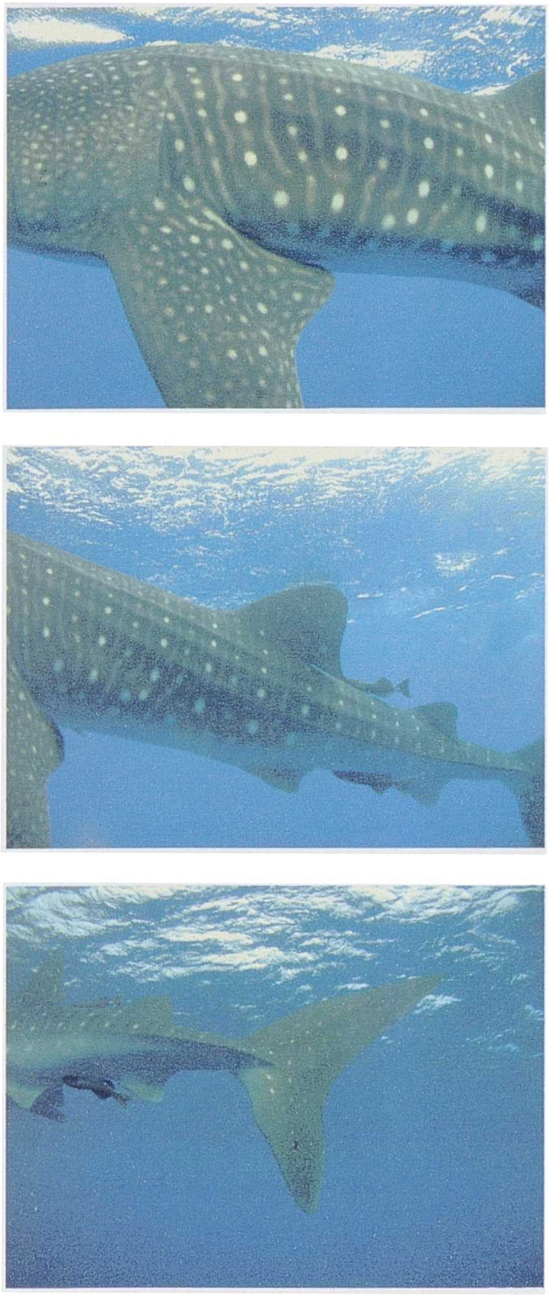


Figure 2.1: Whale shark identification using spot patterns behind the gills, on the 1st dorsal and lower caudal

5. Tag type and number where known: M = marker, AS = acoustic small (V16), AL = acoustic large (V32), SP = satellite pop-off tag, SL = satellite location-only or "Spot" tag.
6. Each tag's location on the shark: rod = right of dorsal, lod = left of dorsal
7. Sex, if available: JM = juvenile male, MM = mature male, JF = juvenile female, MF = mature female.
8. Name or very distinctive scars or characteristics.

Coded images would be listed in the following way:

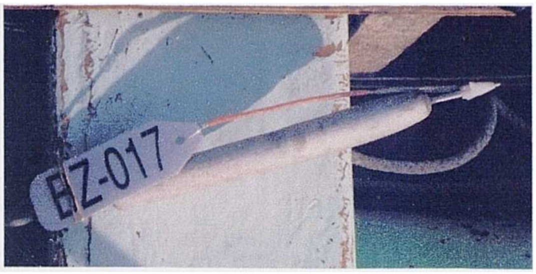
#1473-456_lgd_BZG_20-5-01_M052_lod_AS_rod_MM_Chop

Interpreted as: left side image of gills and dorsal number 1473-456 of a mature male whale shark named Chop (for the chopped dorsal), taken at Gladden in Belize on the 20th of May 2001. The shark had a marker tag # 52 located on the left of its dorsal and a small acoustic on the right of its dorsal.

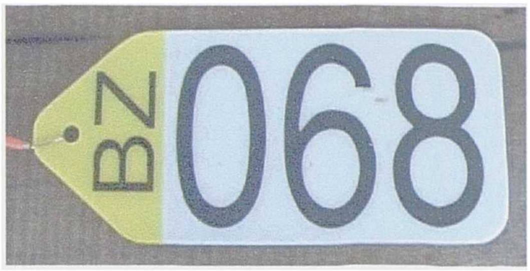
2.2.3 Tagging

Identification of sharks using scars and spot patterns limited popular involvement in resighting of individuals, particularly as these animals moved large distances into areas where people were unfamiliar with the research and identification methods (Chapter 4). A conventional tagging programme began in 1999 to improve resighting of known individuals, involve a greater number of people in the study and estimate population abundance and structure.

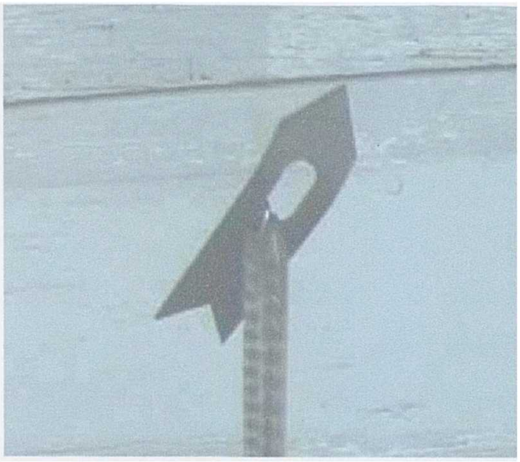
Tags were made of colour-coded, sequentially numbered laminated plastic attached to Floy BFIM nylon darts in 1999, small stainless steel M-type darts in 2000 (Floy FH-69). The letters BZ, for Belize, preceded the numbers to indicate country of tagging. To increase tag retention in 2001 and 2002 and beyond, larger titanium darts (1.5 cm x 6.0 cm) replaced the small darts (Figure 2.2) and a grommet was inserted in the eyehole to increase tag strength. A 140 lb test nylon-coated braided stainless steel wire crimped with stainless crimps and covered with heat-shrinked tubing linked tags and darts. Tag number on tags from 2000 to 2002 could be read underwater at a distance of about 7.0 m if unfouled by algal growth. Numbers could rarely be read from a boat, unless the observer donned a mask and looked over the side of the boat. However, the tag's colour coding and location on the shark provided an indication of deployment year and sometimes even the individual shark. If fouled, tags required a quick clean before a number could be read. Whale sharks would occasionally oblige us during this task by



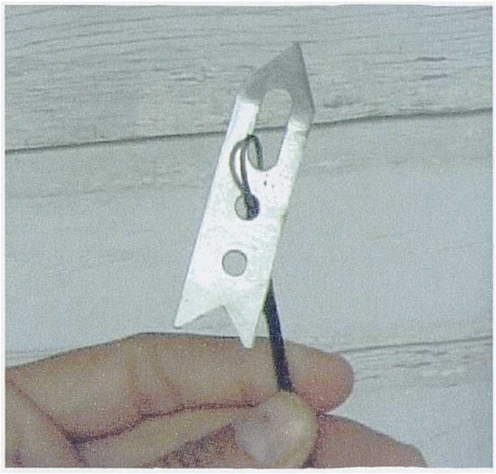
(a)



(b)



(c)



(d)

Figure 2.2: Tag and dart types used during the whale shark tagging program at Gladden Spit. (a) First tag type used on whale sharks at Gladden Spit, white numbered with country code with BFIM nylon dart; (b) larger, colour-coded laminated tag used between 2000 and 2002; (c) stainless steel Floy Tags FH-69 dart head used in 2000; and (d) titanium dart used in 2001 and 2002. White tags were deployed in 1999, yellow and white tags in 2000, orange and white tags in 2001, and green and white tags used in 2002.

swimming slowly and showing no reaction to tag cleaning. In 2002, clear antifouling paint was applied to the tags to decrease algal fouling.

Tagging took place primarily during the two weeks following the full moon of March-June, beginning in April 1999. Tags were deployed mainly at dusk using 2 m pole spears from a 7.5 m skiff manoeuvred next to feeding whale sharks (Figure 2.3). Data recorded per tag deployed included tag number, placement on the animal – left or right of the first dorsal fin (lod or rod), a global positioning system (GPS) point taken (Garmin 12), and total length from tip of the tail to the snout estimated to the nearest 50 cm using the boat length as scale. Where possible a diver entered the water with a digital video or stills camera to sex, size and record the individual's spot patterns and scars. Several sharks were double and even triple tagged with numbered marker and acoustic and/or satellite tags (see Chapters 3 and 5 for explanations on acoustic and satellite tagging). All tagging data recorded with the GPS between 1999 and 2002 were mapped in relation to the location of the spawning snappers at Gladden Spit using the software ArcView (ESRI Corporation) (Figure 2.4). Tagging points for 2002 were segregated to show alteration in the sharks' location during the May moon. Tag and dart retention characteristics were compared and assessed by comparing tagged animals identified through video, conventional stills and observational dives on an annual basis.

Information on the tagging program was disseminated at the local, national and international levels to increase the likelihood of collecting resightings information on tagged sharks. In the region, tour-guides, fishers and marine conservation governmental and non-governmental organisations were contacted and provided with study and tagging information in Belize, Mexico, Honduras, and Texas. Laminated flyers and information sheets were posted in several restaurants and the Placencia Tourism Center and distributed locally to tour-guides, fishers and NGOs[2]. Articles were published in the local press and project newsletters with the study's objectives and request for sightings information were broadly distributed. Both the brochures and the newsletter were also made available on the project's web page set up in 2000. Additionally, resightings log sheets were distributed to tour-guides working out of Placencia and frequent talks with tour-guides, fishers and tourists visiting Gladden Spit provided information on whale sharks and the Belize-based research and reiterated the importance of the tagging program and provided the basis for requesting resightings information.

[2] Brochure, newsletter and information available on the web at www.york.ac/environment/darwin

Figure 2.3: Tag deployment on a whale shark from a 7.5 m outboard boat at the Gladden Spit snapper spawning-aggregation site.

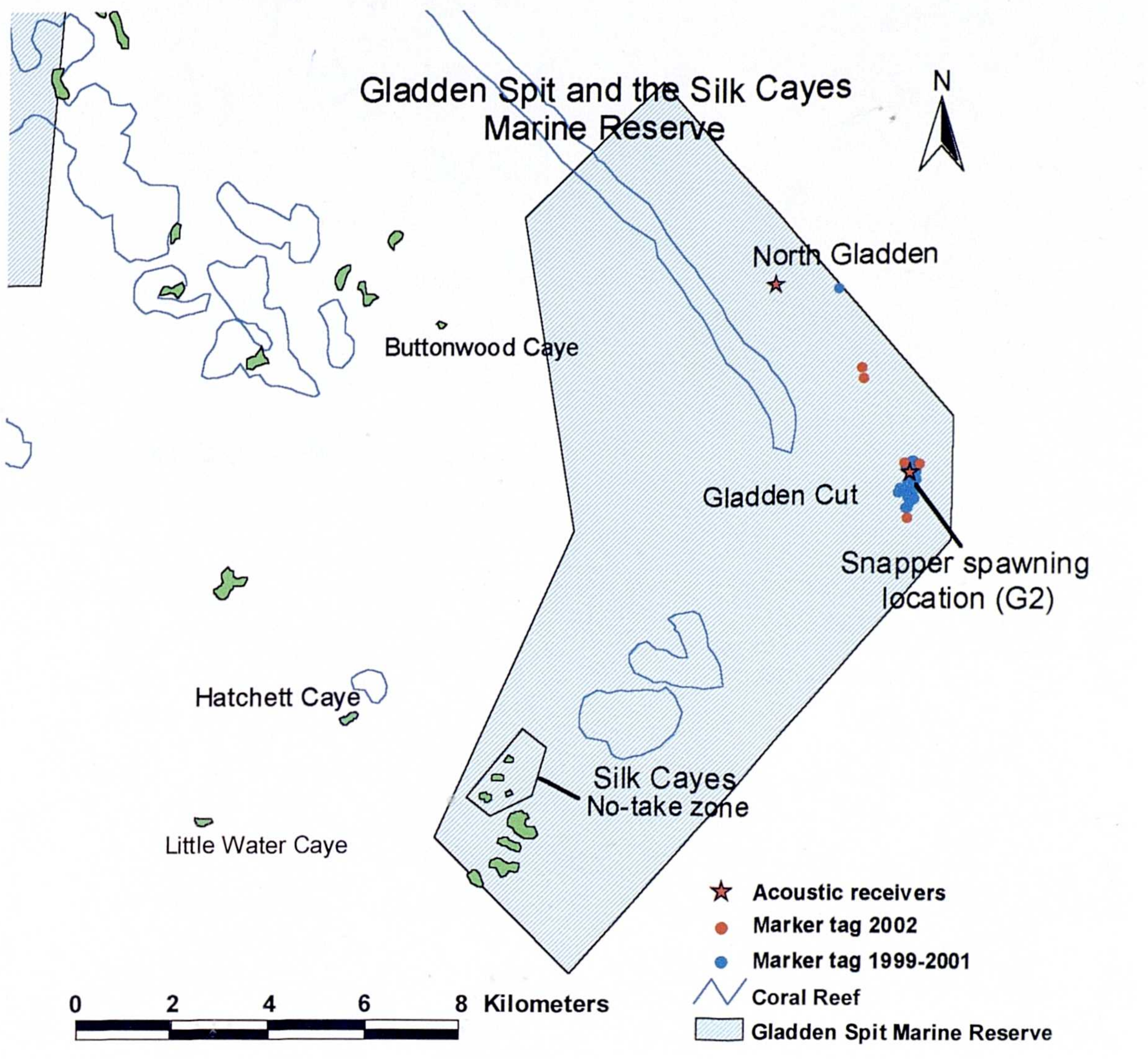


Figure 2.4: Tagging locations of whale sharks in the Gladden Spit and the Silk Cayes Marine Reserve between 1999 and 2002. The two northern most red dots represent tagging that took place during the period of snapper spawning and whale shark unpredictability from 24-29 May 2002.

2.3 *Results*

2.3.1 Population abundance

From 1999-2003, there were 521 recorded encounters of whale sharks at Gladden Spit (Table 2.1). Sharks were measured during 314 (60.3%) encounters and sexed during 163 (31.3%). The highest recorded daily density of whale sharks on the fish spawning aggregation grounds was recorded in 1998 with 25 sharks counted in a diameter of 50 m (Heyman *et al.*, 2001).

Table 2.1: Number of whale sharks (WS) sighted, measured and sexed between 1998 and 2003. TL: total length in meters; JM: juvenile male; MM: mature male: JF: juvenile female; MF: mature female.

	1998	1999	2000	2001	2002	2003
No. WS encounters recorded	50	81	140	133	81	36
No. of WS measured (TL m)	32	71	67	52	58	34
No. sexed	15	15	24	34	53	22
Sexes recorded	11 JM	11 JM	20 JM	27 JM	51 JM	20 JM
	2 MF	2 MM	2 MM	7 MM	2 MM	1 MM
	2 JF	2 JF	1 MF			1 JF
			1 JF			
Mean TL (m)	6.9	5.8	6.1	6.5	6.9	5.7
SD (m)	7.6	1.7	1.6	1.4	1.5	1.0

Mean whale shark sightings per day remained relatively steady throughout 1998-2001 ranging from 3-5 sightings day^{-1}, dropping to two sightings day^{-1} in 2002. A Kruskal-Wallis test comparing the compiled number of whale shark sightings made per day each year using standard search effort within the snapper–spawning season revealed a difference in whale shark sightings between years (df = 4; $X^2 = 14.4$; $p < 0.05$) (Figure 2.5) with a decline noted between 2001 and 2002. This result was primarily due to the decline in mean sightings over a period of 6 days from 24-29 May 2002 when the whale sharks were not seen predictably at the Gladden Spit spawning aggregation site.

The chance of seeing a whale shark on any one day in-season between 1999 and 2001 remained steady at close to 80% (Figure 2.6). Years 1998 and 2002 proved the worst for sightings with only a 67% and 52% chance respectively of seeing a whale shark on a given search day during the peak season. Although sighting days were few in 1998 because of only one month sampled, this was also the year during which the

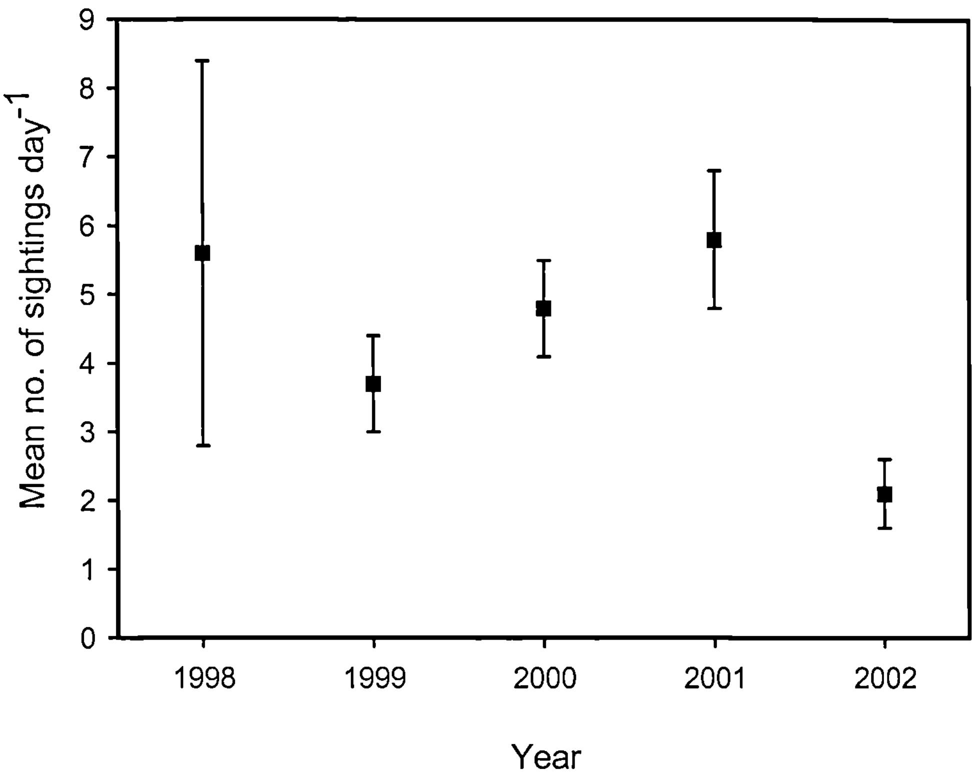


Figure 2.5: The mean number of whale shark sightings per day during the peak whale shark season from March to July between 1998 to 2002 (± SE).

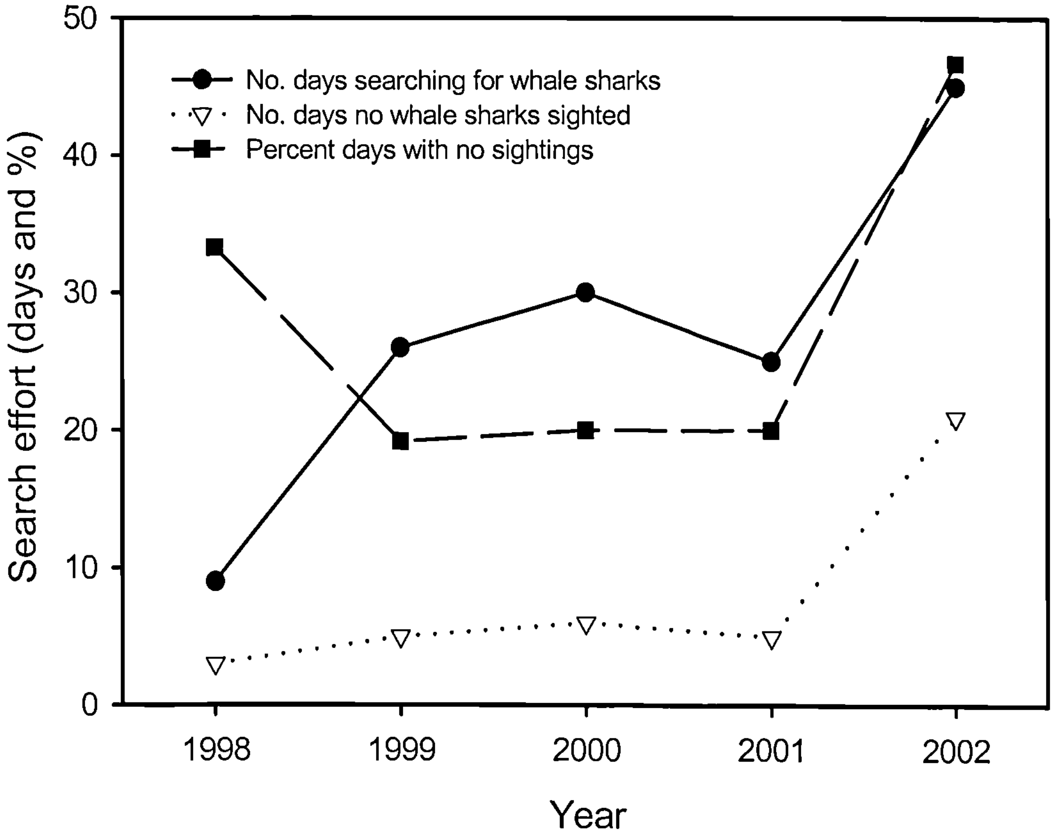


Figure 2.6: The total number of search days for whale sharks in peak snapper spawning season (1998-2002) versus the number of days and percentage of days with no sightings.

greatest number of sharks (n = 25) were sighted on the surface at one time (Heyman *et al.*, 2001).

At least 571 usable images of whale sharks were recorded at Gladden Spit during the same time period, yielding identifications for 123 individuals (Table 2.2; Appendix 2.A). Of these, several sharks were repeatedly resighted between years, thus reducing to 106 the number of identified individuals. Several of the 106 identifications may represent doubles as not all parts of the sharks could be photographed in sequence or at the same time or date, and spot patterns may differ on both sides of the sharks. At least 13 sharks could be uniquely identified through distinctive scars alone. At the time of writing, 69 images were pending further analysis of videotapes or inter-annual image comparisons to potentially generate new identifications or produce further matches with previously identified individuals.

Table 2.2: Whale shark identification numbers using photos and marker tags from 1999-2003.

	1999	2000	2001	2002	2003	Total
No. of whale shark images	87	157	35	227	65	571
Photo identifications	18	41	18	31	15	123
No. of marker tags deployed	16	31	16	7	0	70
No. of marker tags with photo ID	1	14	4	3	0	22
No. of unidentified images	2	31	1	32	3	69

All sharks were tagged within the Gladden Spit and Silk Cayes Marine Reserve (Figure 2.4). Seventy whale sharks were tagged with marker tags (Table 2.3). In addition, eleven tags were lost at sea, accounting for the non-numerical sequence of tagging in the table. Two tags were deployed on the same shark in the same year (no. 2 and 15 in 1999). Two other tags are known to have detached within the year of their deployment based on resightings of the untagged sharks within the same season (M42 and M52 in 2001). At least 23 tagged sharks (33%) were identified photographically (Table 2.2). Most resightings of tagged sharks occurred at Gladden Spit or within 50 km of the reserve. A few notable exceptions include M54 that was seen at Turneffe Elbow (see Figure 1.1) on 20 May 2001, a year after tag deployment and M72 was sighted by two groups of divers near Cancun, four weeks after deployment (see Chapter 4 for details on movements).

Table 2.3: Whale shark marker tag details from 1999-2002. TL: total length in meters; JM: juvenile male; MM: mature male: JF: juvenile female; MF: mature female. Tag letters "BZ" are interchangeable with "M" for marker.

Tag No. (BZ/M)	Date	TL (m)	Sex	Photo ID No.
BZ001	30-May-99	4.5		WS16
BZ002	30-May-99	4.5	JM	
BZ004	30-May-99	4.2		
BZ006	30-May-99	5.5		
BZ007	30-May-99	6.1	JM	
BZ008	30-May-99			
BZ009	31-May-99	4.2		
BZ011	31-May-99	4.2		
BZ012	31-May-99	6.7		
BZ013	31-May-99	6.7		
BZ014	31-May-99	3.9		
BZ015	31-May-99			
BZ016	1-Jun-99	3.9		
BZ017	2-Jun-99	4.8		
BZ018	5-Jun-99	4.8		
BZ019	5-Jun-99	7.6		
BZ020	31-Dec-99	8.2		
BZ033	25-Mar-00	3.9	JM	WS 38
BZ035	25-Mar-00	8.5		WS 43
BZ036	25-Mar-00	5.8		
BZ037	25-Mar-00	6.7		WS 22
BZ038	19-Apr-00	6.1		
BZ039	19-Apr-00	6.7		
BZ040	19-Apr-00	5.5		WS 39
BZ041	19-Apr-00	5.5		
BZ042	20-Apr-00	4.2		
BZ043	20-Apr-00	5.5	JM	
BZ044	23-Apr-00	5.5		WS 19
BZ045	23-Apr-00	4.8	JM	WS 41
BZ046	23-Apr-00	3.0		WS 47
BZ047	23-Apr-00	4.8		
BZ048	24-Apr-00	5.5		WS 18
BZ049	24-Apr-00	6.1	JM	
BZ050	25-Apr-00	5.5	JM	WS 49
BZ051	25-Apr-00	3.9		
BZ052	27-Apr-00	9.7	MM	WS 26
BZ053	18-May-00	9.7	MM	WS 23
BZ054	19-May-00	5.5		
BZ055	19-May-00	7.6		
BZ056	19-May-00	8.5	JF	
BZ057	21-May-00	5.5	JM	
BZ058	21-May-00			WS 48

Tag No. (BZ/M)	Date	TL (m)	Sex	Photo ID No.
BZ059	21-May-00	6.7	JM	WS 44
BZ060	23-May-00	5.5	JM	WS 34
BZ061	25-May-00	5.5	JM	WS 45
BZ062	25-May-00	4.8	JM	
BZ063	23-Jun-00	7.3	JM	
BZ065	23-Jun-00	4.5	JM	
BZ066	23-Jun-00	5.2		
BZ070	9-Apr-01	5.2	JM	
BZ071	9-Apr-01	4.5		
BZ072	9-Apr-01	7.0	JM	
BZ073	10-Apr-01	6.7	JM	WS 59
BZ075	10-Apr-01	9.7	MM	WS 4
BZ076	10-Apr-01			WS 61
BZ077	10-Apr-01	5.5		WS 62
BZ078	10-Apr-01			
BZ079	11-Apr-01	6.1		
BZ080	10-May-01	5.5		
BZ081	10-May-01	6.1		
BZ082	10-May-01	8.5		
BZ083	10-May-01			
BZ084	10-May-01	6.4	JM	
BZ085	11-May-01	6.4	JM	
BZ086	11-May-01			
BZ090	3-Apr-02	6.0	JM	
BZ091	5-Apr-02	6.1	JM	WS 78
BZ092	29-Apr-02	6.7	JM	WS 76
BZ094	2-May-02	9.7	JM	
BZ095	2-May-02	7.3	JF	WS 102
BZ096	1-Jun-02	5.2	JM	
BZ098	1-Jun-02	6.7	JM	
Mean TL		6.0		
SD TL		1.6		

2.3.2 Population structure

All sharks encountered, identified and tagged were measured with a sightings error of ± 0.50 m. The mean size of the 521 whale sharks encountered was 6.3 m ± 1.7 m SD (range 3.00 m – 12.7 m). Of all sexed sharks, juvenile males predominated (85.9%). The population composition of photo-identified sharks is based on the tagged sharks.

The mean size of whale sharks tagged at Gladden is 6.0 m ± 1.6 m SD (range 3.0 m to 9.7 m). The smallest shark recorded at Gladden was a juvenile male of 3.0 m in 1999 and the largest was an untagged mature female estimated at 12.7 m in 1998. A similar sighting made by several tour guides on a 12.7 m boat in 1998 supported this size estimate where the shark exceeded the boat's length by about 0.5-1.0 m (J. Berry, pers. comm.).

The relatively small size of sharks tagged or encountered at Gladden Spit indicates that the majority of visiting sharks were immature. Of the 521 whale shark encounters recorded, 86% (n = 163) were sexed as juvenile males, similar to the 70 tagged whale sharks, of which 29 (41%) were sexed with confidence and 83% (n = 24) were found to be juvenile males based on an observed presence of claspers but lack of clasper development. Only two mature females have been sighted since 1998. Similarly, only six juvenile females were sighted, two of which were tagged (M56 and M95). At least 14 mature males were sighted, of which three were identified and subsequently tagged with tags M52 "Chop", M53 "Dong" and M75).

Growth of three male whale sharks was estimated based on total length at first sighting and last resighting. The three individuals were readily identified based on their patterns of spots and scars. Arca and Lower-tail-off (LTO), both untagged juvenile males also known as WS 8 and WS 21, measured 5.5 m and 4.5 m ± 0.50 m respectively when first identified in 1999. When resighted in 2002, Arca measured 6.6 m ± 0.50 m and LTO in 2003 was estimated at 6.1 m ± 0.50 m. This would give a growth rate for Arca of between [(6.6-0.50) – (5.5 + 0.50)/3] and [(6.6+0.50) – (5.5-0.50)/3], indicating a growth rate of between 0.03 m and 0.70 m $year^{-1}$. For LTO, the result would be [(6.1-0.50) – (4.5 + 0.50)/4] and [(6.1+0.50) – (4.5-0.50)/4] or 0.15 m to 0.65 m growth $year^{-1}$. Both were still juvenile when resighted. Chop, a mature male first measured in 2000 at 8.5 m ± 0.50 m was resighted most recently in 2003 and estimated measuring 9.5 m while swimming on the surface. This represents a growth rate of [(9.6-0.50) – (8.5 + 0.50)/3] and [(9.6+0.50) – (8.5-0.50)/3] or 0.03 m to 0.70 m growth $year^{-1}$.

2.3.3 Resightings and tag retention

Photo identification facilitated the recognition of several sharks from one year to the next. Of the 18 individuals identified in 1999, eight were recognised on the fish spawning ground in 2000. Four of the same sharks from 1999 and 2000 were recognized again in 2001. At least five sharks including Arca, Chop and Lower Tail Notch were recognised three out of the five years that photo identifications were taken at Gladden Spit. An increase in the number of sharks identified each year and between years may take place following further analysis of videos and still images supplied by people outside of the study.

Marker tag retention appeared low throughout the study. Only two of the 16 sharks tagged in 1999 with nylon darts and small white tags were resighted with tags in

2000 despite the high resightings rate (44%) of photographically identified sharks during the same period. One tag was legible after cleaning off algal fouling (M07), and the second tag had broken off after the first 2 cm precluding number identification. No tags from 1999 were recorded in years 2001 onwards. Of the 31 sharks tagged in 2000 with FH-69 stainless steel darts, only two (M43 and M54) or 6.5% were resighted in 2001 with intact but heavily biofouled tags. Within season resightings indicated that some sharks shed their tags within weeks or days of deployment: M42 shed its tag within a week of deployment and M52 was sighted without its tag within two months of tag deployment. Three of 16 sharks with tags deployed in 2001 were resighted in 2002, but only one of the tags was legible (M73). At least eight sharks reappeared in successive years at Gladden Spit with only lanyards to indicate that they had previously been tagged, although some of these represented shed acoustic or satellite tags. Although tag shedding may be attributable to tagging technique, the method used had been perfected in 1999 with 16 tag deployments and further consolidated with the 31 deployments in 2000. By comparison, results from the acoustic tagging indicate that tag retention was high with over half (53%, n = 9) of all acoustically tagged sharks in 2001 (n = 17) returning in 2002 (see Chapter 3). Following the development of a stronger marker tag and use of a larger dart in the 2001 field season, tag recognition and retention from 2001 onwards appeared higher. Tags resighted in 2002 and 2003 were not broken and no sharks were seen with 2001 lanyards that would further indicate breakage.

Less than 10% of whale shark tag deployments (n = 67 reactions recorded for markers, satellite and acoustic tags) showed any reaction to tagging. Reactions ranged in strength from a slight flinching when the dart penetrated to vigorous swimming away. There appeared to be no difference in strength of response in relation to shark size.

2.3.4 Popular involvement in resightings

The tagging resightings information campaign was not successful. Tour-operators were too busy to fill out log sheets and rarely remembered or communicated tag numbers if a tag was sighted. Most tourists were too overwhelmed by their experience of diving or snorkelling with a whale shark to remember if the shark was tagged, let alone recalling a number or tag type. A few visitors proved keen observers, recording tag colour, type and number but usually only provided this information if asked directly after the dive (this occurred when tourists were surveyed to characterise visitation of the marine reserve; see Chapter 7). A tourism and whale shark tagging organisation based in Honduras received a resightings report of the Belize tagged shark that moved to the

Yucatan Peninsula and promptly emailed the information. However, information provision on sightings of several Belize tagged sharks in Honduran waters took place at international conferences several weeks or months later and lacked information on dates, locations or other information on the sharks.

2.4 Discussion

It was originally hoped that a mark-release-resighting (MRR) method based on an open-population model such as the Jolly-Seber could be used in this study to estimate population abundance of whale sharks tagged and resighted at Gladden Spit. Strong *et al.* (1996) employed this method of estimating population sizes with moderate success on a relatively small population of white sharks in Spencer Gulf, South Australia, yielding population estimates of 191.7 and 18 with 95% confidence limits of 36.5-1612.2 and 3.9 to 157.6 respectively.

As the Belize-based whale shark study progressed it became evident that the small number of tagged and resighted individuals per sampling period (either per moon or per year) precluded the use of MRR models despite the predictability of shark visitation at Gladden Spit and their relatively high density and large aggregation size (Heyman *et al.*, 2001). Additionally, it was also apparent that the population was not functional or representative of a wider population as it consisted of transient (with several individuals only sighted once), highly mobile individuals (Chapters 3 and 4) most of which were juvenile males. Additionally, marker tag retention appeared low, undermining attempts to estimate numbers based on resightings of tagged sharks. The World Conservation Union (IUCN, 2000) considers a functional population as one encompassing mature individuals that are capable of reproduction. It is difficult to apply this definition to the whale shark aggregations at Gladden Spit. There were only 16 mature individuals observed in five years, several of which may have been repeatedly counted and only one male was seen during the same period with frayed claspers, indicating that it had recently mated.

In this study, population counts based on encounters were not considered reliable since these involved the numerous resighting of many individuals. Population abundance based on tagging was not deemed sufficiently reliable due to tag shedding. Photo identification was considered the most reliable means of estimating the whale shark population at Gladden Spit although photo-based programmes marking individuals may only represent a fraction of the total population (Carbone *et al.*, 2001). There is, however, a small risk that some photo identifications are duplicates, representing different non-contiguous parts of the shark or two separate sides that could not be matched. Yet, if only half of all photo identifications are used (to account for the possible differences in identification of a shark's two sides) the minimum population visiting Gladden would be 53 individuals. This figure definitely underestimates the visiting population as many sharks were only sighted and photographed once or were sighted underwater or surface-feeding but could not be photographed or tagged at the time, often due to decreasing light levels as most sharks aggregated close to sunset.

Why whale sharks appeared to segregate by sex and size with mainly juvenile males visiting Gladden Spit is unclear. However, segregation by sex and size in whale shark populations is not unusual: similar findings have been recorded for this species in the Seychelles (Graham, unpublished data) and Ningaloo Reef, Western Australia (Colman, 1997). In fact, many species of animals display segregation of the sexes, often as a means of reducing competition for resources. In the elasmobranchs, Springer (1967) suggested that sharks segregated into ontogenetically similar groups as well as sexes when adult (juveniles, adult males, adult females) because of differences in dietary preferences, swimming capabilities, or to reduce intra-specific aggression and/or predation. Whale shark searches were conducted throughout most months of the year from 1999 to July 2002. Based on acoustic tag results and sightings, whale shark abundance at the fish spawning site was low to nonexistent outside of the peak snapper spawning season of March through June so mature sharks of both sexes are not visiting the fish spawning grounds at different times of the year. Larger individuals (over 9 m) were occasionally observed at Gladden Spit outside of the peak season (Graham, pers. obs.; tour-guide and fishermen's observations), but are often found several kilometres away from the fish spawning site or offshore over deep water, feeding among tuna (*Thunnus atlanticus* and *Katsuwomus pelamis*) and bonito (*Sarda sarda*).

By comparison, male and female white sharks are segregated spatio-temporally in relation to a physical and biological gradient in a small geographic area in Spencer Gulf, South Australia, where females were more abundant near inshore islands in winter and males more abundant near remote islands in the summer (Strong *et al.*, 1996). Similarly, Klimley (1987) found that scalloped hammerheads (*Sphyrna lewini*) segregated by sex and size while feeding and commuting between the El Bajo Espiritu Santo seamount and the open sea in Baja California, Mexico. Female hammerheads occupied a different habitat than the males by leaving the seamount at a smaller size, schooling in like groups, and feeding more on pelagic prey, which permitted rapid growth to reproductive size. Morrissey and Gruber (1993) found that the size of a lemon shark (*Negaprion *brevirostris*) is positively correlated with home range size and Gruber *et al.* (1988) showed that juvenile lemon sharks occupied different activity spaces from adults in the Bimini Lagoon, Bahamas. Segregation also occurs during dispersal and large-scale movements. Using genetic markers, Pardini *et al.* (2001) suggested that white sharks dispersed differently from feeding and natal grounds based on sex, with females showing coastal philopatry to natal grounds and males roving across ocean basins. It is therefore possible that female whale sharks have different dietary preferences to males, which leads them to feed away from Gladden. Similarly, feeding on offshore schools of small fish and patches of abundant plankton may prove more nutritionally and energetically rewarding for adult whale sharks than feeding on fish spawn. No instance of intra-specific aggression was ever recorded between juvenile or juvenile and adult whale sharks in Belize or the Seychelles.

Whale shark natural mortality is thought to be low (Pauly, 2002) and there is no current evidence that populations in the Caribbean Sea and Western Atlantic Ocean are impacted by fisheries since no dedicated fisheries exists in these regions, although a fishery has been recorded in Senegal (COP12, 2002). Based on large-scale movements exhibited by whale sharks (Eckert & Stewart, 2001; Chapter 4), a fishery on the Eastern Atlantic could impact populations sighted in the West and cause a reduction in the recorded number of large individuals. Landings data from India taken between 1938 and 1997 do not indicate a predominance of one size class or sex over the other (Hanfee, 2001). Why larger, mature sharks and females in particular do not frequent the spawning aggregation is not known. Large sharks may find that fish spawn does not represent a sufficiently energetically attractive food in relation to capture effort expended. The feeding apparatus of larger sharks may be less suited to the filtering and ingestion of microscopic snapper eggs. It is possible that females feed on more pelagic prey, to grow faster and reach a larger size at maturity similar to scalloped hammerheads near the El Bajo Espiritu Santo seamount in Baja California (Klimley, 1987). However, these reasons should not preclude juvenile females from feeding at the site and only six juvenile females were recorded feeding on spawn at Gladden Spit between 1998 and 2003. Although the fish spawning aggregations form the focus of a feeding aggregation, whale sharks appear to be reproducing in the Western Caribbean region based on the observation of frayed claspers on one mature male indicating that mating could have taken place within the previous 14 days (G. Cailliet, pers. comm. 2001).

Whale shark population abundance at Gladden Spit was variable during the peak snapper spawning periods between 1998 and 2003. In addition, in 1998 (a La Niña year[3]), relative shark density on the fish spawning grounds was high with 25 individuals encountered on the surface in a diameter of 50 m (Heyman *et al.*, 2001). No other year of this study yielded as high a density or number of sharks recorded at a single time. Wilson *et al.* (2001) also noted higher abundances of whale sharks at Ningaloo Reef, Western Australia during La Niña years. The area where whale sharks aggregated and were counted from 1998 to 2001 remained standard due to the predictable presence of spawning snappers and agreed with tagging locations. However, in 2002, whale sharks were more dispersed throughout the marine reserve apparently due to changes in the location of the spawning fish (Figure 2.1). Whale shark population abundance at Gladden Spit is more likely to be regulated by rates of immigration and emigration in relation to spawning fish abundance than by rates of birth and death in the sharks themselves. Pauly (2002) suggests a very low mortality for whale sharks (0.088 $year^{-1}$) based on a longevity range 60 or 100 years ($K = 0.031$ $year^{-1}$-0.051 $year^{-1}$).

On a methodological note, peaks in shark photo identification during the study were correlated with availability of suitable camera equipment, with a low occurring in 2001. Purchase of two digital cameras and a video camera in 2002 dramatically increased the number of images taken and usable identifications made. Although there is insufficient environmental data to determine whether changes in the number of encounters are correlated with external factors between 1998 and 2003, it is worth noting that there was a significant difference in whale shark sightings detected between 2001 and 2002 based on a standard search per unit effort of time (Chapter 7) apparently based on reduced abundance and predictability of prey (Chapter 3).

2.4.1 Tag shedding

It was difficult to estimate rates of tag shedding due to highly variable rates of shark revisitation to Gladden Spit and the low percentage of tagged sharks identified photographically (33%). Additionally, multiple identifications were often not possible over the years. Poor positioning in the water with respect to the shark, shark swimming speed, etc. further compounded lack of tag resighting. Nonetheless, tag retention appeared low throughout the study based on a lack of resightings of tagged sharks both in the water and from boats. Greatest tag losses appeared to occur between 1999 and

[3] http://www.cdc.noaa.gov/%7Ekew/MEI/#LaNina

2001 when the nylon darts and the Floy FH-69 M-type stainless steel darts were used. This is unusual since the nylon darts were apparently successful in tagging of marlin (*Makaira* spp.) (E. Prince, pers. comm. 2001) and the FH-69 have been successfully used by the National Marine and fisheries Service's cooperative shark tagging programme (Kohler *et al.*, 1998), by Gruber (1982) on lemon sharks and by Carrier (1985) on nurse sharks (*Ginglymostoma cirratum*).

However, Heupel and Bennett (1997) found that although tagging epaulette sharks (*Hemiscyllium ocellatum*) with M-type darts provoked a localized but acute response in tagged tissues, tag sequestration occurred through build up of fibrous tissues and no secondary infections were noted. However, Davies and Joubert (1967) found that M-type tags cut through flesh and were shed up to four months in three different species of shark. The majority of deployed tags on whale sharks showed no visible tissue response, e.g., necrosis, both immediately after tagging and after a year's deployment. However, a shark with a large acoustic tag showed an acute tissue response with lack of healing after 3 days, showing a 2 cm wound at the point of insertion. The tag was shed within 14 days of deployment based on resighting of the shark. Drag of the laminated plastic marker tags may have led to premature tag shed or breakage with FH-69 tagged whale sharks at Gladden. Additionally, in at least one instance a marker tag was seen to have abraded the skin against which it was positioned. Even if the marker tags stay on, their effectiveness as a capture-independent means of recognising individuals over the long term is limited. Carrier (1985) found high levels of fouling with tags on animals over a mean of 415 days at liberty. Tags deployed on whale sharks at Gladden Spit resighted within the three-month snapper season were not fouled, however tags resighted after a 6 months or more were often illegible due to heavy algal fouling. Use of clear antifouling paint on 2002 tags helped to reduce fouling where M094 and M095 were readily recognized in 2003 (Figure 2.7).

Permanent scars that involved partial or total fin loss or alterations made to fins (notches, etc.) readily recognized from either side of the shark were useful in the whale sharks identification and recognition. At least 17 individuals were sighted with scars and wounds at Gladden, and 13 of these could be confidently used for identification purposes as Cailliet (1996) warned that recognition of individuals may be impaired if sharks display similar scars. Many of the wounds appeared to be directly caused by boat or propeller impact, similar to what Norman (pers. comm.) found at Ningaloo Reef. Gashes or wounds to the body and fins that did not involve partial fin loss were not necessarily useful indicators, as whale shark skin appears to heal leaving little visible

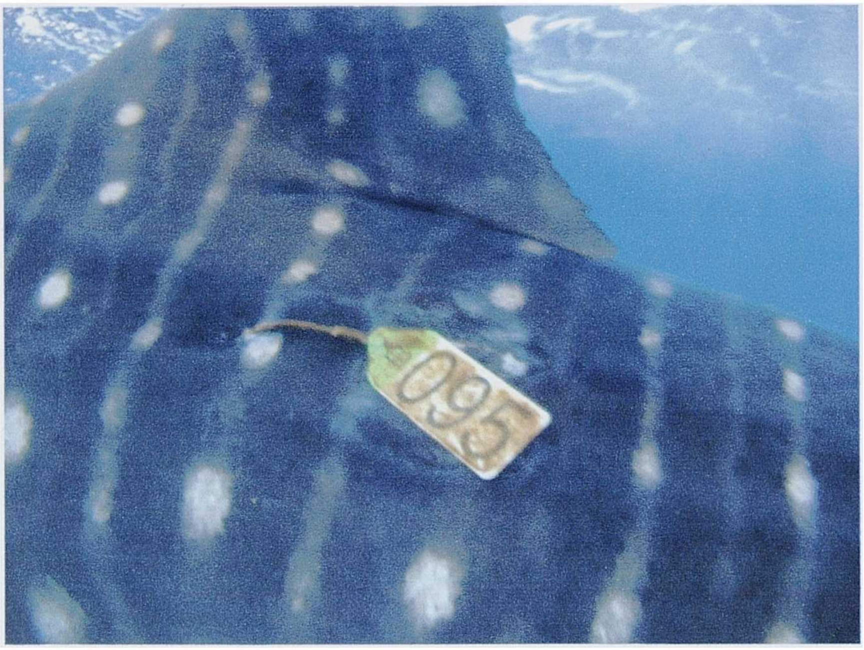


Figure 2.7: Image taken in 2003 of a 2002 marker tag deployment on a whale shark. The level of algal fouling is minimal after anti-fouling treatment prior to deployment. Skin abrasion under tag is evident after a year's deployment.

scarring. Heupel *et al.* (1998) recorded rapid healing in wounded carcharinid sharks in Australia. Two whale sharks named "Chop" and "Prop-chop" both suffered gashes apparently inflicted by a propeller. Chop's wound consisted of a gash 60 cm by 10 cm anterior to the left keel that occurred in 2000 and healed completely by 2001, and Prop-chop's first dorsal left side was slashed vertically several times in 2001 but was found healed with trace marks remaining in 2002 (Appendix 2.A). Norman (pers. comm.) also noted rapid healing in whale shark wounds recorded in Australia's Ningaloo Reef.

Shark tagging campaigns requesting information on recapture or resightings of tagged sharks for research purposes can be successful, for example the National Oceanographic and Atmospheric Administration's National Marine Fisheries Service' Cooperative shark tagging program which involves over 4,000 recreational anglers (Kohler & Turner, 2001). However, information on resightings of marked whale sharks in Belize by the public was sparse despite a broad information campaign. It is possible that resightings were limited due to non-recognition or recording of tags and subsequent non-reporting of tag information where tags were recognized. Tag resighting information may have been directed to two organisations linked to whale sharks that operated in the region. Both had web site forms where tourists could fill in sightings data online. Such lacklustre feedback is not unusual and was also observed in the Seychelles, even following an article in the national newspaper and a talk presented nationally (Graham, unpublished data).

2.4.2 Growth

It was difficult to determine catch-independent rates of growth for whale sharks in the wild. The ± 0.50 m error on size estimates may have negated any meaningful growth estimates. However, estimated growth rates over three years for three sharks observed at Gladden ranged from 0.03 m to 0.70 m year^{-1} (Chop, Arca and LTO), and encompass growth rates measured for whale sharks in captivity. Uchida (2000) noted that mean TL growth year^{-1} for a 3.65 m female whale shark held in captivity was 29.5 cm (survival time: 2056 days), for a 4.5 m male shark was 21.6 cm (1040 days) and for a 4.85 m male totalled 25.5 cm (458 days). By comparison, Parker and Stott (1965) calculated an increase in mean length of about 0.43 m over a period of about 6 months from mid-summer to mid-winter in basking sharks measuring between 2.5-4.0 m. This is similar to findings by Sims *et al.* (2000b) who estimated that a highly recognizable female basking shark resighted several times over a 3.1 years period grew 2.4 m (0.77 m year^{-1}). These growth rates are rapid compared to that of a predatory shark the oceanic whitetip (*C. longimanus*). Lessa *et al.* (1999)and noted that a fisheries-caught oceanic whitetip sharks grew rapidly in their first year (0.25 m $year^{-1}$), with growth slowing to 0.09 m $year^{-1}$ from the ages of 9 years onwards.

2.4.3 Intra- and inter-specific associations and interactions

Whale sharks showed little obvious intra-specific interactions during their time at the fish spawning aggregation site, unlike several other species of shark including scalloped hammerheads (Klimley & Nelson, 1981), grey reef sharks (*Carcharhinus amblyrhynchos*) (McKibben & Nelson, 1986) and lemon sharks (Gruber *et al.*, 1988). There were no instances recorded of behaviour where sharks closely follow each other or circle each other with head to tail as observed in Australia or in the UK with basking sharks (Sims *et al.*, 2000a). Movement at the site and to and from the site appeared solitary (Chapters 3 and 4). Sharks appeared to aggregate and feed on the fish spawn opportunistically and the aggregations did not appear to serve a reproductive purpose based on the high percentage of juvenile sharks observed (Chapter 3).

At Gladden Spit, whale sharks were often sighted in association with several other species of fish or marine mammals. Fish species observed moving with whale sharks included two species of remora, *Escheneidae* spp., the cobia (*Rachycentron canadum*) and the silky shark (*C. falciformis*). Whale sharks feeding away from the spawning site were often found swimming with and feeding on the same pelagic baitfish as bonito, blackfin tuna (*Thunnus atlanticus*) and occasionally skipjack tuna (*Katsuwonus pelamis*). Silky sharks and blacktip sharks (*Carcharhinus limbatus*) were often present in the tuna aggregations but blacktips were never seen to move with whale sharks. There was one recorded interaction of a juvenile male whale shark and a male loggerhead turtle (*Caretta caretta*). The turtle swam towards the whale shark's snout and both remained head to head for almost a minute underwater until the turtle turned and swam back down to the reef and the whale shark moved towards the surface. Although three species of dolphins were recorded at Gladden Spit including the rough toothed (*Steno bradenensis*), common pan-tropical spotted (*Stenella bradenensis*) and bottlenose dolphins (*Tursiops truncatus*), only bottlenose dolphins were observed interacting with whale sharks on a frequent basis. Interactions included swimming in front of the whale shark, reminiscent of riding the bow-wave of boats, nipping at the pectoral fins, hanging upside down in front of a stationary whale shark less than a foot away from the shark's snout, and tapping the sharks' pectoral fins with their own fins.

2.4.4 Conventional tagging programs: are they worthwhile?

Are conventional shark tagging programs worthwhile? If the tagging study had not been conducted we would not have known that whale sharks feeding at Gladden Spit had travelled to the northern Yucatan Peninsula or even the Bay Islands of Honduras (Chapter 4). However, tagging small yet open populations of animals to estimate overall populations using MRR methods such as the Jolly-Seber model may be construed as ineffective due to the large confidence intervals. This is particularly true for the ontogenetically and sexually segregated whale sharks feeding at Gladden Spit that only represent a sector of the population. Ultimately, all the identification and size data generated from the study came from the researchers, and the objective of involving a greater number of people in the study to increase resightings failed. Consequently, non-invasive identification techniques such as photographic identification is recommended for the study of whale shark populations over the implementation of more conventional tagging projects.

The tagging process did not generally affect whale sharks and the majority of tourists seeing tagged sharks did not mind the tags (Chapter 7). However, tag retention rates appeared poor and the lack of resightings information make this an onerous and relatively ineffective means of assessing movement, population abundance and site fidelity. Satellite and acoustic tagging have proven highly a successful means of assessing the patterns of movement and site fidelity of whale sharks. Although these techniques are more expensive than marker tags, they yield unbiased sightings-independent data and display higher rates of tag retention. The development of more robust techniques to identify individual whale sharks and confidently estimate population sizes could be based on the application of computer-generated pattern matching of spot patterns. This technique is used by the International Fund for Animal Welfare's (IFAW) sperm whale identification program (Whitehead, 1990). Genetic tagging is another feasible option to recognize individual whale sharks and determine local and global population sizes. This method was usefully implemented to assess humpback whale (*Megaptera novaeangliae*) populations and movements in the North Atlantic between 1988 and 1995 (Palsboll *et al.*, 1999).

2.4.5 Conclusions and management implications

This study has important implications for the management and conservation of whale sharks and other elusive migratory fish species. The whale shark population in Belize is transient and linked to the availability of prey. Results from this study indicate that the whale sharks visiting Gladden Spit do not constitute a functional population due to the bias towards juvenile males and their undefined range of movement and habitat that would help to define a "population". However, for management purposes it is worth noting that the number of whale sharks visiting Gladden Spit is small, with approximately 100 individuals counted over five years. Although this figure appears top be an underestimate as not all individuals encountered could be identified. It is not possible to tell at this stage if the number of individuals is increasing, decreasing or stable due the range of movement and a range of biological and environmental factors that can bias counts such as abundance of snappers, sea-surface temperature, availability of other food types, etc. However, sightings per unit effort over time can provide a proxy for counts and a guideline for management of the spawning fish and sharks. The significant decline in sightings in 2002 should therefore be taken as a warning to strengthen tourism management at Gladden Spit and focus on the conservation of the spawning aggregations, as these appear to be important nutritional food sources for juvenile males and appear to form the basis of whale shark sightings predictability.

Resightings of whale sharks based on acoustic and observation data indicate that the managed population has a strong memory of the aggregation site. The high return rate of individual whale sharks to the area indicates that management of this population should observe the precautionary principle and be geared towards reducing anthropogenic impacts so as not to establish avoidance patterns in sharks. Changes in predictable aggregation behaviour will undermine the nascent lucrative tourism industry, a key economic alternative to the spawning aggregation fishery and a means of offsetting the costs of operating the marine reserve.

Although the Gladden Spit and Silk Cayes Marine Reserve provides the spatial framework to protect juvenile male whale sharks during their predictable and highly vulnerable spring feeding bouts, this population is transient and forms part of a larger population whose individuals are frequently sighted near the Bay Islands of Honduras and at the tip of the Yucatan Peninsula (Chapter 4 for large-scale movements). Feeding areas targeted by all individuals may be distributed along high productivity ocean fronts such as the Yucatan upwelling (Merino, 1997), where large numbers of whale sharks are sighted yearly from July to September (M. Garcia, pers. comm. 2000). Widespread movement of this population across multiple political boundaries requires the implementation of regional instruments to promote the management and conservation of this species in addition to local and national measures. Photo identification efforts should be continued locally and expanded in this and other regions[4] as a non-invasive means of cataloguing whale shark populations and recording the large-scale movements of individuals. Identification of feeding and breeding areas for the other elements of the whale shark population is an important next step towards the protection of whale shark populations in the region.

2.5 References

Alava M. N. R., Dolumbalo E. R. Z., Yaptinchay A. A. & Trono R. B. 2002. Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In: *Elasmobranch Biodiversity Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997.* (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 132-147. Sabah, Malaysia. IUCN, Gland, Switzerland.

Anislado-Tolentino V. & Robinson-Mendoza C. 2001. Age and growth for the scalloped hammerhead shark, *Sphyrna lewini* (Griffith and Smith, 1834) along the Central Pacific Coast of Mexico. *Ciencias Marinas.* **27** (4): 501-520.

Arnbom T. 1987. Individual identification of sperm whales. *Reports of the International Whaling commission.* **37** (201-204):

Baum J. K., Myers R. A., Kehler D. G., Worm B., Harley S. J. & Doherty P. A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science.* **299** (5605): 389-392.

Begon M., Harper J. L. & Townsend C. R. 1996. *Ecology, Individuals, Populations and Communities.* Blackwell Science, Oxford. 1068 pp.

Best P. B. 1990. Trends in the Inshore Right Whale Population Off South-Africa, 1969-1987. *Marine Mammal Science.* **6** (2): 93-108.

Bonfil R. 1997. Status of shark resources in the Southern Gulf of Mexico and Caribbean: implications for management. *Fisheries Research.* **29** (2): 101-117.

Branstetter S. 1987. Age, growth and reproductive-biology of the Silky Shark, *Carcharhinus falciformis*, and the Scalloped Hammerhead, *Sphyrna lewini*, from the Northwestern Gulf of Mexico. *Environmental Biology of Fishes.* **19** (3): 161-173.

[4] The Shark Trust based in the UK recently developed a global whale shark database that aims to collect data on individuals and populations from around the world for management and conservation purposes.

Cailliet G. M. 1996. An evaluation of methodologies to study the population biology of white sharks. In: *Great White Sharks: the Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. A. eds.), pp 415-416. San Diego, California. Academic Press.

Camhi M., Fowler S., Musick J., Brautigam A. & Fordham S. 1997. Sharks and their relatives: ecology and conservation. Occasional Paper of the IUCN Species Survival Commission. IUCN 20. 1-40 pp.

Carbone C., Christie S., Conforti K., Coulson T., Franklin N., Ginsberg J. R., Griffiths M., Holden J., Kawanishi K., Kinnaird M., Laidlaw R., Lynam A., Macdonald D. W., Martyr D., McDougal C., Nath L., O'Brien T., Seidensticker J., Smith D. J. L., Sunquist M., Tilson R. & Shahruddin W. N. W. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*. **4**: 75-79.

Carrier J. C. 1985. Nurse shark of big pine key: comparative success of three types of external tags. *Florida Scientist*. **48** (3): 146-154.

Cerchio S. 1998. Estimates of humpback whale abundance off Kauai, 1989 to 1993: evaluating biases associated with sampling the Hawaiian Islands breeding assemblage. *Marine Ecology-Progress Series*. **175**: 23-34.

Cerchio S., Gabriele C. M., Norris T. F. & Herman L. M. 1998. Movements of humpback whales between Kauai and Hawaii: implications for population structure and abundance estimation in the Hawaiian Islands. *Marine Ecology-Progress Series*. **175**: 13-22.

Chao A. 2001. An overview of closed capture-recapture models. *Journal of Agricultural Biological and Environmental Statistics*. **6** (2): 158-175.

Chen C.-T., Liu K.-M. & Joung S.-J. 1996. Preliminary report on Taiwan's whale shark fishery. In: Fowler S. L., Reed T. M. & Dipper F. A. (eds) *Elasmobranch Biodiversity, Conservation and Management*. The IUCN Species Survival Commission, Sabah, Malaysia, July 1997, pp 162-167.

Cliff G., Elst R. P. V. d., Govender A., Witthun T. K. & Bullen E. M. 1996. First estimates of mortality and population size of white sharks on the South African Coast. In: *Great White Sharks: the Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. G. eds.), pp 393-399. San Diego, California. Academic Press, Inc.

Colman J. G. 1997. A review of the biology and ecology of the whale shark. *Journal of Fish Biology*. **51** (6): 1219-1234.

COP12. 2002. Proposal for inclusion of whale sharks on Appendix II - Proponents India and Philippines. CITES. 24 pp.

Davies D. H. & Joubert L. S. 1967. Tag evaluation and shark tagging in South African waters, 1964-1965. In: *Sharks, Skates and Rays*. (Gilbert P. W. ed.), pp 111-140. Baltimore, Maryland. Johns Hopkins.

de Silva J. A., Condrey R. E. & Thompson B. A. 2001. Profile of shark bycatch in the US Gulf of Mexico menhaden fishery. *North American Journal of Fisheries Management*. **21** (1): 111-124.

Eckert S. A., Dolar L. L., Kooyman G. L., Perrin W. & Rahman R. A. 2002. Movements of whale sharks (*Rhincodon typus*) in South-East Asian waters as determined by satellite telemetry. *Journal of Zoology*. **257**: 111-115.

Eckert S. A. & Stewart B. S. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environmental Biology of Fishes*. **60** (1-3): 299-308.

Fairfax D. 1998. *The Basking Shark in Scotland, Natural History, Fishery and Conservation*. Tuckwell Press, East Linton, Scotland. 206 pp.

FAO. 1994. Overview of world elasmobranch fisheries (341): 1-11, 102-107.

Ferreira C. A. & Ferreira T. P. 1996. Population dynamics of white sharks in South Africa. In: *Great White Sharks: The Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. A. eds.), pp 381-391. San Diego, California. Academic Press.

Fowler S. L. 2000. Whale sharks *Rhincodon typus* policy research and scoping study. The Nature Conservation Bureau. UK. 27 pp.

Fowler S. L., Reed T. M. & Dipper F. A. (eds.). 2002. Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia July 1997. IUCN SSC Shark Specialist Group, Gland, Switzerland and Cambridge, UK. 258 pp.

Francis M. P., Griggs L. H. & Baird S. J. 2001. Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine Freshwater Research*. **52**: 165-178.

Gruber S. H. 1982. Role of the lemon shark, *Negaprion brevirostris* (Poey) as a predator in the tropical marine environment: a multidisciplinary study. *Florida Science*. **45** (1): 46-75.

Gruber S. H., Nelson D. R. & Morrissey J. F. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian Lagoon. *Bulletin of Marine Science*. **43** (1): 61-76.

Hanfee F. 2001. Gentle Giants of the Sea: A report on trade in whale shark off the Gujarat coast. TRAFFIC-India/WWF-India. 38 pp.

Heupel M. R. & Bennett M. B. 1997. Histology of dart tag insertion sites in the epaulette shark. *Journal of Fish Biology*. **50** (5): 1034-1041.

Heupel M. R., Simpfendorfer C. A. & Bennett M. B. 1998. Analysis of tissue responses to fin tagging in Australian carcharhinids. *Journal of Fish Biology*. **52**: 610-620.

Heyman W. D., Graham R. T., Kjerfve B. & Johannes R. E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology-Progress Series*. **215**: 275-282.

IUCN. 2000. *2000 IUCN Red List of Threatened Species*. World Conservation Union, Gland, Switzerland.

Joung S. J., Chen C. T., Clark E., Uchida S. & Huang W. Y. P. 1996. The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma' supreme. *Environmental Biology of Fishes*. **46** (3): 219-223.

Karanth K. U. 1995. Estimating tiger *Panthera tigris* populations from camera-trap data using capture-recapture models. *Biological Conservation*. **71** (3): 333-338.

Karanth K. U. & Nichols J. D. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology*. **79** (8): 2852-2862.

Katona S., Baxter B., Brazier O., Kraus S., Perkins J. & Whitehead H. 1979. Identification of humpback whales by fluke photographs. In: *Behaviour of Marine Animals Vol. 3: Cetaceans*. (Olla H. W. a. B. ed.), pp 33-44. New York. Plenum Press.

Klimley A. P. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes*. **18** (1): 27-40.

Klimley A. P. 1996. Residency patterns of white sharks at the South Farallon Islands, California. In: *Great White Sharks: The Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. A. eds.), pp 365-374. San Diego, California. Academic Press, Inc.

Klimley A. P. & Nelson D. R. 1981. Schooling of the Scalloped Hammerhead Shark, *Sphyrna lewini*, in the Gulf of California. *Fishery Bulletin*. **79** (2): 356-360.

Kohler N. E., Casey J. G. & Turner P. A. 1998. NMFS Cooperative shark tagging program, 1962-93: An atlas of shark tag and recapture data. *Marine Fisheries Review*. **60** (2): 1-87.

Kohler N. E. & Turner P. A. 2001. Shark tagging: a review of conventional methods and studies. *Environmental Biology of Fishes*. **60** (1/3): 191-210.

Le Boeuf B. J., H. Perez-Cortes M., J. Urban R., Mate B. R. & F. Ollervides U. 2001. High gray whale mortality and low recruitment in 1999: potential causes and implications. *Journal of Cetacean Resource Management*. **2** (2): 85-99.

Lessa R., Santana F. M. & Paglerani R. 1999. Age, growth and stock structure of the oceanic whitetip shark, *Carcharhinus longimanus*, from the southwestern equatorial Atlantic. *Fisheries Research*. **42** (1-2): 21-30.

McKibben J. N. & Nelson D. R. 1986. Patterns of movement and grouping of grey reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science*. **38** (1): 89-110.

Merino M. 1997. Upwelling on the Yucatan Shelf: hydrographic evidence. *Journal of Marine Systems*. **13** (1-4): 101-121.

Morrissey J. F. & Gruber S. H. 1993. Home range of juvenile lemon shark, *Negaprion brevirostris*. *Copeia*. **1993** (2): 425-434.

Myers R. A. & Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*. **423**: 280-281.

Palsboll P. J., Allen J., Berube M., Clapham P. J., Feddersen T. P., Hammond P. S., Hudson R. R., Jorgensen H., Katona S., Larsen A. H., Larsen F., Lien J., Mattila D. K., Sigurjonsson J., Sears R., Smith T., Sponer R., Stevick P. & Oien N. 1999. Genetic tagging of humpback whales. *Nature*. **388**: 767-769.

Pardini A. T., Jones C. S., Noble L. R., Kreiser B., Marlcolm H., Bruce B. D., Stevens J. D., Cliff G., Scholl M. C., Francis M., Duffy C. A. & Martin A. P. 2001. Sex-biased dispersal of great white sharks. *Nature*. **412**: 139-140.

Parker H. W. & Stott F. C. 1965. Age, size and calcification in the basking shark, *Cetorhinus maximus* (Gunnerus). *Zoologische Mededelingen*. **40** (34): 305-319.

Pauly D. 2002. Growth and mortality of the basking shark *Cetorhinus maximus* and their implications for management of whale sharks *Rhincodon typus*. In: *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Worjkshop, Sabah, Malaysia, July 1997*. (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 199-208. Gland, Switerland and Cambridge, UK. IUCN SSC Shark Specialist Group.

Punt A. E., Pribac F., Walker T. I., Taylor B. L. & Prince J. D. 2000. Stock assessment of school shark, *Galeorhinus galeus*, based on a spatially explicit population dynamics model. *Marine and Freshwater Research*. **51** (3): 205-220.

Rabinowitz A. 1993. Estimating the Indo-Chinese tiger *Panthera tigris* Corbetti population in Thailand. *Biological Conservation.* **65** (3): 213-217.

Romanov E. V. 2002. Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. *Fishery Bulletin.* **100** (1): 90-105.

Schwarz C. J. 2001. The Jolly-Seber model: More than just abundance. *Journal of Agricultural Biological and Environmental Statistics.* **6** (2): 195-205.

Schwarz C. J. & Seber G. A. F. 1999. Estimating animal abundance: Review III. *Statistical Science.* **14** (4): 427-456.

Seber G. A. F. 2001. Some new directions in estimating animal population parameters. *Journal of Agricultural, Biological and Environmental Statistics.* **6** (2): 140-151.

Silver S. C., Ostro L. E. T., Marsh L. K., Maffei L., Noss A. J., Kelly M. J., Wallace R. B., Gomez H. & Ayala G. in press. The use of camera traps for estimating jaguar (*Panthera onca*) abundance and density using capture/recapture analysis:

Simpfendorfer C. A., Hueter R. E., Bergman U. & Connett S. M. H. 2002. Results of a fishery-independent survey for pelagic sharks in the western North Atlantic, 1977-1994. *Fisheries Research.* **55** (1-3): 175-192.

Sims D. W. & Reid P. C. 2002. Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland). *Fisheries Oceanography.* **11** (1): 59-63.

Sims D. W., Southall E. J., Quayle V. A. & Fox A. M. 2000a. Annual social behaviour of basking sharks associated with coastal front areas. *Proceedings of the Royal Society of London Series B-Biological Sciences.* **267**: 1897-1904.

Sims D. W., Speedie C. D. & Fox A. M. 2000b. Movements and growth of a female basking shark re-sighted after a three year period. *Journal of the Marine Biological Association of the United Kingdom.* **80** (6): 1141-1142.

Springer S. 1967. Social organization of shark populations. In: *Sharks, Skates and Rays.* (Gilbert P. W., Mathewson R. F. & Rall D. P. eds.), pp 149-174. Baltimore. Johns Hopkins Press.

Stevens J. D., Norman B. M., Gunn J. S. & Davis T. L. O. 1998. Movement and behavioural patterns of whale sharks at Ningaloo Reef: the implications for tourism. National Ecotourism Final Report: Application Ref. No. 30051. CSIRO Marine Research. 35 pp.

Strong W. R., Bruce B. D., Nelson D. R. & Murphy R. D. 1996. Population Dynamics of White sharks in Spencer Gulf, South Australia. In: *Great White Sharks: The*

Biology of Carcharodon carcharias. (Klimley A. P. & Ainley D. G. eds.), pp 401-415. San Diego, California. Academic Press, Inc.

Sundstrom L. F. & Gruber S. H. 2002. Effects of capture and transmitter attachments on the swimming speed of large juvenile lemon sharks in the wild. *Journal of Fish Biology*. **61** (3): 834-838.

Taylor J. G. 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*. **47** (4): 637-642.

Tuyttens F. A. M., Macdonald D. W., Swait E. & Cheeseman C. L. 1999. Estimating population size of Eurasian badgers (*Meles Meles*) using mark-recapture and mark-resight data. *Journal of Mammalogy*. **80** (3): 950-960.

Uchida S., Toda M., Kamei Y. & Teruya H. 2000. The husbandry of 16 whale sharks, *Rhincodon typus*, from 1980 to 1998 at Okinawa Expo Aquarium. *American Elasmobranch Society Annual Meeting, La Paz, Mexico.*:

Whitehead H. 1990. Computer-assisted individual identification of sperm whale flukes. *Reports of the International Whaling Commission Special Issue*. **12**: 71-77.

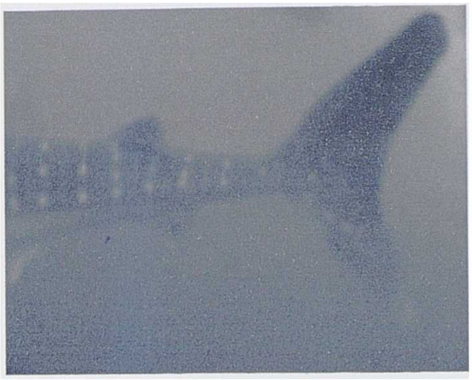
Wilson G. J. & Delahay R. J. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research*. **28** (2): 151-164.

Wilson S. G., Taylor J. G. & Pearce A. F. 2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/Southern Oscillation. *Environmental Biology of Fishes*. **61** (1): 1-11.

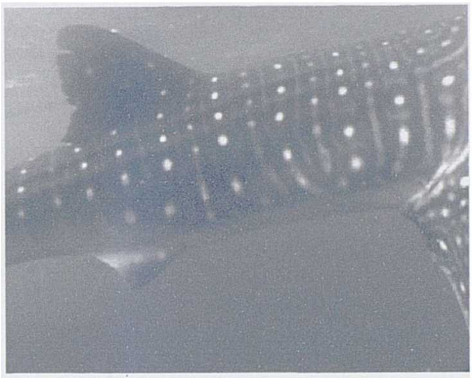
York E. C., Moruzzi T. L., Fuller T. K., Organ J. F., Sauvajot R. M. & DeGraaf R. M. 2001. Description and evaluation of a remote camera and triggering system to monitor carnivores. *Wildlife Society Bulletin*. **29** (4): 1228-1237.

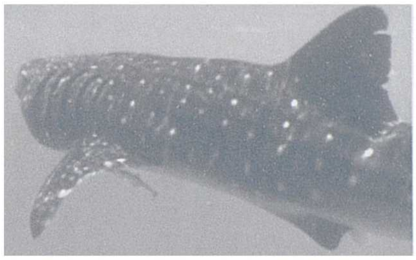
Appendix 2.A Whale shark photo identification catalogue for Gladden Spit, Belize.

WS 1
1999

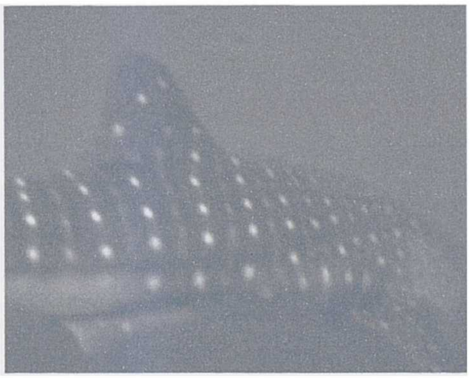


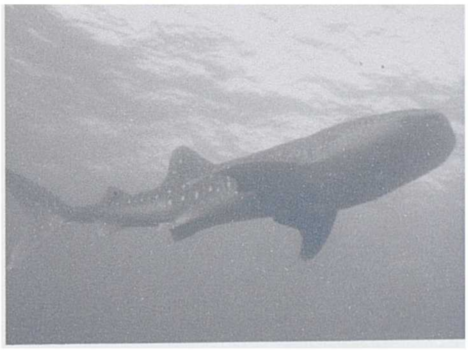
WS 2 -
Fringy-Kinky
1999



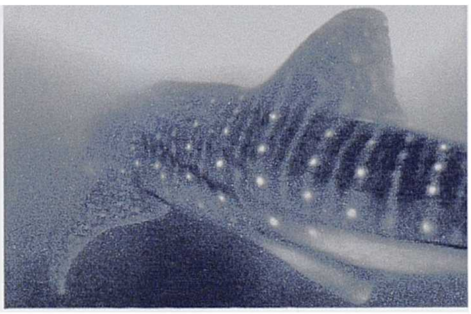


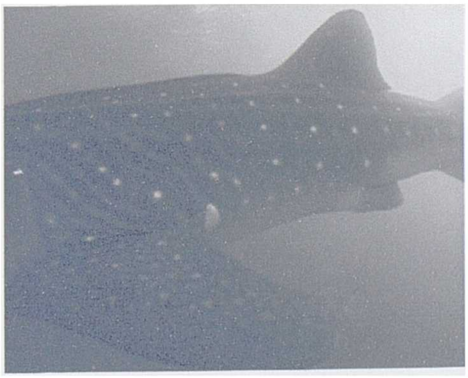
WS 3 - Lower tail
notch
1999
2000
2001
2002



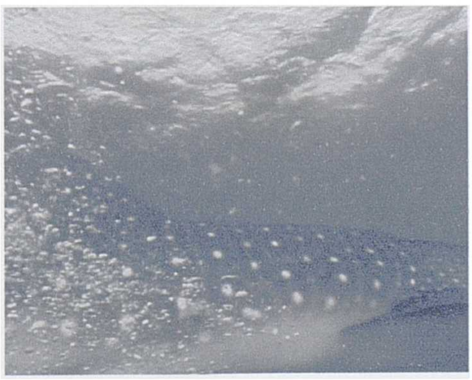


WS 4 - Stumpy
no spots M75
1999
2001
2002

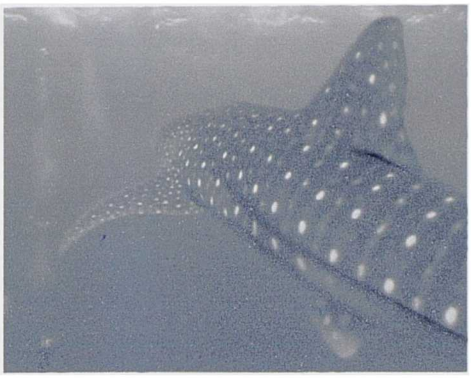




WS 5
1999

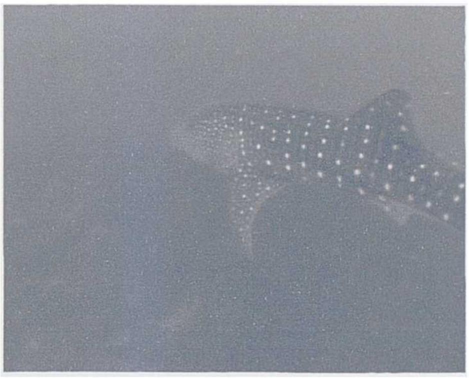


WS 6
1999

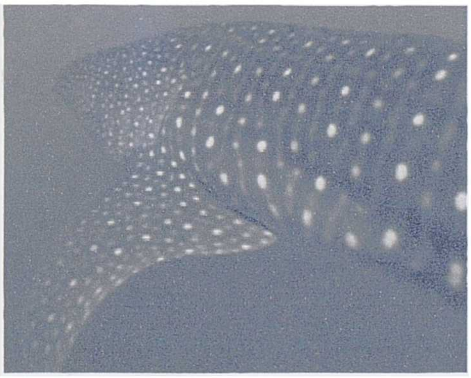


WS 7
1999

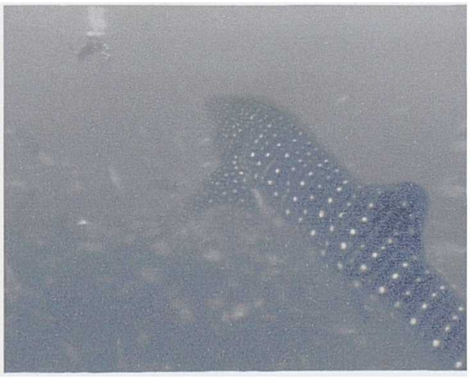
WS 8 - Arca
1999
2000
2001
2002



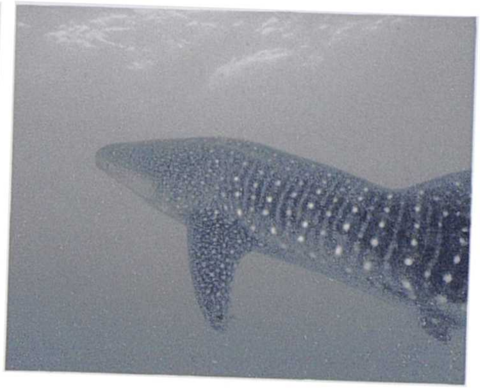
WS 9
1999



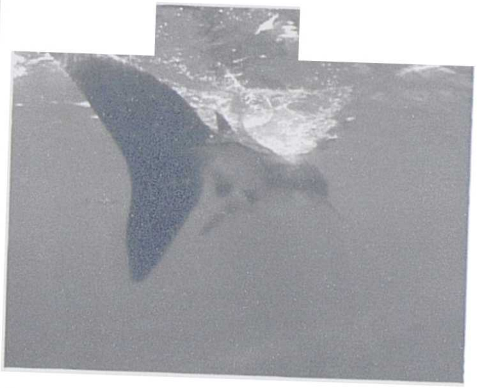
WS 10
1999



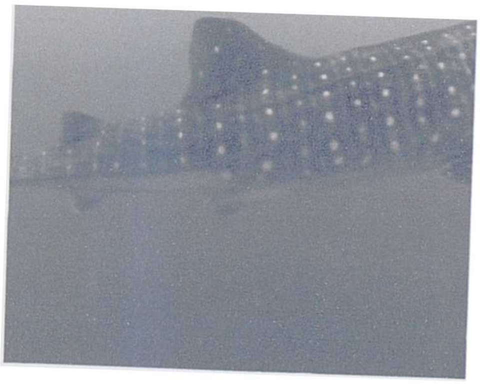
WS 11
1999

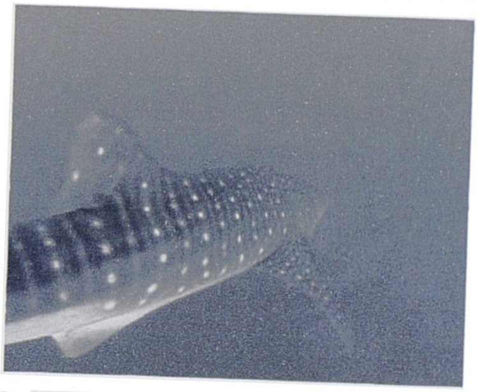


WS 12
1999
2000



WS 13 - Blunt
1999
2000

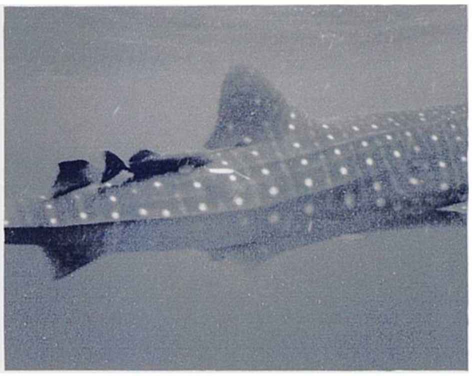




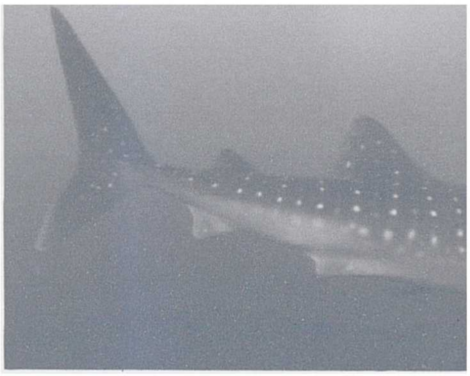
WS 14
1999
2000

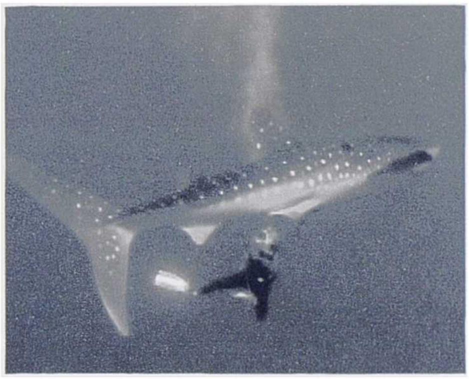
WS 15
2000

WS 16 - M01
1999

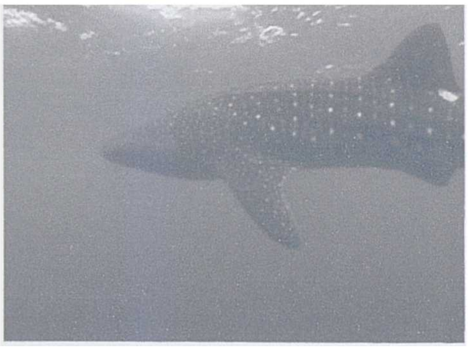


WS 17 - Arca too
1999
2000
2001

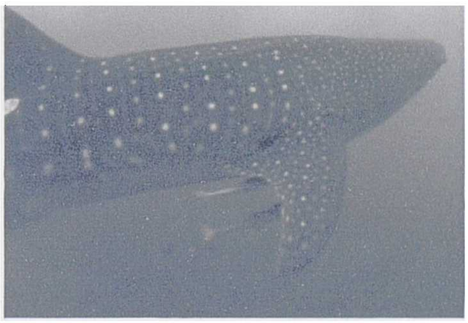




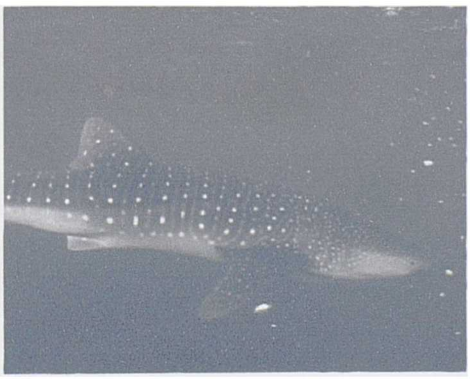
WS 18 - M48
2000

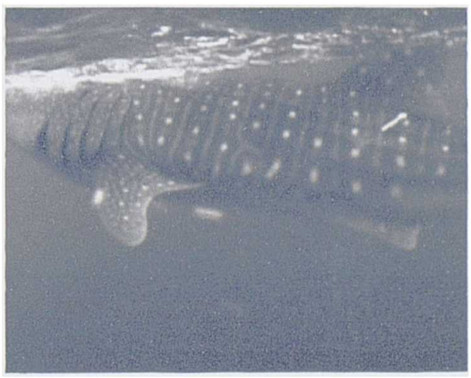


WS 19 - M44
2000



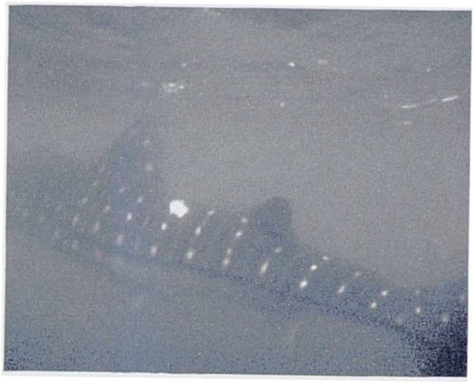
WS 20 - M58
1999
2000

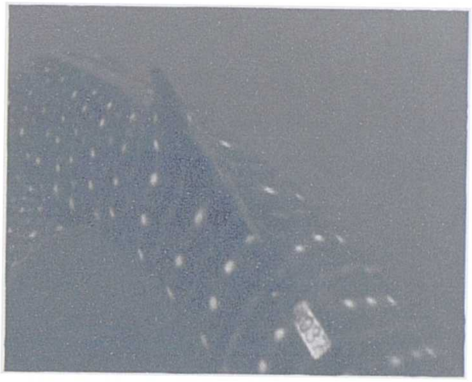




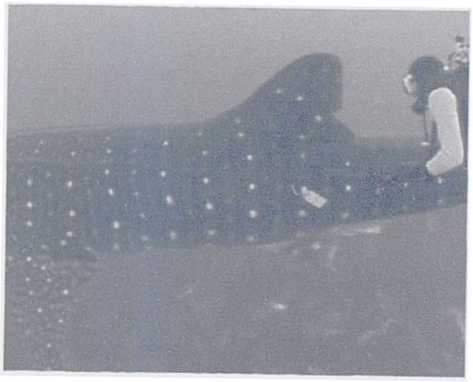
WS 21 - Lower
tail off
1999
2003

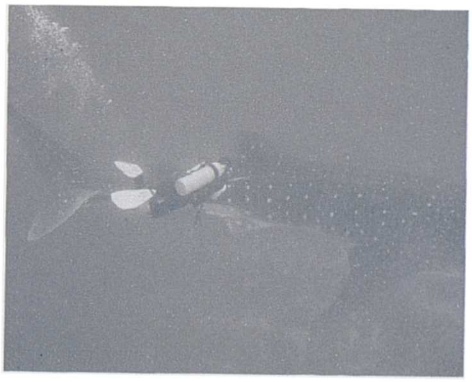
WS 22 - M37
2000





WS 23 - Dong
M53
2000





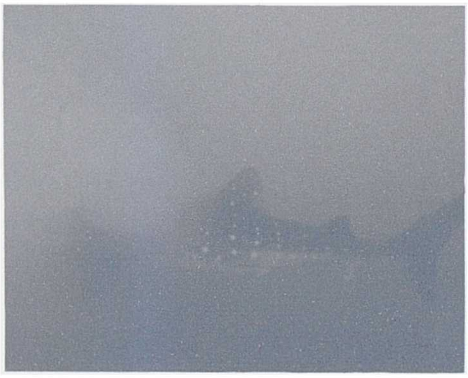
WS 24
2000

WS 25 - SRI
0533
2000

WS 26 - Chop
M52
2000
2001
2003

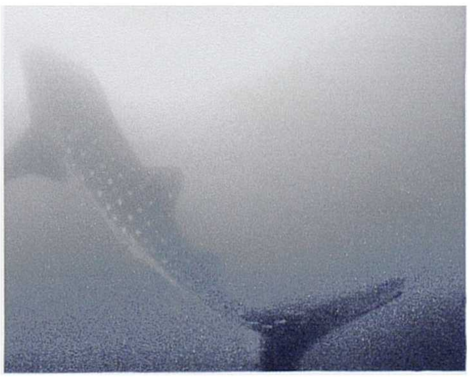
WS 27
2000

WS 28
2000

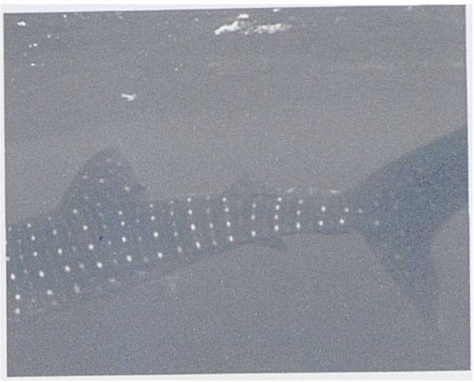


WS 29
2000

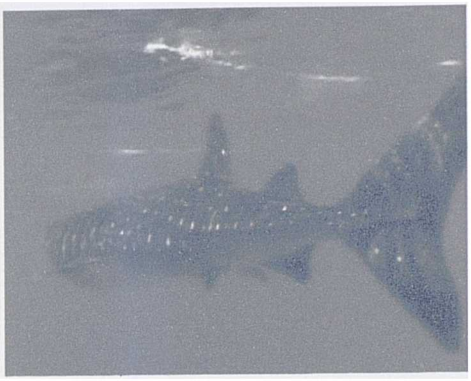
WS 30
2000



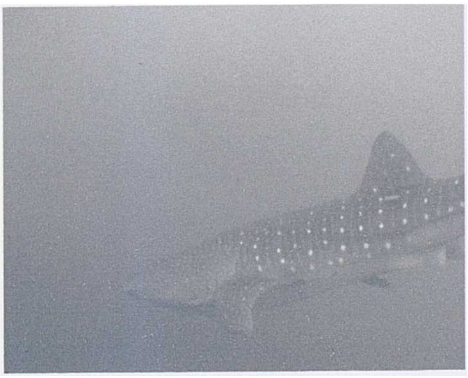
WS 31
2000

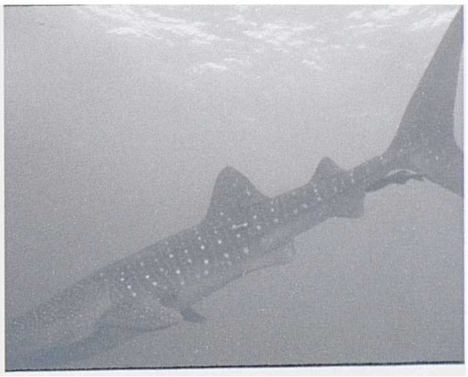


WS 32
2000

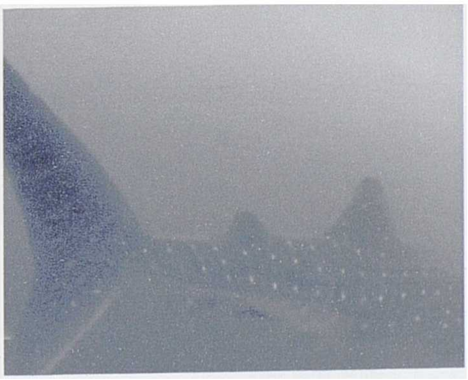


WS 33
2000

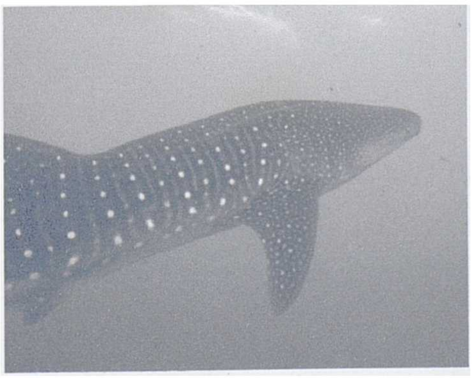


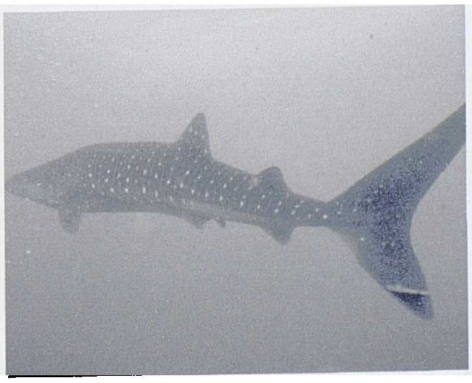


WS 34 - M60
2000

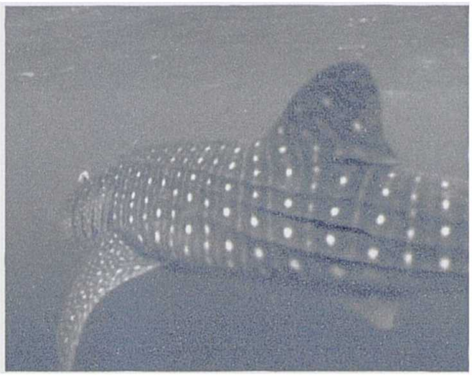


WS 35
2000

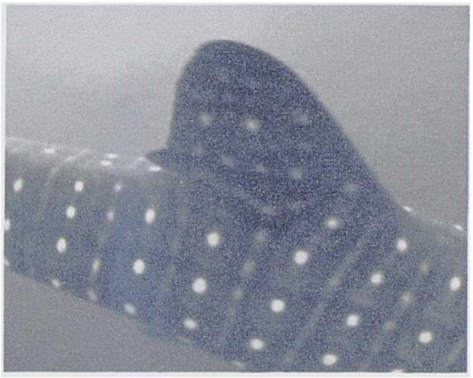




WS 36
2000

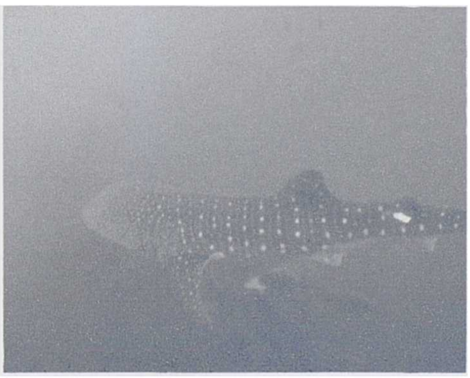


WS 37
2000

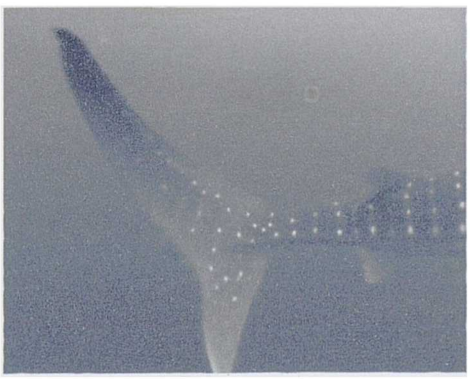


WS 38 - M33
2000

WS 39 - M40
2000

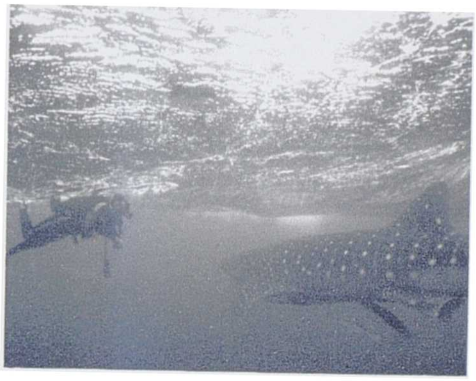


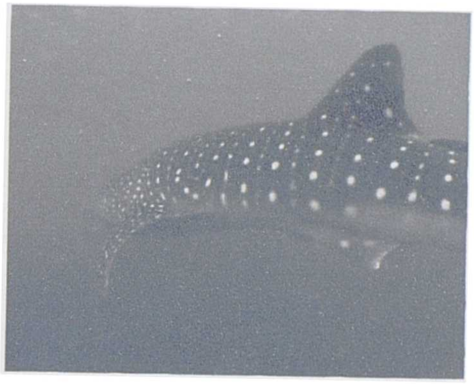
WS 40
2000



WS 41 - M45
2000

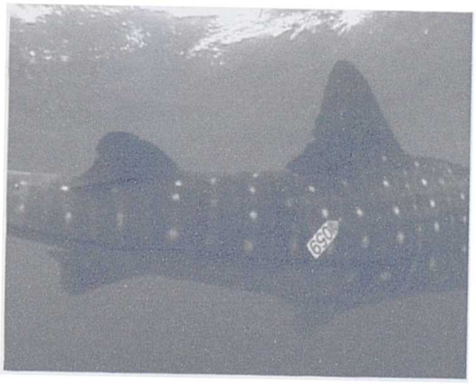
WS 42
2000



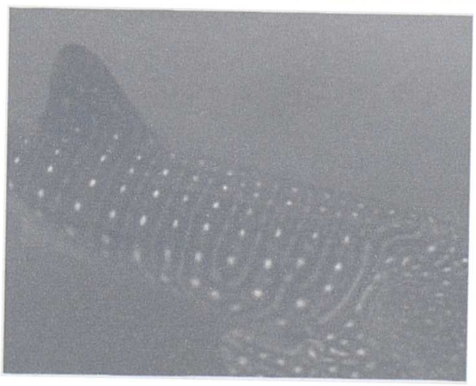


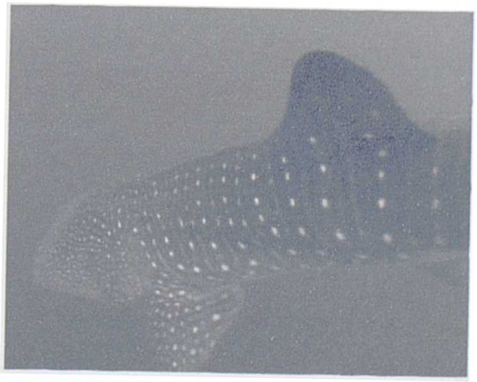
WS 43 - M35
2000

WS 44 - M59
2000

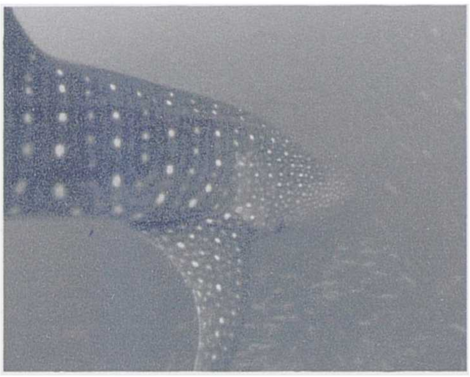


WS 45 - M61
2000



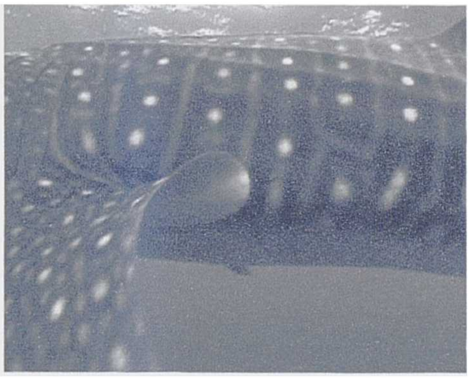
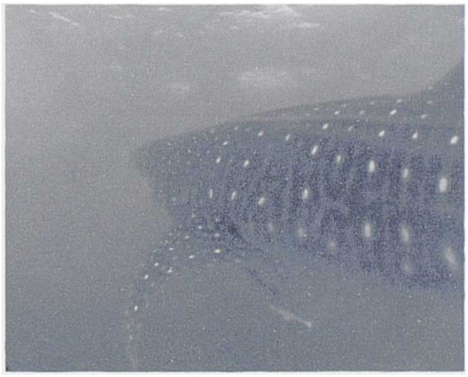


WS 46
2000

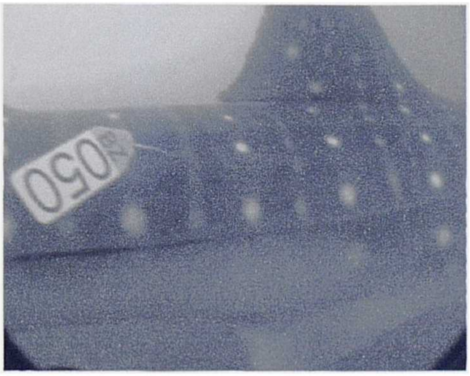



WS 47 - M46
2000

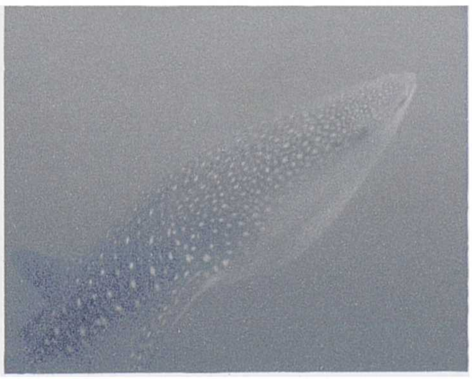
WS48 - M58
2000

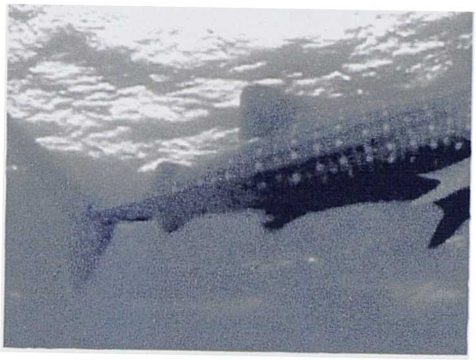
WS 49 - M50
2000



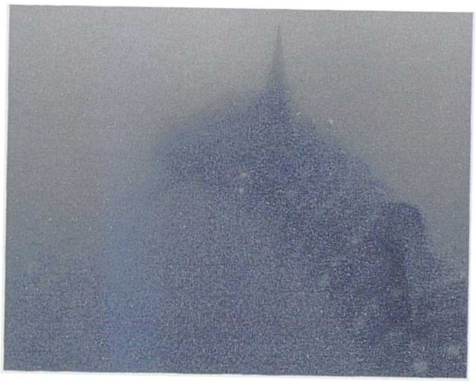
WS 50
2000



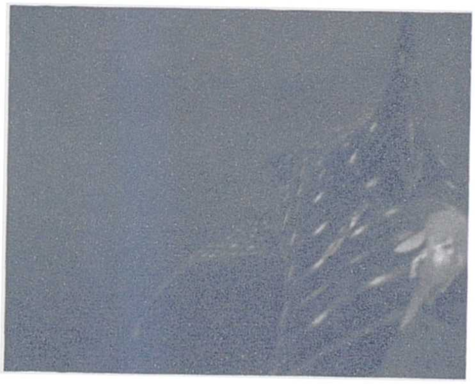
WS 51
2000



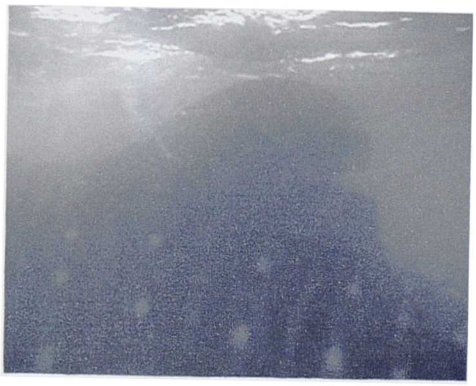
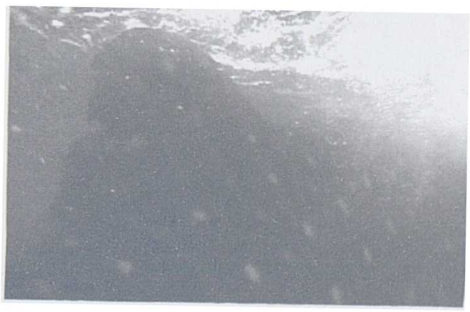
WS 52
2001



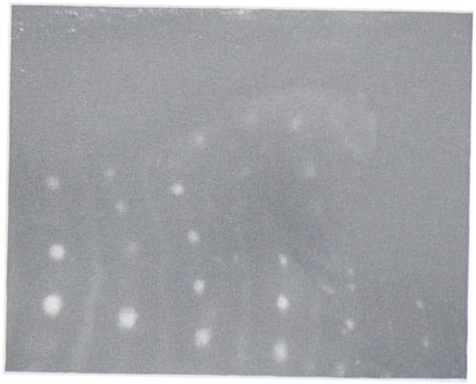

WS 53 - SRI M?
2001




WS 54 - D Cut
2001

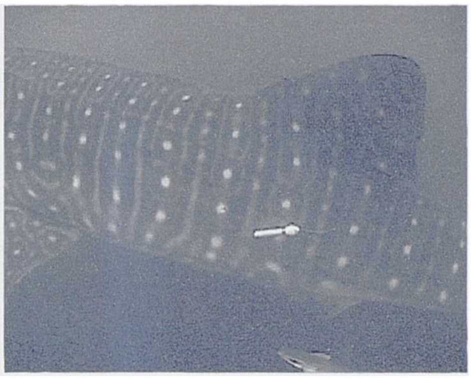



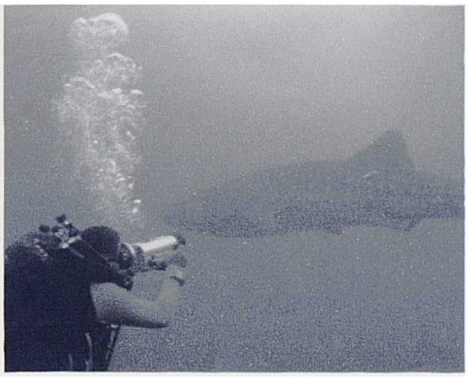
WS 55 - Prop
chop
2001
2002

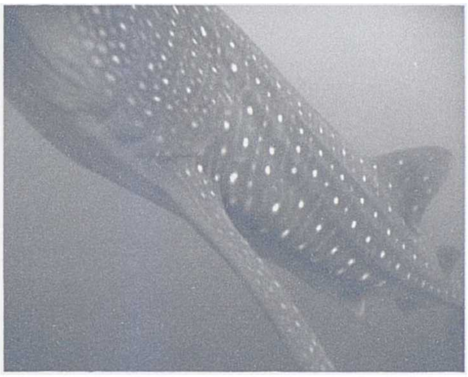
WS 56
2001

WS 57 - Aztec
2001

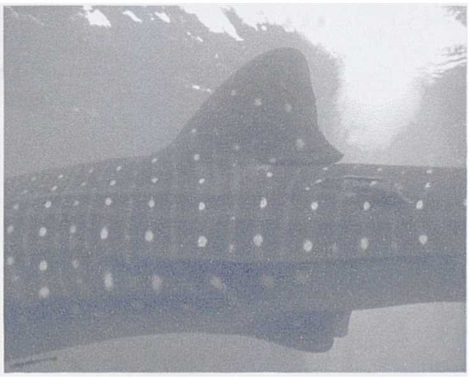


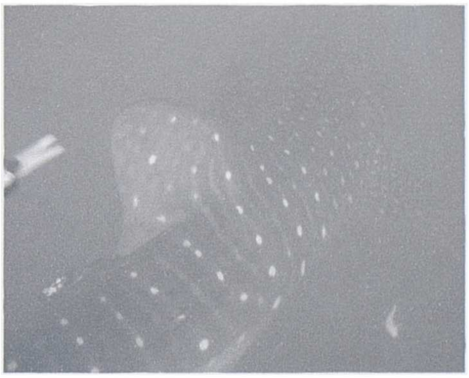


WS 58
2001

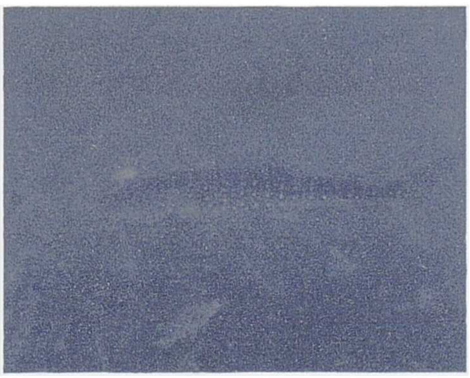


WS 59 - M73
2001
2002



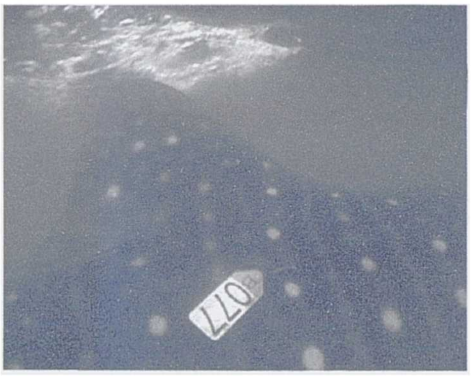


WS 60
2001



WS 61 - M76
2001

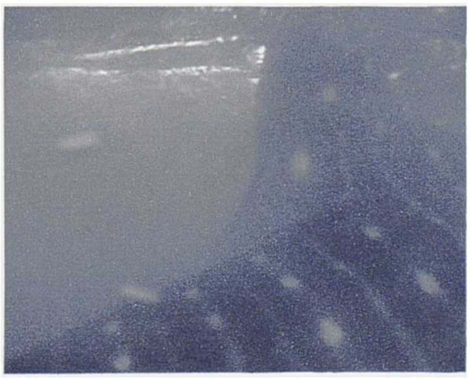
WS 62 - M77
2001



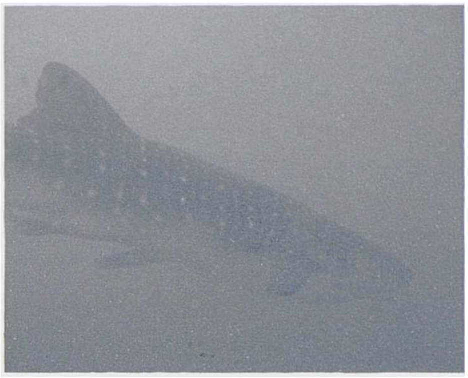
WS 63
2001

WS 64
2001

WS 65
2001



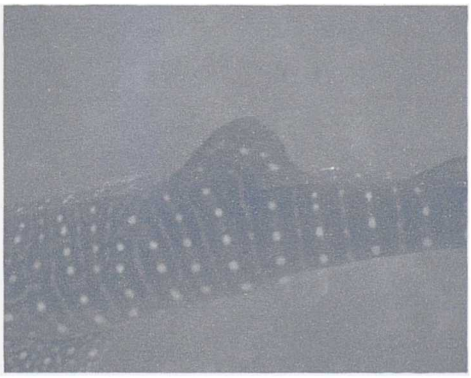
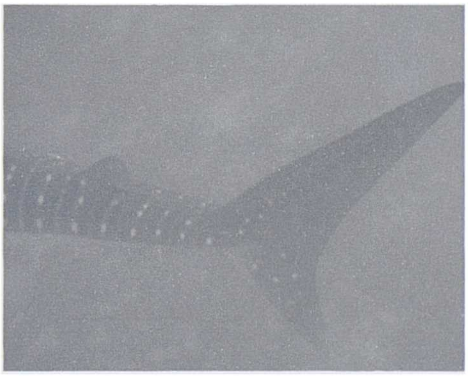
WS 66 - 1 Yr
Sat-tag
2001
2002

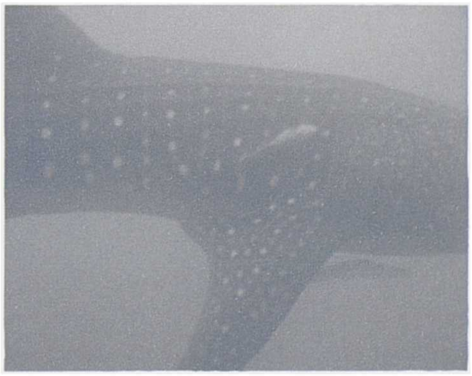
WS 67
2002


WS 68 - Upper
cut tail
2002

WS 69
2002

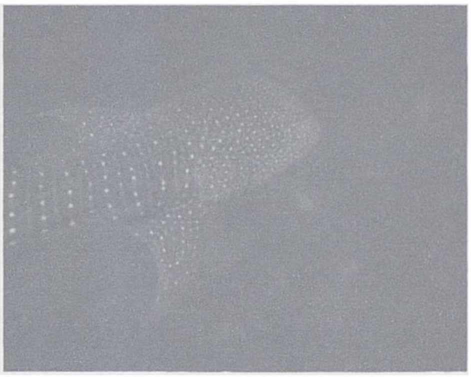
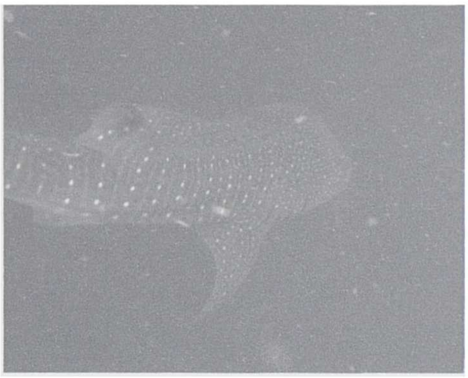



WS 70
2002

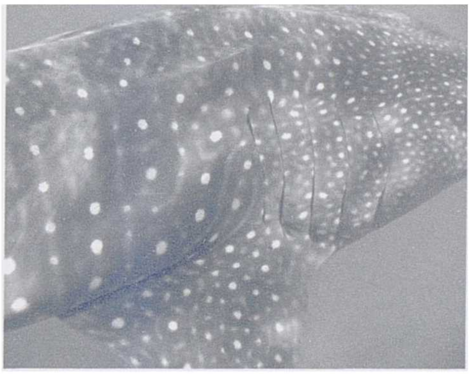



WS 71
2002

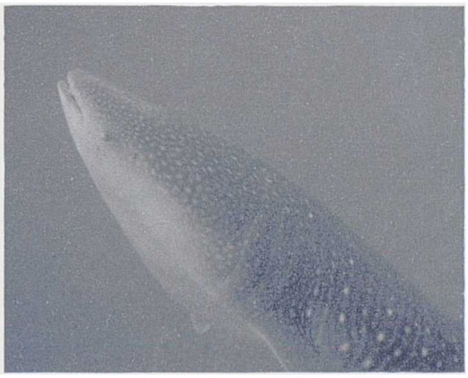

WS 72
2002

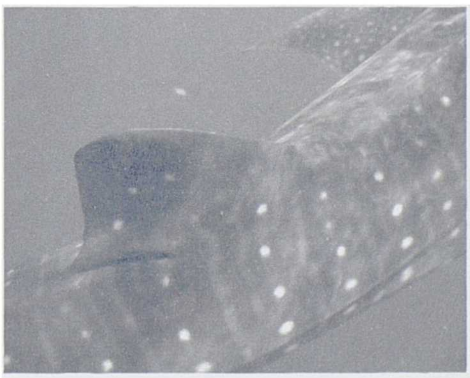
WS 73
2002



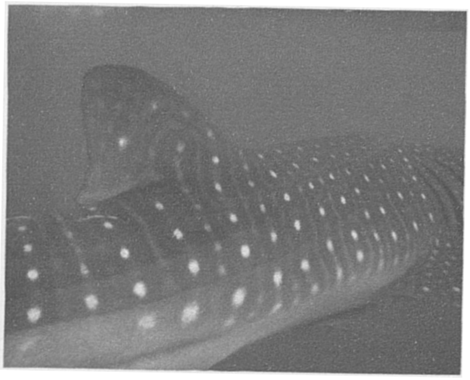

WS 74 - Drill 1
2002

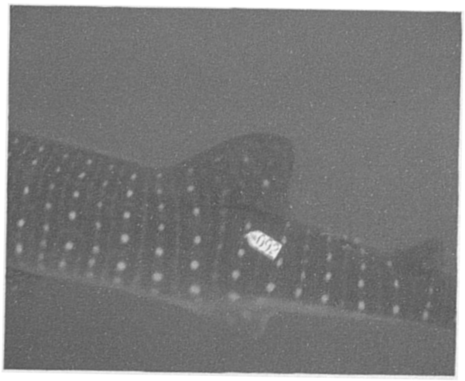



WS 75
2002

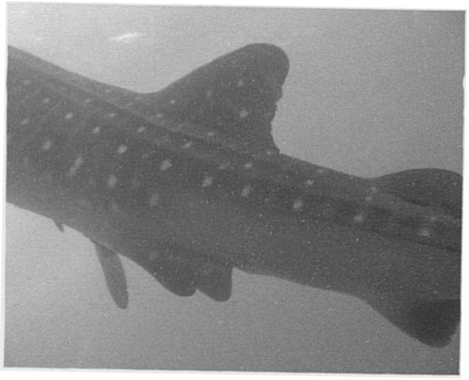



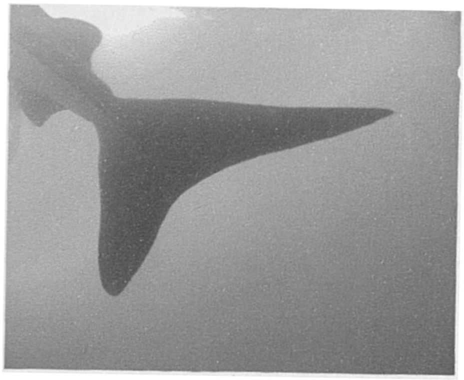
WS 76 - M92
2002
2003



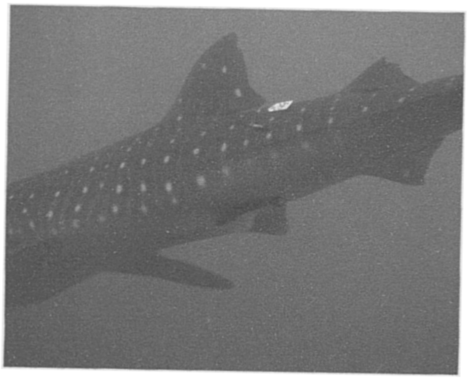


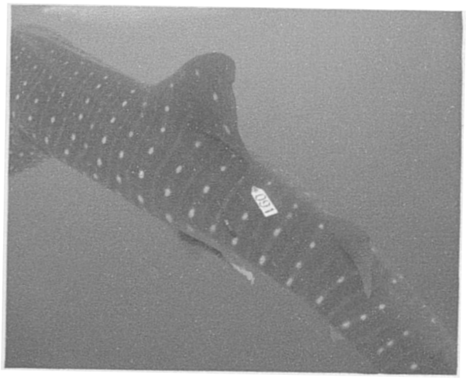
WS 77
2002



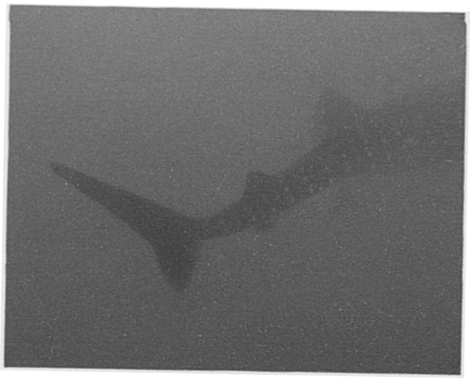


WS 78 - M91
2002

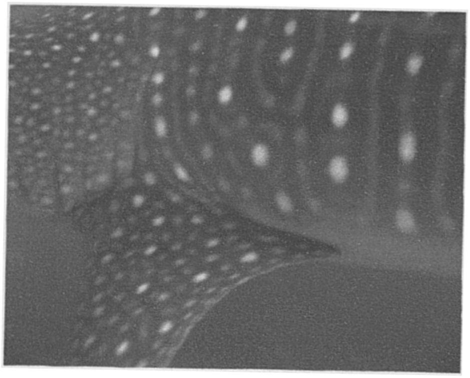


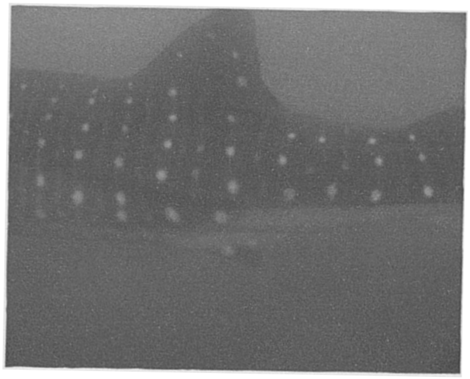


WS 79 - Low tail
gone 2
2002

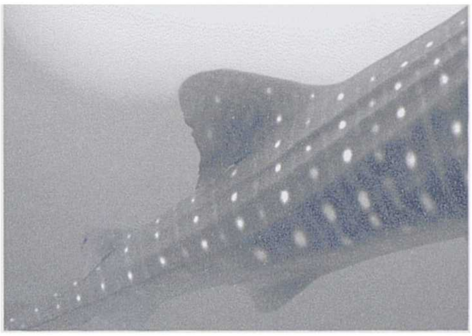


WS 80
2002

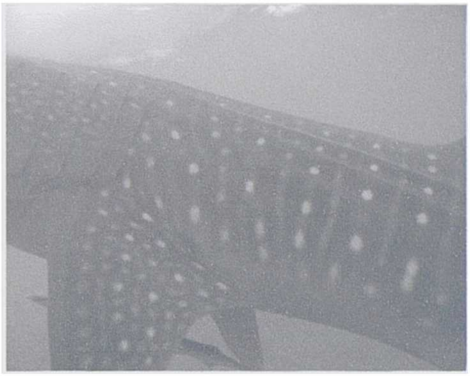




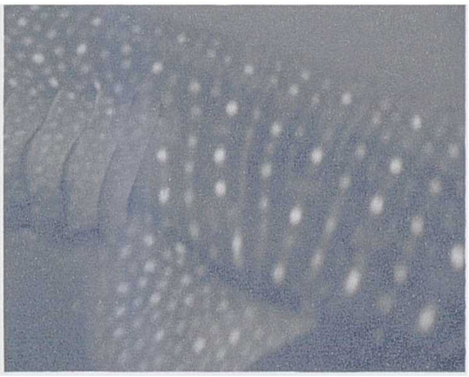
WS 81 - Mr. Facey
2002
2003

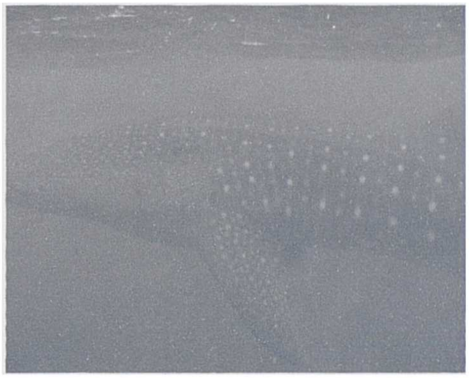


WS 82
2002

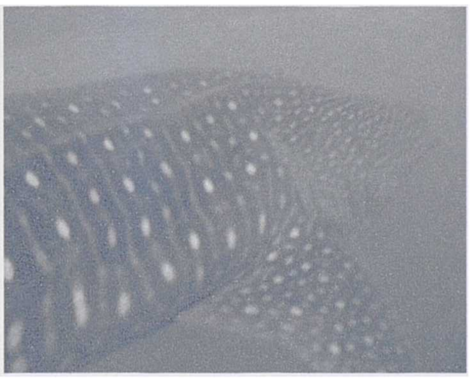


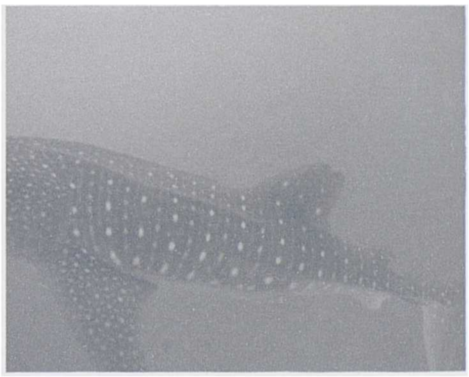
WS 83
2002





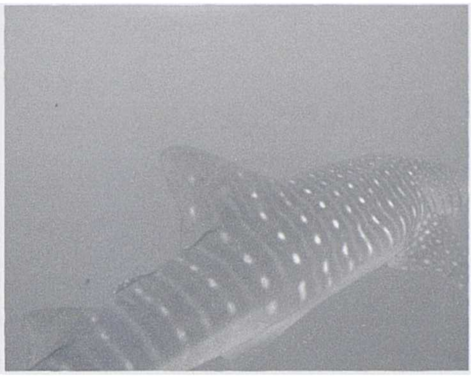
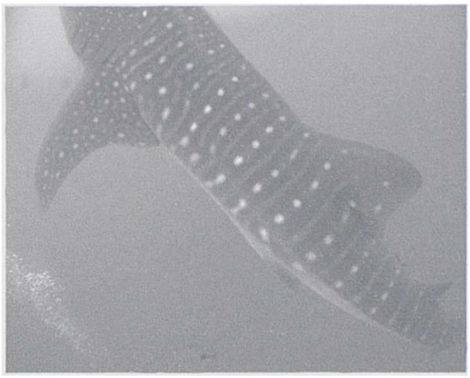
WS 84 - Cut and Roll
2002



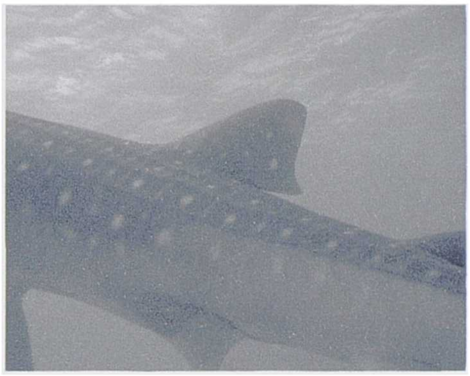


WS 85
2002

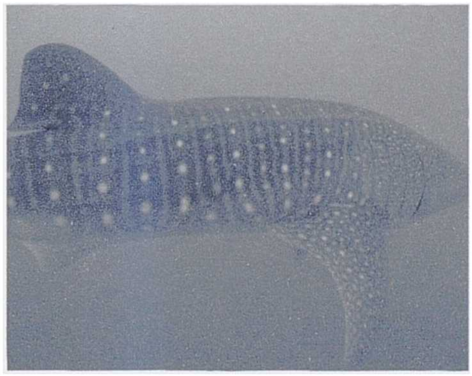
WS 86 - Liney
2002

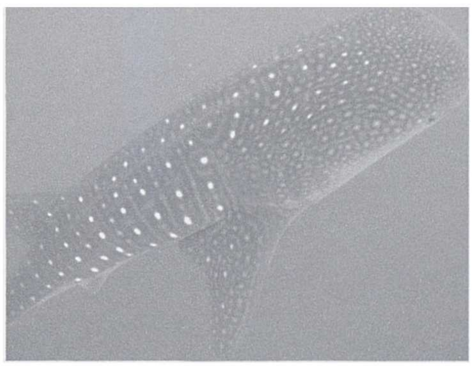
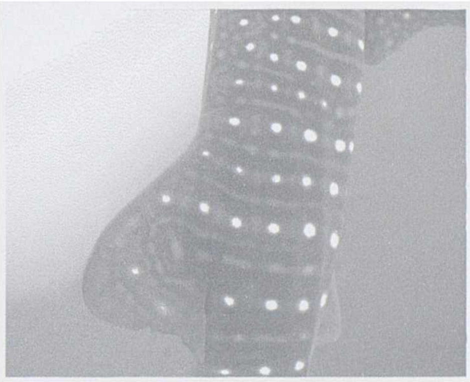
WS 87 - Drill too
2002

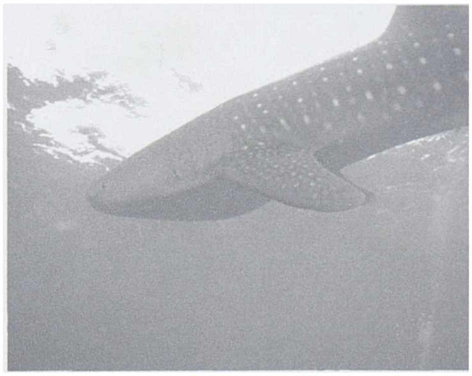
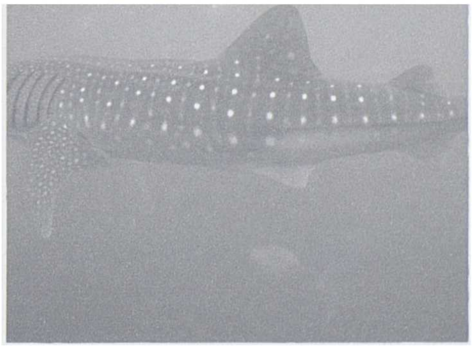
WS 88
2002




WS 89
2002

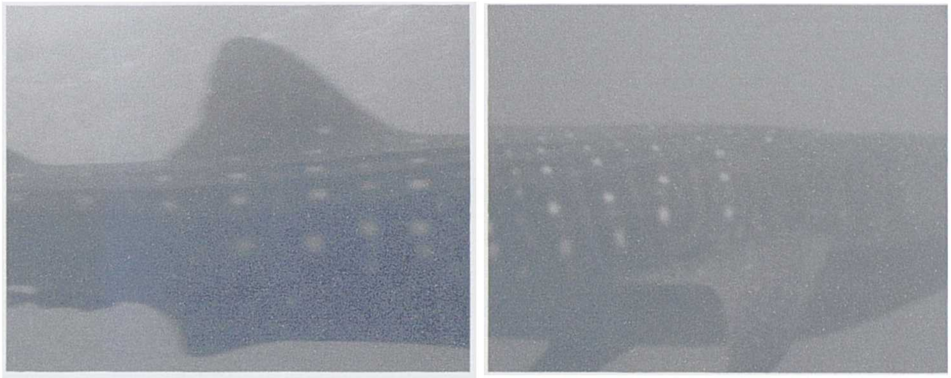



WS 90
2002

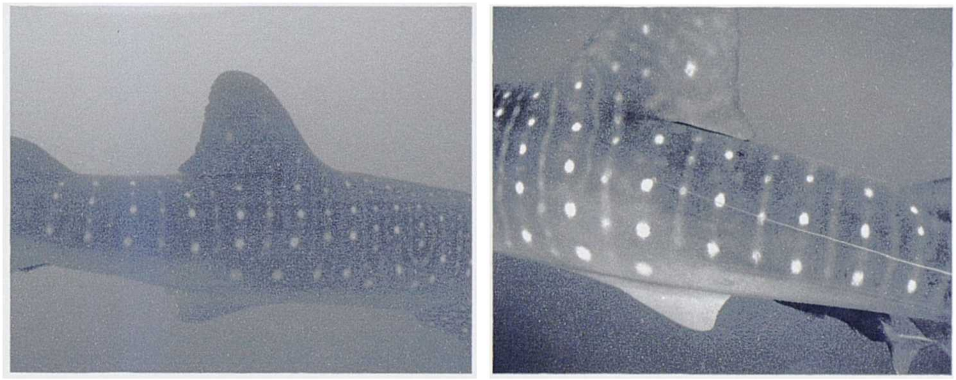



WS 91
2002

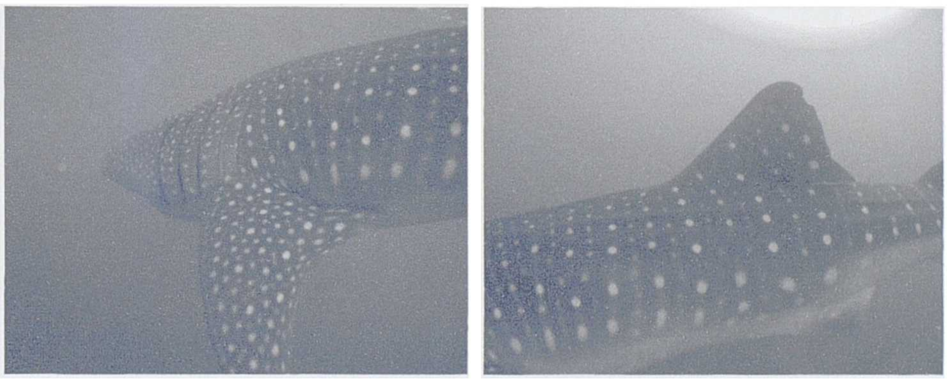
WS 92
2002



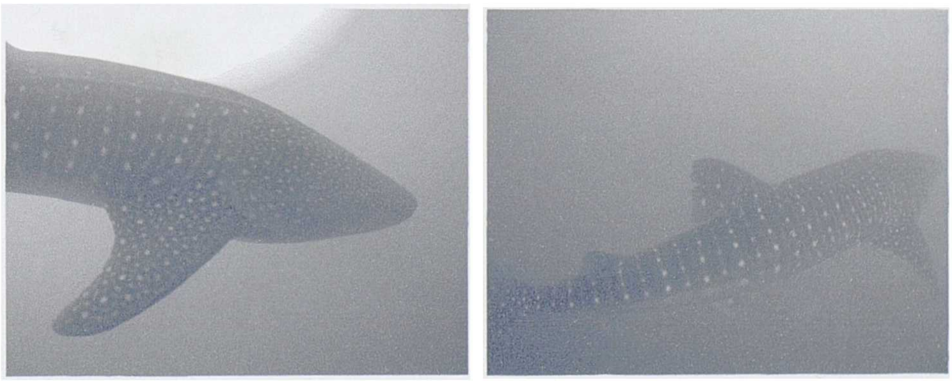
WS 93 - Spot
2002
2003



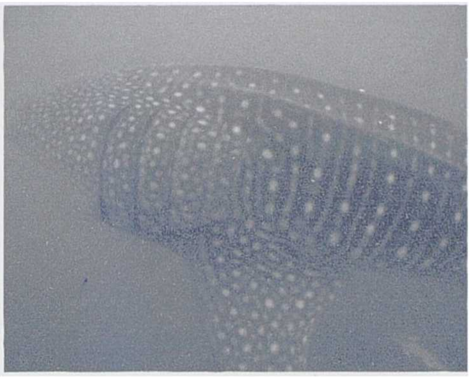
WS 94
2003

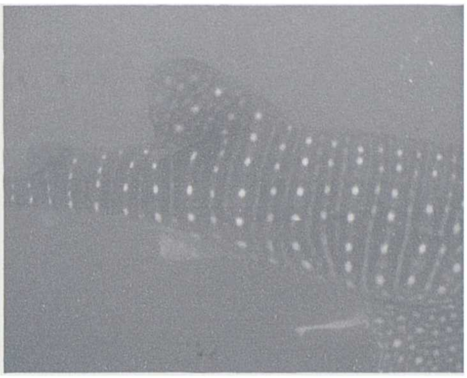


WS 95 - Spot 2
2003

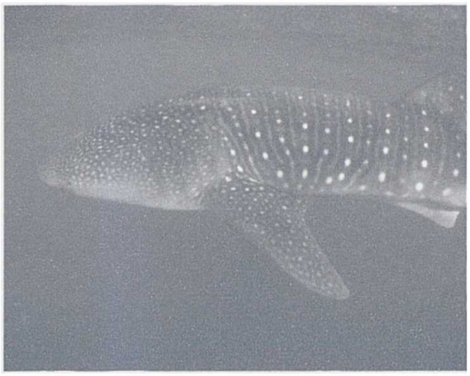


WS 96
2003

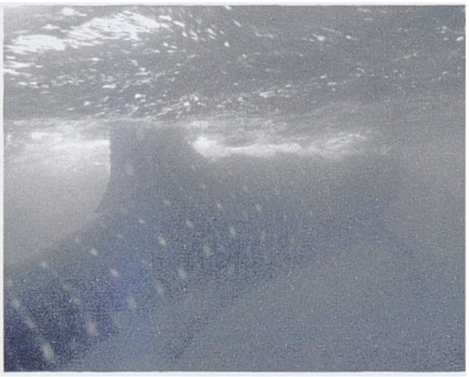


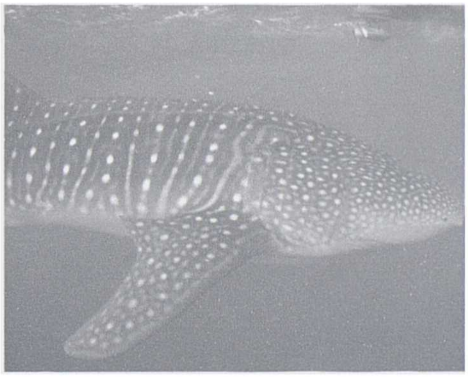


WS 97
2003

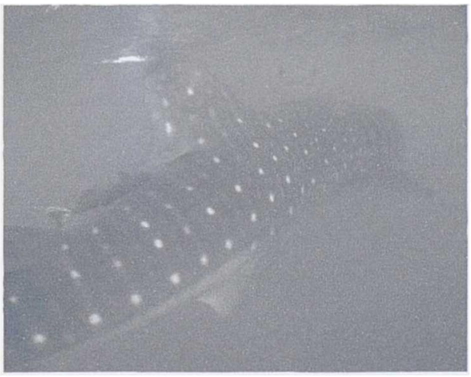


WS 98
2003

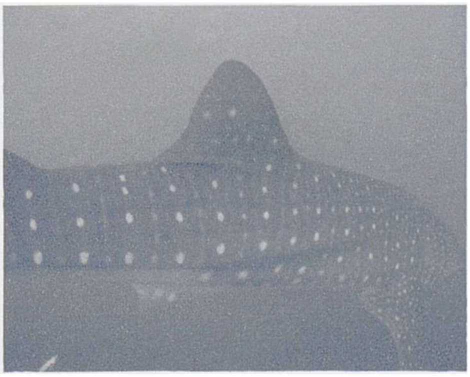




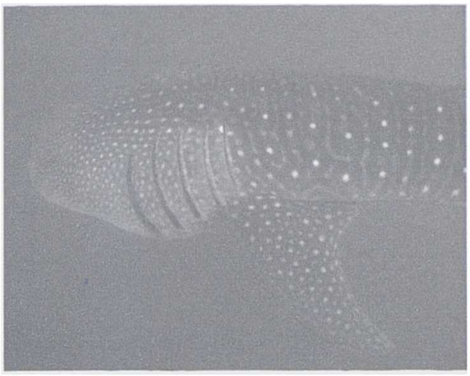
WS 99
2003



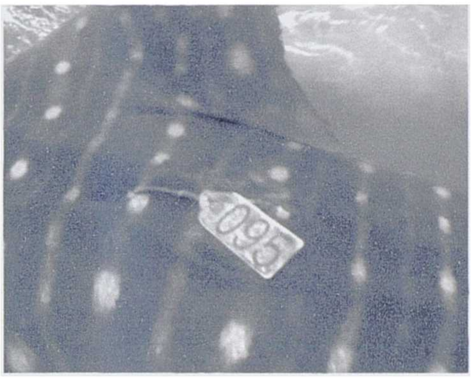
WS 100
2003

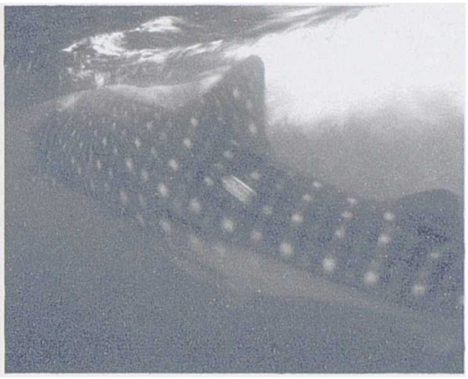


WS 101
2003



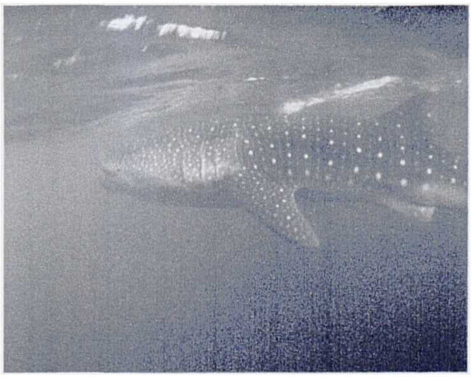
WS 102 - M95
2002
2003



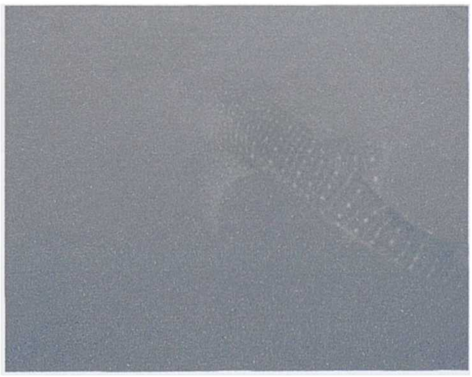


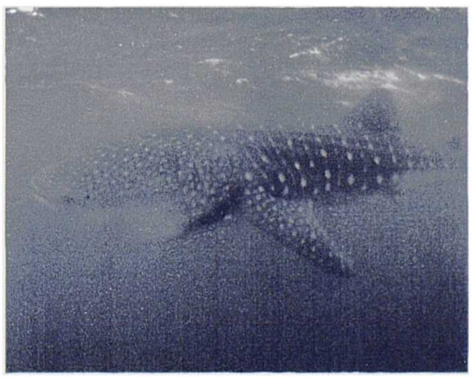
WS 103
2003

WS 104
2003

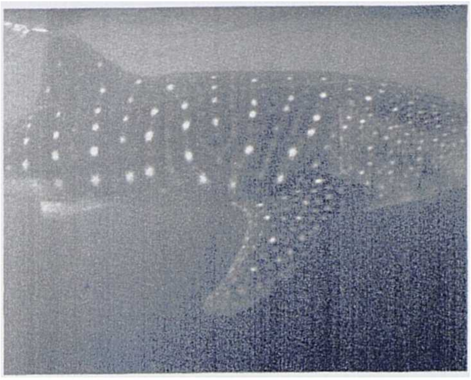


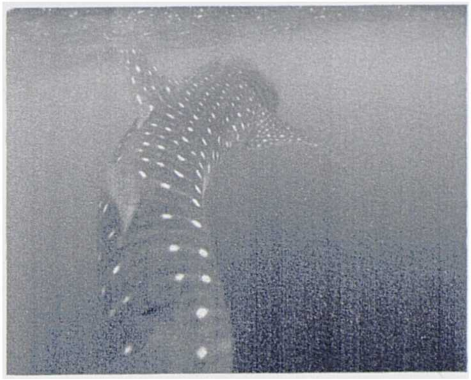
WS 105
2003



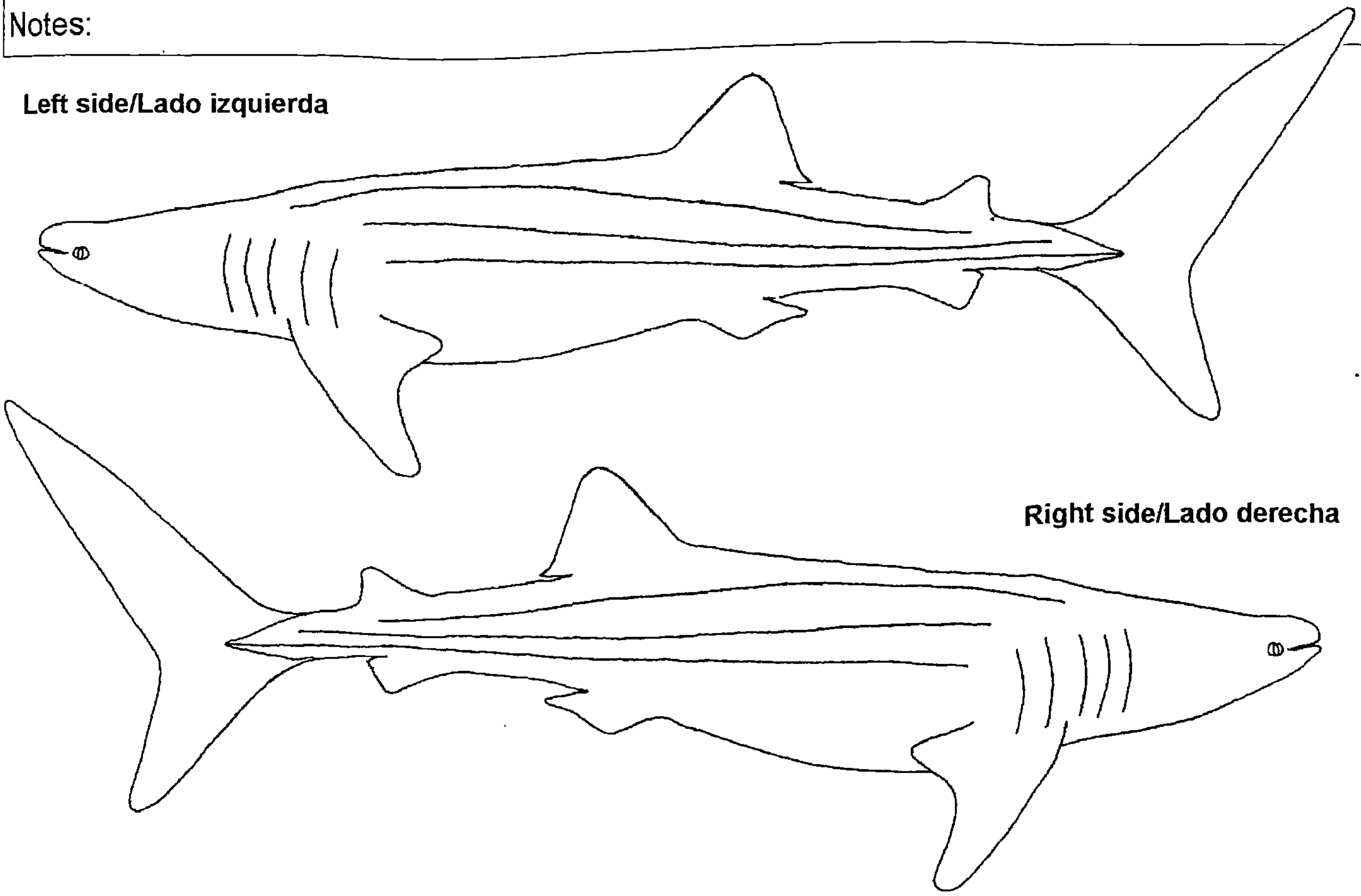


WS 106
2003





Whale Shark Identification Sheet - Belize	**WS ID No.:**
WS Name:	Sex (M/F/JM/JF):
Location & date 1st ID:	Est. Length (m/ft):
Notes:	



Scars or distinctive characteristics	
Left/Izquierda	Right/Derecho

Tagging log

Date	Tag type/color	Tag no.

Sightings log

Date	Time	Location-photo/video?

R. Graham—University of York (rtg@btl net)

Chapter 3. Whale shark site fidelity in relation to a temporal food source and a marine reserve

Abstract

This three-year study shows fine-scale site fidelity in whale sharks (*Rhincodon typus* Smith, 1828) visiting a temporally heterogeneous food source. Patterns of movement and feeding behaviour of whale sharks at a multi-species reef fish spawning site at Gladden Spit, Belize, are characterized in relation to the seasonal spawning of large aggregations of cubera and dog snappers (*Lutjanus cyanopterus* and *L. jocu*). Gladden Spit was declared a marine reserve in May 2000 - the first of its kind established to protect the seasonal aggregations of snappers and feeding whale sharks. A submersed passive acoustic receiver moored at the spawning site recorded patterns of diel, intra- and inter-seasonal visitation from April 2000 to July 2002 for 22 whale sharks tagged with externally attached acoustic tags. Whale sharks showed strong diel and intra-seasonal (n = 17), and inter-seasonal (n = 10) site-fidelity to Gladden Spit. These data indicate that snapper spawn is an attractive food source for whale sharks. The sharks further altered their behaviour during the snapper spawning season by remaining primarily in the upper water column and reducing the frequency of deep dives. However, a preliminary $\delta^{15}N$ analysis of whale shark tissues sampled after two fish spawning moons suggested that sharks displayed a prey preference for zooplankton rather than spawn. Site fidelity results indicate that the marine reserve's design encompasses the key shark aggregation areas, providing site protection during their vulnerable surface feeding periods. Results further suggest that extension of the eastern boundary of the reserve by 5 km could provide a greater buffer for vulnerable surface-feeding whale sharks from nearby cargo traffic. Yet, acoustic and observational data suggest that the sharks did not reside year-round in the Gladden Spit and Silk Cayes Marine Reserve, indicating that the marine reserve may primarily protect juvenile male whale sharks during vulnerable yet limited periods of their life.

3.1 Introduction

Predictable animal behaviour forms the basis of human-based strategies for exploitation and conservation. Many species of fish, including sharks, display predictable patterns of movement and site visitation at different periods in their life-cycle (Klimley & Nelson, 1984; Klimley, 1996; Colman, 1997b) making them vulnerable to fisheries (Bonfil, 1994; Camhi *et al.*, 1997). On the benign side, site fidelity helps to focus research, management and conservation efforts (Sadovy, 1994; Rhodes & Sadovy, 2002) and promote tourism (Arnold & Birtles, 1993; Colman, 1997a; Olson *et al.*, 1997), an alternative to consumptive animal usc. Animals that visit a particular site repeatedly over time display one of the key attributes of site fidelity. Also known as philopatry, site attachment, site fixity, or temporary residency, this predictable behaviour has been associated primarily with reproduction and feeding and is observed in vertebrates and invertebrates, both terrestrial and marine, at different stages in the species' life-cycle and throughout heterogeneous temporal and spatial scales (Hartney, 1996; Lewis *et al.*, 1996; Luckhurst, 1998; Defran & Weller, 1999; Buzby & Deegan, 2000; Meyer *et al.*, 2000; Nemerson *et al.*, 2000; Schaefer *et al.*, 2000; Brown, 2001; Salo & Rosengren, 2001; Willis *et al.*, 2001; Brager *et al.*, 2002; Boles & Lohmann, 2003). For example, scalloped hammerhead sharks (*Sphyrna lewinii*) display temporal and spatial patterns of fidelity to specific seamounts and to sites within a discrete area on a particular seamount in Baja California, Mexico (Klimley *et al.*, 1988), and gray whales (*Eschrichtius robustus*) display intra- and inter-annual site fidelity to specific sites to reproduce and calve such as the Bahia de los Angeles also located in Baja California (Weller *et al.*, 1999). Arctic graylings (*Thymallus arcticus*) only display inter-annual fidelity to summer feeding sites (Buzby & Deegan, 2000) and female turtles such as the green (*Chelonia mydas*) turtle and loggerhead (*Caretta caretta*) will return to the same beaches where they were hatched to lay eggs (Carr & Carr, 1972; Weishampel *et al.*, 2003).

Definitions for site fidelity are as broad and variable as the spatial and temporal scales it encompasses. Gruber *et al.* (1988) defined it as "a behavioural continuum between nomadic and home-ranging life styles". However, this definition does not necessarily fit those species that do not show discrete home ranges or activity spaces. Humpback whales (*Megaptera novaeangliae*) return each summer to regional feeding sites such as the Prince William Sound in Southern Alaska or the Gulf of Maine that measure hundreds of square kilometres (Baker *et al.*, 1986; Clapham *et al.*, 1993). By contrast, spawning salmon home to a very specific section of their natal stream at a specific time of the year following a migration of hundreds or thousands of kilometres (Candy & Beacham, 2000). White and Garrott (1997) and Born *et al.* (1997) note that "fidelity is the tendency of an animal to return to an area previously occupied or to remain within the same area for an extended period of time". While assessing the temporal dimension of site fidelity of Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand's Banks Peninsula, Brager *et al.* (2002) expressed site fidelity as "the proportion of summers with sightings in Akaroa Harbour out of all years the animal was known to be alive".

Switzer (1993) notes that specific sites may confer characteristics that will enhance reproductive fitness and returning to these locations may be considered as evolutionarily stable strategies. Characteristics that may shape the development of site attachment in a marine environment can include abundant and or diverse food, favourable habitat (shelter, complexity), favourable oceanographic factors (temperature, salinity, currents, bathymetry), and proximity to conspecifics or to prey. Some of the best examples of site fidelity related to reproductive behaviour are observed in fish spawning aggregations where fish may migrate large distances to aggregate and reproduce at very specific areas and times (Johannes, 1978; Fine, 1990; Domeier & Colin, 1997; Bolden, 2000; Rhodes & Sadovy, 2002). Sharks demonstrate strong site attachment to areas that confer reproductive advantages (Gruber *et al.*, 1988; Castro, 1993; Morrissey & Gruber, 1993; Lowe *et al.*, 1996). Seasonally abundant food sources can also help to aggregate normally isolated individuals and to facilitate courtship and mating. Basking sharks (*Cetorhinus maximus*) aggregate from May to July along prey-rich oceanographic fronts off the south-west coast of England when feeding together in dense plankton patches and proceed to display courtship behaviour (Sims *et al.*, 2000).

Many patterns of site-attachment behaviour in fish are linked to search for patchy or seasonally-abundant sources of food (Arnold, 1981; Arnold & Walker, 1992; Arnold *et al.*, 1993; Arnold *et al.*, 1994; Zeller, 1997; Zeller & Russ, 1998). This has also been widely documented for elasmobranchs (Gruber *et al.*, 1988; Klimley *et al.*, 1988; Klimley *et al.*, 1992; Holland *et al.*, 1996; Taylor, 1996; Born *et al.*, 1997; Goldman & Anderson, 1999; Holland *et al.*, 1999). Among these, white sharks (*Carcharodon carcharias*) modulate their roving behaviour to visit sites with pinniped colonies such as Dangerous Reef, South Australia (Strong *et al.*, 1992) and the Farallon Islands of California (Klimley *et al.*, 1992; Klimley, 1996). At the Farallons, sharks showed a dual pattern in site attachment behaviour where most remained in the vicinity of the pinniped colony for one to several days, with a few individuals displaying stronger inter-seasonal philopatry (Klimley, 1996).

Food sources and habitats can be ephemeral, leading to a dispersal of populations and individuals and the discovery of new sources of food and sites for reproduction (Travis & Dytham, 1998). The use of navigational cues such as polarized light (Dacke *et al.*, 1999), geomagnetic fields (Zoeger *et al.*, 1981; Kalmijn, 1982; Lohmann & Johnsen, 2000), celestial cues (Sandberg *et al.*, 2000), chemical cues (Nevitt *et al.*, 1995; Montgomery & Walker, 2001) and the development of memory maps that encompass several or all of these cues are suggested as a means of increasing an animal's foraging success or enabling the relocation of sites or prey (Mellgren & Roper, 1986; Benhamou, 1997; South, 1999; Mouritsen, 2001; Salo & Rosengren, 2001). Additionally, animals must time their arrival to coincide with pulses of food or optimal reproductive conditions (see Chapter 4 for details on navigation and memory maps and Chapter 5 on rhythmicity). Active acoustic tracking has provided most of the data on patterns of feeding behaviour and site attachment in large elasmobranchs to date (Sundstrom *et al.*, 2001). This method provides fine-scale data on depth and habitat preferences over a short time scale and has been successfully used with a range of large elasmobranch species including scalloped hammerhead sharks (Holland *et al.*, 1993), white sharks (Klimley *et al.*, 1992; Strong *et al.*, 1992; Goldman & Anderson, 1999), lemon sharks (*Negaprion brevirostris*) (Gruber *et al.*, 1988; Morrissey & Gruber, 1993), tiger sharks (*Galeocerdo cuvier*) (Holland *et al.*, 1999), blue sharks (*Prionace glauca*) (Sciarrotta & Nelson, 1977; Carey & Scharold, 1990; Klimley *et al.*, 2002) and whale sharks (*Rhincodon typus*) (Gunn *et al.*, 1999). However this laborious technique cannot provide researchers with independent data on seasonal scales of foraging and site attachment.

A modification of the active tracking is the passive-acoustic tracking using submerged acoustic receivers that record the time and date of a shark's passage within the range of the receiver. The receiver is either downloaded via a radio signal or following manual removal from its mooring. The radio-linked system was successfully used to elucidate patterns of movement and presence versus absence of Nassau groupers (*Epinephelus striatus*) in the Bahamas (Bolden, 2000), dusky groupers (*E. marginatus*) in Sicily, Italy (Lembo *et al.*, 2002) and white sharks at California's Año Nuevo Island (Klimley *et al.*, 2001). The underwater passive-acoustic system has been used with great success in this study and with scalloped hammerhead sharks (Klimley & Nelson, 1984; Klimley, 1993). Recent developments of the passive system include receiver ability to download depth and temperature data from passing animals tagged with depth and temperature sensing acoustic tags.

Even passive acoustic systems have their drawbacks. Most notably, receiver reception is limited, often to less than 1 km diameter so some knowledge of the study animals' movement behaviour is required for optimal placement. Additionally, data is limited to the point where the fish is tagged or first recorded to other sites where receivers are placed, and there is no indication of an individual's pattern of movement between the two points. To circumvent these limitations, satellite-linked tags that record depth, temperature and location were developed to provide site and researcher-independent insights in diving behaviour, site attachment and habitat preferences throughout a specified period of time. Such tags have been successfully used with several species of fish including whale sharks in this study (Chapters 4 and 5), in Australia (J. Stevens, pers. comm.) and the Pacific (Eckert & Stewart, 2001; Eckert *et al.*, 2002), on basking sharks (Priede, 1984; Sims *et al.*, 2003), on white sharks (Boustany *et al.*, 2002), blue marlin (*Makaira nigricans*) (Graves *et al.*, 2002), halibut (*Hippoglossus stenolepsis*) (Seitz *et al.*, 2002), and Atlantic bluefin tuna (*Thunnus thynnus thynnus*) (Lutcavage *et al.*, 1999; Block *et al.*, 2001).

Site fidelity studies can provide key spatio-temporal data critical for animal conservation efforts, particularly of large migratory species. In the marine realm, these data can be used to site protected areas that encompass key periods of an animal's lifecycle such as reproduction and development (Bonfil, 1997; Roberts, 1997; Roberts & Sargant, 2002). Marine reserves, where no extractive activities are permitted, are declared for a range of reasons (Jones, 1994) including economic (Dixon, 1993), biological (Roberts, 1995, 1998), socio-cultural (Fiske, 1992; Lam, 1998; Pomeroy, 1999), and physical (Lindeman *et al.*, 2000; Mangel, 2000). Although marine reserves have generally been considered ineffective or limited for the protection of large highly mobile marine species or species with large home ranges during all of their life-stages, they can be effective if they encompass the activities of target species during a key life-stage or a predictable and hence vulnerable activity such as feeding or reproduction (Jones, 1994; Bonfil, 1997; Allison *et al.*, 1998). As such, marine reserves are increasingly considered important in the enhancement of fisheries stocks and therefore target the protection of spawning biomass of several commercially important species (Roberts, 1997; Mangel, 1998; Dayton *et al.*, 2000; Lindeman *et al.*, 2000). In other instances a protected area will focus on a single highly mobile species if considered lucrative to do so, fuelling a rapidly developing tourism, as seen with whale-watching based on the gray whales that migrate to Baja California's protected Magdalena Bay to breed (Moore, 1999).

For a protected area to be effective it needs therefore to be designed and sited in a way that will maximize benefits according to the original objectives. Occasionally, enough biological data are available to help define these criteria, however, in many instances a mixture of biological and anecdotal or historical data (Johannes, 1998) mixed with precautionary overtones (Lauck *et al.*, 1998) dictates marine reserve design and siting. However, the lack of biological data especially can lead to marine protected areas that are ineffective or even damage fisheries (Crowder *et al.*, 2000).

The whale shark is an example of a large migratory species that could benefit from localised and global protective measures such as marine protected areas. Circumtropical dwelling and planktivorous (Gudger, 1915; Wolfson, 1986; Colman, 1997b), whale sharks display patterns of movement including "coastal patrolling" over a restricted spatial scale during seasonal visitations to Ningaloo Reef in Western Australia (Gunn *et al.*, 1999) and trans-oceanic migrations (Eckert & Stewart, 2001; Eckert *et al.*, 2002). They further display predictable seasonal site fidelity to a range of sites globally (Colman, 1997b) (Graham, unpublished data) including Ningaloo Reef, Australia (Taylor, 1996; Stevens *et al.*, 1998). Whale sharks appear to use a range of navigational aids coupled with an internal clock to reach patchy food sources as these develop (see Chapters 4 and 5). However, whale shark site fidelity has not been characterized at Ningaloo Reef or demonstrated at several other sites where they have been sighted predictably including the coastal waters of India, Seychelles, Baja California, South Africa, and Honduras. Off the coast of Belize, whale sharks have been observed to congregate in groups of up to 25 individuals in an area less than 50 m across at Gladden Spit, a promontory on the Belize Barrier Reef, to feed on the spawn of reproducing snappers (Heyman *et al.*, 2001). This predictable gathering of whale sharks provided the basis for the research presented here.

The objective of this study was to characterise patterns of site fidelity of whale sharks tagged with coded acoustic transmitters using a single passive acoustic receiver located at a known aggregation site. For the purpose of this study, the spatial aspect of site fidelity is defined as the return of study animals to the feeding grounds as demarcated by the receiver range. Temporally, site fidelity is examined in relation to the presence versus absence of spawning snappers.

3.2 *Materials and methods*

3.2.1 Study site

A full description and map of the site is given in Chapter 1. This study focused specifically on Gladden Spit, Belize (Figure 3.1).

3.2.2 Acoustic telemetry

Daily, seasonal and annual whale shark visitation at Gladden Spit was monitored by tagging 22 individuals with coded single-channel acoustic tags: Vemco V32-6H (n = 9) and V16-6H (n = 13). Tags were factory set to a frequency 69 kHz to emit six pulses of sound with a random repeat rate of 25-49 seconds to minimize clashes with other acoustic tags present. Individual sharks were identified by the unique combination of the tag's pulses and pauses. At these settings the V32 tags have a manufacturer's estimated battery life of 4 years and the V16 tags have a lifespan of around 2.5-3 years. Tag reception was tested individually in air and underwater before deployment using a single-channel acoustic receiver (Vemco VR1 and VR2) and boat-based receiver (Vemco VR60) coupled to an omni-directional hydrophone (Vemco VR10).

VR1 and VR2s are submersible single-channel acoustic receivers set to receive pulses from 69 KHz coded acoustic tags. Both instruments have 1 megabyte of memory and use a lithium long-life C-cell battery with a 6-month data-collection life span. The receiver at the snapper spawning site referred to as "G2" in Figure 3.1, recorded continuously for 796 days from the 27 April 2000 until 1 July 2002. Initially a VR1 was used at Gladden from 27 April 2000 to May 2002 (when the battery ran out) followed by a VR2 deployed from 7 February to 1 July 2002. The VR1 decodes up to 256 different coded tags and stores a maximum of 150,000 detections whereas the more recently developed VR2 decoded up to 65,536 coded tags and stores up to 300,000 detections. The acoustic receiver used was moored at approximately 30 m depth in the middle of the site termed G2 (Figure 3.1) where the spawning of cubera and dog snappers were repeatedly observed in 1998 and 1999. Braided stainless steel (3/32), was crimped and shackled to the receiver and an engine block or crankshaft that was subsequently tied to the reef. The receiver was suspended in mid-water at approximately 24 m depth by a metal float. This depth helped reduce attenuation of signals reflected off the reef or the sea surface.

To identify the trophic importance of different prey to whale sharks feeding at Gladden Spit, tissue samples of the sharks, mutton snapper muscle, mutton snapper roe, zooplankton and the coelenterate *Linuche unguiculata* were taken in April and May 2002 (2^{nd} and 3^{rd} month of snapper spawning at Gladden) and preserved in 100% EtOH or 70% isopropyl alcohol. One faecal sample was obtained directly from a whale shark and preserved by drying. A full description of the sampling, analysis and results is noted in Appendix 3.A.

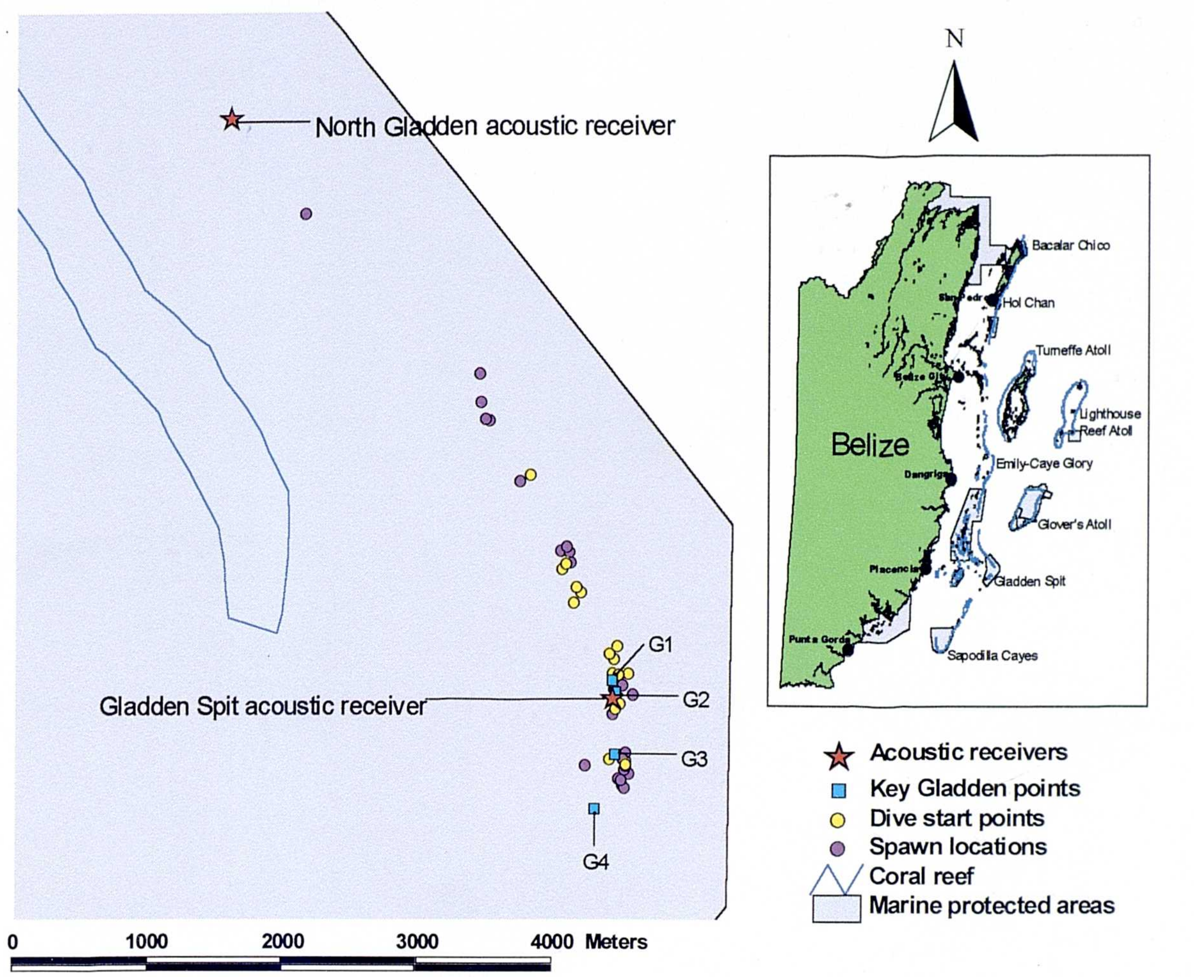


Figure 3.1: Locations where spawn circles were observed on the surface and dive entry sites 2001 and 2002. Key Gladden sites include G1: grouper rock, G2: acoustic receiver and primary dog and cubera spawning site; G2-G3: multiple species of reef fish spawning aggregations; G4: no recorded spawning witnessed past this site. (Base map kindly provided by CZMA).

Receiver reception was tested with the VR1 located at Gladden Spit during a calm sea-state day. The boat engine and depth sounder were turned off and five V16-6H tags were lowered on a rope and submerged to 10 m for 10 minutes in 250 m intervals away from the receiver as measured by a Garmin 12 GPS. A VR60 boat-based acoustic receiver with hydrophone was used to ensure that the tags were functioning during the test. Spraying the body of the receiver with clear anti-fouling paint minimized fouling by marine organisms. Receiver battery life was tested by allowing the VR1 to function until the battery wore out (manufacturer estimate was six months). The VR2 was placed one metre away to ensure continuity of reception at the Gladden Spit site.

3.2.3. Data analysis

The spatial position of the acoustic receiver G2 in relation to the snapper spawning-site was recorded using a GPS and mapped using ArcView. Lunar phases were taken from the US naval observatory's chart and were adjusted from Universal Time/ Greenwich Mean time to local Belize time (http://aa.usno.navy.mil/data/docs/ MoonPhase.html). Day versus night calculations for all dates and diel data were based on sunrise and sunset data obtained from the Belize Hydrometeorological Department web page (http://www.hydromet.gov.bz/). All data were tested for normality using a Kolmogorov-Smirnov test before being submitted to statistical tests. Non-normal data were analysed using non-parametric tests.

3.3 Results

3.3.1 Receiver tests

Receiver reception tests measuring the maximal reception distance of acoustic tags with the VR1 indicated that recorded pulse number for the five tested tags diminished between 0-250 m from the receiver until no pulses were recorded at 500 m distance away (Figure 3.2). Receiver battery life stretched beyond the manufacturer's indications of 185 days to 235 days in water with a mean temperature 27.7^{0}C ± 0.90 SD, as recorded by a submersible temperature logger (Onset Corp. X-Tidbit) from 2 January 2002 to 19 March 2003. During the overlap of both functioning receivers, the VR2 was found to record fewer pulses per shark and overall than the VR1.

3.3.2 Intra- and inter-annual site fidelity

Records of acoustically tagged whale sharks indicated that they showed a high degree of intra-monthly, inter-monthly and inter-annual site fidelity to Gladden Spit. Of the 22

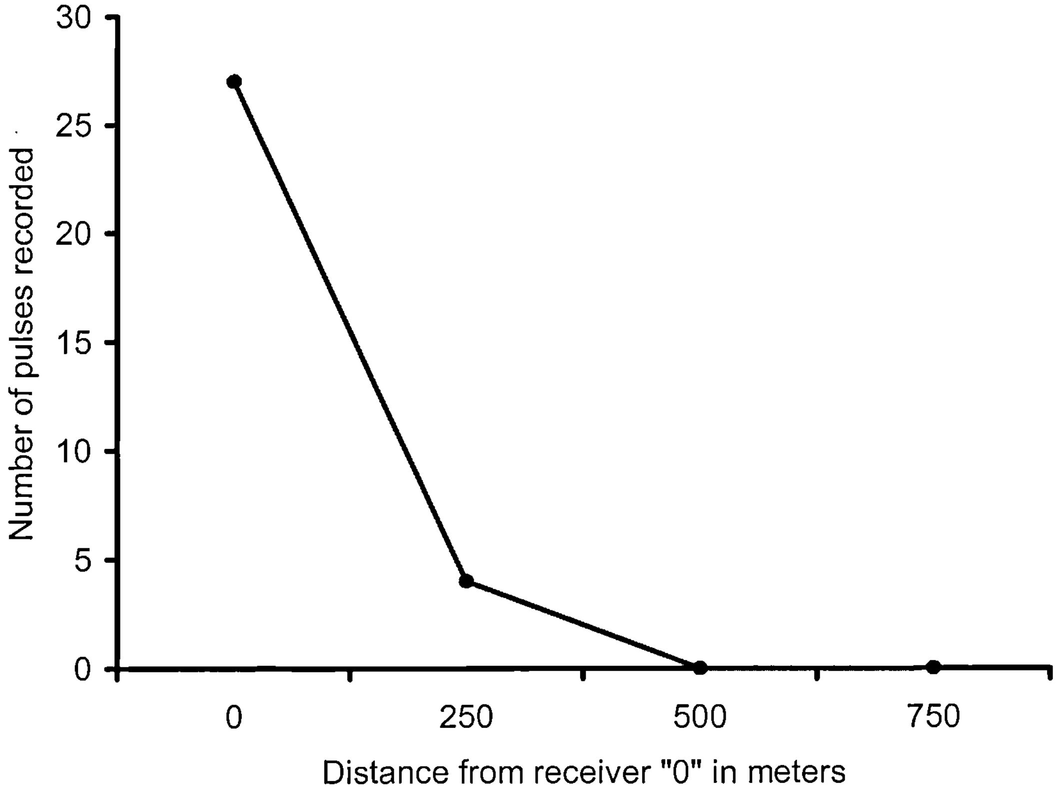


Figure 3.2: Reception range in meters of acoustic tags by the VR1 receiver at Gladden Spit. The number of pulses were recorded over 10 minutes at each station.

whale sharks acoustically tagged in 2000 and 2001 (Table 3.1), 17 sharks returned to Gladden Spit for at least one successive moon and 10 sharks returned to Gladden the year after being tagged (Figure 3.3). The highest recorded cumulative time for whale shark visitation on any one day (2373 min, mean 263.7 min ± 110.8 SD) was recorded for 9 sharks on 12 April 2001, 4 days after the full moon (Figure 3.4). This high visitation rate is primarily due to the rapid deployment of 11 additional tags between 16 March and 11 April 2001 and the presence of a returning shark tagged in 2000.

Differences in monthly whale shark visitation were recorded at Gladden Spit with a greater number of visits during the months of March to October compared to November through February, with May the peak visitation month recorded between 2000 and 2002 (Kruskal-Wallis test; df = 27; $\chi^2 = 51.297$; $p < 0.05$) (Figure 3.5). A secondary peak in visitation was recorded during September 2000 and July and August 2001. Although whale sharks were not sighted near the receiver during this period, large aggregations of cubera snapper (up to n = 3000) were observed and dog snappers were recorded spawning during these months (see Chapter 6 on fish census methodology). Whale shark visitation coincided with an increased abundance of fish and the production of spawn, which in turn was linked to the phase of the moon during the peak snapper spawning-season. Whale shark large-scale movements and dispersal outside of Gladden Spit and the spawning periods are discussed in Chapter 4.

Table 3.1: Deployment of acoustic tags on whale sharks at Gladden Spit, 2000 to 2001. TL: estimated total length in meters; JM: juvenile male; MM: mature male: JF: juvenile female; MF: mature female; F: female, stage of maturity unknown.

Tag number	Date Deployed	Sex	TL (m)	Marker tag no.
A1	27-Apr-00	JM	5.5	50
A2	21-May-00	JM	5.5	57
A3	23-May-00	JM	5.5	60
A4	23-May-00	JM	4.8	45/62
A5	24-May-00	F	8.5	56
A6	9-Apr-01	JM	7.0	72
A7	9-Apr-01	-	5.5	-
A8	9-Apr-01	-	-	-
A9	9-Apr-01	JM	6.7	73
A10	16-Mar-01	-	-	-
A11	9-Apr-01	JM	5.2	-
A12	10-Apr-01	-	-	-

Tag number	Date Deployed	Sex	TL (m)	Marker tag no.
A13	10-Apr-01	-	-	-
A14	10-Apr-01	-	-	-
A15	11-Apr-01	-	6.1	79
A16	11-May-01	-	-	-
A17	10-Apr-01	-	-	-
A18	10-May-01	MM	9.7	75
A19	11-May-01	MM	9.7	52
A20	13-May-01	-	-	-
A21	11-May-01	-	-	-
A22	11-May-01	JM	4.2	-

"–": data not available

Tagged sharks periodically visited the spawning grounds in the week immediately preceding the full moon. However, whale shark visits were more frequent and longer in duration at Gladden Spit from the start of the full moon to the end of the last quarter moon (days sampled n = 407) (Figures 3.4, 3.5) compared to visitation during the new moon and first quarter moon (days sampled n = 398) (Mann-Whitney U test: $z = -6.316$; $p < 0.001$). This period coincided with peak snapper spawning and did not indicate that whale shark visitation was necessarily cued by the lunar phase (see Chapter 6).

Acoustically tagged sharks account for 21% of all sharks counted with photo identification since 1998 (n = 106) (see Chapter 2 for more information on photo identification). The remaining five sharks that were not recorded at Gladden Spit again may have shed their tags or dispersed to other sites. Receiver records indicate that although intra- and inter-annual tag retention was high with 77% return rate of previously tagged sharks between April 2000 and July 2002, one of the larger V32 tags deployed in 2000 was in the process of being shed only 2 days after deployment. That shark was not recorded by the receiver in the month following tagging or in 2001 despite a resighting, and is not included in the 22 tagged sharks monitored in this study. The acoustic tag for shark A9 (also tagged with marker M073) detached between 25 October 2001 and 28 March 2002 when the shark was resighted with its marker tag but without the acoustic tag. No other sharks were seen with malfunctioning or broken tags in 2001 and 2002. Although few acoustic tags showed evidence of fouling, one heavily fouled tag sighted underwater in April 2002 (Shark A17) was clearly recorded by the receiver, indicating that fouling does not appear to prevent acoustic transmission.

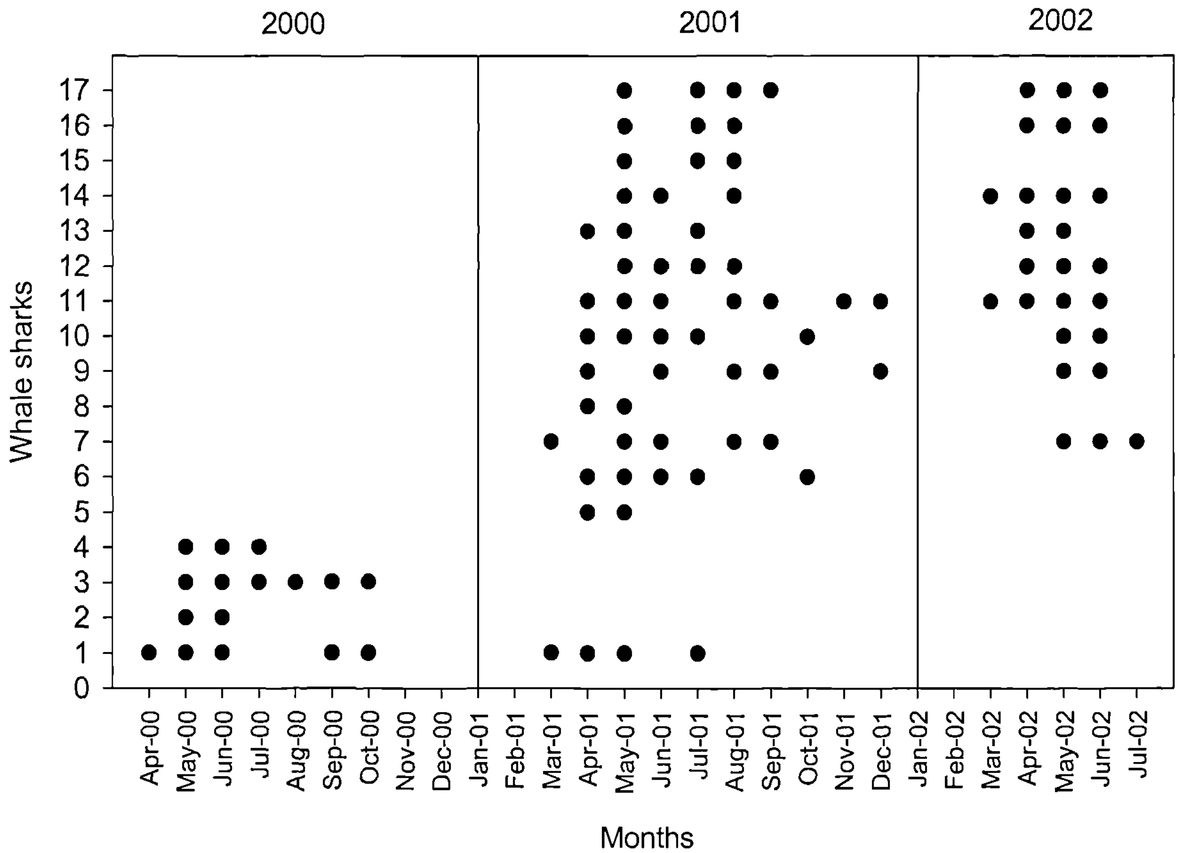


Figure 3.3: Patterns of intra- and inter-seasonal philopatry of 17 acoustically tagged whale sharks at the acoustic receiver located at the Gladden Spit snapper spawning aggregation site from 27 April 2000 to July 2002. Each point represents visitation by a whale shark during a specific month.

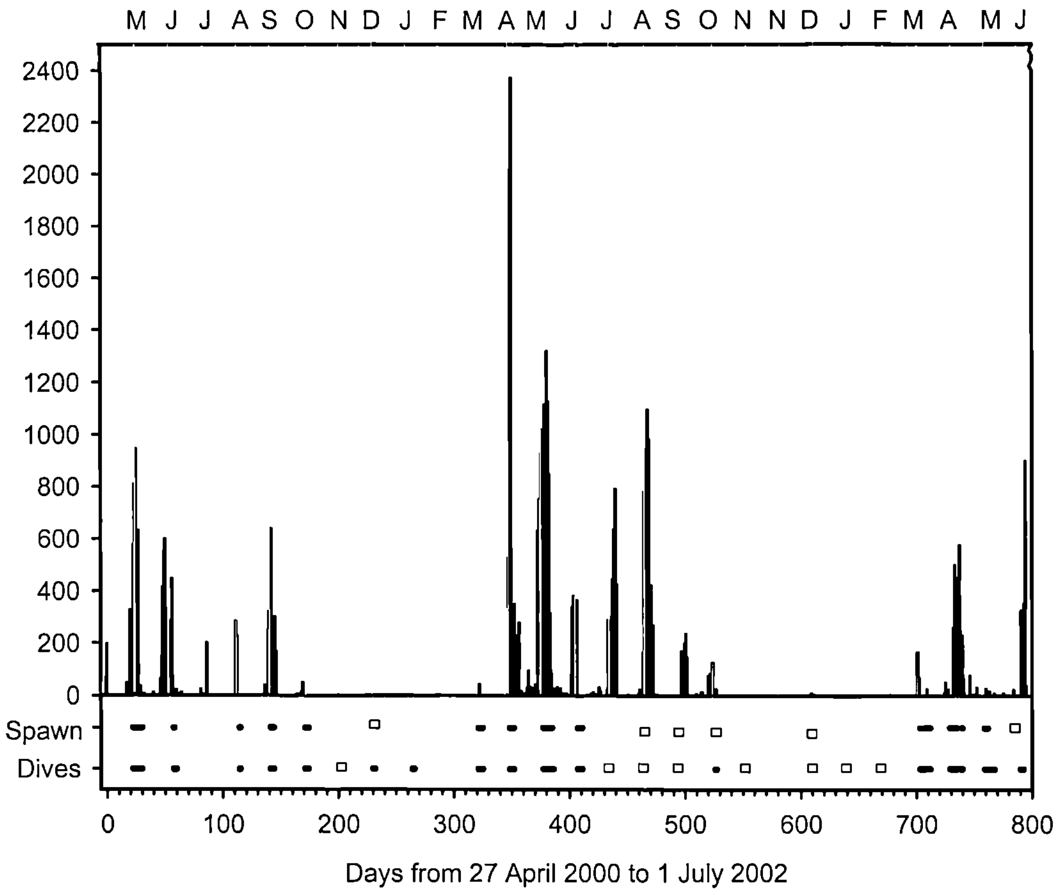
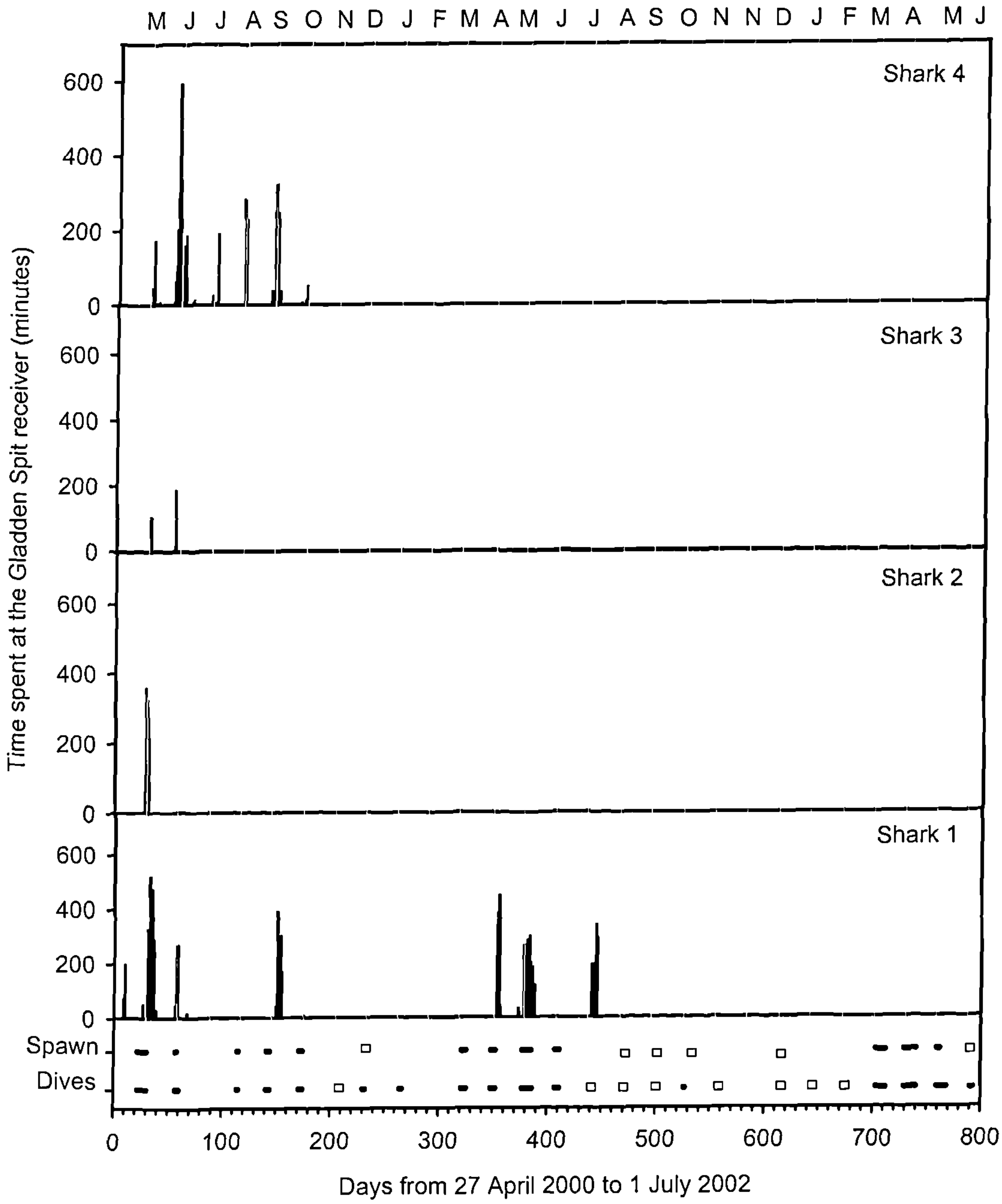
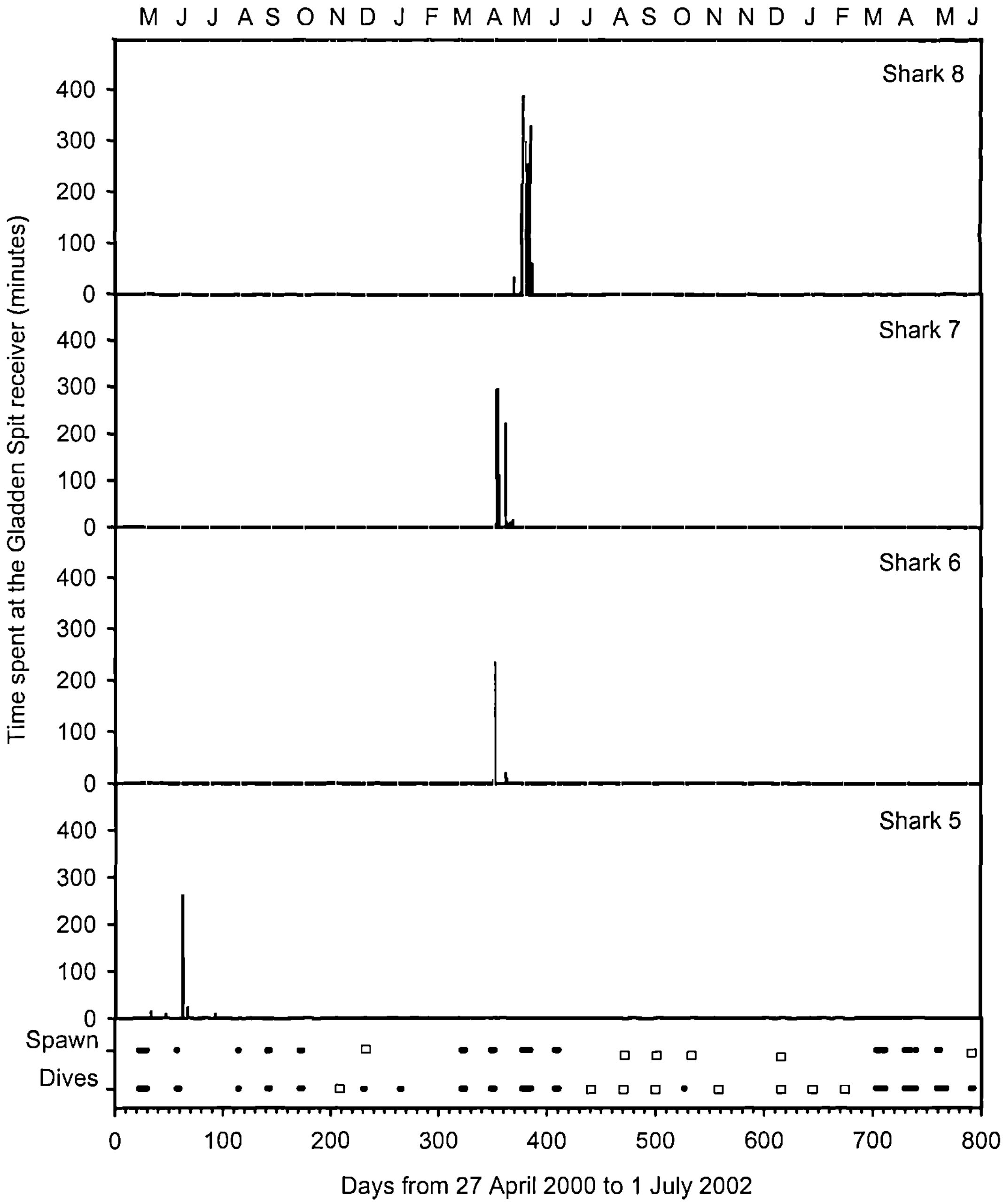


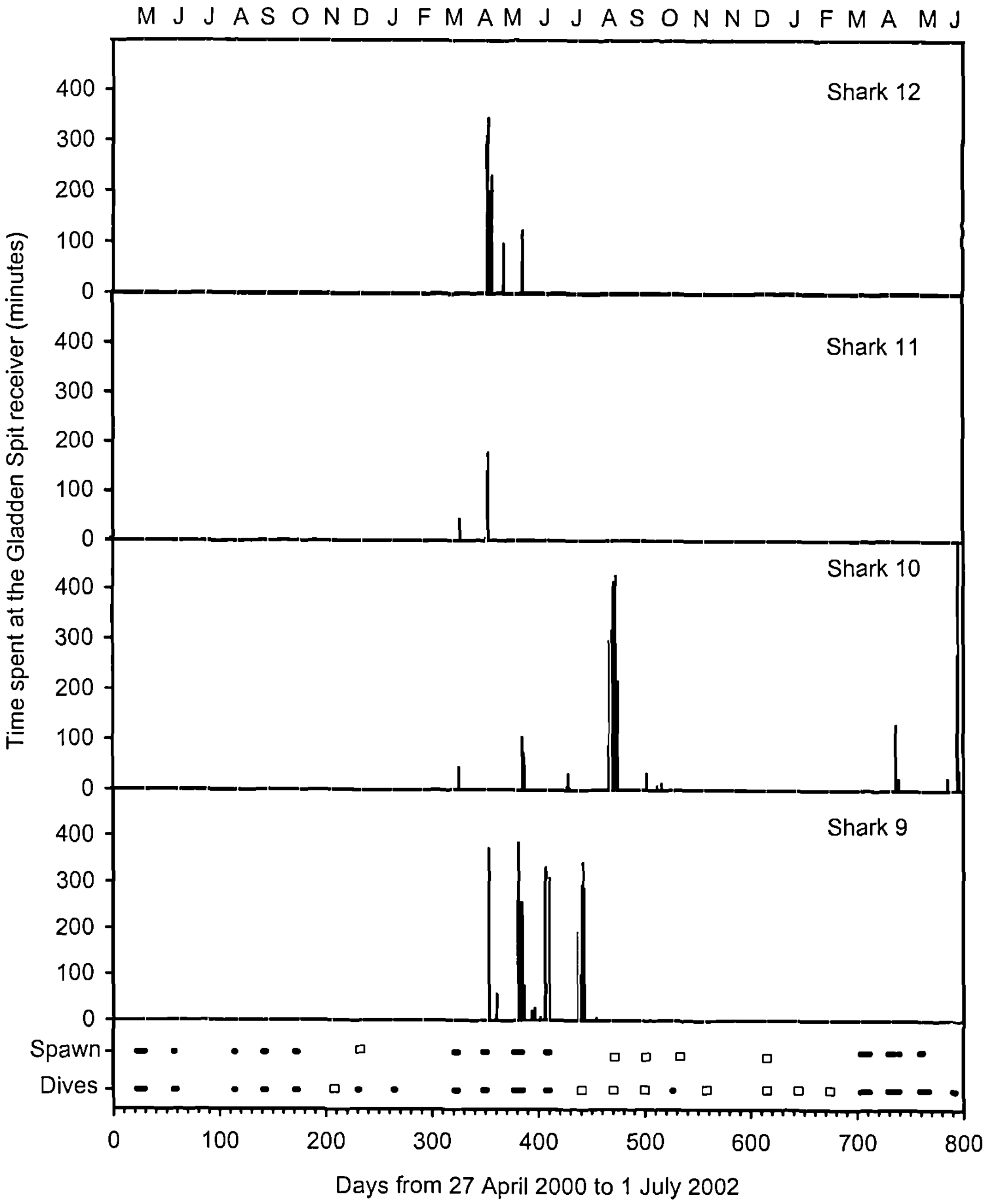
Figure 3.4: Total time spent at the Gladden Spit receiver in minutes per day by all 22 acoustically tagged whale sharks from 27 April 2000 to 1 July 2002. Grey vertical lines coincide with the full moon, half way between each line coincides with the new moon. Dashes in the "Spawn" and "Dives" graph indicate when snappers have been observed to spawn and when divers have dived the Gladden Spit spawning site. White dashes indicate spawning and diving observations made during specific months prior to the 2000-2002 study period.



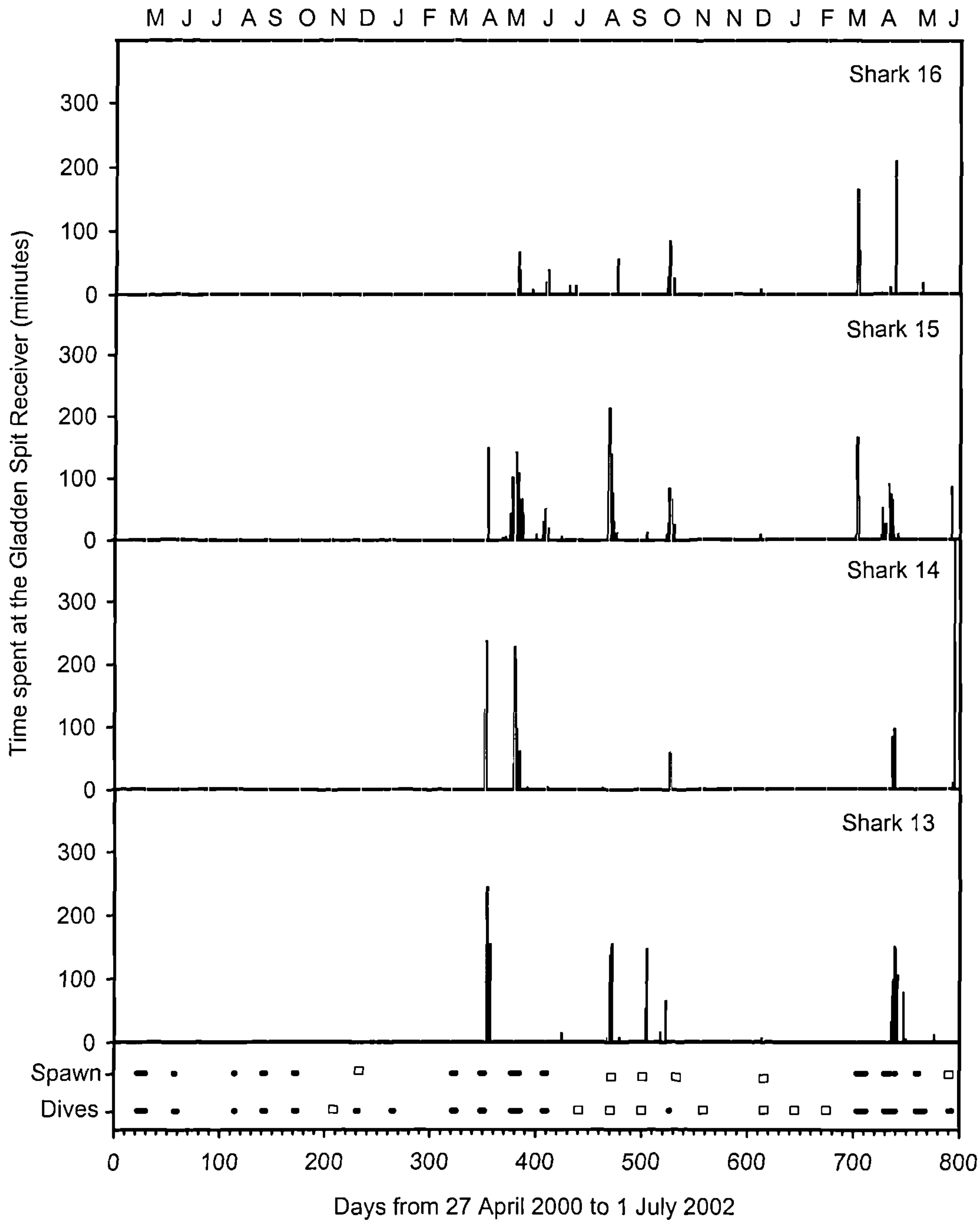
M J J A S O N D J F M A M J J A S O N N D J F M A M J
Shark 4
Shark 3
Shark 2
Shark 1
600
400
200
0
Time spent at the Gladden Spit receiver (minutes)
Spawn
Dives
0
100
200
300
400
500
600
700
800
Days from 27 April 2000 to 1 July 2002

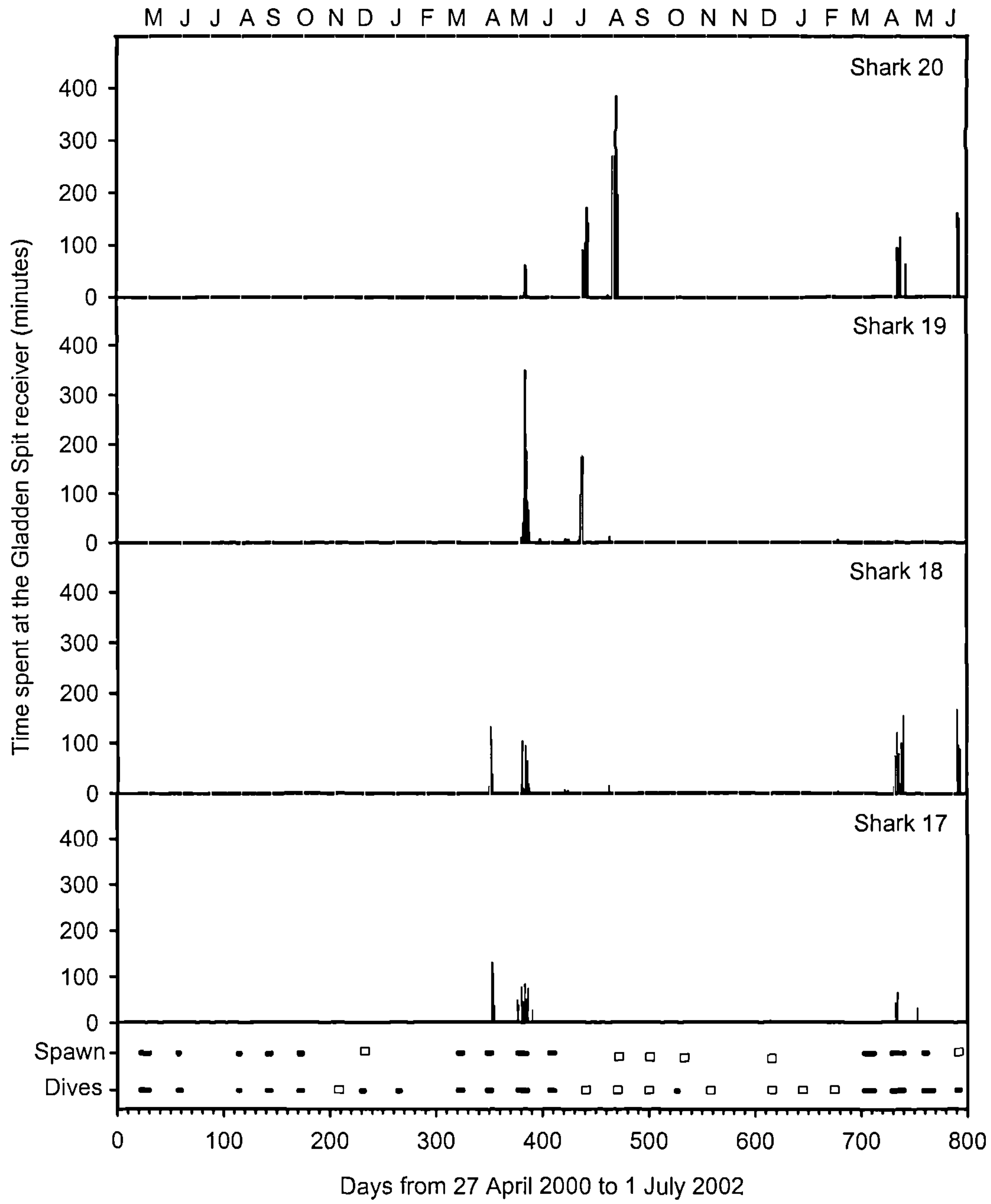


M J J A S O N D J F M A M J J A S O N N D J F M A M J
Shark 8
Shark 7
Shark 6
Shark 5
Time spent at the Gladden Spit receiver (minutes)
400
300
200
100
0
Spawn
Dives
0
100
200
300
400
500
600
700
800
Days from 27 April 2000 to 1 July 2002



M J J A S O N D J F M A M J J A S O N N D J F M A M J
Shark 12
Shark 11
Shark 10
Shark 9
Time spent at the Gladden Spit receiver (minutes)
400
300
200
100
0
Spawn
Dives
0
100
200
300
400
500
600
700
800
Days from 27 April 2000 to 1 July 2002


M J J A S O N D J F M A M J J A S O N N D J F M A M J
Shark 16
Shark 15
Shark 14
Shark 13
Time spent at the Gladden Spit Receiver (minutes)
0
100
200
300
Spawn
Dives
0
100
200
300
400
500
600
700
800
Days from 27 April 2000 to 1 July 2002



M J J A S O N D J F M A M J J A S O N N D J F M A M J
Shark 20
Shark 19
Shark 18
Shark 17
Time spent at the Gladden Spit receiver (minutes)
0
100
200
300
400
Spawn
Dives
0
100
200
300
400
500
600
700
800
Days from 27 April 2000 to 1 July 2002

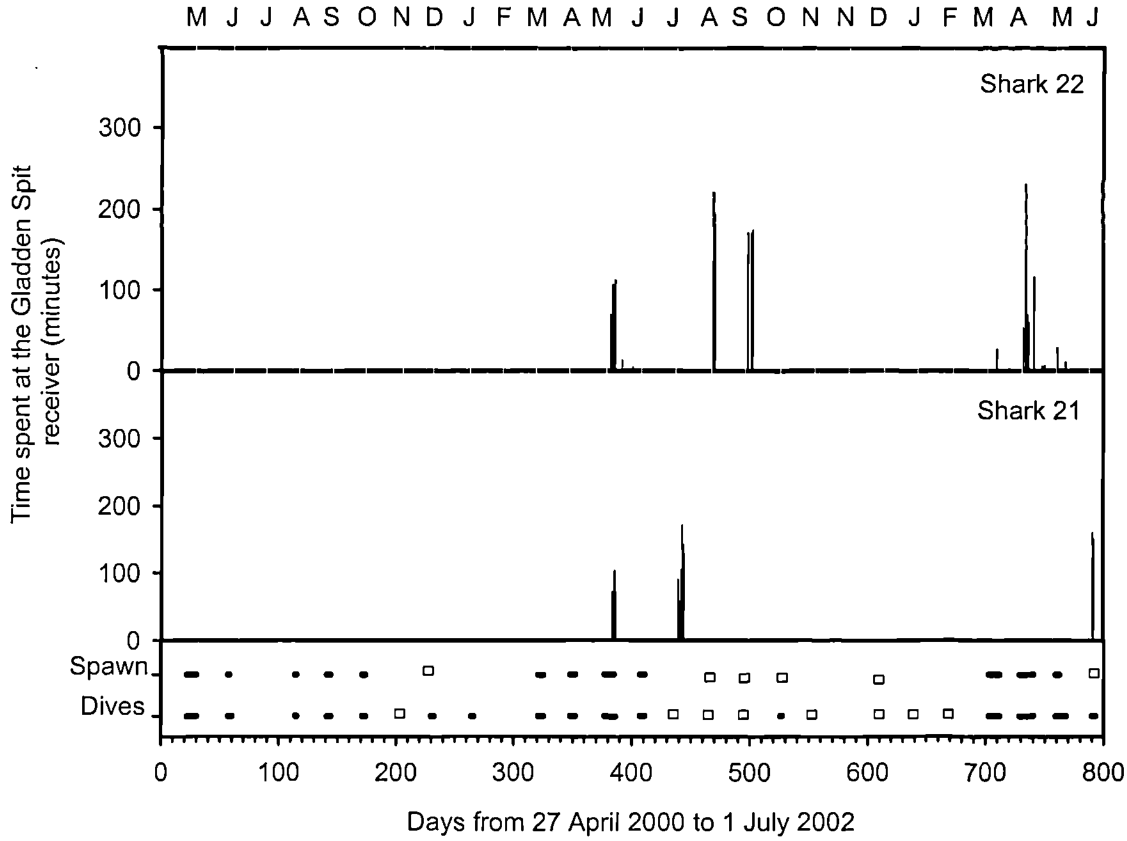


Figure 3.5: Time spent in minutes by 17 individual whale sharks at the acoustic receiver located at the Gladden Spit snapper spawning aggregation site deployed over 796 days from 27 April 2000 to July 2002. Grey vertical lines coincide with the full moon, half way between each line coincides with the new moon. Dashes in the "Spawn" and "Dives" graph indicate when snappers have been observed to spawn and when divers have dived the Gladden Spit spawning site. White dashes indicate spawning and diving observations made during specific months prior to the 2000-2002 study period.

3.3.3 Timing of visitation

Whale shark timing of arrival and departure at Gladden indicated that this species may have been able to monitor prey abundance. They may have been able to detect changes in prey abundance and cessation of spawning of Gladden's snappers perhaps using olfactory or auditory cues. During the May moon in 2001, 13 sharks left the Gladden spawning site within 7 days of one another (13-19 May 2001), with 6 leaving on 15 May. Departure from the spawning grounds usually occurred at or a few days after underwater observations had ceased and before the start of the new moon. At least 81.3% of daily visitation (n = 358, mean 16.3, ± 11.6 SD) took place within the fish spawning season's full moon periods (March through June, full moon to start of new moon). Between and within all years, visitation was significantly greater during the full moon periods versus new moon periods where 79.4% of visitation took place from the full moon to the new moon (n = 452, mean 20.5, ± 15.1 SD).

3.3.4 Diel patterns of fidelity

Whale sharks spent more time at the receiver and spawning site during the day (n = 1627), compared to the night (n = 676) (Mann-Whitney U test; Z = -3.362; $p < 0.001$). To assess similarity in philopatric behaviour at the spawning grounds, the difference in time spent by all acoustically tagged whale sharks at the Gladden Spit receiver was investigated using a one-way between groups analysis of variance. Whale sharks spent different amounts of time at Gladden compared to one another (a one-way between-groups ANOVA: df = 21; F = 3.1; $p < 0.001$).

At least 10 sharks (nos. A1, A2, A4, A7, A8, A9, A10, A12, A19 and A20) spent over 5 hours in a 24 h period within the <500 m radius reception range of the acoustic receiver. Shark A4 (juvenile male, ~5.0 m total length) spent almost 10 consecutive hours close to the receiver in June 2000. Whale sharks arrive and leave the receiver site at different times of the day (Figures 3.6 and 3.7). Most sharks arrived in the afternoon between 12:00 h and 18:00 h. Individuals appeared to cue arrival times to the onset of fish aggregating activity and spawning. All sharks recorded different rates of visitation in a 24 h period (a one-way between-groups ANOVA: df = 23; F = 6.127; $p < 0.001$). Comparisons of visitation at the spawning site in minutes per time of day revealed a significant difference between 17:00 h and all other hours of the day (Tukey HSD, $p < 0.001$) (Figure 3.6). In the majority of cases, this arrival period preceded the

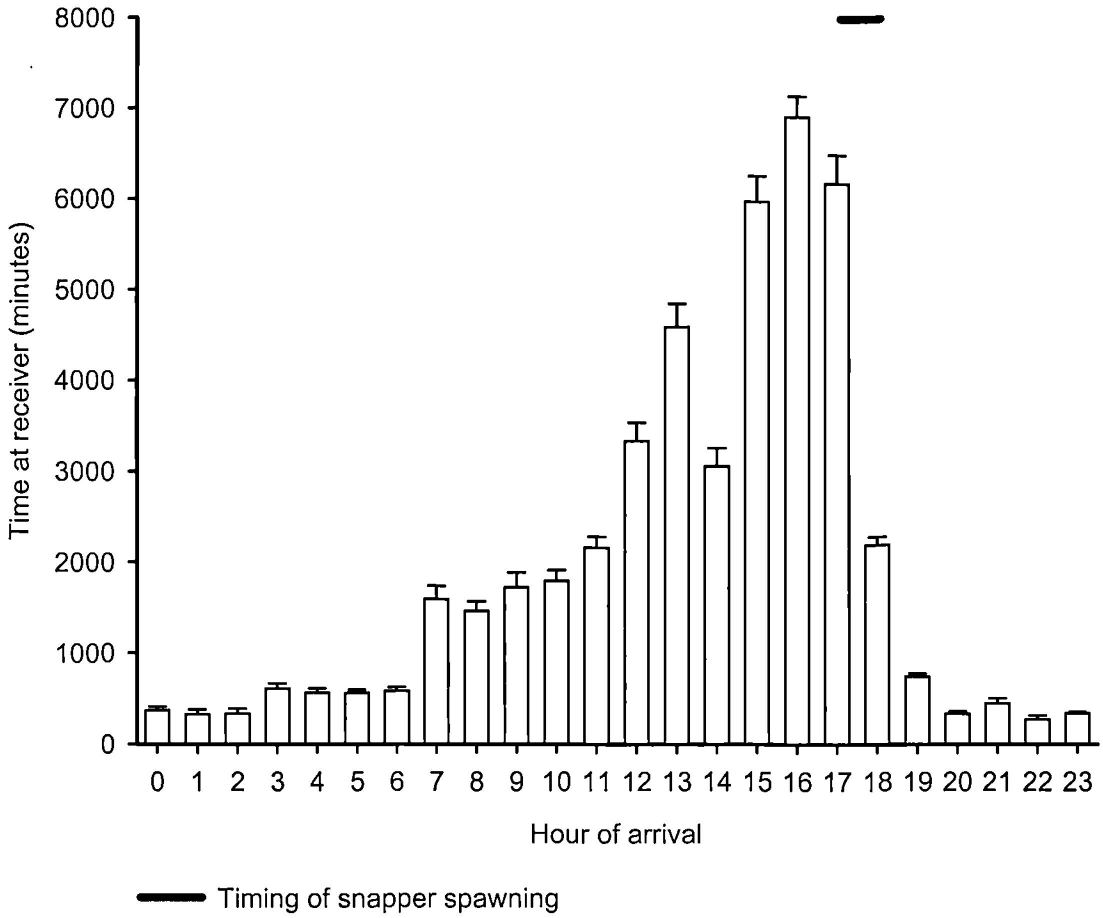
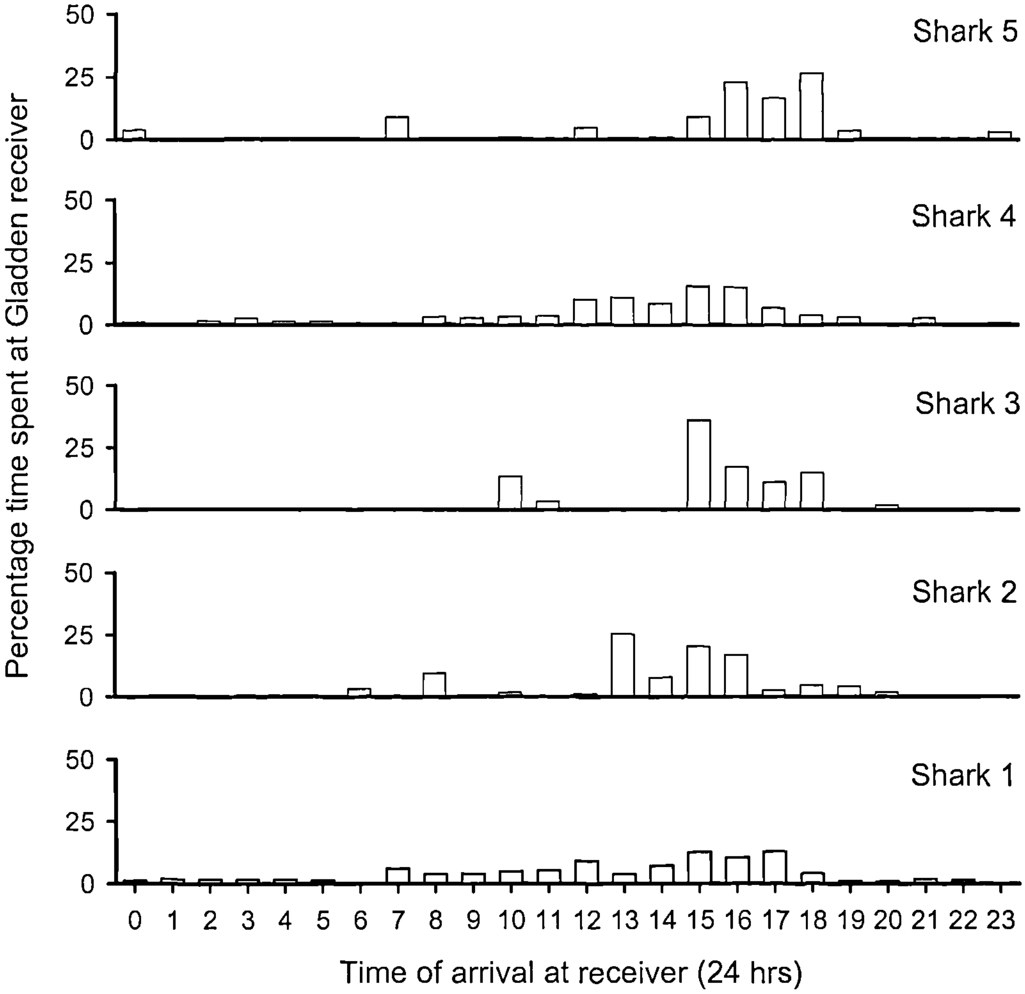
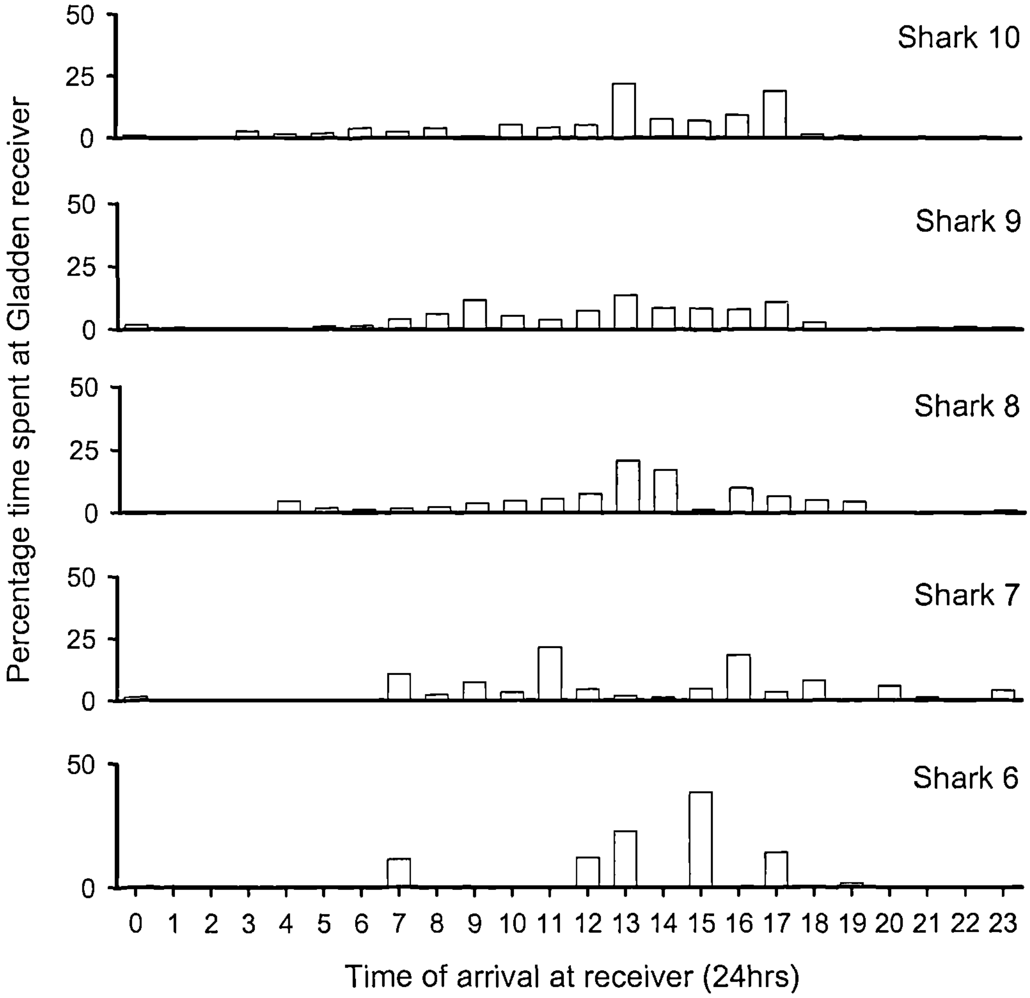
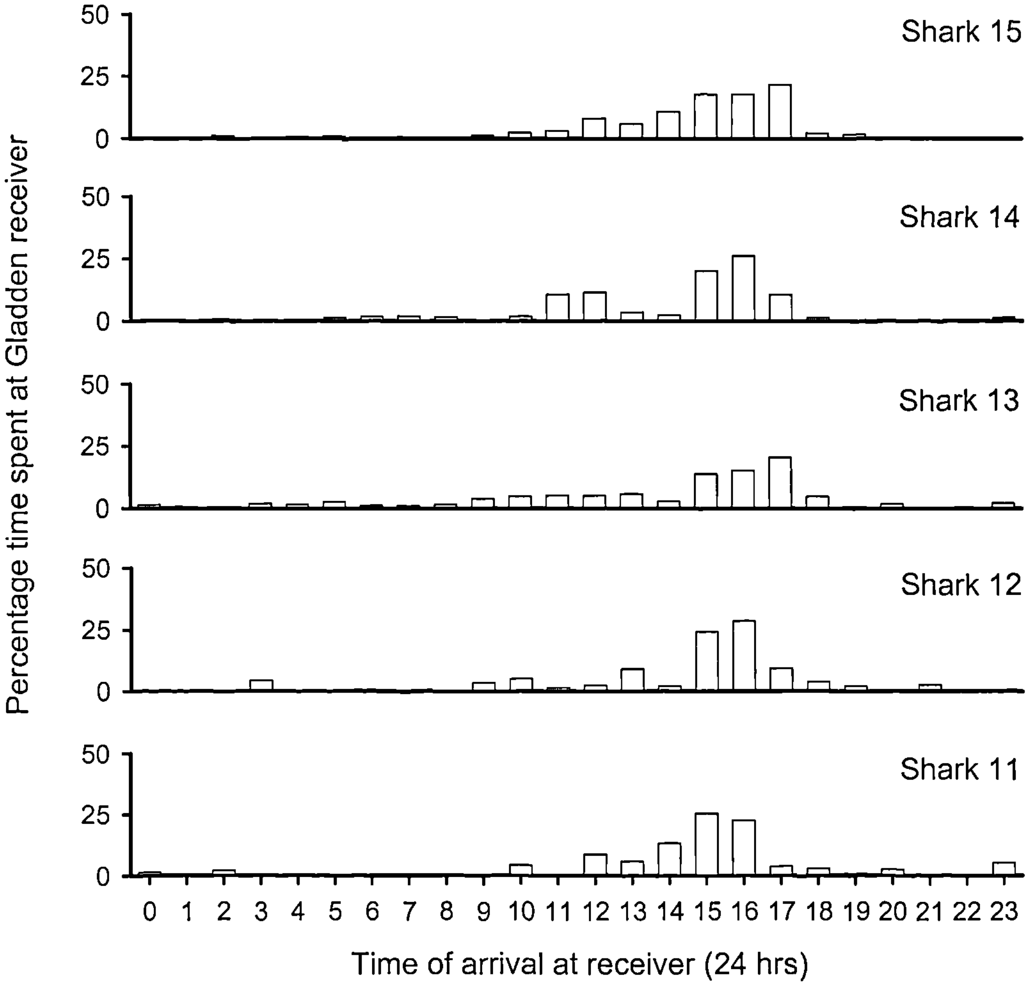
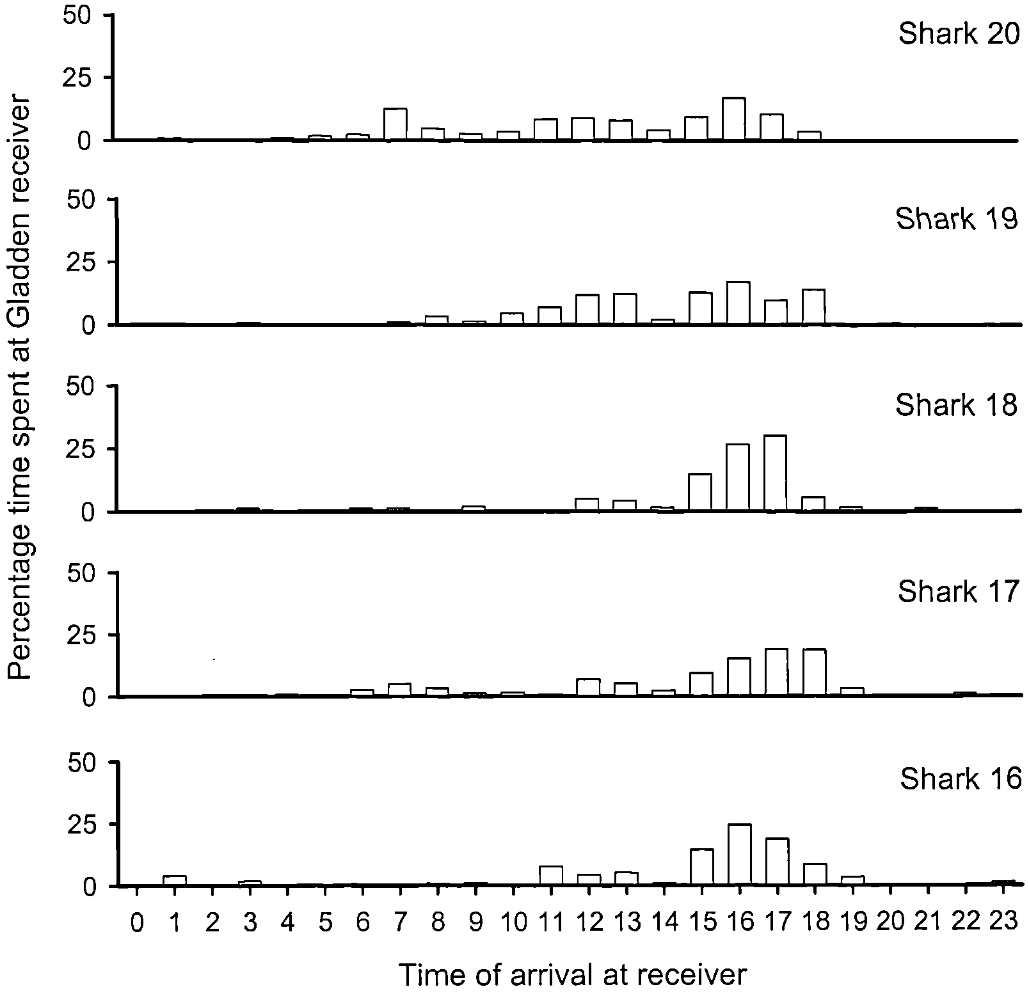


Figure 3.6: Mean time spent at Gladden in minutes (± SE) by all sharks based on time of arrival at the Gladden Spit receiver Between 27 April 2000 and 1 July 2002.


Shark 5
Shark 4
Shark 3
Shark 2
Shark 1
50
25
0
Percentage time spent at Gladden receiver
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time of arrival at receiver (24 hrs)


Shark 10
Shark 9
Shark 8
Shark 7
Shark 6
50
25
0
Percentage time spent at Gladden receiver
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time of arrival at receiver (24hrs)


Shark 15
Shark 14
Shark 13
Shark 12
Shark 11
50
25
0
Percentage time spent at Gladden receiver
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time of arrival at receiver (24 hrs)



Shark 20
Shark 19
Shark 18
Shark 17
Shark 16
50
25
0
Percentage time spent at Gladden receiver
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time of arrival at receiver

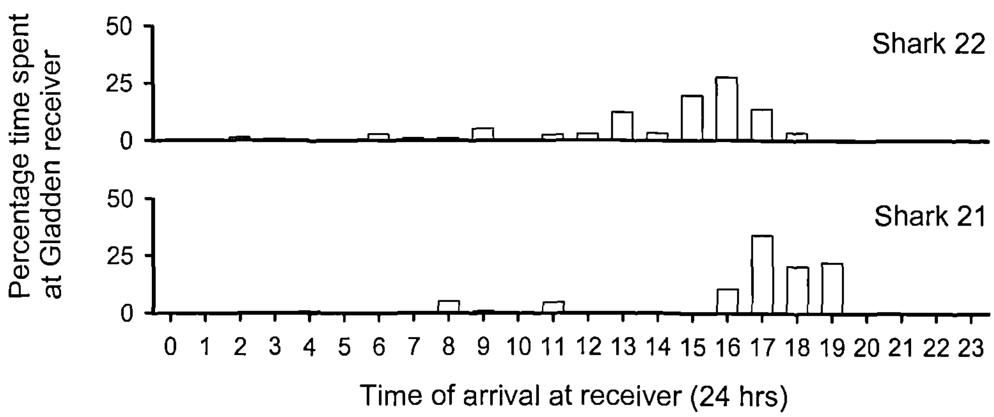


Figure 3.7: Percent time spent per day (24 hours) by 22 acoustically tagged sharks at the Gladden Spit acoustic receiver. Calculations are based on the time of arrival of individual sharks at the receiver.

onset of dog and cubera spawning with a mean onset of spawning of 17:35 ($n = 37$, range 17:08-18:05) observed for both species of snappers combined (Figure 3.6).

3.3.5 Whale shark feeding behaviour in the spawning aggregation

Both dog and cubera snappers were seen to aggregate in increasing numbers from the early afternoon about 14:00 onwards. Dog snappers tended to aggregate on the reef platform between 20 m and 30 m, occasionally streaming down to the reef and rising again to form a dense school in the mid-water. Cuberas streamed in the hundreds or thousands towards the spawning site and occasionally swam in a tight circle on the reef platform. As the mean onset of spawning for both cuberas and dogs neared (17:35 h), the fish broke out of the circle, streamed towards the fore-reef drop-off and aggregated between 45 m and 25 m depth. Several cuberas, presumed females due to their gravid appearance and white colour morph, displayed a head down twitching behaviour that attracted several other fish that nuzzled it (see Chapter 6 for more on the behaviour of spawning fish). At this time, whale sharks commonly circled both dog snappers on the reef platform and the nearby cuberas in slightly deeper water. Whale sharks ascended in the water column with the spawning fish and began feeding as the spawn was released (Figure 3.8). When the spawn rose to the surface it created circles of relatively flat water with an oil-like appearance (Figure 3.9). New spawn circles formed on the surface until ~18:30, after which it became too dark to see. During this time, whale sharks began surface-feeding (Figure 3.8), turning in tight circles around the spawn cloud, moving off to a new spawn circle when the first dissipated and the oil-like surface was no longer visible.

Whale sharks were often observed swimming or "surfing" with or against the waves, possibly to minimize energy expenditure and increase feeding efficiency. They were also observed swimming against wave direction and concentrating prey into their open mouths. Underwater feeding speeds were estimated at under 1.0 m s^{-1} or less when the spawn was released and a snorkeler could keep up with the sharks. On the surface as the spawn dispersed with surface wind-driven currents, whale sharks increased their swimming speed to over 1.0-1.3 m s^{-1} where even the fittest snorkelers were unable to keep up with them.

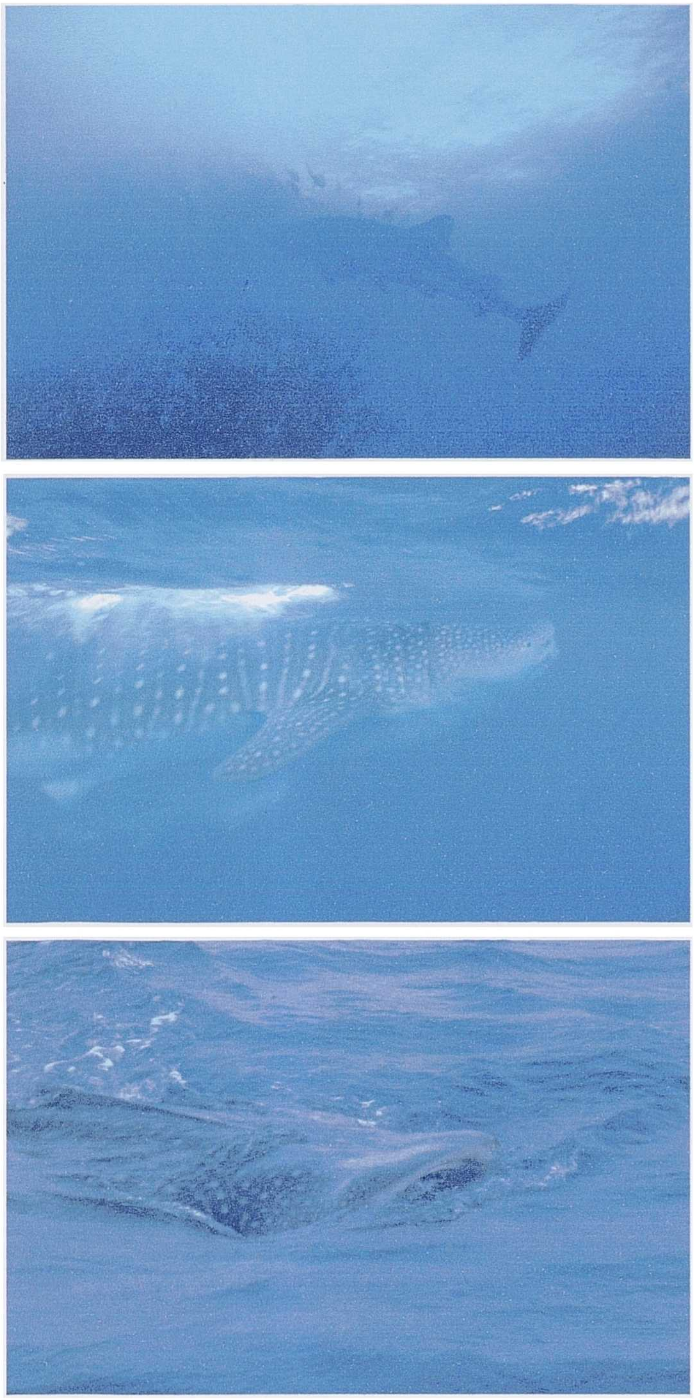


Figure 3.8: Whale sharks feeding on recently released spawn, and a whale shark feeding on eggs that have floated to the surface.

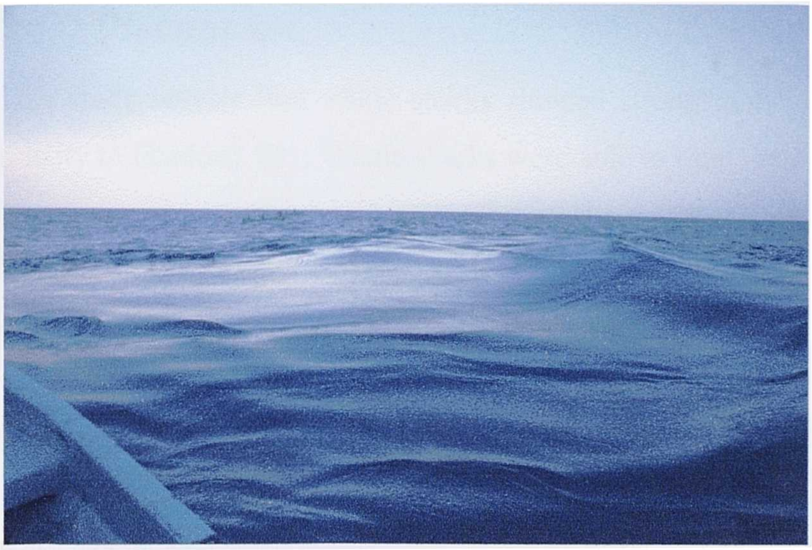


Figure 3.9: Oil-like appearance of a spawn bubble on the surface created by spawn rising up to the surface.

3.4 *Discussion*

This study reveals that whale sharks showed strong diel, intra- and inter-annual site fidelity to Gladden Spit. Whale sharks were able to time their movements and modulate their foraging behaviour to focus feeding on the seasonally abundant snapper spawn. Navigation to Gladden Spit and timing of arrival at the spawning grounds is discussed in detail in Chapter 4.

Aggregating behaviour can also provide species with protection from predation (Hamilton, 1971) or with opportunities for reproduction. Neither of these selective pressures appears key for whale sharks visiting the snapper spawning aggregation as most sharks identified were juvenile males with a mean size of 6.0 m. Wilson *et al.* (2001) and Graham (Chapter 2 and unpublished data) drew the same conclusions after observing aggregations of primarily juvenile males in areas of high zooplankton abundances at Ningaloo Reef, Western Australia and in the Seychelles. However, patterns of site fidelity described for Gladden Spit cannot only be ascribed to juvenile males since at least two of the sexed sharks with acoustic tags were either adult or female. Additionally, several mature individuals, both male and female that were not acoustically tagged, have been observed to feed on the spawn at Gladden Spit (see Chapter 2 for more details on population structure and size).

Seasonal offshore productivity near Gladden Spit may attract mature individuals and serve as a focal point for reproduction, as postulated by Sims *et al.* (2000) for basking sharks off the southeast coast of England. Larger whale sharks that were not seen at the snapper spawning grounds were occasionally seen offshore in schools of tuna. It is possible that the feeding apparatus of adult sharks is less efficient at filtering spawn than that of juveniles. Additionally, larger, adult sharks are able to swim more efficiently and feed with tuna than smaller juveniles by moving at fewer body lengths per second.

3.4.1 Key considerations in assessing site fidelity

This study was surprisingly successful in characterising patterns of site fidelity in whale sharks despite the low reception range recorded for the acoustic receiver deployed at the snapper spawning aggregation site. The high temporal and spatial specificity of site attachment recorded for whale sharks on the spawning grounds indicates that the placement of acoustic receivers is critical to recording presence versus absence data for tagged sharks. Prior knowledge of the site and behaviour of the study animals, and incorporation of local knowledge enabled the best placement of this and other receivers sited along the Belize Barrier Reef (See Chapter 4). Klimley *et al.* (1988) studying patterns of movement in scalloped hammerheads at a Gulf of California seamount and Dewar (pers. comm. 2001) working on manta rays (*Manta birostris*) in Komodo, Indonesia, also recorded reception ranges of less than 500 m radius while working in open ocean environments. Surprisingly, Heupel (pers. comm. 2002) found the reverse while working with juvenile blacktip sharks (*Carcharhinus limbatus*) in a shallow lagoon environment with reception ranges of up to 1.75 km recorded for each receiver.

Even with strategic positioning, receivers cannot keep track of shifts in distribution of prey that can alter site fidelity patterns in predators. This was evident in May 2002 when the snappers shifted away from their normal spawning site and spawned irregularly to the north-northwest (G1 in Figure 3.1). Consequently, whale sharks were observed patrolling along the reef as opposed to remaining close to the receiver site during spawning time. This is reflected in the dispersed nature of whale shark tagging efforts in 2002 as opposed to the clumped tagging that took place from 2000 to 2001 (Chapter 2, Figure 2.4).

Tag retention was assumed to be high throughout the study period. However, one shark tagged in 2000 with the heavier V32 tag was observed with the tag being shed within 2-3 days of deployment. Scientists have recorded variable rates of tag retention in several programs using different types of darts (Gruber, 1982; Carrier, 1985; Stevens, 1990; Heupel & Bennett, 1997; Heupel *et al.*, 1998; Metcalf & Arnold, 1999; Xiao *et al.*, 1999; Godo & Michalsen, 2000; Xiao, 2000; Eckert & Stewart, 2001). No acoustic tag deployed at Gladden Spit in 2000 was resighted in 2002, indicating non-return to Gladden or tag shed (particularly as these were the heavier V32 tags). However, if well inserted, tags can remain deployed for years. The National Marine Fisheries Service shark tagging program recorded a sandbar shark (*C. plumbeus*) carrying a marker tag for 27.8 years before recapture (Kohler *et al.*, 1998). Heavier acoustic tags that create more drag than marker tags present greater challenges. Yet, a whale shark carried a working satellite tag for three years as it migrated across the Pacific from Mexico (Eckert & Stewart, 2001). At Gladden Spit, tag type, dart style and insertion techniques appeared to be key factors in promoting retention (see Chapter 2 for more details on tag retention rates and application).

3.4.2 Temporal fidelity

Anticipating snapper spawning, whale sharks waited up to 10 hours for the fish to spawn in an area less than 500 m in diameter, based on the results of the receiver tests.

This form of anticipatory behaviour was conditioned by the recurring presence of food and has been observed in many species of animals. Grizzly bears (*Ursus arctos*) congregate to prey on spawning pink salmon during the fall months to increase their weight before hibernation (Olson *et al.*, 1997). Several species of whale time their summer migrations with the emergence of highly concentrated blooms of krill and show high degrees of foraging area philopatry, including humpback whales foraging in the Gulf of Maine (Clapham *et al.*, 1993), and gray whales feeding seasonally off Sakhalin Island, Russia (Weller *et al.*, 1999). Among the elasmobranchs, several shark species show food-oriented diurnal site attachment behaviour prompting opportunistic aggregations. Blue sharks patrol the coast of California's Santa Catalina Island at night in search of squid and move offshore during the day (Sciarrotta & Nelson, 1977). In Baja California, scalloped hammerheads show very site specific and defined site attachment to one specific location on the El Bajo Espiritu Santo seamount when aggregating (Klimley & Nelson, 1984). White sharks time their arrival at pinniped colonies for the pupping seasons to prey on recently-weaned pups (Klimley, 1996; Strong *et al.*, 1996; Goldman & Anderson, 1999). Gunn *et al.* (1999) also speculated that the early aggregation of whale sharks off the Ningaloo Reef anticipated the zooplankton bloom that follows the seasonal coral spawning event.

Although whale sharks demonstrated strong site attachment timed with the spawning cubera and dog snappers, these sharks have not been observed to feed on mutton snapper spawn. Fisher and underwater observations coupled with macroscopic analysis of ripe mutton snapper gonads suggests that this species spawns at night or in the early morning (see Chapter 6). Additionally, the 22 acoustically tagged whale sharks did not register another peak of visitation at the receiver outside of 1600-1800 h (peak cubera and dog snapper spawning time). This might indicate that muttons are either spawning outside of the receiver's range accounting for the lack of data and observations, or that they spawn in smaller more dispersed groups, generating a less concentrated food source than that of the large aggregations of dog and cubera snappers and therefore less attention from whale sharks. However, visitation to the spawning ground as evidenced by receiver data was generally sparse between 2000 h and 0700 h indicating that whale sharks may move offshore following the spawning event. These movements offshore are corroborated by the satellite tag diving data where dives made at night initially exceed the depth of the reef shelf. Dive profiles at night also indicate that whale sharks are moving horizontally for periods of up to and over one hour before rising up to a shallower depth (see Chapter 5 on diving behaviour). Movement offshore at night was also noted in an acoustically tracked whale shark in the Seychelles (Graham, unpublished data) and has been recorded for several other species of sharks including the filter-feeding megamouth shark (*Megachasma pelagios*), tiger sharks (Holland *et al.*, 1999), and lemon sharks (Gruber *et al.*, 1988). However, blue sharks (*P. glauca*) have displayed an inverse pattern of moving in towards the coast at night between March and June to feed on abundant squid (Sciarrotta & Nelson, 1977).

Ascending in the water column over time mimics the diel vertical migration of many species of zooplankton (Folt & Burns, 1999) which whale sharks may feed on. Megamouths also display a distinct diel pattern of foraging that brings them close to the surface at night (Nelson *et al.*, 1997). Yet they are able to feed on deep-water jellyfish and euphausiid shrimps (Diamond, 1985) indicating that whale sharks may also be able to find food at depth while offshore. A circular plug wound observed in the side of a swimming whale shark in the Gulf of Mexico may have been caused by the deep-dwelling cookie cutter shark (*Isistius brasiliensis*) (E. Hickerson, pers comm. 2002) further indicating that whale sharks dive to great depths during their foraging. Predation by the cookie cutter shark is similarly documented by LeBoeuf *et al.* (1987) in the deep-diving elephant seal, *Mirounga angirostris*.

3.4.3 How important is fish spawn to a whale shark's diet?

Based on site attachment to Gladden Spit, snapper spawn appears to be an important component of juvenile male whale sharks diet during the spring. Most marine pelagic fish eggs are energy dense due to their protein and oil droplets and are buoyant (Riis-Vestergaard, 2002). Buoyancy enables eggs to be transported by surface-driven currents to larval recruitment areas. Whale shark feeding mechanism and behaviour are thought to be best adapted to concentrated patches of food (Colman, 1997b) and its mouth morphology enables it to maximize intake while surface feeding. Unlike the basking shark which is an obligate ram-filter-feeder (Sims, 2000), whale sharks are capable of remaining stationary while feeding (Colman, 1997b), a strategy that minimizes energy expenditure compared to the drag induced by the open mouth of a filter feeder (Sanderson *et al.*, 1994). However, this strategy is only efficient and effective if the prey are densely aggregated and abundant, e.g. spawn or tightly formed schools of pelagic baitfish. This helps to explain whale shark behaviour at Gladden where individuals actively patrolled the spawning grounds before spawning took place and began feeding when the gametes were most highly concentrated and emerging from the spawning fish.

The amount of eggs ingested or their calorific content could not be determined in this study. However, analysis of $\delta^{15}N$ values indicates that snapper spawn does not constitute an important proportion of the whale shark diet overall (see Appendix 3.A). These figures need to be interpreted with caution, as turnover time of whale shark tissues and the variability in isotope composition of prey during the sharks' migratory path are unknown. However, the samples were taken at the third spawning moon and two of the sampled sharks had been at Gladden Spit feeding on spawn the two previous moons. Faeces have a high turnover rate and the sample analysed mirrors the tissue sample results supporting the lack of importance of eggs in the sharks overall diet. By comparison, whale sharks held in captivity in Japan's Okinawa Expo Aquarium ingested about 5-7 kg of food once a day six days per week. Uchida *et al.* (2000) report that they were fed krill (*Euphausia pacifica* and *E. superba*), pelagic shrimp (*Sergia lucens*), squid (*Loligo japonica*) and fish (*Spratelloides gracilis*). It was not possible in this study to determine if this quantity of different food types could serve as a proxy for the amount of spawn ingested per day by a single whale shark in the wild or if whale sharks in the wild require greater amounts of food to survive.

Whale shark predation on snapper eggs is a contentious issue with local fishers. Although the sharks have only been observed to feed on cubera and dog snapper eggs, fishers believe that they are also consuming mutton snapper (*L. analis*) eggs and are therefore responsible for the decline in the fishery (see Chapter 6). A range of data (acoustic, observational and trophic) indicates that whale sharks do not appear to feed on mutton snapper spawn. Mutton snappers do not spawn at the exact same time and location as dog and cubera snappers. Neither have they been observed to spawn during the day despite over 700 hours of diving in the spawning site over five years. Combined with macroscopic examination of fully hydrated roe from landed mutton snappers it appears that they likely spawn at night or in the early morning. Additionally, the receiver at G2 (Figure 3.1) does not record another peak of site fidelity during the night or early morning that would indicate aggregating or feeding behaviour. It is possible that mutton snappers spawn outside of the receiver's range or whale sharks show a lack of interest in feeding on mutton snapper spawn (for more detail on snapper spawning, please refer to Chapter 6).

Whale sharks fed on a range of food types during the snapper spawning-period. During the morning, they were seen swimming along the fore-reef in the upper water column and occasionally on the surface feeding on small pelagic sprat alongside near-reef schools of tuna, similar to behaviour recorded by Gunn *et al.* (1999) at Ningaloo

Reef, Australia and Graham in the Seychelles (unpublished data). Sharks were also observed to feed on the seasonally-occurring bloom of thimble jellyfish (*Linuche unguiculata*) and zooplankton. Such blooms are not unusual and occur in relation to increased abundances of plankton (Mills, 2001). A rapid examination of surface sampling of zooplankton at Gladden Spit revealed a predominance of calanoid copepod spp., a favoured food of whale sharks (Clark & Nelson, 1997), mixed with smaller numbers of polychaete worms, fish eggs and larvae, megalopas and diatoms.

The mechanisms whereby whale sharks decide which type of prey to consume and the order to eat them are unknown. As with all foraging fish these decisions must be balanced against the costs of searching for food (Jennings *et al.*, 2001). Charnov (1976) developed the marginal value theorem to predict the movement of predators between patches where the optimal time to stay should be greater in more productive patches than less productive ones depending on the density of predators. This would suggest that a whale shark would stay longer in patches if they were located further apart. However, this assumes that the shark has prior knowledge of where the next patch is located, which it may or may not possess.

Swimming and feeding incur metabolic costs based on the food types preyed on (James & Findlay, 1989; James & Probyn, 1989), particularly if ram filter feeding which relies on keeping the mouth agape during swimming as observed with basking sharks (Sims, 1999). Videler (1993) noted that hungry fish swim more slowly during routine swimming but faster after they begin feeding and they change swimming strategies for different food sources in order to maximize energy gain. Using snorkelers deployed nearby, whale sharks were estimated to swim slowest, ~0.3-0.8 m s^{-1}, when waiting for the fish to spawn and when feeding on plankton and jellyfish. Swim speed increased underwater to over ~0.8 m s^{-1} following the onset of spawning and reached a maximum (~1.2-1.5 m s^{-1}) during surface feeding bouts following dispersal of the spawn and during movement to other spawn patches. It is possible that by increasing the speed of feeding and movement towards new patches, an individual whale shark can capitalize on the concentrated food and outcompete conspecifics in new patches. Basking sharks similarly slow down while filter feeding on zooplankton and increase their rate of movement while cruising towards areas of higher prey abundance (Sims, 2000).

Aggregating behaviour can work in favour of the sharks by increasing local enhancement whereby discovery of food by conspecifics can help focus foraging efforts. Whale sharks are occasionally seen to move directly from one spawn patch to another yet it is not known if they are directed by the spawning noises made by snappers or the feeding noises of other sharks. Sight may play an important part in identifying food sources or feeding behaviour of conspecifics as sharks generally have highly developed visual system (Gruber & Cohen, 1978). Yet, aggregating behaviours may also work against the sharks through the rapid depletion of prey as suggested by Le Boeuf *et al.* (2001) in relation to the high mortality level of gray whales in Mexico and California in 1999. Dispersal in different directions or range shifts can minimize or avoid rapid depletion of temporary food patches. Ferguson *et al.* (2001) noted that Arctic tundra caribou (*Rangifer tarandus*) in Nunavut, Canada, may have mass emigrated from their traditional winter foraging site in the 1980s to another site that contained a greater abundance of fruticose lichens. Although there are high costs associated with dispersal into unknown areas, these risks are reduced for whale sharks due to their large size, their ability to cruise relatively rapidly, their three feeding mechanisms that enable them to exploit a range of planktonic and patchily distributed food, and perhaps even their large liver and thick blubber-like layer of skin (see Chapter 4 for more on large-scale movements and 5 on diving physiology). Fat stores may enable them to survive for relatively long periods of time with little or no food in similar fashion to sperm whales (Whitehead, 1996).

3.4.5 Patterns of site fidelity: Residents, transients or somewhere in between?

The patterns of intra- and inter-annual site fidelity to Gladden Spit indicate that whale sharks displayed a broad spectrum of spatial and temporal patterns of attachment but are not resident at Gladden Spit. Patterns ranged from strong diel and annual spatial and temporal fidelity to the spawning site, an area of less than 100 m in diameter to a broader pattern of fidelity to the Gulf of Honduras and ultimately transience through all monitored sites that extend throughout the 250 km of the Belize Barrier Reef (See Chapter 4). It is possible that the whale sharks move to other seasonally abundant patches of food located outside of the acoustic array deployed in Belize. They may move systematically to a new patch as resources become depleted competing a cycle of movement with the annual return to Gladden and its seasonal fish spawn. This would emulate many examples of multiple site fidelity on with variable spatio-temporal scales, such as the seasonal movement of wildebeest between three sites in the Serengeti Park, Tanzania, where they display site attachment based on seasonally-available resources (Dingle 1996). Multiple scales of site fidelity related to specific life-stages have been revealed in a range of animals. Atlantic bluefin tuna (*Thunnus thynnus thynnus*) feed in the northern Atlantic, migrate predictably past a small stretch of Sicily's coastal waters and yet spawn in a larger area of the Mediterranean basin (Block, 2000; Block *et al.*, 2001). Nassau groupers (*Epinephelus striatus*) aggregate to spawn in small discrete areas of forereef between December and March in Belize but are not considered resident to that area based on acoustic or tag recoveries at least 250 km away from the point of capture (Carter, 1989) and post-spawning counts of fish (Graham, unpublished data). Gray whales feed in the cool shallow and highly productive waters of the Chirikov Basin in the Bering Sea (measuring about 40,000 km^2) between May and October (Le Boeuf *et al.*, 2001). The whales then migrate over 8,000 km southward to specific breeding lagoons in Baja California, Mexico such as Magdalena Bay (Le Boeuf *et al.*, 2001).

Even though a minimum of 17 sharks revisited the spawning aggregation grounds from one spawning moon to the next within the peak snapper spawning-period of March through June, there was no pattern of schooling or clear migration during movement as seen with tuna or gray whales (Chapter 4). Over 80% of all whale shark visits to Gladden were temporally specific and took place from the full moon to the new moon with peaks in visitation to the fish spawning aggregation site taking place in the late afternoon of each day during that period. Similar temporal fidelity linked to a specific site was also observed in scalloped hammerhead sharks. Klimley *et al.* (1988) recorded diurnal fidelity in 18 scalloped hammerhead sharks over a ten-day period to a specific area on the El Bajo Espiritu Santo seamount in the Gulf of California, followed by movement into the pelagic environment at night to feed on fish and cephalopods. However, Klimley and Nelson (1984) termed this behaviour "refuging" whereby animals group together, activity is minimized and restricted to the centre of the animals' home range. Whale sharks do not appear to use this type of social refuging system while waiting for fish to spawn and when not foraging in the Gladden Spit area based on their apparent solitary movements and the variable times of arrival of individuals at the spawning site.

The lack of whale shark sightings at Gladden Spit during the peak May moon in 2002 was strongly correlated to the lack of spawning activity in the fish. Only three acoustically tagged sharks visited Gladden for a mean of two days each during the May moon before leaving the area. Six sharks in total were sighted on the surface. By comparison, at least nine sharks were acoustically recorded visiting during the April moon and five sharks visited during the June moon. Therefore it appears that whale shark predictability at Gladden Spit is based on the presence and abundance of spawning dog and/or cubera snappers.

3.4.6 Do whale sharks sleep?

Continuous movement incurs high energetic costs. It is possible that the physiological and behavioural mechanisms that enable site fidelity help to minimize energy expenditure through rapid relocation of prey e.g., whale sharks and spawn or zooplankton patches. However, to further offset energetic costs, many species of elasmobranchs show decreases in locomotory behaviour during the night or day (Finstad & Nelson, 1975; McKibben & Nelson, 1986; Gruber *et al.*, 1988; Carey & Scharold, 1990; Klimley *et al.*, 2002). Patterns of variable visitation at the receiver throughout 24 hr periods combined with diving data from the satellite tags indicate that whale sharks feed diurnally and do not sleep. Gunn *et al.* (1999) further support continuous wakefulness in whale sharks when they observed an individual feeding at night during tracking off Ningaloo reef. Many species of vertebrates that swim continuously such as sharks do not require sleep, but at night reduced visual input provides the brain with a "rest" due to a decrease in the processing of complex visual information (Kavanau, 1998). Whale sharks do not need to swim continuously to ventilate their gills as do lamnids or carcharhinids and as evidenced by their occasional stationary behaviour. However, they will sink if they do not provide the occasional tail beat (Graham, pers. obs). Although whale sharks can pump-ventilate their gills while in a stationary position, they have never been observed laying on the seabed like their orectolobid relatives the nurse sharks (*Ginglymostoma cirratum*).

3.4.7 Site fidelity and the design of marine reserves

Habitat use and population persistence are key criteria in determining marine reserve size and protecting target species during vulnerable life stages, including migratory species. Targeting strong protection at discrete sites where species are most vulnerable and most economically valuable is often an acceptable compromise for dispersed protection over broader areas, one of the means of protecting migratory species. Although predictability and site fidelity in animals can also be created through feeding programs, the sustainability and ecological worth of these are questionable. Lemon and bull sharks are predictably sighted at Walker's Caye, Bahamas, because they have been attracted for years by the fish entrails cast-off by local fishers. Nurse sharks are encouraged to congregate around tourists by tour-guides offering food in the Shark Ray

Alley and Hol-Chan Marine Reserves in Belize (Graham, pers. obs). Yet their natural behaviour and home range in this site are not known and cannot be correlated with the marine reserve boundaries.

Gladden Spit and the Silk Cayes is the first marine reserve declared to protect natural aggregations of temporally spawning fish and highly mobile whale sharks. In this study, Gladden Spit was identified as the primary area along the Belize Barrier Reef where whale sharks displayed fine-scale spatial and temporal site fidelity (See Chapter 4 on movement along the reef and time spent at other sites). Although movement behaviour and patterns of site fidelity were not known at the time, the Belize Government recognized the aggregation of whale sharks in conjunction with spawning snappers at Gladden Spit as a unique event. The government consequently declared Gladden Spit and the Silk Cayes as a marine reserve (GSSCMR) in May 2000 to protect both the sharks and fish during their vulnerable life-period (Statutory Instrument no. 68 of 2000) (Chapter 1 and Figure 1.2). This study's results have since indicated this marine reserve effectively encompasses the key snapper spawning and whale shark feeding area. Effective siting of marine protected areas has also taken place at several other sites including the Leigh Marine Reserve in New Zealand. Marker and acoustically tagged sparids (*Pagrus auratus*) displayed strong site fidelity year round between 1997-2000 to areas only a few hundred meters wide located within the reserve (Willis *et al.*, 2001). The boundaries of the Coconut Island Fisheries Conservation Zone in Kaneohe Bay in Hawaii were also shown to encompass the diel movement behaviours and habitat use of the blue trevally (*Caranx melampygus*) (Holland *et al.*, 1996) and the commercially important whitesaddle goatfish (*Parupeneus porphyreus*) during its juvenile phase (Meyer *et al.*, 2000).

Predictability of whale shark sightings in Belize has been key to raising Gladden Spit's profile as a marine reserve. However, predictability can change and impact the effectiveness of marine reserves. During the peak spawning season in 2002, snappers altered their spawning behaviour from 24 to 30 May. Consequently, visitors and researchers had difficulties locating whale sharks predictably and only three whale sharks were recorded in the GSSCMR using the boat-based receiver and the moored receiver. In Belize initially, local tour-guides thought that tagging affected shark visitation. The 77% resighting rate of acoustically tagged sharks, and numerous resightings of marker and satellite-tagged sharks throughout the course of this study indicated that tagging did not affect whale shark visitation rates at Gladden Spit. Additionally, over 90% of all sharks tagged showed no reaction to the tagging process.

The few that reacted usually flinched momentarily, resumed feeding on the surface and were resighted in the days following.

The alteration in snapper spawning behaviour and subsequent decline in whale shark sightings in May 2002 may have been due to the highest level of visitors and boats recorded in the reserve (see Chapter 7). Underwater, snappers were observed to actively avoid divers by moving off the reef slope and were often seen to dive deep (R. Graham, D. Castellanos, S. Pech and J. Berry, pers. obs.), a drastic change in behaviour from previous seasons and one that continued in 2003 with high tourist visitation rates to the spawning site (D. Castellanos, pers. comm. 2003). Changes in target species distribution in relation to prey availability have also been recorded in Gray whales in Clayoquot Sounds, Canada – also possibly impacted by visitor behaviour (Duffus, 1996), in humpback whales in the Southern Gulf of Maine (Weinrich *et al.*, 1997), in basking sharks in Britain (Sims & Reid, 2002), and in skipjack tuna in the Pacific (*Katsuwonus pelamis*) (Lehodey *et al.*, 1997). Similarly, in Ningaloo Reef, Western Australia, whale shark sightings became sparse possibly due to distributional shifts in prey linked to changes in ocean conditions brought on by El Niño Southern Oscillation (ENSO) (Wilson *et al.*, 2001).

Marine reserves are not always able to protect fish during their entire life cycle due to ontogenetic preferences in habitat use. With any marine reserve's attempts to protect a migratory species, Gladden's effectiveness in protecting whale sharks is limited: the feeding aggregation is highly segregated and temporal, consisting primarily of juvenile males aggregating mainly during the full moon periods of March through June. However, *post hoc* mapping of feeding and tagged whale sharks and the distributional shifts in snapper spawning that occurred in 2002, indicated that the reserve was well sited, with the main spawning activity and aggregated whale sharks remaining within its boundaries. All recorded spawning activity took place about 1 km from the eastern limit of the reserve, suggesting that this boundary should be extended out by at least 5 km.

An eastern expansion of the Gladden Spit and Silk Cayes reserve would help to better encompass the deeper waters off the reef shelf-edge that snappers, groupers and whale sharks have been observed to use[1]. Moving the boundaries would also help to protect the whale sharks that are feeding with the coastal-pelagic schools of tuna located

[1] While diving in the single-womanned submersible Deepworker (Nuytco Corp/NOAA) off the reef shelf drop-off to 170 m at Gladden Spit, Graham observed mutton snappers, yellowfin groupers (*Mycteroperca venenosa*), bonito (*Sarda sarda*) and barracuda (*Sphyrna picuda*) in ~100-125 m deep, and black grouper (*M. bonaci*) at 130 m. Two whale sharks were observed patrolling the reef wall at ~75 m.

offshore and in a busy cargo shipping lane running north-south from Guatemala's ports of Puerto Barrios and Santo Thomas de Castillo to Belize City and beyond. Ship strikes have been the cause of numerous whale shark mortalities worldwide (Gudger, 1937b, 1937a, 1937c, 1938, 1939). This study revealed repeated movements by whale sharks along and across many shipping lanes fringing the Belize Barrier Reef and its atolls (Chapter 4). As a promontory jutting out into the Gulf of Honduras, Gladden Spit is vulnerable to the passage of large cargo ships that often move within 5-10 km of the reserve. An expansion of the reserve by an additional 5 km offshore would help to reduce the likelihood of ship strikes while whale sharks are feeding close to the reef at this highly strategic and vulnerable location.

Site fidelity of reef fish during their spawning period is an effective biological and economic basis for the protection of commercially important species – many of which are migratory. These reasons further prompted the Belize Government in November 2002 to declare full protection for 11 spawning aggregation sites that host several species of reef fish that aggregate seasonally to spawn. They further announced a closed season on the capture of Nassau groupers between December and March, the spawning period recorded for this species at Belize's latitudes (Sadovy & Ecklund, 1999). The fully protected sites do not include Gladden Spit, which falls under the management jurisdiction of Friends of Nature. The future for the reserve is uncertain as fishing is still permitted, which even at a reduced level has led to a decline in fish size and catch per unit effort between 2000 and 2002 (see Chapter 6). In fact, despite the relative ease and efficiency of siting marine reserves in spawning aggregation areas, few of the 11 spawning sites declared in Belize currently benefit from strong protection against illegal fishing due to a lack of human and financial resources. Many spawning aggregation areas are located far offshore and are difficult and expensive to patrol, e.g. Glover's Reef Marine Reserve, Gladden Spit, Riley's Hump/Dry Tortugas in Florida.

Appropriate siting and even a subsequent alteration of the Gladden Spit and Silk Cayes marine reserve's boundaries will not be sufficient to limit disturbance of fish spawning behaviour and feeding whale sharks. Tourist management and enforcement of regulations is essential if the marine reserve is to remain effective at sustaining fish spawning behaviour and predictable whale shark visitation. Measures suggested include the enforcement of a minimum diver approach distance to spawning aggregations (15 m), upholding the no-touch policy with sharks, a 15 m minimum distance between tour boats and whale sharks, and adhering to a time cut-off (suggested 1700 h) for site visitation that precedes the onset of fish spawning.

3.5 References

Allison G. W., Lubchenco J. & Carr M. H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications*. **8** (1): S79-S92.

Arnold G. P. 1981. Movement of fish in relation to water currents. In: *Animal Migration*. (Aidley D. J. ed.), pp 55-79. Cambridge. Cambridge University Press.

Arnold G. P., Metcalfe J. D. & Holford B. H. 1993. Orientation of plaice (*Pleuronectes platessa*) in the open sea: evidence for the use of external directional clues. *ICES Journal of Marine Science*. **117**: 559-566.

Arnold G. P. & Walker M. G. 1992. Vertical movements of cod (*Gadus morhua* L.) in the open sea and the hydrostatic function of the swimbladder. *ICES Journal of Marine Science*. **49**: 357-372.

Arnold G. P., Walker M. G., Emerson L. S. & Holford B. H. 1994. Movements of cod (*Gadus morhua* L.) in relation to the tidal streams in the southern North Sea. *ICES Journal of Marine Science*. **51**: 207-232.

Arnold P. W. & Birtles R. A. 1993. Towards sustainable management of the developing dwarf minke whale tourism industry in Northern Queensland. CRC Reef Research Technical Report. Townsville, Australia. 30 pp.

Baker C. S., Herman L. M., Perry A., Lawton W. S., Straley J. M., Wolman A. A., Kaufman G. D., Winn H. E., Hall J. D., Reinke J. M. & Ostman J. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Marine Ecology Progress Series*. **31**: 105-119.

Benhamou S. 1997. On systems of reference involved in spatial memory. *Behavioural Processes*. **40** (2): 149-163.

Block B. A. 2000. Mattanza - Love and death in the Sea of Sicily. *Science*. **289** (5481): 876-877.

Block B. A., Dewar H., Blackwell S. B., Williams T. D., Prince E. D., Farwell C. J., Boustany A., Teo S. L. H., Seitz A., Walli A. & Fudge D. 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science*. **293** (5533): 1310-1314.

Bolden S. K. 2000. Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fishery Bulletin*. **98** (3): 642-645.

Boles L. C. & Lohmann K. J. 2003. True navigation and magnetic maps in spiny lobsters. *Nature*. **421**: 60-63.

Bonfil R. 1994. Overview of world elasmobranch fisheries. *FAO Fisheries Technical Paper*. **341**: 1-6.

Bonfil R. 1997. Marine protected areas as a shark fisheries management tool *Proc. 5th Indo-Pacific Fish Conference, Noumea, 1997*. Societe Francaise Ichtyologie, Noumea, pp 217-230.

Born E. W., Wiig O. & Thomassen J. 1997. Seasonal and annual movements of radio-collared polar bears (*Ursus maritimus*) in northeast Greenland. *Journal of Marine Systems*. **10** (1-4): 67-77.

Boustany A. M., Davis S. F., Pyle P., Anderson S. D., Le Boeuf B. J. & Block B. A. 2002. Satellite tagging: expanded niche for white sharks. *Nature*. **415** (6867): 35-36.

Brager S., Dawson S. M., Slooten E., Smith S., Stone G. S. & Yoshinaga A. 2002. Site fidelity and along-shore range in Hector's dolphin, an endangered marine dolphin from New Zealand. *Biological Conservation*. **108** (3): 281-287.

Brown J. S. 2001. Foraging ecology of animals. In: *The Ecological Consequences of Environmental Heterogeneity*. (Hutchings M. J., John E. A. & Stewart A. J. A. eds.), pp 181-214. London. British Ecological Society.

Buzby K. M. & Deegan L. A. 2000. Inter-annual fidelity to summer feeding site in Arctic grayling. *Environmental Biology of Fishes*. **59**: 319-327.

Camhi M., Fowler S., Musick J., Brautigam A. & Fordham S. 1997. Sharks and their relatives: ecology and conservation. Occasional Paper of the IUCN Species Survival Commission. IUCN 20. 1-40 pp.

Candy J. R. & Beacham T. D. 2000. Patterns of homing and straying in southern British Columbia coded-wire tagged chinook salmon (*Oncorhynchus tshawytscha*) populations. *Fisheries Research*. **47** (1): 41-56.

Carey F. G. & Scharold J. V. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*. **106**: 329-342.

Carr A. & Carr M. H. 1972. Site fixity in the Caribbean green turtle. *Ecology*. **53**: 425-429.

Carrier J. C. 1985. Nurse shark of big pine key: comparative success of three types of external tags. *Florida Scientist*. **48** (3): 146-154.

Carter J. 1989. Grouper sex in Belize. *Natural History* (October 1989): 61-68.

Castro J. I. 1993. The shark nursery of Bulls Bay, South-Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes*. **38** (1-3): 37-48.

Charnov E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology*. **9**: 129-136.

Clapham P. J., Baraff L. S., Carlson C. A., Christian M. A., Mattila D. K., Mayo C. A., Murphy M. A. & Pittman S. 1993. Seasonal occurrences and annual return of humpback whales, *Megaptera novaeangliae*, in the southern Gulf of Maine. *Canadian Journal of Zoology*. **71**: 440-443.

Clark E. & Nelson D. R. 1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes*. **50** (1): 63-73.

Colman J. 1997a. Whale shark interaction management, with particular reference to Ningaloo Marine Park. Western Australia Department of Conservation and Land Management, Marine Conservation Branch 27. Freemantle, Western Australia. 61 pp.

Colman J. G. 1997b. A review of the biology and ecology of the whale shark. *Journal of Fish Biology*. **51** (6): 1219-1234.

Crowder L. B., Lyman S. J., Figueira W. F. & Priddy J. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science*. **66** (3): 799-820.

Dacke M., Nilsson D. E., Warrant E. J., Blest A. D., Land M. F. & O'Carroll D. C. 1999. Built-in polarizers form part of a compass organ in spiders. *Nature*. **401**: 470-473.

Dayton P. K., Sala E., Tegner M. J. & Thrush S. 2000. Marine reserves: Parks, baselines, and fishery enhancement. *Bulletin of Marine Science*. **66** (3): 617-634.

Defran R. H. & Weller D. W. 1999. Occurrence, distribution, site, fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Marine Mammal Science*. **15**: 366-380.

Diamond J. M. 1985. Filter-feeding on a grand scale. *Nature*. **316**: 679-681.

Dingle H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, New York. 474 pp.

Dixon J. A. 1993. Economic benefits of marine protected areas. *Oceanus*. **36** (3): 35-40.

Domeier M. L. & Colin P. L. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science*. **60** (3): 698-726.

Duffus D. A. 1996. The recreational use of grey whales in southern Clayoquot Sound, Canada. *Applied Geography*. **16** (3): 179-190.

Eckert S. A., Dolar L. L., Kooyman G. L., Perrin W. & Rahman R. A. 2002. Movements of whale sharks (*Rhincodon typus*) in South-East Asian waters as determined by satellite telemetry. *Journal of Zoology*. **257**: 111-115.

Eckert S. A. & Stewart B. S. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environmental Biology of Fishes*. **60** (1-3): 299-308.

Ferguson M. A. D., Gauthier L. & Messier F. 2001. Range shift and winter foraging ecology of a population of Arctic tundra caribou. *Canadian Journal of Zoology*. **79** (5): 746-758.

Fine J. C. 1990. Spawning aggregations of Nassau grouper in Honduras: Groupers in Love. *Sea Frontiers* (Jan/Feb): 42-45.

Finstad W. O. & Nelson D. R. 1975. Circadian activity rhythm in the horn shark *Heterodontus francisci*: effect of light intensity. *Bulletin of the Southern California Academy of Science* **74**: 20-26.

Fiske S. J. 1992. Sociocultural Aspects of Establishing Marine Protected Areas. *Ocean & Coastal Management*. **17** (1): 25-46.

Folt C. L. & Burns C. W. 1999. Biological drivers of zooplankton patchiness. *Trends in Ecology & Evolution*. **14** (8): 300-305.

Godo O. R. & Michalsen K. 2000. Migratory behaviour of north-east Arctic cod, studied by use of data storage tags. *Fisheries Research*. **48** (2): 127-140.

Goldman K. J. & Anderson S. D. 1999. Space utilization and swimming depths of white sharks, *Carcharodon carcharias*, at the south Farallon Islands, central California. *Environmental Biology of Fishes*. **56**: 351-364.

Graves J. E., Luckhurst B. E. & Prince E. D. 2002. An evaluation of pop-up satellite tag technology for estimating post release survival of blue marlin (*Makaira nigricans*) from a recreational fishery. *Fishery Bulletin*. **100**: 134-142.

Gruber S. H. 1982. Role of the lemon shark, *Negaprion brevirostris* (Poey) as a predator in the tropical marine environment: a multidisciplinary study. *Florida Science*. **45** (1): 46-75.

Gruber S. H. & Cohen J. L. 1978. Visual system of the elasmobranchs: state of the art 1960-1975. In: *Sensory Biology of Sharks, Skates and Rays*. (Hodgson E. S. & Mathewson R. F. eds.), pp 11-116. Arlington, Va. US Office of Naval Research.

Gruber S. H., Nelson D. R. & Morrissey J. F. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian Lagoon. *Bulletin of Marine Science.* **43** (1): 61-76.

Gudger E. W. 1915. Natural history of the whale shark, *Rhineodon typus* Smith. *Zoologica.* **1** (19): 345-389.

Gudger E. W. 1937a. A whale shark impaled on the bow of a steamer near the Tuamotus, South Seas. *Science.* **85** (2204): 314.

Gudger E. W. 1937b. A whale shark rammed by a steamer off Colombo, Ceylon. *Nature.* **139**: 549.

Gudger E. W. 1937c. A whale shark speared on the bow of a steamer in the Caribbean Sea. *Copeia.* **1937** (1): 60.

Gudger E. W. 1938. A whale shark rammed by a vessel off the Pacific coast of western Panama. *Nature.* **141**: 516.

Gudger E. W. 1939. Four whale sharks rammed by steamers in the Red Sea region. *Copeia.* **1938** (4): 170-175.

Gunn J. S., Stevens J. D., Davis T. L. O. & Norman B. M. 1999. Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Marine Biology.* **135**: 553-559.

Hamilton W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology.* **31**: 295-311.

Hartney K. B. 1996. Site fidelity and homing behavior of some kelp-bed fishes. *Journal of Fish Biology.* **49**: 1062-1069.

Heupel M. R. & Bennett M. B. 1997. Histology of dart tag insertion sites in the epaulette shark. *Journal of Fish Biology.* **50** (5): 1034-1041.

Heupel M. R., Simpfendorfer C. A. & Bennett M. B. 1998. Analysis of tissue responses to fin tagging in Australian carcharhinids. *Journal of Fish Biology.* **52**: 610-620.

Heyman W. D., Graham R. T., Kjerfve B. & Johannes R. E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology-Progress Series.* **215**: 275-282.

Holland K. N., Lowe C. G. & Wetherbee B. M. 1996. Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fisheries Research.* **25** (3-4): 279-292.

Holland K. N., Wetherbee B. M., Lowe C. G. & Meyer C. G. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Marine Biology.* **134**: 665-673.

Holland K. N., Wetherbee B. M., Peterson J. D. & Lowe C. G. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia*. **1993** (2): 495-502.

James A. G. & Findlay K. P. 1989. Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis*. *Marine Ecology Progress Series*. **50**: 279-294.

James A. G. & Probyn T. 1989. The relationship between respiration rate swimming speed and feeding behaviour in the cape anchovy, *Engraulis capensis* Gilchrist. *Journal of Experimental Marine Biology and Ecology*. **131**: 81-100.

Jennings S., Kaiser M. J. & Reynolds J. D. 2001. *Marine Fisheries Ecology*. Blackwell Science Inc. 415 pp.

Johannes R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes*. **3** (1): 65-84.

Johannes R. E. 1998. The case for data-less management: examples from tropical nearshore fisheries. *Trends in Ecology and Evolution*. **13** (6): 243-246.

Jones P. J. S. 1994. A review and analysis of the objectives of marine nature reserves. *Ocean & Coastal Management*. **24** (3): 149-178.

Kalmijn A. J. 1982. Electric and magnetic field detection in elasmobranchs. *Science*. **218** (26): 916-918.

Kavanau J. L. 1998. Vertebrates that never sleep: implications for sleep's basic function. *Brain Research Bulletin*. **46** (4): 269-279.

Klimley A. P. 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology*. **117** (1): 1-22.

Klimley A. P. 1996. Residency patterns of white sharks at the South Farallon Islands, California. In: *Great White Sharks: The Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. A. eds.), pp 365-374. San Diego, California. Academic Press, Inc.

Klimley A. P., Anderson S. D., Pyle P. & Henderson R. P. 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia*. **1992** (3): 680-690.

Klimley A. P., Beavers S. C., Curtis T. H. & Jorgensen S. J. 2002. Movements and swimming behaviour of three species of sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*. **63**: 117-135.

Klimley A. P., Butler S. B., Nelson D. R. & Stull A. T. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *Journal of Fish Biology*. **33**: 751-761.

Klimley A. P., Le Boeuf B. J., Cantara K. M., Richert J. E., Davis S. F. & Van Sommeran S. 2001. Radio-acoustic positioning as a tool for studying site specific behaviour of the white sharks and other large marine species. *Marine Biology*. **138**: 429-446.

Klimley A. P. & Nelson D. R. 1984. Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. *Behavioral Ecology and Sociobiology*. **15** (1): 45-54.

Kohler N. E., Casey J. G. & Turner P. A. 1998. NMFS Cooperative shark tagging program, 1962-93: An atlas of shark tag and recapture data. *Marine Fisheries Review*. **60** (2): 1-87.

Lam M. 1998. Consideration of customary marine tenure system in the establishment of marine protected areas in the South Pacific. *Ocean & Coastal Management*. **39** (1-2): 97-104.

Lauck T., Clark C. W., Mangel M. & Munro G. R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications*. **8** (1): S72-S78.

Le Boeuf B. J., H. Perez-Cortes M., J. Urban R., Mate B. R. & F. Ollervides U. 2001. High gray whale mortality and low recruitment in 1999: potential causes and implications. *Journal of Cetacean Resource Management*. **2** (2): 85-99.

Le Boeuf B. J., McCosker J. E. & Hewitt J. E. 1987. Crater wounds on northern elephant seals: the cookiecutter shark strikes again. *Fisheries Bulletin*. **85** (2): 387-392.

Lehodey P., Bertignac M., Hampton J., Lewis A. & Picaut J. 1997. El Niño Southern Oscillation and tuna in the western Pacific. *Nature*. **389**: 715-718.

Lembo G., Spedicato M. T., F. O., Carbonara P., Fleming I. A., McKinley R. S., Thorstad E. B., Sisak M. & Ragonese S. 2002. A wireless communication system for determining site fidelity of juvenile dusky groupers *Epinephelus marginatus* (Lowe, 1834) using coded acoustic transmitters. *Hydrobiologia*. **483** (1-3): 249-257.

Lewis M., Campagna C. & Quintana F. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. *Marine Mammal Science*. **12** (1): 138-147.

Lindeman K. C., Pugliese R., Waugh G. T. & Ault J. S. 2000. Developmental patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas. *Bulletin of Marine Science.* **66** (3): 929-956.

Lohmann K. J. & Johnsen S. 2000. The neurobiology of magnetoreception in vertebrate animals. *Trends in Neurosciences.* **23** (4): 153-159.

Lowe C. G., Wetherbee B. M., Crow G. L. & Tester A. L. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes.* **47** (2): 203-211.

Luckhurst B. E. 1998. Site fidelity and return migration of tagged red hinds (*Epinephelus guttatus*) to a spawning aggregation site in Bermuda *50th Gulf and Caribbean Fisheries Institute*, Bermuda, pp 750-763.

Lutcavage M. E., Brill R. W., Skomal G. B., Chase B. C. & Howey P. W. 1999. Results of pop-up satellite tagging of spawning size class fish in the gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries Aquatic Science.* **56**: 173-177.

Mangel M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters.* **1** (2): 87-90.

Mangel M. 2000. On the fraction of habitat allocated to marine reserves. *Ecology Letters.* **3** (1): 15-22.

McKibben J. N. & Nelson D. R. 1986. Patterns of movement and grouping of grey reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science.* **38** (1): 89-110.

Mellgren R. L. & Roper T. J. 1986. Spatial learning and discrimination of food patches in the European badger (*Meles meles L.*). *Animal Behaviour.* **34**: 1129-1134.

Metcalf J. D. & Arnold G. P. 1999. Tracking fish with electronic tags. *Nature.* **387**: 665-666.

Meyer C. G., Holland K. N., Wetherbee B. M. & Lowe C. G. 2000. Movement patterns, utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. *Environmental Biology of Fishes.* **59**: 235-242.

Mills C. E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia.* **451** (1-3): 55-68.

Montgomery J. C. & Walker M. M. 2001. Orientation and navigation in elasmobranchs: which way forward? *Environmental Biology of Fishes.* **60**: 109-116.

Moore M. 1999. In Baja, economy vs. ecology, whale-watching craze brings cash-and environmental threat *The Washington Post*, Washington DC. March 28, 1999. pp A25.

Morrissey J. F. & Gruber S. H. 1993. Home range of juvenile lemon shark, *Negaprion brevirostris*. *Copeia*. **1993** (2): 425-434.

Mouritsen H. 2001. Navigation in birds and other animals. *Image and Vision Computing*. **19** (11): 713-731.

Nelson D. R., McKibben J. N., Strong W. R., Lowe C. G., Sisneros J. A., Schroeder D. M. & Lavenberg R. J. 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes*. **49**: 389-399.

Nemerson D., Berkeley S. & Safina C. 2000. Spawning site fidelity in Atlantic bluefin tuna, *Thunnus thynnus*: the use of size-frequency analysis to test for the presence of migrant east Atlantic bluefin tuna on Gulf of Mexico spawning grounds. *Fish Bulletin*. **98**: 118-126.

Nevitt B. A., Veit R. R. & Kareiva P. 1995. Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds. *Nature*. **376**: 680-682.

Olson T. L., Gilbert B. K. & Squibb R. C. 1997. The effects of increasing human activity on brown bear use of an Alaskan River. *Biological Conservation*. **82** (1): 95-99.

Pomeroy C. 1999. Social considerations for marine resource management: evidence from Big Creek Ecological Reserve. *California Cooperative Oceanic Fisheries Investigations Reports*. **40**: 118-125.

Priede I. G. 1984. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote-sensing. *Fisheries Research*. **2** (3): 201-216.

Rhodes K. L. & Sadovy Y. 2002. Temporal and spatial trends in spawning aggregations of camouflage grouper *Epinephelus polyphekadion*, in Pohnpei, Micronesia. *Environmental Biology of Fishes*. **63**: 27-39.

Riis-Vestergaard J. 2002. Energy density of marine pelagic fish eggs. *Journal of Fish Biology*. **60**: 1511-1528.

Roberts C. M. 1995. Rapid buildup of fish biomass in a Caribbean marine reserve. *Conservation Biology*. **9** (4): 815-826.

Roberts C. M. 1997. No-take marine reserves: unlocking the potential for fisheries. In: *Marine Environmental Management: Review of Events in 1997 and Future Trends*. (Earl R. C. ed.), pp 127-132. Gloucester. Kempley.

Roberts C. M. 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries*. **23** (7): 16-19.

Roberts C. M. & Sargant H. 2002. Fishery benefits of fully protected marine reserves: why habitat and behaviour are important. *Natural Resource Modeling*. **15** (4): 487-507.

Sadovy Y. 1994. Grouper stocks of the Western Central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute*. **43**: 42-64.

Sadovy Y. & Ecklund A. M. 1999. Synopsis of biological data on the Nassau grouper *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA NOAA Technical Report NMFS 146. 65 pp.

Salo O. & Rosengren R. 2001. Memory of location and site recognition in the ant *Formica uralensis* (Hymenoptera: Formicidae). *Ethology*. **107**: 737-752.

Sandberg R., Backman H., Moore F. R. & Lohmus M. 2000. Magnetic information calibrates celestial cues during migration. *Animal Behaviour*. **60**: 453-462.

Sanderson S. L., Joseph J. Cech J. & Cheer A. Y. 1994. Paddlefish buccal flow velocity during ram suspension feeding and ram ventilation. *Journal of Experimental Biology*. **186**: 145-156.

Schaefer J. A., Bergman C. M. & Luttich S. N. 2000. Site fidelity of female caribou at multiple spatial scales. *Landscape Ecology*. **15** (8): 731-739.

Sciarrotta T. C. & Nelson D. R. 1977. Diel behaviour of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. *Fishery Bulletin*. **75** (3): 519-528.

Seitz A., Wilson D. & Nielsen J. L. 2002. Testing pop-up satellite tags as a tool for identifying critical habitat for Pacific halibut (*Hippoglossus stenolepsis*) in the Gulf of Alaska. USGS. Anchorage, Alaska. 43 pp.

Sierra L. M., Claro R. & Popova O. A. 2001. Trophic biology of the marine fishes of Cuba. In: *Ecology of the Marine Fishes of Cuba*. (Claro R., Lindeman K. C. & Parenti L. R. eds.), pp 115-148. Washington DC. Smithsonian Institution Press.

Sims D. W. 1999. Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife edge? *Proceedings of the Royal Society of London Series B-Biological Sciences*. **266**: 1437-1443.

Sims D. W. 2000. Filter-feeding and cruising swimming speeds of basking sharks compared with optimal models: they filter-feed slower than predicted for their size. *Journal of Experimental Marine Biology and Ecology*. **249** (1): 65-76.

Sims D. W. & Reid P. C. 2002. Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland). *Fisheries Oceanography*. **11** (1): 59-63.

Sims D. W., Southall E. J., Quayle V. A. & Fox A. M. 2000. Annual social behaviour of basking sharks associated with coastal front areas. *Proceedings of the Royal Society of London Series B-Biological Sciences*. **267**: 1897-1904.

Sims D. W., Southall E. J., Richardson A. J., Reid P. C. & Metcalfe J. D. 2003. Seasonal movements and behaviour of basing sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series*. **248**: 187-196.

South A. 1999. Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal. *Ecological Modelling*. **117** (2-3): 343-360.

Stevens J. D. 1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. *Journal of Marine Biology Association of the UK*. **70**: 707-720.

Stevens J. D., Norman B. M., Gunn J. S. & Davis T. L. O. 1998. Movement and behavioural patterns of whale sharks at Ningaloo Reef: the implications for tourism. National Ecotourism Final Report: Application Ref. No. 30051. CSIRO Marine Research. 35 pp.

Strong W. R., Bruce B. D., Nelson D. R. & Murphy R. D. 1996. Population Dynamics of White sharks in Spencer Gulf, South Australia. In: *Great White Sharks: The Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. G. eds.), pp 401-415. San Diego, California. Academic Press, Inc.

Strong W. R., Murphy R. C., Bruce B. D. & Nelson D. R. 1992. Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: A preliminary report. *Australian Journal of Marine and Freshwater Research*. **43**: 13-20.

Sundstrom L. F., Gruber S. H., Clermont S. M., Correia J. P. S., Marignac J. R. C. d., Morrissey J. F., Lowrance C., Thomassen L. & Oliveira M. T. 2001. Review of elasmobranch behavioral studies using telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes*. **60**: 225-250.

Switzer P. V. 1993. Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*. **7**: 533-555.

Taylor J. G. 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*. **47** (4): 637-642.

Travis J. M. J. & Dytham C. 1998. Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London Series B-Biological Sciences*. **266**: 723-728.

Uchida S., Toda M., Kamei Y. & Teruya H. 2000. The husbandry of 16 whale sharks, *Rhincodon typus*, from 1980 to 1998 at Okinawa Expo Aquarium. *American Elasmobranch Society Annual Meeting, La Paz, Mexico.*:

Videler J. J. 1993. *Fish Swimming*. Chapman and Hall, London. 284 pp.

Weinrich M., Martin M., Griffiths R., Bove J. & Schilling M. 1997. A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine. *Fishery Bulletin*. **95**: 826-836.

Weishampel J. F., Bagley D. A., Ehrhart L. M. & Rodenbeck B. L. 2003. Spatiotemporal patterns of annual sea turtle nesting behaviors along an East Central Florida beach. *Biological Conservation*. **110** (2): 295-303.

Weller D. W., Wursig B., Bradford A. L., Burdin A. M., Blokhin S. A., Minakuchi H. & Jr. R. L. B. 1999. Grey whales (*Eschrichtius robustus*) off Sakhalin Island, Russia: seasonal and annual patterns of occurrence. *Marine Mammal Science*. **15** (4): 1208-1227.

White G. C. & Garrott R. C. 1997. *Analysis of Wildlife Radiotracking Data*. Academic Press, San Diego, California. 383 pp.

Whitehead H. 1996. Variation in the feeding success of sperm whales: temporal scale, spatial scale and relationship to migration. *Journal of Animal Ecology*. **65** (4): 429-438.

Willis T. J., Parsons D. M. & Babcock R. C. 2001. Evidence for long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve. *New Zealand Journal of Marine and Freshwater Research*. **35**: 581-590.

Wilson S. G., Taylor J. G. & Pearce A. F. 2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/Southern Oscillation. *Environmental Biology of Fishes*. **61** (1): 1-11.

Wolfson F. H. 1986. Occurrences of the whale shark, *Rhincodon typus*, Smith. In: Uyeno T. & et. al. (eds) *Indo -Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*. Ichthyological Society of Japan, Tokyo, pp 208-226.

Xiao Y., Brown L. P., Walker T. I. & Punt A. E. 1999. Estimation of instantaneous rates of tag shedding for school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, by conditional likelihood. *Fish B-NOAA*. **97** (1): 170-184.

Xiao Y. S. 2000. An individual-based approach to evaluating experimental designs for estimating rates of fish movement from tag recoveries. *Ecological Modelling*. **128** (2-3): 149-163.

Zeller D. C. 1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Marine Ecology Progress Series*. **164**: 65-67.

Zeller D. C. & Russ G. R. 1998. Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). *Canadian Journal of Fisheries and Aquatic Sciences*. **55**: 917-924.

Zoeger J., Dunn J. R. & Fuller M. 1981. Magnetic material in the head of the common Pacific dolphin. *Science*. **213**: 892-894.

Appendix 3.A Trophic analysis

Methods

To assess the relative trophic importance of reef fish spawn to a whale shark's diet within the peak snapper spawning period of March to June, 10 tissue samples from 10 individual whale sharks (preserved in 100% ethanol (EtOH)) were collected using a purpose-made biopsy punch kit fitted onto a pole spear. One large whale shark faecal sample was also collected directly from the shark (subsequently dehydrated in the sun). Towing a 220μm plankton net at the aggregation site on three occasions and during the early afternoon (non-snapper spawning hours) samples of surface-based mesozooplankton were collected and preserved in EtOH. Three collections were made of the thimble jellyfish, *Linuche unguiculata,* that whale sharks been observed to feed on; half of the samples were preserved and half dehydrated in the sun. Five samples of hydrated eggs were taken directly from ovaries of landed mutton snapper (*L. analis*) and one sample of snapper abdominal tissue that was preserved in 100% EtOH. All samples were analysed for $\delta^{15}N$ and $\delta^{13}C$ stable isotope composition using a continuous flow isotope ratio mass spectrometer at the Centre for Environment, Fisheries, and the Aquaculture Sciences (CEFAS) Laboratories in Lowestoft, UK in the following manner (description by Simon Jennings, CEFAS):

"The samples were washed in distilled water to remove traces of preservative, frozen and freeze dried. Freeze dried samples were then ground to a fine powder. The $\delta^{15}N$ composition of the freeze-dried and ground tissue samples was determined using continuous flow isotope ratio mass spectrometry (CF-IRMS). Weighed samples of 1.0 mg ground tissue were oxidised and the N_2 passed to a single inlet dual collector mass spectrometer (Automated Nitrogen Carbon Analysis (ANCA) Integra system). Two samples of reference material (a standard mix of ammonium sulphate and beet sugar) were analysed after every five tissue samples in order to calibrate the system and compensate for drift with time. The ^{15}N composition was expressed in conventional delta notation, relative to the level of ^{15}N in atmospheric N_2:

$$\delta^{15}N = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

where R is the ratio ^{15}N:^{14}N. Experimental precision (based on the standard deviation of replicates of the internal standard) was < 0.15‰. The ^{13}C composition was expressed in conventional delta notation, relative to the level of ^{13}C in Pee Dee Belamite (PDB):

$$\delta^{13}C = \left(\frac{R_{sample}}{R_{s\tan dard}} - 1 \right) \times 1000$$

where R is the ratio ^{13}C:^{12}C. The experimental precision for $\delta\ ^{13}C$ was only 0.1‰, but these data are unreliable because the samples are almost pure lipid and almost no material remains after lipid extraction."

Results

Results from the trophic analysis outlined in Table 3.2 indicate that whale shark tissue was very lipid rich, with sufficient N present to run the analyses effectively. However, the density of lipid in the tissue meant that the $\delta^{13}C$ values could not be used for interpreting food web structure. During these analyses, it was assumed that mutton snapper roe is near equal in nutritional content and isotopic signature to that of cubera and dog snappers based on their similar diets. Although, fish appear to make up a larger proportion of a dog snapper's diet than mutton snappers (Sierra *et al.*, 2001). If local geographical consistency existed in base $\delta^{15}N$, the data indicated that whale sharks were feeding predominantly on animals at low trophic levels (e.g. zooplankton and coelenterates). Although whale sharks may have fed on plankton feeding fish and fish eggs at Gladden, these prey did not make a large overall contribution to their diet in the longer term based on higher values of $\delta^{15}N$ of mutton snapper eggs (2-3 ‰ higher) as compared to those of whale shark tissue. Even though whale shark tissue turn-over times are unknown, it is possible that tissues analysed represented a transitional phase for whale sharks as they arrived at the fish spawning aggregations and switched from feeding on zooplankton to fish roe. Yet, samples were taken during the final encounter with two sharks that were observed to feed on spawn during two previous spawning moons, suggested that fish spawn should have been assimilated into the tissues. Results in Table 3.2 show little difference between the isotopic signatures of the different whale shark tissues sampled. Additionally, analysis of the faecal sample, taken in the middle of the fish spawning season and which should represent high tissue turnover, also suggested that food intake during the fish spawning period was dominated by animals lower in the food chain than fish eggs.

These data need to take into consideration that little is known about the (1) tissue turn-over time in whale sharks, (2) details of the feeding migrations of the whale sharks, (3) the variation in base $\delta^{15}N$ over the migration routes and with season and that (4) samples that contain less lipid could therefore give better information on $\delta^{13}C$.

Table 3.2: Results from the $\delta\ ^{15}N$ and $\delta\ ^{13}C$ analysis of whale shark tissues and prey at Gladden Spit, Belize.

RG code	$\delta\ ^{15}N$	$\delta\ ^{13}C$	Sample	Preser-vative	Date
1	10.6671	-16.1141	*Lutjanus analis* roe	ip	03/04/02
2	9.18191	-14.6947	*Lutjanus analis* roe	ip	03/04/02
3	10.6906	-13.8322	*Lutjanus analis* roe	eh	01/06/02
4	10.6719	-16.5852	*Lutjanus analis* roe	eh	01/06/02
5	10.1097	-16.848	*Lutjanus analis* roe	eh	01/06/02
6	12.1808	-17.5422	*Lutjanus analis* tissue	eh	01/06/02
7	1.83082	-17.6061	*Linuche unguiculata*	Eh	02/05/02
8	0.859476	-18.1734	*Linuche unguiculata*	Dried	02/04/04
9	1.33321	-17.5921	*Linuche unguiculata*	Ip	29/03/02
10	1.41007	-18.4069	Plankton	Eh	28/05/02
11	3.84853	-18.4333	Plankton	Eh	31/05/02
12	3.72585	-18.2039	Plankton	eh	02/06/02
13	7.06328	-14.5273	*Rhincodon typus* tissue	eh	01/06/02
14	7.00589	-14.4102	*Rhincodon typus* tissue	ip	29/03/02
15	7.48664	-14.435	*Rhincodon typus* tissue	eh	01/06/02
16	7.29489	-14.5029	*Rhincodon typus* tissue	ip/ eh	02/04/02
17	7.09157	-15.0106	*Rhincodon typus* tissue	ip/ eh	03/04/02
18	7.34577	-15.323	*Rhincodon typus* tissue	eh	01/06/02
19	7.3101	-14.9653	*Rhincodon typus* tissue	ip	02/04/02
20	7.24306	-15.3573	*Rhincodon typus* tissue	ip	01/04/02
21	7.11961	-15.4868	*Rhincodon typus* tissue	ip	29/03/02
22	6.47209	-15.0232	*Rhincodon typus* tissue	ip	03/04/02
23	7.32551	-19.9479	Faeces of *Rhincodon typus*	dry	02/05/02

ip: 70% isopropyl alcohol preservative; eh: 100% ethanol preservative.

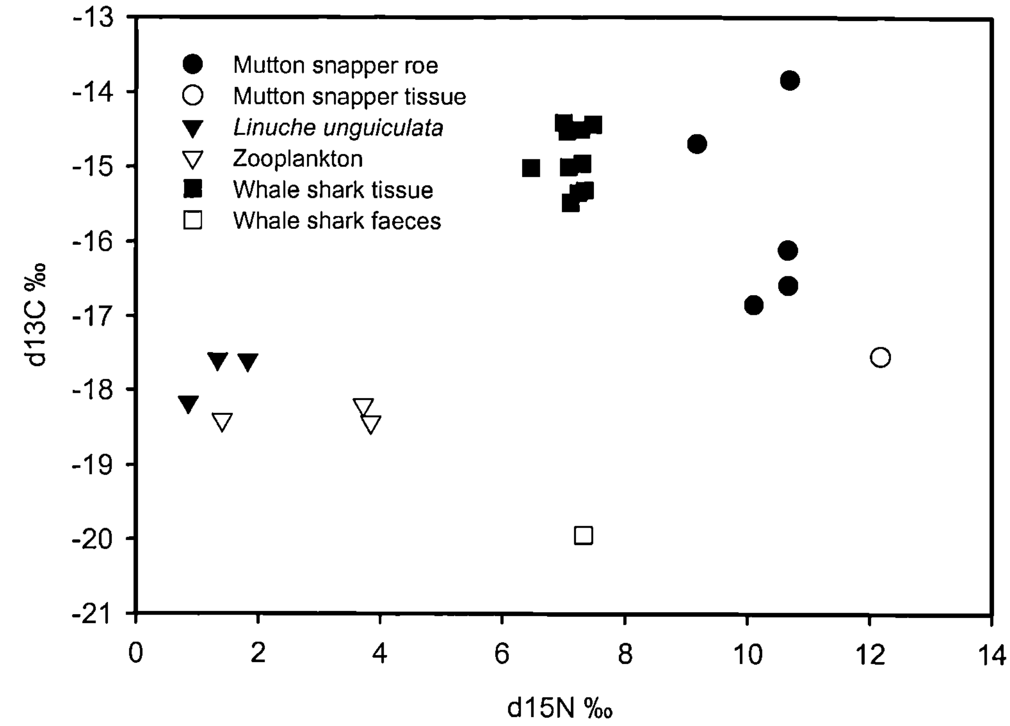


Figure 3.10: Relationship between mean δ ^{15}N and δ ^{13}C for whale sharks, mutton snappers, mutton snapper roe, and known prey items *Linuche unguiculata* and zooplankton.

Chapter 4. Patterns of movement of whale sharks on the Belize Barrier Reef

Abstract

This chapter presents results from a three-year study on the patterns of movement of whale sharks along the Mesoamerican Barrier Reef. Marker tags applied to 70 whale sharks provided data on movements along the reef. Coded acoustic transmitters deployed on 22 whale sharks coupled with passive receivers moored at 23 locations throughout the Belize Barrier Reef provided information on site presence versus absence, large-scale movements and timing of movement. The importance of fish spawning aggregations in whale shark foraging behaviour was investigated with eight acoustic receivers sited in areas hosting multi-species spawning aggregations. Results indicate that whale sharks range throughout the entire Mesoamerican Barrier Reef and seven of Belize's 12 marine reserves. All 22 tagged whale sharks displayed different patterns of movement and residency, with sharks demonstrating a mixed strategy of individual and group foraging. No diel home ranges could be determined for whale sharks in this study but several sharks display meso-scale residency to the Gulf of Honduras. On the Belize Barrier Reef, site fidelity is highest at Gladden Spit where sharks time their arrival and departure in accordance with the availability of patchy and ephemeral food, the spawn of large aggregations of reproducing snappers. Tagged whale sharks do not show similar site attachment to any of the other spawning aggregations investigated along the Belize Barrier Reef. This study's results have implications for the conservation of large migratory fish.

4.1 Introduction

Although whale sharks (*Rhincodon typus*) are found throughout the world's tropical waters (Wolfson, 1986; Colman, 1997), little is known about their ecology and even less about their patterns of movement (Colman, 1997; Fowler, 2000). Considered highly migratory, whale sharks range throughout the territorial waters of 124 countries (COP12, 2002). They are capable of trans-oceanic migrations (Eckert & Stewart, 2001) and yet localised or broad-scale movements have been investigated in only seven of these countries (Australia, Belize, Malaysia, Baja California (Mexico), Honduras, Seychelles and South Africa), with no published literature for whale shark movements in the Atlantic and Caribbean. This lack of information makes the monitoring and conservation of whale sharks and other species of pelagic highly migratory fish challenging. Recent findings indicate that whale sharks appear to incorporate coastal phases with the open ocean in their life-cycle, demonstrating that they are capable of large-scale movements (Eckert & Stewart, 2001; Eckert *et al.*, 2002) (Graham, unpublished data). This study presents the first results on patterns of movement and habitat use for whale sharks in the Western Caribbean-Atlantic. Specifically, whale sharks ranged throughout the length of the Mesoamerican Barrier Reef and were capable of highly directed and precisely timed movements to ephemeral yet dense patches of prey.

Sightings, strandings and catches have provided most of the data on whale shark distribution and behaviour to date (Wolfson, 1986; Chen *et al.*, 1996; Beckley *et al.*, 1997; Hanfee, 2001). However, new tagging technologies have enabled fisheries-independent research on patterns of movement. Acoustic tags have been used to actively track whale sharks in Australia (Gunn *et al.*, 1999) and the Seychelles (Graham, unpublished data) and passively monitor presence versus absence in Belize (this study). Researcher-independent satellite tags that collect, store and transmit information to satellites have been successfully used on a host of marine animals (Priede, 1984; Heide-Jorgensen & Dietz, 1995; Mate *et al.*, 1995; Hughes *et al.*, 1998; Block, 2000; Hays *et al.*, 2001; Boustany *et al.*, 2002; Graves *et al.*, 2002; Harcourt *et al.*, 2002; Seitz *et al.*, 2002; Sims *et al.*, 2003). In elasmobranchs, satellite-tags have yielded results for whale sharks (Eckert & Stewart, 2001; Eckert *et al.*, 2002) and white sharks (Boustany *et al.*, 2002) in the Pacific and basking sharks in the Atlantic (Priede, 1984; Sims *et al.*, 2003), providing insights into patterns of movements, habitat use and diving behaviour. Characterising the migratory behaviour and areas of site fidelity of highly mobile fish such as the whale shark can play an important role in their effective management and protection from threats such as fishing and ship strikes. Better understanding of their predictability in time and location will further provide the basis for successful niche tourism operations, considered strong economic alternatives to fishing.

Animals move to fulfil a series of needs during the course of their life-cycle: they must find food, reproduce, raise their young in the case of some species, and avoid harm. All of these activities require movement, either self-propelled as with most species or dependent on external transportation from other species, winds or currents. Movements may be undirected and encompass foraging and ranging behaviours or directed and form part of a migratory pattern (Dingle, 1996). Although migration can encompass several different types of movement that fulfil feeding, reproductive or protective needs (Dingle, 1996), migratory behaviour is defined by Kennedy (1961) as a

> "persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrencc".

A range of terrestrial, airborne and marine animals undertake large-scale migrations, often using the same migratory pathways throughout their life-time (Dingle, 1996). In fish, Atlantic bluefin tuna (*Thunnus thunnus thynnus*) show variable patterns of movement. Several satellite-tagged individuals moved from their feeding grounds in the northern Atlantic Ocean several thousands of kilometres south to spawning grounds in the Gulf of Mexico and at least three individuals moved from the western Atlantic to the eastern Atlantic or Mediterranean Sea (Block *et al.*, 2001). Such large-scale movements are also common for several species of elasmobranchs. Sharks move in the aquatic seascape in socially, spatially and temporally different ways. Movement may be undertaken by individuals or groups and may also be segregated by sex and size (Sciarrotta & Nelson, 1977; McKibben & Nelson, 1986; Klimley, 1987; Gruber *et al.*, 1988; Klimley *et al.*, 1988; Morrissey & Gruber, 1993; Boustany *et al.*, 2002). Lemon sharks (*Negaprion brevirostris*) and grey reef sharks (*Carcharhinus amblyrhynchos*) show highly social schooling behaviour while foraging (McKibben & Nelson, 1986; Morrissey & Gruber, 1993). White shark (*Carcharodon carcharias)* males range widely across ocean basins whereas females remain closer to their coastal natal home, ranging over smaller distances (Pardini *et al.*, 2001). Whale sharks from the Gulf of California were recently shown by satellite-tagging to undertake variable and large-scale movements whereby one individual (7.1 m total length, sex unknown), tracked over the course of three years, moved 12,620 km west across the Pacific Ocean (Eckert and Stewart 2001). Another of the 15 satellite-tagged whale sharks (female, length unknown) moved 7,762 km into the Pacific from the Gulf of California, and all other sharks remained close to or inside the Gulf of California for the variable duration of tag deployment.

Movements follow not only spatial patterns but also temporal patterns with certain species of shark displaying rhythmic diel and seasonal behaviour, often in relation to abundant yet temporary sources of food. Lemon sharks display a diel pattern of repeated movements from east to west in the Bimini Lagoon possibly to enable resource replenishment in one area versus the other (Gruber *et al.*, 1988; Sundstrom *et al.*, 2001). Scalloped hammerhead sharks (*Sphyrna lewini*) move rhythmically between the El Bajo Espiritu Santo seamount into the surrounding pelagic waters in the Gulf of California to search for prey in the late afternoon (Klimley & Nelson, 1984; Klimley *et al.*, 1988), and blue sharks (*Prionace glauca*) move offshore during the day and onshore at night where prey such as squid are more abundant (Sciarrotta & Nelson, 1977).

Seasonal patterns are evident in white sharks that aggregate in greater densities and actively patrol specific areas of the coastline at California's Farallon Islands during the spring seal-pupping season to prey on weaned northern elephant seal (*Mirounga angustirostris*) and California sea lion pups (*Zalophus californianus*) (Klimley *et al.*, 1992; Klimley *et al.*, 1996a; Goldman & Anderson, 1999). Seasonal zooplankton blooms attract temporary aggregations of filter-feeding whale sharks in Ningaloo Reef, Western Australia (Stevens *et al.*, 1998) and the Seychelles (Graham, unpublished data), and basking sharks (*Cetorhinus maximus*) off the southeast coast of England (Sims *et al.*, 1997). Several studies indicate that patterns of movement are highly variable within species (McKibben & Nelson, 1986; Eckert & Stewart, 2001; Pardini *et al.*, 2001; Boustany *et al.*, 2002; Eckert *et al.*, 2002). McKibben and Nelson (1986) noted that different groups of grey reef sharks behave differently in the Enewetak Lagoon with one group remaining inside the lagoon while another group forages on the forereef.

Several species of shark can show variable degrees of site attachment (site fidelity) within patterns of movement (Sciarrotta & Nelson, 1977; Klimley & Nelson, 1984; McKibben & Nelson, 1986; Klimley *et al.*, 1992; Morrissey & Gruber, 1993; Klimley, 1996; Taylor, 1996; Sims *et al.*, 1997). And for those species whose activity spaces can be defined, Morrissey and Gruber (1993) found that activity spaces appear to be positively correlated with body size, and increase at a greater rate than body growth. Juvenile lemon sharks (mean TL = 73.4 cm) in Bimini lagoon were found to occupy a mean home range area of 0.68 km^2 compared to areas occupied by adults, e.g., 93 km^2 for a 230 cm TL and 18 km^2 for a 168 cm TL shark (Morrissey & Gruber, 1993).

Fish have developed numerous means to orient themselves or navigate that enable them to move in a directed manner and cue their arrival with patchily distributed food sources. They may orient using landmarks or fixed reference points (piloting) or without landmarks or known destination point yet knowing their direction of movement (compass orientation) (Dingle, 1996). True navigation or "the ability to move toward a particular goal in completely unfamiliar territory in the absence of any sensory contact" (Dingle, 1996) has been described and reviewed extensively for a range of terrestrial animals and birds (Mouritsen, 2001), turtles (Lohmann *et al.*, 2001), teleost fish and sharks (Kalmijn, 1982; Klimley, 1993; Montgomery & Walker, 2001; Klimley *et al.*, 2002). Sensory cues that help fish to orient, and ultimately to navigate, include currents (Arnold, 1981; Montgomery *et al.*, 1997), temperature and chemical gradients (Carey & Scharold, 1990; Dittman & Quinn, 1996; Salo & Rosengren, 2001), landmarks (Klimley, 1993; Klimley *et al.*, 2002), the sun and its polarised light (Winn *et al.*, 1964; Loyacano *et al.*, 1977; Gruber *et al.*, 1988; Dacke *et al.*, 1999), the moon (Klimley *et al.*, 2002), and the discrimination of magnetic fields (Kalmijn, 1982; Walker, 1984; Klimley, 1993; Walker *et al.*, 1997). Whale sharks may orient themselves using several or all of these cues in series or in parallel depending on ambient conditions, cues which may form the basis of a cognitive map. An endogenous clock entrained by external cues may help to predict or interpret changes in the environment, underpin a cognitive map (Huntingford, 1984), and therefore control the timing of movements (see Chapter 5 for more details on rhythmicity).

Their large-scale movements bring whale sharks into contact with several directed fisheries based specifically in India (Hanfee, 2001), Philippines (Alava *et al.*, 2002) and Taiwan (Chen *et al.*, 1996) that supply primarily Asian markets. These have led to rapid declines in catch per unit effort and have resulted in fishing bans in India and the Philippines and catch quotas in Taiwan. Additionally they are occasionally targeted in the open ocean, where incidental catches from net fisheries such as the tuna fishery (Romanov, 2002) lead occasionally to mortality (Graham, unpublished data) (for more detail on whale shark biology and distribution please refer to Chapter 1). Characterising movement behaviour is helping to focus regional management and conservation efforts for whale sharks.

This chapter aims to characterise the spatio-temporal patterns of movements of whale sharks along the Mesoamerican Barrier Reef. Specifically this study (1) characterises where whale sharks move to following seasonal reef fish spawning aggregation events at Gladden Spit, (2) characterises whale shark congregations at Gladden Spit versus other sites on the Belize Barrier Reef, (3) determines whether whale sharks form schools and show social behaviour during their foraging and large-scale movements, and (4) ascertains if horizontal movements display diel, lunar, and seasonal rhythms. Implications of the findings for management and conservation of large mobile pelagic fish species are discussed.

4.2 *Materials and methods*

Several overlapping methodologies were used in this study to increase the likelihood of obtaining results in a highly variable environment while studying the usually elusive whale shark. Sightings of whale sharks were recorded through visual observation using SCUBA and video (see Chapter 2 for methods). Identification of individual sharks was done using distinctive scarring and spot patterns, and conventional tagging (see Chapter 2 for methods). Sightings-independent methods relied on the use of satellite pop-off tags (see chapter 5 for satellite-tag methods) and acoustic transmitting tags coupled with underwater acoustic receivers. All data used in this study were collected between April 2000 and July 2002.

4.2.1 Study area

A full description of the Mesoamerican Barrier Reef System (MBRS), the Belize Barrier Reef Complex (BBRC), the study site and timing of fieldwork is provided in Chapter 1. Acoustic receivers were placed along the Belize Barrier Reef in areas identified by local fishermen as reef fish spawning aggregation sites and/or locations where whale sharks had been sighted previously (Figure 4.1). Fishermen generally considered the aggregations other than Gladden Spit as either no longer commercially viable or extirpated. The primary study site was Gladden Spit, Belize, where all of the tagging was performed. Gladden Spit was the only area in Belize where whale sharks were known to aggregate in large numbers and on a predictable basis.

4.2.2 Tagging

In total 70 marker tags, 22 acoustic tags and 11 satellite tags were deployed within the Gladden Spit Marine Reserve between 1999 and 2002 (See Chapter 2 for marker tag deployment, Chapter 3 for acoustic tag deployment and Chapter 5 for satellite tag deployment methods and results). Since 106 individual whale sharks were identified from 1998 to 2003 (Chapter 2), the tagging rate represented 21% of the visiting population. 70% of individuals sexed were juvenile males (Chapter 2).

4.2.3 Acoustic telemetry

Whale shark movements on the BBRC were monitored by tagging 22 individuals with coded acoustic tags (refer to Methods in Chapter 3 for acoustic tag specifications and testing). A total of 23 acoustic receivers were moored along the barrier reef during the study period from 2000-2002 (Figure 4.1 and Table 4.1) (refer to Methods in Chapter 3

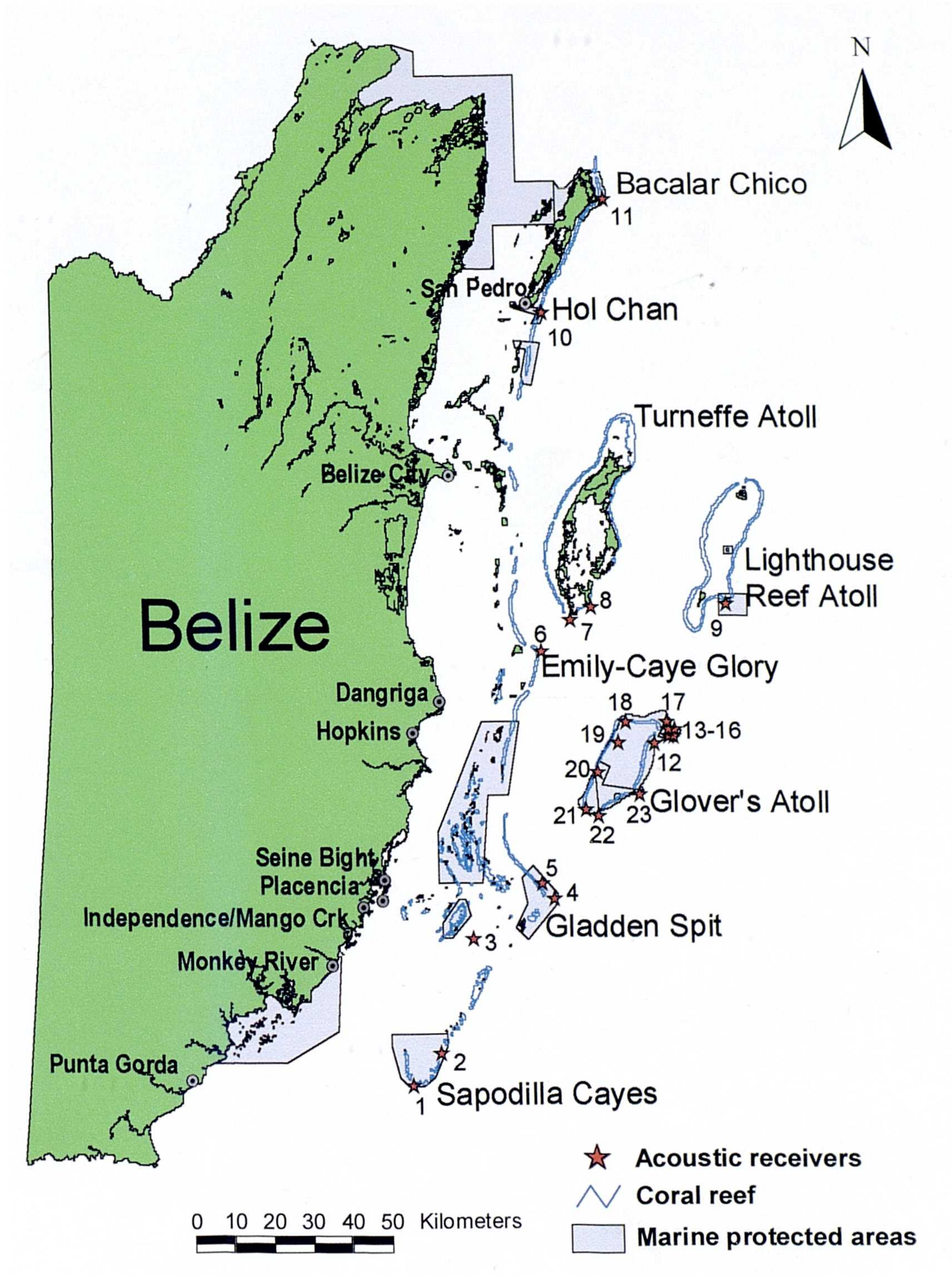


Figure 4.1: Acoustic receiver locations along the Belize Barrier Reef from 27 April 2000 to July 2002 (Base map kindly provided by Belize's Coastal Zone Management Authority (CZMA)).

Table 4.1: Location and deployment duration of all acoustic receivers deployed Between April 2000 and July 2002 on the Belize Barrier Reef Complex. MPA = marine protected area; spag = grouper/snapper spawning aggregation site. NA = Data not available. All receivers located at Glover's were installed and maintained by the Wildlife Conservation Society and the Scripps Institution of Oceanography.

No.	Receiver	Location Latitude (^{0}N)	Location Longitude (^{0}W)	In MPA	Installation date	Months of data collected	Location description
1	Sapodilla Tip	16.08	88.30	Yes	May 2000	12	Sloping shelf promontory
2	Sapodilla N	16.15	88.24	Yes	Oct. 2000	18	Wall
3	W Pompion	16.42	88.16	No	March 2001	9	Wall
4	Gladden Spit	16.51	87.96	Yes	April 2000	26	Sloping shelf to wall, promontory
5	Gladden N	16.55	87.99	Yes	April 2000	23	Sloping shelf to wall
6	Emily-Caye Glory	17.08	87.98	No	Jan. 2001	18	Sloping shelf to wall, promontory
7	Turneffe Elbow	17.15	87.91	No	Oct. 2000	18	Sloping spur and groove to wall, promontory
8	N Turneffe	17.19	87.86	No	Oct. 2000	6	Wall
9	Half Moon Caye - Lighthouse	17.20	87.54	Yes	Dec. 2000	7 then lost	Sloping shelf to wall, promontory
10	Hol Chan	17.86	87.97	Yes	May 2002	2	Sloping shelf
11	Bacalar Chico	18.13	87.82	Yes	May 2001	2 lost/stolen	Sloping shelf to wall, promontory
12	Glover's Fishut	16.87	87.72	No	Nov. 2001	7	NA
13	Glover's NE Cut	16.89	87.69	Yes	Nov. 2001	7	NA
14	Glover's Spag S	16.89	87.68	Yes	Jan. 2002	5	NA
15	Glover's Spag	16.90	87.68	Yes	Jan. 2001	14	Sloping spur and groove to wall, promontory
16	Glover's Spag N	16.91	87.68	Yes	Jan. 2002	5	NA
17	Glover's NE Point	16.91	87.70	No	Nov. 2001	7	NA
18	Glover's NW Point	16.93	87.79	No	Jan. 2001	6	NA
19	Glover's NW Mid	16.88	87.81	No	Nov. 2001	7	NA
20	Glover's West Cut	16.81	87.86	No	Jan. 2001	18	NA
21	Glover's SW Caye	16.71	87.85	No	Nov. 2001	7	NA
22	Glover's SW Point	16.72	87.89	No	Nov. 2001	7	NA
23	Glover's NE Caye	16.76	87.76	No	Nov. 2001	7	NA

for acoustic receiver and mooring specifications). Of the 23 receivers, 12 ringing Glover's reef atoll were set up and run by the Wildlife Conservation Society and the Scripps Institute of Oceanography starting in January 2001. These receivers used the same frequency of transmitter reception (69 kHz), permitting data exchange between the two complementary arrays. Ten acoustic receivers were located within existing marine protected areas: Bacalar Chico (1), Half Moon Caye (1), Glover's Reef (4), Gladden Spit (2), and the Sapodilla Cayes (2). In several of these sites (Turneffe, Emily, Glover's, Gladden Spit) pre-spawning or spawning behaviour of snappers (*Lutjanus cyanopterus* and *L. jocu primarily*) and groupers near the receiver was confirmed based on criteria defined by Domeier and Colin (1997). A further seven receivers were moored at non-promontory sites on the edge of the reef shelf or in channels where whale sharks had been sighted or which were thought to be used as a migratory corridor (Figure 4.1).

Site checks to maintain and download receivers also took place outside the peak snapper spawning-season at all sites. Fish censuses were also run at Gladden, Turneffe and Emily in January 2001 and January 2002 to assess sizes and behaviour of spawning aggregations of Nassau grouper (*Epinephelus striatus*), black grouper (*Mycteroperca bonaci*), yellowfin grouper (*M. venenosa*) and tiger grouper (*M. tigris*)(see Chapter 6 on spawning aggregation details and fish census methods).

4.2.4 Data analysis

Data were analysed using the statistical package SPSS and tested for normality using Kolmogorov-Smirnov. Non-normal results were analysed using non-parametric tests and normal results tested with parametric methods. Distance data between specific points were determined through mapping and using the distance function in ESRI's software ArcView. Satellite tag pop-off locations were estimated with an accuracy of up to ± 350 m according to the Argos satellite system. Geopositional data from satellite tags deployed at Gladden Spit (see Chapter 5 for sat-tag details) were based on the times of dawn and dusk and the maximum changes in light intensity recorded by the light sensor and hence the estimated local time of midnight or noon (Hill, 1994). Positional estimates were derived from irradiance data filtered using an algorithm embedded in the manufacturer's dedicated software (Wildlife Computers Pat Host software and GeoDecoder). Manufacturer longitudinal accuracy is estimated at 0.5 degrees (30 nm or 55.5 km at the equator or 53.4 km at Lat 16^0 N, Gladden Spit tagging site). All longitudes with a mean square difference of over 5 were rejected, as were values west of

88.85^{0}W as these represent land based positions. Additionally, any longitudinal data recorded beyond the maximum possible distance travelled by a whale shark (± 53.4 km tag error) for the time elapsed between longitudinal fixes were removed. Latitude could not be estimated as the tags and software could not provide accuracy greater than 3-10 degrees and sea surface temperature (SST) variability in the region was not great enough to provide clear or useful latitudinal fixes. Maximum possible distance travelled was based on the maximum speed recorded for whale shark movement during the study (See "Results" below) multiplied by the time between longitudinal fixes and compared to distance between fixes.

4.3 Results

4.3.1 Large-scale movements

Combined tagging results indicated that whale sharks tagged at Gladden Spit range widely throughout the Mesoamerican Barrier Reef Complex. Marker tagged sharks were recorded moving as far as the northern most point of the Yucatan Peninsula in Mexico to the north, and south east off the Northern coast of Honduras. A whale shark (7.0 m total length (TL), juvenile male) tagged on 9 April 2001 with marker tag M072, was resighted by two groups of divers on 5 and 7 May 2001, near Cancún on the Yucatan peninsula. It swam a distance of over 570 km from Gladden Spit (direct line distance). Tourists and a shark tagging team near Utila in the Bay Islands of Honduras, about 135 km away from Gladden Spit, sighted two tagged sharks (one with a 2000 acoustic tag and another with an unidentified 1999 marker tag)[1] several months after tag deployment (number and sighting dates could not be provided; A. Antoniou, pers. comm. 2001). A satellite-tagged shark (S5, see Chapter 5) was recorded off the north coast of Honduras ~214 km from Gladden to the south-east after 14 days at sea post-tagging (Figure 4.2 and 5.1). A shark tagged in the Bay Islands of Honduras by the Shark Research Institute and tourists was recorded at Gladden Spit on 23 June 2000 and 14 March 2001 (tag no. 0533 located left of dorsal, juvenile male, ~5.5 m TL). Boat captains and the ARGOS satellite reception system recorded additional Belize-tagged whale sharks near the forereef between Gladden Spit and the Sapodillas (n = 7), offshore in the deep waters of the Cayman Trench between Belize and Honduras (n = 3), and inshore near Pompion and Ranguana Cayes (n = 3) or Seal Caye (n = 1). Some

[1] No sex or size estimates given with this information although based on Belize tagging logs the acoustically tagged shark was very likely a juvenile male between 4-6 m. Of 6 acoustically tagged sharks in 2000, only one was a juvenile female.

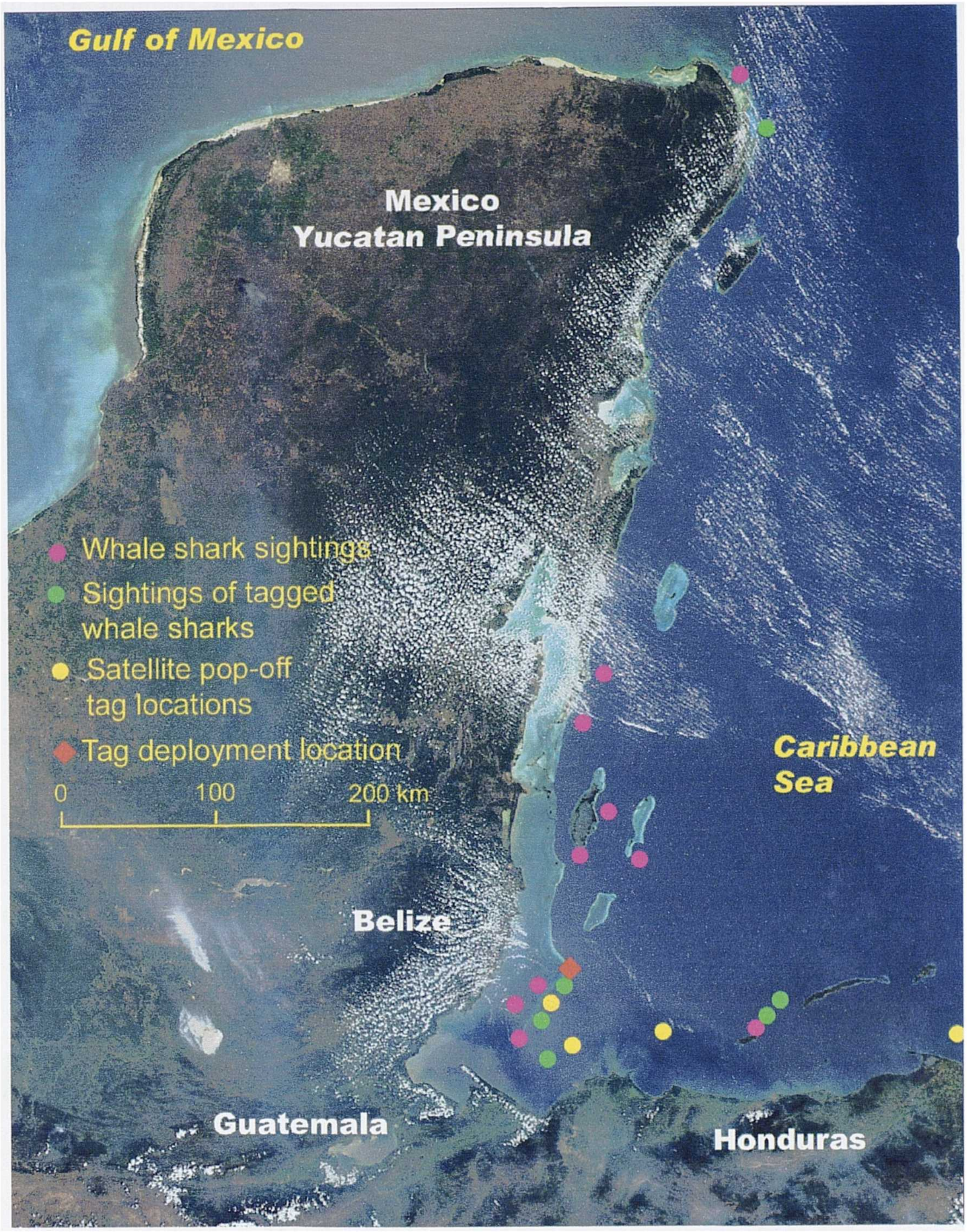


Figure 4.2: Locations of whale shark sightings along the Mesoamerican Barrier Reef and sightings of sharks tagged at Gladden Spit. Figure includes tag deployment location and satellite tag pop-off locations (base photo courtesy of NASA/MODIS 2000).

of these sightings may represent repeat sightings as tag numbers or other distinguishing features were not provided.

Longitudinal data from two satellite tags that collected data for 188 and 206 days respectively (nos. S3 and S4, see Chapter 5 for tag details) supported philopatry to the Mesoamerican Barrier Reef region (Figure 4.3). Tags S3 and S4 provided 110 and 102 usable longitude fixes during their respective deployments. These represented usable data rates of 50.2% and 44.9% of total. The comparatively small amount of usable longitudinal data in S4 may have been due to excessive fouling – that did not fully block the light sensor, and tag malfunction after several months of deployment. However, sensor drift due to fouling is not readily apparent since data indicate movements east followed by return movements west during deployment. Data for both sharks indicated that they remained in a restricted longitudinal range for most of the 6-month deployment. Throughout the period of effective deployment, the tags primarily recorded movement between 88.80^{0}W and 86.00^{0}W for the first 5 months, with occasional movements east as far as 81.25^{0}W.

Taking into account tag accuracy (53.4 km), this would indicate that whale shark S3 could have ranged from 88.81^{0}W-81.25^{0}W ± 0.5^0 or 807 km ± 53.4 km from west to east and back. S4 may have ranged from 88.79^{0}W-83.51^{0}W ± 0.5^0 or 563 km ± 53.4 km. deployed on the same shark. Tag transmission and resightings data from S5 further supported the movement across the Gulf of Honduras from Gladden Spit to the north coast of Honduras and back. Both sharks moved at least to 84^{0}W, a longitude that coincides with the Swan Islands (Honduras) where whale sharks have been sighted previously (M. Van Rensburg, pers. comm. 2002). Although latitudinal fixes could not be determined, S3 and S4's possible visit to this site is further supported by the movements of another shark tagged in Honduras by the Shark Research Institute that moved over deep waters (> 2,000 m) towards the Swan Islands (A. Antoniou, pers comm. 2001). In April 2001, shark with tag S5 was tagged again with tag no. S4.

Whale sharks were recorded on at least 14 of the 23 acoustic receivers indicating that they ranged throughout the entire length of the reef, from the Sapodillas in the south to the Hol Chan Marine Reserve in the north, including the three atolls Turneffe, Lighthouse and Glover's (Table 4.2 and Figure 4.4). Records indicated that 18 of the 22 acoustically tagged sharks visited at least two receivers during the deployment of their tags. Lack of representation at some receivers may have been due to tag shedding or swimming out of the 500 m range of the receiver. At least two of the larger, heavier V32 tags were shed prematurely (see Chapter 3). In Figure 4.4, 15 of the 22 acoustically

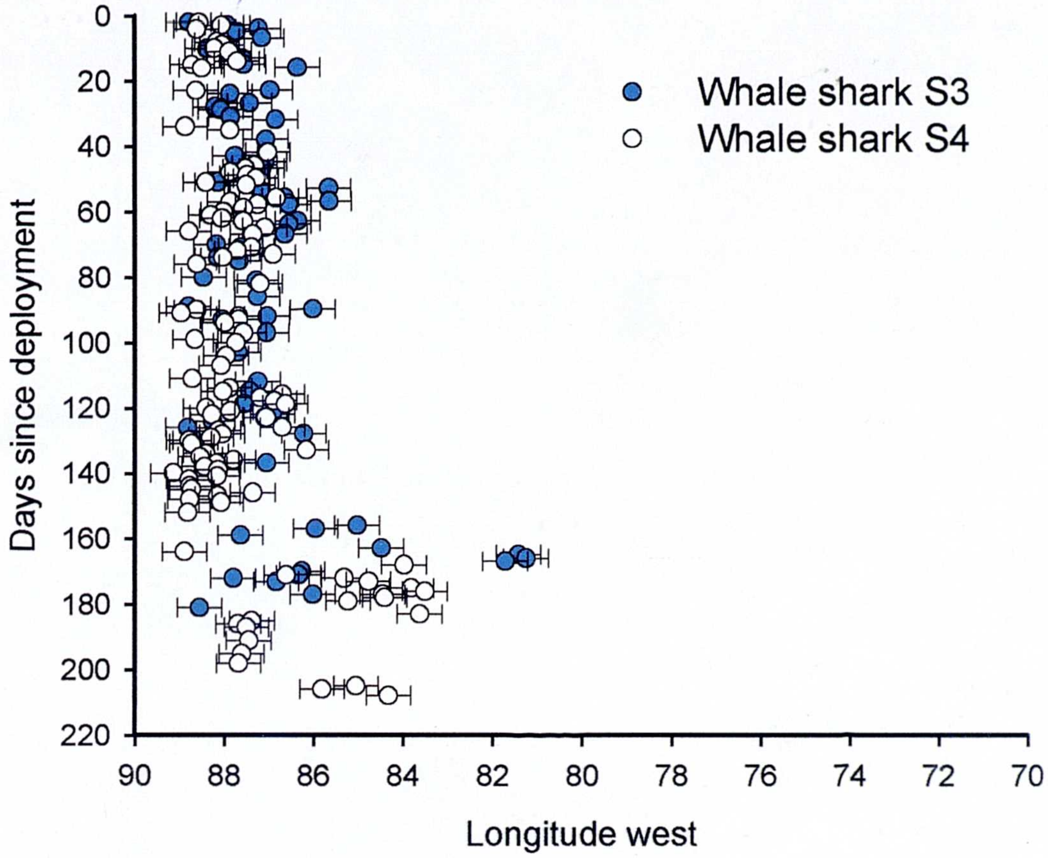


Figure 4.3: Longitudinal data recorded by satellite tags deployed on whale sharks S3 and S4 from 11 April to 4 November 2001 for 188 and 206 days of data collection and effective deployment respectively. Error bars represent 0.5^0 error Longitude.

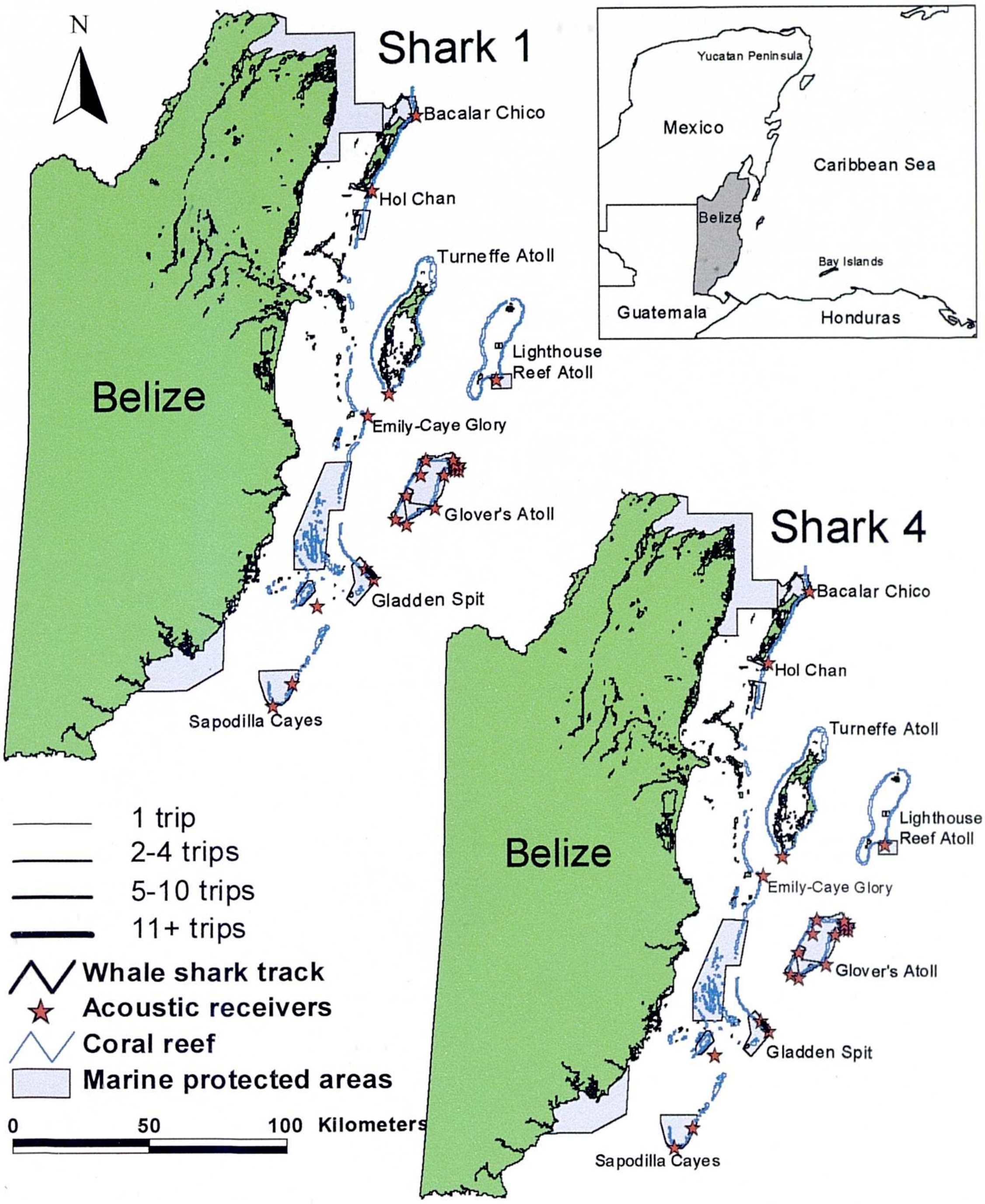
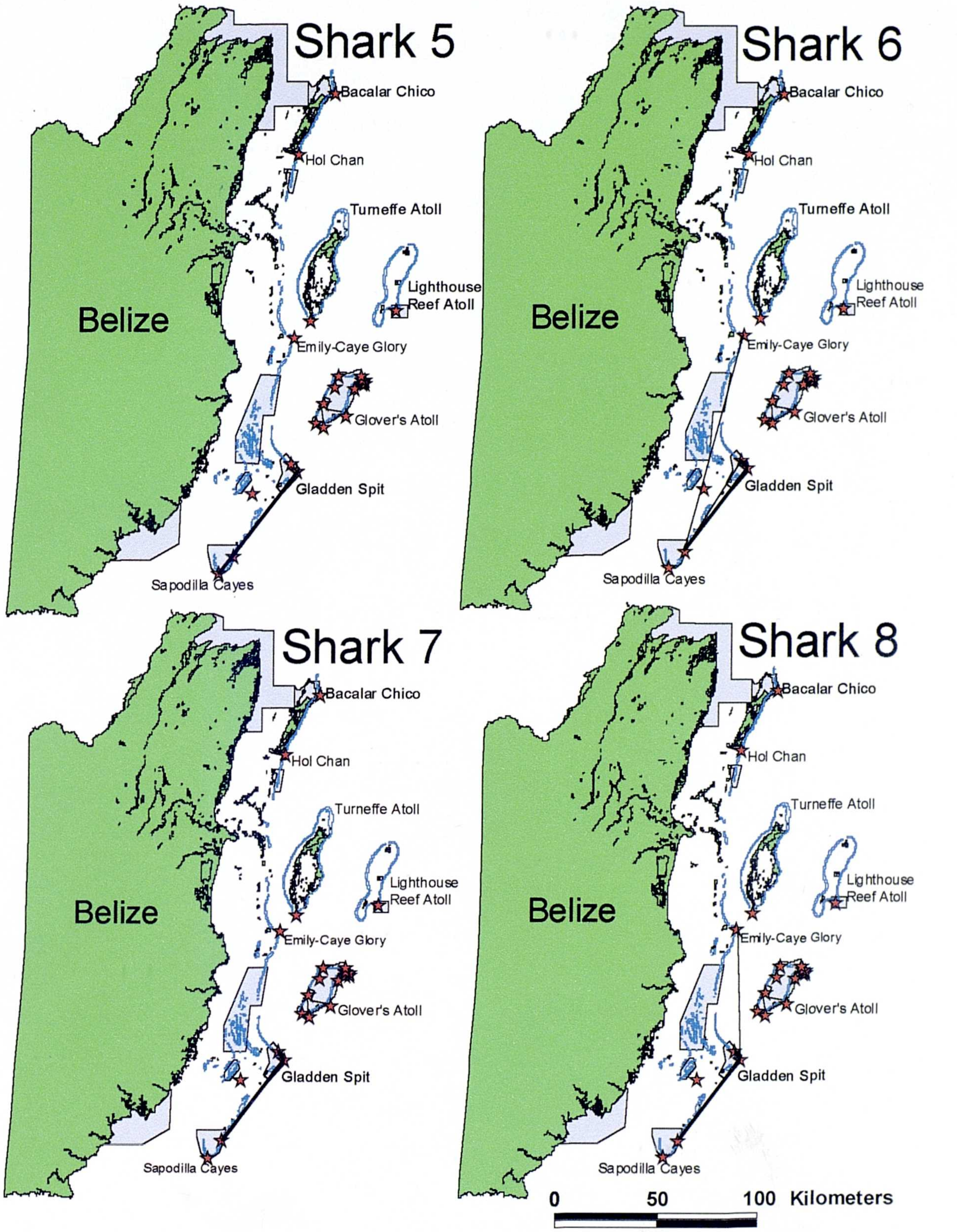
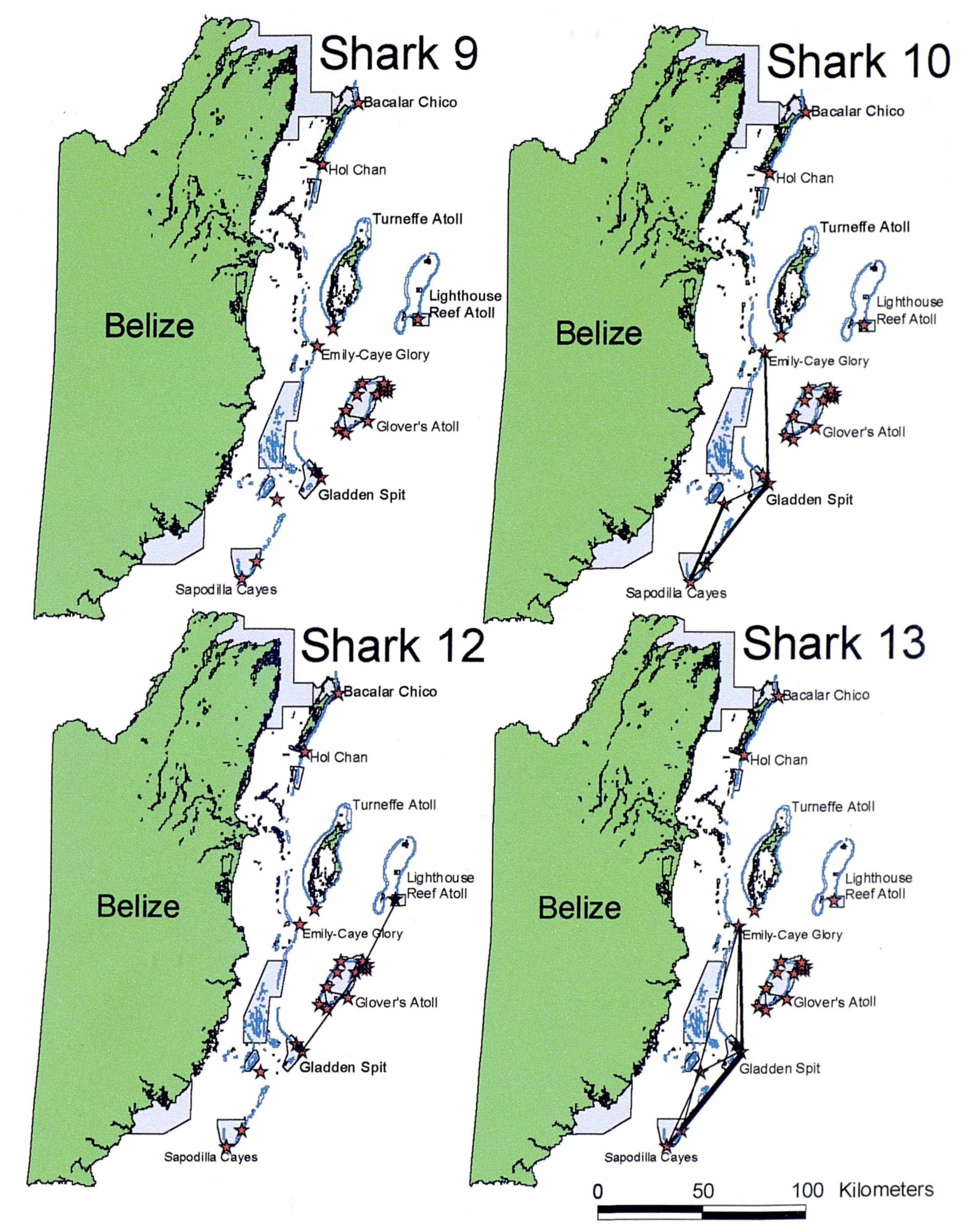
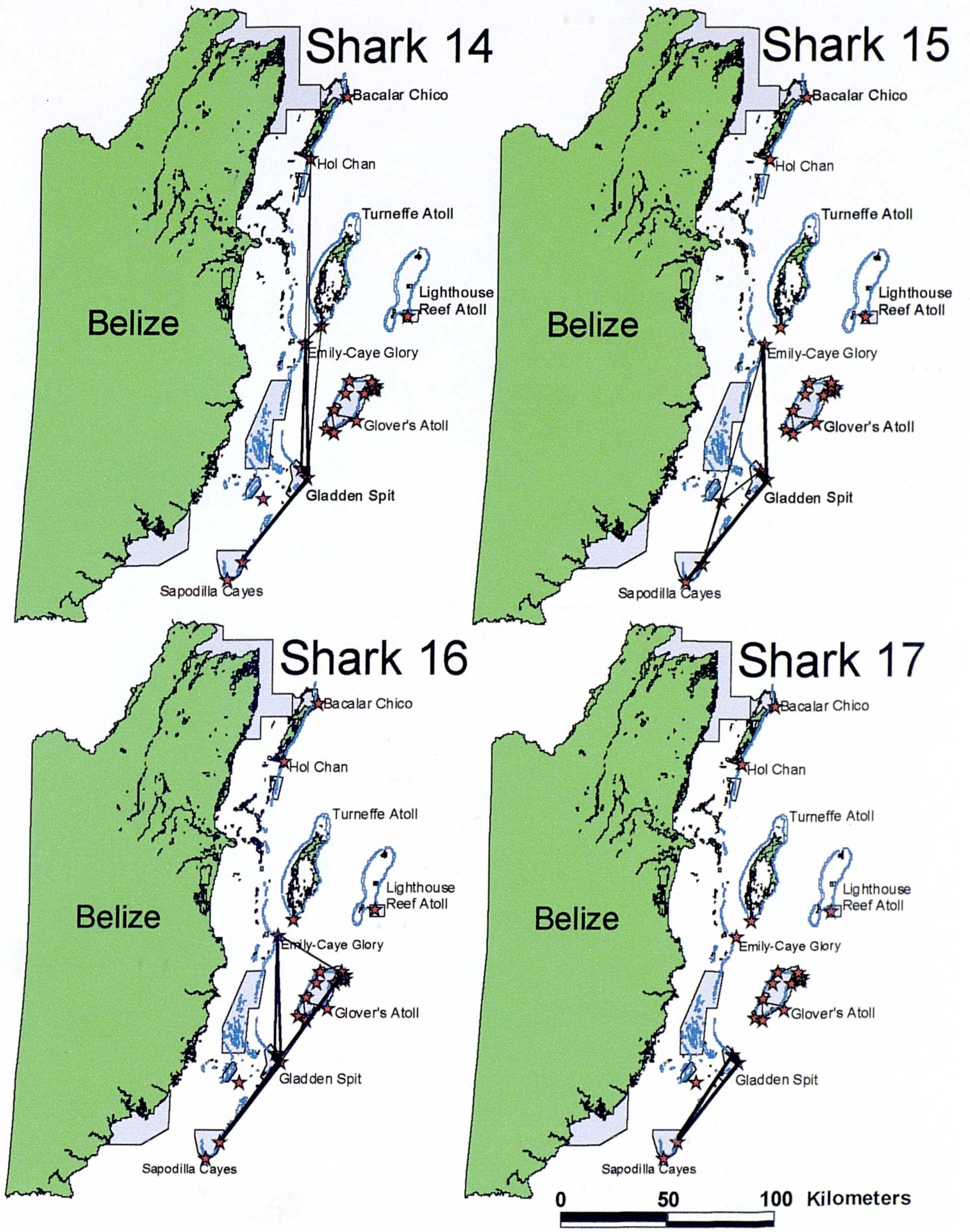


Figure 4.4: Tracks of 18 whale sharks with acoustic tags that visited at least one other receiver apart from Gladden Spit's aggregation site receiver from 27 April 2000 to 9 July 2002. Thickness of movement lines represents the number of trips made between different receivers (Base map: CZMA).


Shark 5
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 6
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 7
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 8
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
0 50 100 Kilometers


Shark 9
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 10
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 12
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 13
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
0 50 100 Kilometers


Shark 14
Shark 15
Shark 16
Shark 17
Belize
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse
Reef Atoll
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
0
50
100 Kilometers

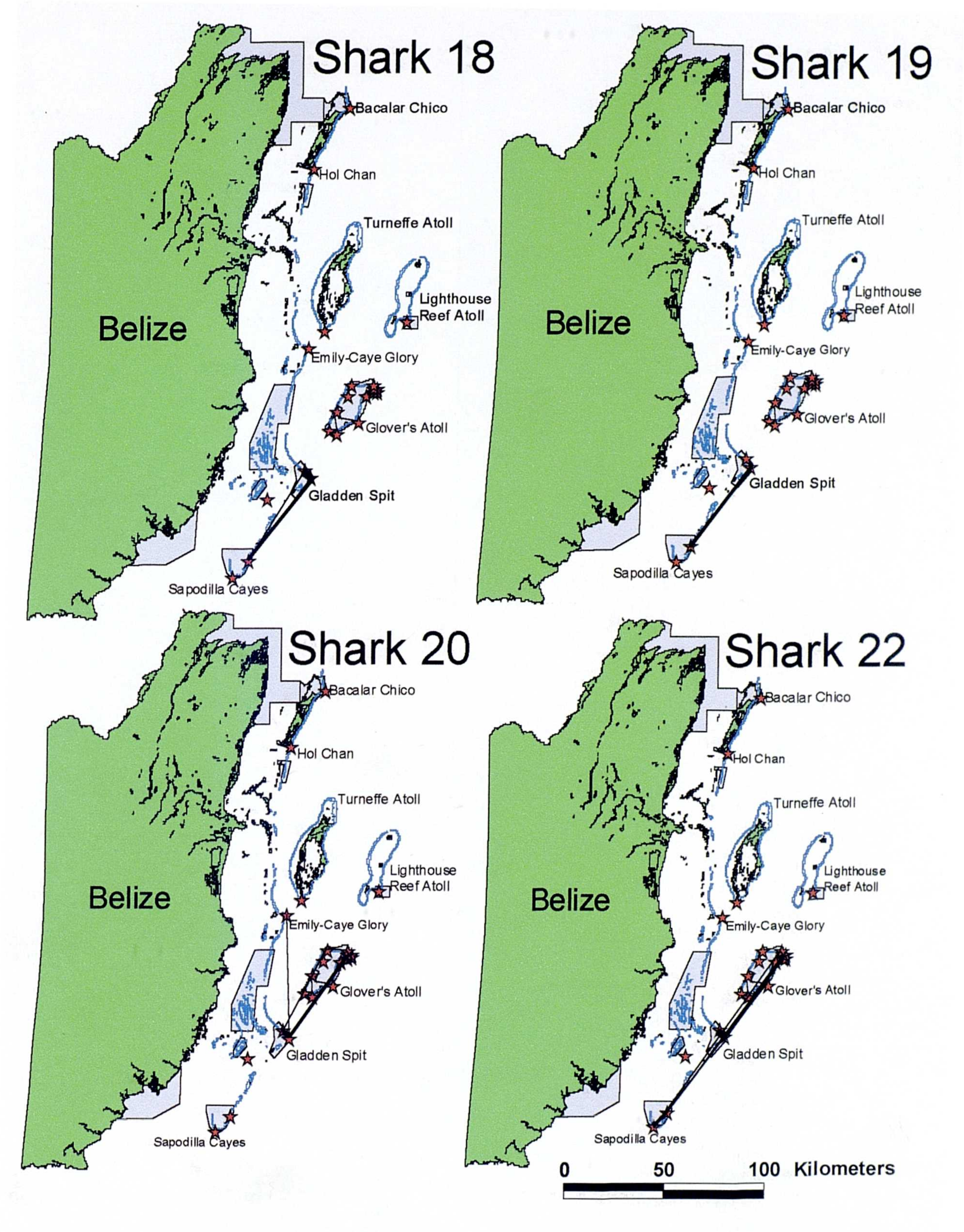

Shark 18
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 19
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 20
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
Shark 22
Bacalar Chico
Hol Chan
Turneffe Atoll
Lighthouse Reef Atoll
Belize
Emily-Caye Glory
Glover's Atoll
Gladden Spit
Sapodilla Cayes
0 50 100 Kilometers

Table 4.2: Summary of movements of 18 whale sharks on the Belize Barrier Reef between 27 April 2000 and 1 July 2002 in relation to 23 moored acoustic receivers. A hit on a receiver is equivalent to a minimum of a minute in the receiver's range. One trip = a single move between two receivers.

Shark number	Dates	Number of recorded trips	Number of hits on all receivers	Acoustic receivers visited *
1	27 April 00 – 12 July 01	26	8404	4, 5
4	23 May 00 – 14 Oct 00	14	3852	4, 5
5	24 May 00 – 23 July 00	2	396	1, 4
6	10-26 April 01	6	239	2, 4, 5, 6
7	10-26 April 01	4	809	2, 4, 5
8	10 April 01 – 19 May 01	5	1719	2, 4, 5, 6
9	10 April 01 – 19 May 01	2	3720	4, 5
10	16 March 01 – 1 July 02	15	2764	1, 2, 3, 4, 5, 6
12	10 April 01 – 17 May 02	12	1247	4, 5, 9, 15
13	11 April 01 – 11 June 02	31	2197	1, 2, 3, 4, 5, 6
14	11 April 01 – 30 June 02	22	1136	2, 4, 5, 6, 7, 10
15	11 April 01 – 28 June 02	43	1855	1, 2, 3, 4, 5, 6
16	9 may 01 – 8 June 02	25	466	2, 4, 5, 6, 15, 16
17	10 April 01 – 1 June 02	21	1130	2, 4, 5
18	9 May 01 – 29 June 02	18	1721	2, 4, 5
19	9 May 01 – 11 Sep 02	7	945	2, 4
20	13 May 01 – 29 June 02	12	1854	4, 5, 6, 15, 17, 18
22	9 may 01 – 3 June 02	22	2042	1, 2, 4, 5, 15, 17, 23

* See Table 4.1 for receiver numbers, names and locations.S4 and S5 represent two tags Fig 4.4.

tagged sharks made at least 5-10 trips between Gladden Spit and North Gladden, 4.2 km away (Figure 4.1, receivers nos. 4 and 5). This area coincides with the broad fore-reef distribution of the Gladden Spit mutton snapper spawning aggregation. Sharks were observed underwater and on the surface moving between both receivers, usually avoiding the shallow portions of the reef platform in preference to navigating along the edge of the fore-reef steep drop-off. Another frequently used route recorded for 13 sharks making a minimum of 5-10 trips, ran from Gladden Spit to the Northern Sapodillas receiver (Figure 4.1, receivers nos. 4 and 2), a distance of 49.5 km. Although sharks showed high site fidelity particularly to Gladden Spit (See Chapter 3), combined movement data from sightings, acoustic data and satellite pop-off data indicate that some whale sharks visit for one moon a year only, and sometimes only once before moving to other sites along the Belize Barrier Reef or beyond. Some sharks are therefore short-term temporal residents and others transients.

4.3.2 Rate of movement

Shark M072 was resighted near Cancún after 25 days at liberty. It had covered ~570 km (point-to-point distance) for an estimated minimum travel rate of 22.8 km day^{-1}, (equivalent to 0.95 km h^{-1}; 0.26 m s^{-1}; 0.04 body lengths second^{-1} (BL s^{-1})) (day of deployment and resighting not included in days at liberty). Sat-tag S5 deployed on a juvenile male of 6.7 m TL detached near the north coast of Honduras after 14 days to give an average travel rate estimated at 17.2 km day^{-1}, 0.72 km h^{-1}, 0.20 m s^{-1} or 0.03 BLs^{-1}.

Rates of movement between receivers varied greatly from hours to months and in many instances movement did not appear directed from one receiver site or a known spawning aggregation site to another, especially if compared to a known speed of 22.8 km day^{-1}. There were exceptions that highlighted a whale shark's ability to undertake very directed travel and time an arrival at Gladden Spit to coincide with a snapper spawning-period. On 14 May 2001 A22, a juvenile male 4.2 m TL, left Gladden at 18:53 and after crossing a deep channel arrived 333 minutes later at 05:26 on the 15 May at Glover's NE Caye (a known snapper spawning aggregation site located 34.7 km away from Gladden ± 1 km for the detection range of two receivers) and recorded a travel speed of 6.3 km h^{-1} (1.74 m s^{-1} or 0.42 BL s^{-1}) (Figure 4.1, receiver no. 23). However, there was no information on whether snappers were spawning at that site during those dates so it was not known if the shark fed on spawn at that time. A22 passed by the NE Caye receiver again at 17:26 h on 15 May and returned to Gladden

Spit where it was picked up on the receiver at 17:48 h on 16 May, while snappers may still have been spawning. It repeated this route moving towards another documented spawning aggregation site further north on Glover's Atoll, 57.7 km away, on 21 May (Figure 4.1, receivers 13-16). It returned to Gladden Spit very briefly on 22 May, 13.38 h later at 4.31 km h^{-1} (1.20 m s^{-1} or 0.29 BL s^{-1}). The shark's immediate departure from Gladden may have been due to the cessation of snapper spawning. As distance travelled from Gladden Spit increases, sharks appear to slow their rate of travel e.g. to the Yucatan, Honduras and even Hol Chan Marine Reserve, possibly due to less directed travel based on a greater frequency of meandering.

Longitudinal data recorded for satellite tagged sharks S3 and S4 indicate that both sharks appear to have made strongly directed movements east during the same period of the year. S3 moved east from 87.64^{0}W to 81.25^{0}W ± 53.4 km and back to 87.8^{0}W ± 53.4 km from 17-30 September 2001. This would indicate an estimated distance travelled of 1,436 km ± 213.6 km or a mean of 110 km day^{-1} or 4.6 km h^{-1} (1.28 m s^{-1}, 0.13 BL s^{-1}). These figures lie well within the abilities of a whale shark swimming purposefully. S4 displayed a similar move east from 88.07^{0}W to 83.51^{0}W ± 53.4 km and back to 87.38^{0}W ± 53.4 km from 6 September to 12 October 2001. This shark would have travelled 935 km ± 213.6 km at a mean pace of 25 km day^{-1} or 1.0 km h^{-1} (0.28 m s^{-1}, 0.4 BL s^{-1}). During the period of tag deployment for S3 and S4, the sharks could have ranged the entire length of the Mesoamerican Barrier Reef as it extends from 88.8^{0}W in the south below the Sapodilla range to 86.5^{0}W at the NE corner of the Yucatan Peninsula. However, it would appear from the recorded longitudes and placement of land that the sharks remained close to the Belize Barrier Reef with possible forays to the Belize atolls and the Bay Islands of Honduras. This is particularly evident for S3 whose sat-tag detached on 15 October 2001 midway between the Belize Barrier Reef and the Bay Islands shortly after returning from a move to the east (Figures 4.3 and 5.1). Rates of movement during the day and night could not be accurately differentiated in the current set of data. This study was also not able to assess the existence or levels of geopositional drift due to the effect of moonlight, biofouling and prolonged deep diving or subsurface swimming on light sensor function. However these impacts have impacted geopositional accuracy in the brand of satellite-tags used (Welch & Eveson, 1999) and dive-induced changes in maximal light intensity were discarded in a study of basking shark movements (Sims *et al.*, 2003).

The effect of currents on whale shark travel speed could not be determined since no usable data exist. However, deployment of satellite-linked drifters by the National

Oceanographic Partnership Program (NOPP)[2] indicated that the prevailing current runs east to west, colliding midway along the Mesoamerican Barrier Reef and turning north along the Yucatan Peninsula (Figure 4.5). It is possible that whale sharks swim with the current to minimize energy expenditure when travelling north from Gladden Spit. The number of resightings of whale sharks in the Gulf of Honduras may be due to a gyre identified by Heyman and Kjerfve (2001), an effect demonstrated by the drift pattern of six satellite tags that popped-off in the region (Figure 4.6).

4.3.3 Movement characteristics

Based on the lack of simultaneous signals recorded from different sharks on all receivers except Gladden Spit, it appears that whale sharks did not move synchronously in groups. Sharks often moved away from Gladden Spit in opposite directions following cessation of fish spawning and were recorded at different, widely spaced receivers during the same dates (Figure 4.7). Of the 18 tagged sharks recorded at the Gladden receiver during the May 2001 spawning moon, four moved south and were picked up at different times by the N. Sapodilla's receiver (no. 2), five moved north, two to Emily and three to Glover's. Of the four that left Gladden and were not recorded by another receiver, three returned the following moon.

Lack of recordings may be due to certain sharks swimming beyond the range of a receiver. Although they only appeared to aggregate opportunistically to feed at Gladden Spit, a dive guide working off the NE coast of Turneffe Atoll observed 14 whale sharks aggregated to feed in April 1999 near no known spawning aggregation site (P. Comerly, pers. comm. 2000). The Gladden Spit snapper aggregation is unlikely to serve as a focal point for whale shark reproduction as 70% of all sharks sexed there were juvenile males, and those that were not sexed rarely attained a TL >8.5 m to qualify them as mature (See Chapter 2).

4.3.4 Site attachment

The only site where whale sharks displayed strong diel site attachment behaviour was at Gladden Spit, where one shark remained within 500 m of the spawning aggregation for close to 10 hours within a 24 h period (see Chapter 3 for details on site fidelity). However, whale sharks were transient at six other known spawning aggregation sites (Receivers 1, 6, 7, 9, 23, 13-16), some extant (Glover's, Lighthouse and Turneffe) and

---

[2] For more information on the National Oceanographic Partnership Program (NOPP) drifters please consult http://drifters.doe.gov/. For the specific drifter tracks recorded in the Western Caribbean go to: http://drifters.doe.gov/data.html.

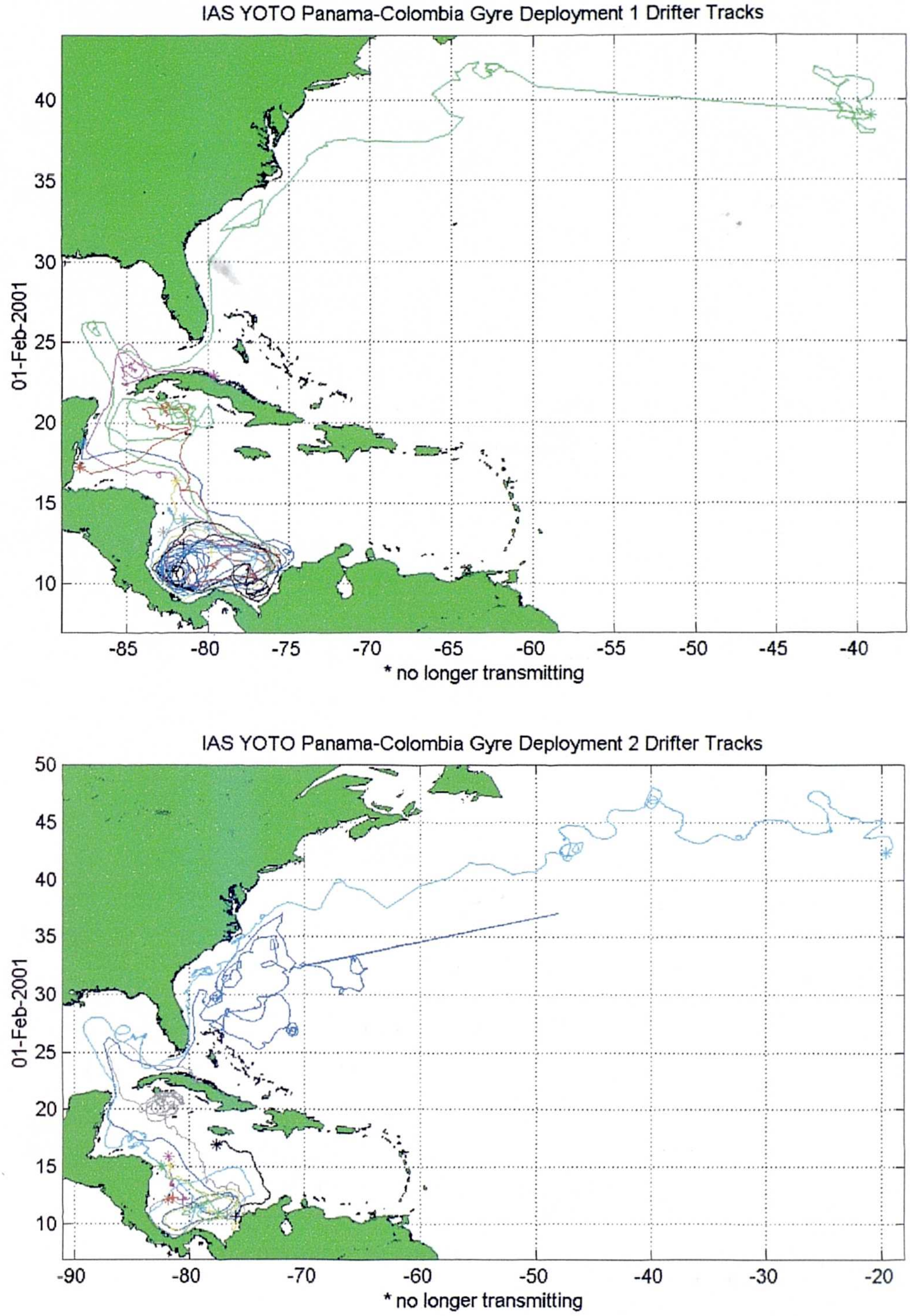


Figure 4.5: Satellite linked drifter tracks in the western Caribbean as compiled in February 2001. (Maps courtesy of the Intra Americas Seas program and the National Oceanographic Partnership Program). + deployment location and start of transmission, ✱ loss of transmission.

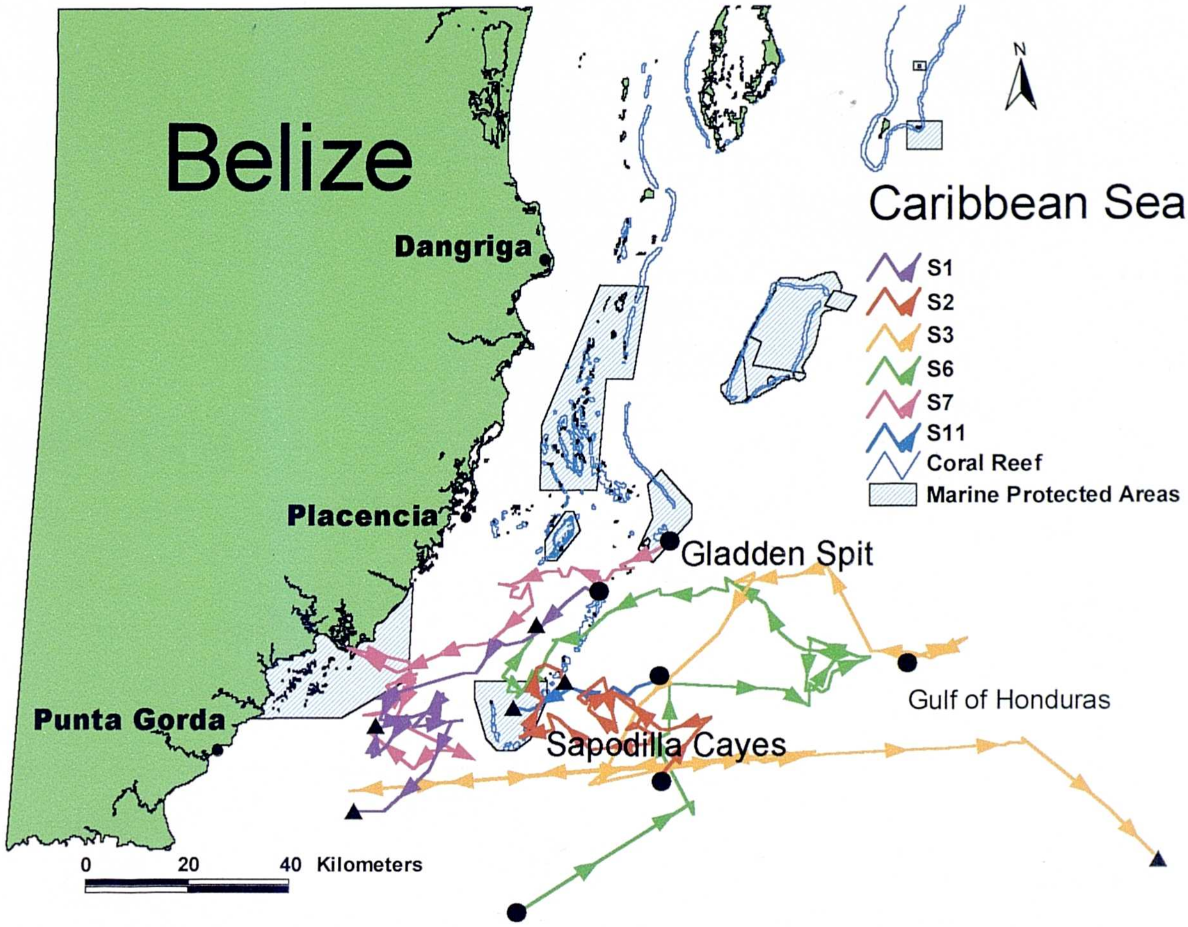


Figure 4.6: Detached satellite-tag drifter tracks in the Gulf of Honduras (n = 6, positions all Argos location quality of "1" or above). "●" Pop-off location and start of transmission and track; "▲" loss of transmission and end of track (Base map of Belize kindly provided by CZMA).

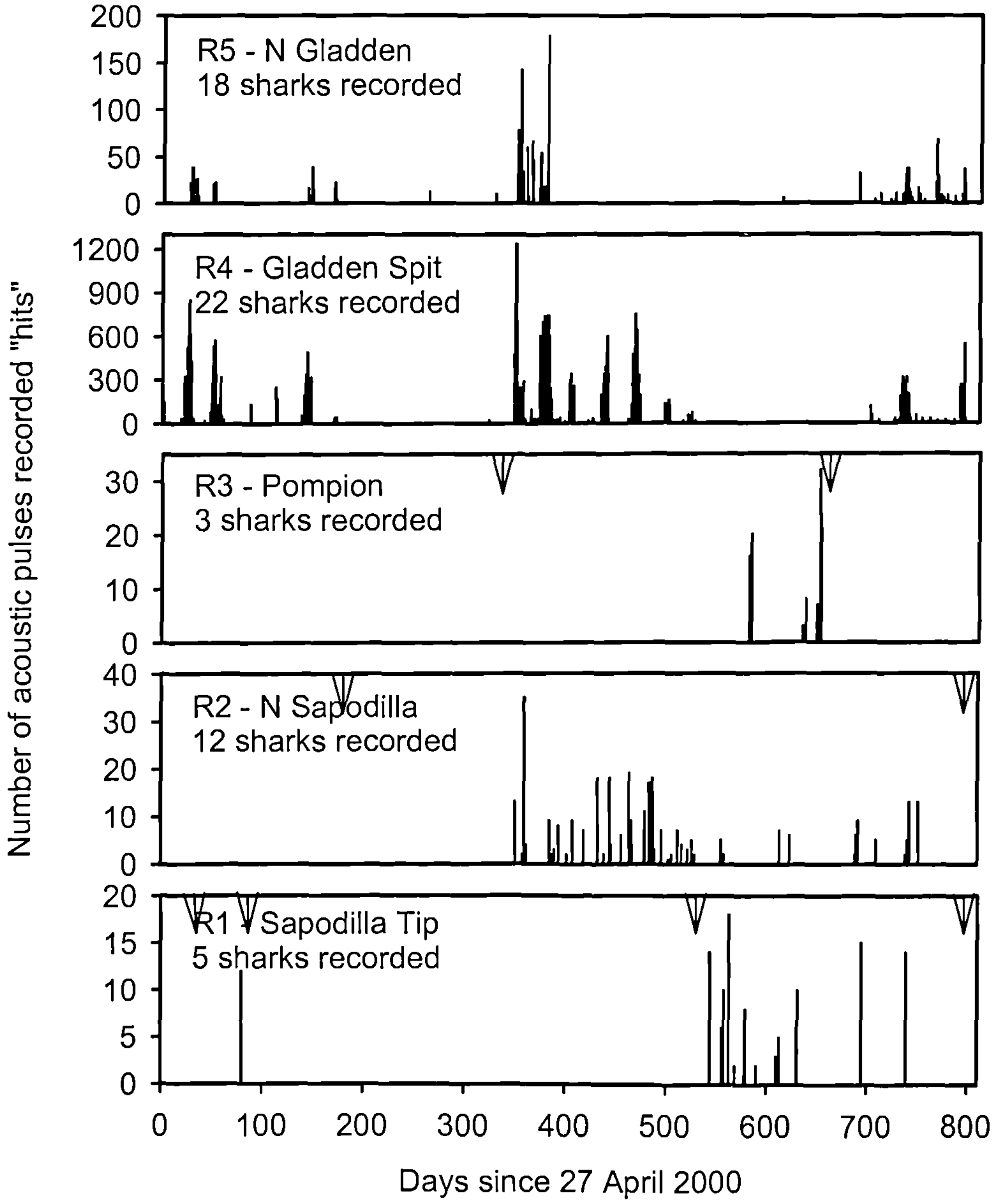
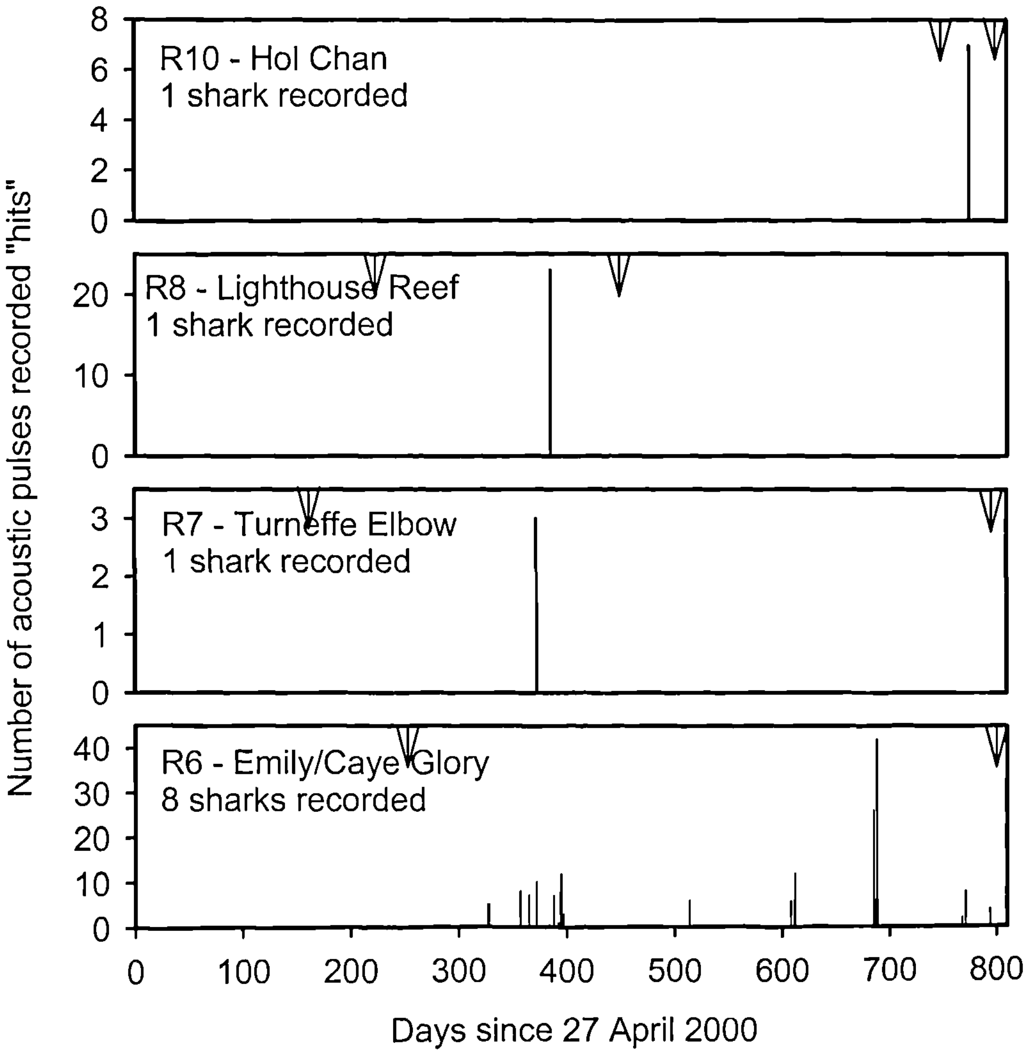
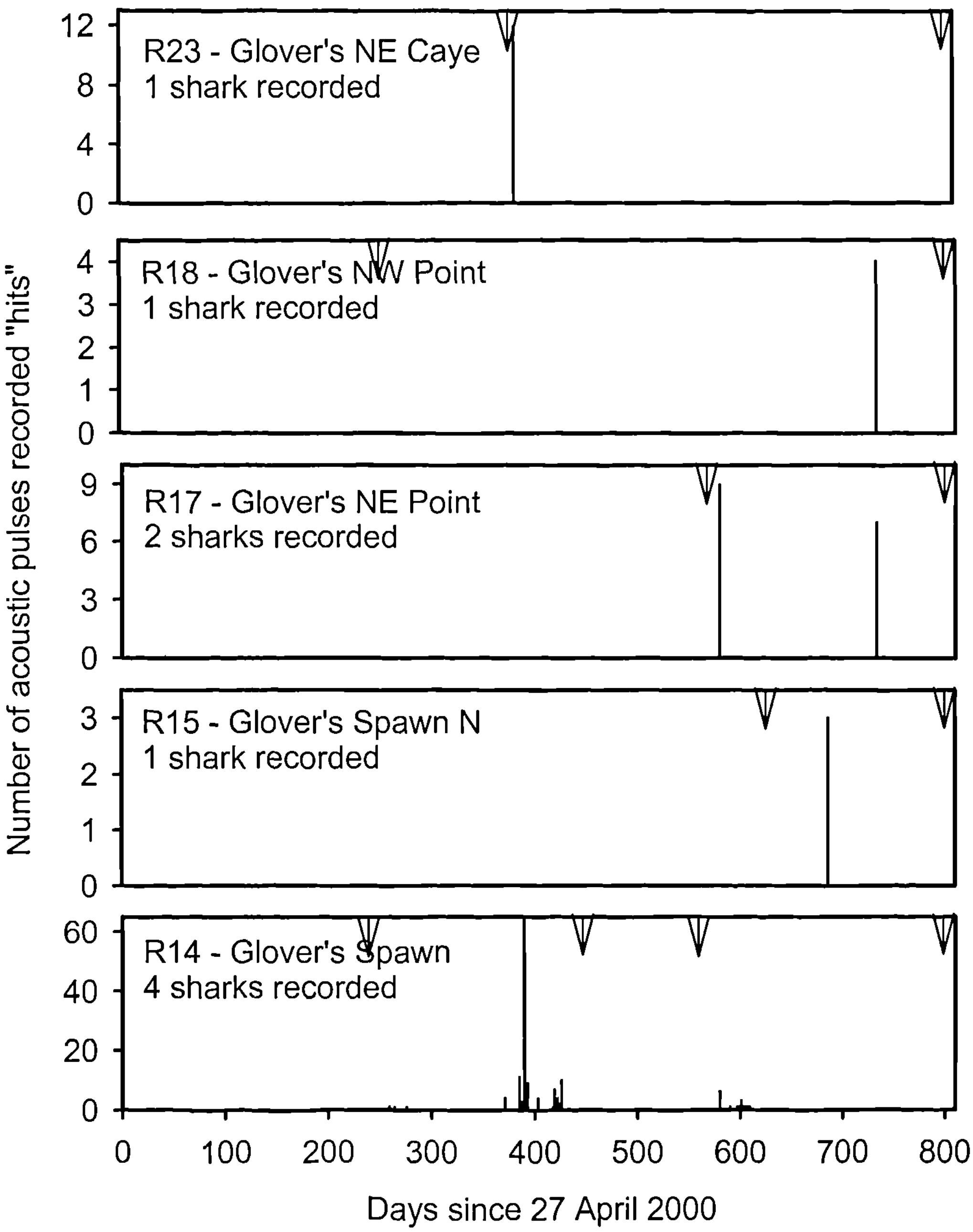


Figure 4.7: Number of pulses recorded or "hits" made by acoustically-tagged whale sharks visiting acoustic receivers moored along the Belize Barrier Reef between 27 April 2000 to 9 July 2002. Only receivers visited by whale sharks are represented. Arrows indicate start and end of receiver deployment; no arrows indicate that the receiver was deployed continuously from study start to finish.


R10 - Hol Chan
1 shark recorded
R8 - Lighthouse Reef
1 shark recorded
R7 - Turneffe Elbow
1 shark recorded
R6 - Emily/Caye Glory
8 sharks recorded
Number of acoustic pulses recorded "hits"
Days since 27 April 2000


R23 - Glover's NE Caye
1 shark recorded
R18 - Glover's NW Point
1 shark recorded
R17 - Glover's NE Point
2 sharks recorded
R15 - Glover's Spawn N
1 shark recorded
R14 - Glover's Spawn
4 sharks recorded
Number of acoustic pulses recorded "hits"
Days since 27 April 2000
0
100
200
300
400
500
600
700
800

others extirpated (Emily and Sapodillas). Outside of Gladden Spit, there were no significant difference in the amount of visitation (number of "hits" at receivers) spent near spawning aggregation sites (Mean: 92.00 ± 63.39 SD) versus non-spawning aggregation sites (Mean: 447.60 ± 736.72 SD) where receivers were located (Independent samples t-test: df = 4; t (14) = 1.08; $p = 0.342$). Figure 4.4 highlights 14 sites that whale sharks have visited, eight of which showed repeated visitation (Receivers 1-6, 14, 17). These results yielded a few surprises: three whale sharks visited the receiver no. 3 "Pompion", located inside the reef. This site is not formally documented in Belize as a spawning aggregation site. However, local fishers note that yellowtail snappers (*Ocyurus chrysurus*) spawn there in March and April and whale sharks are frequently seen in the area at that time (D. Castellanos, E. Leslie, L. Leslie, pers. comm.). Nonetheless, the sharks spent the majority of time (200 minutes recorded) at this receiver between the months of November and February and outside of the yellowtail snapper spawning season. Although we observed cubera and dog snapper spawning several times at Turneffe from 1999 to 2002, only one acoustically tagged whale shark was recorded at the site and a dive resort located nearby reported two juvenile male sharks, one untagged and the other tagged with marker M056 (S. Babatz, pers. comm. 2001).

4.4 Discussion

This study's acoustic and satellite-tag data revealed new insights into whale shark patterns of small- and large-scale movements. Whale sharks moved broadly throughout the Mesoamerican Barrier Reef and Atolls during the year. They were capable of undertaking both exploratory ranging and purposeful navigation making very directed movements across deep channels at night. Several individuals were transient at all 23 monitored sites and others were temporary residents at Gladden Spit. Acoustic results indicate that the tagged whale sharks did not display strong site attachment to any fish spawning aggregation site in Belize that was acoustically monitored, other than Gladden Spit.

It is important to note that the 22 whale sharks tagged with acoustic tags represent 21% of the total number of individuals identified (n = 106) at Gladden Spit over 5 years. The tagged sample is highly representative of the male juvenile portion of the whale shark population. Although it is difficult to extrapolate these movements to the entire population of whale sharks due to the probability of ontogenetic segregation occurring at Gladden Spit, results were nonetheless indicative of how whale sharks could move and what habitats they use and traverse along the Mesoamerican Barrier Reef.

4.4.1 Large-scale movements and distribution

This study provided the first records of large-scale movements for whale sharks in the Atlantic and Caribbean with a whale shark recorded moving ~570 km from Gladden Spit to the tip of the Yucatan Peninsula and another at least 214 km to the south east off the north coast of Honduras. These represent relatively small movements, as this species is capable of trans-oceanic migrations and ranging into temperate waters. Movements recorded in this study were much more limited than the oceanic movements recorded in the Western Indian Ocean from the Seychelles to the Andaman Sea off the west coast of Thailand (~1,800 km) (Graham, unpublished data) and in the Pacific from Baja California to the north of Tonga (12,620 km) (Eckert & Stewart, 2001).

Whale sharks range widely latitudinally with sightings records from the Cape of Good Hope in South Africa (34°21S, 18°28E) to the Hudson River in New York (40°50N, 74°00W) (Wolfson, 1986). Recently, there was a sighting further north off the island of Gran Malan in New Brunswick, Canada of a whale shark caught in a herring weir at ~45.18°N, 63.45°W (T. Cheney, pers. comm. 2003). Whale sharks are not unusual in their geographic plasticity. Similar wide-ranging distributions and movements are recorded for numerous predatory sharks. The globally distributed blue shark currently holds the record for long distance migration based on a tag recapture with one tagged shark recaptured in Natal, Brazil 6,926 km away from its tagging location near New York (Kohler *et al.*, 1998). Genetic analysis of white sharks by Pardini *et al.* (2001) revealed sex-biased dispersal with males possibly undertaking movements from the eastern coast of South Africa to Australia (~10,000 km) and females remaining close to the coast and natal areas.

Many animal species display patterns of movement driven by the search for food, warmth, refuge and reproduction. Patterns of movement along the Belize Barrier Reef for whale sharks recorded at Gladden were primarily linked to the search for food. As identified sharks were predominantly juvenile males (see Chapter 2), this discounts the likelihood of movement for reproductive purposes and their mean size of 6 m discounts schooling for refuge from predators. Graham (unpublished data) and Taylor (1994) reached a similar conclusion in the Seychelles and Ningaloo Reef respectively, where the majority of whale sharks aggregating to feed were also juvenile males.

Movement patterns recorded for whale sharks included site attachment at Gladden Spit (see Chapter 3 for more on site fidelity at this site), commuting to nearby sites such as North Gladden, ranging throughout several sites in Belize, and possibly migrating to other areas of abundant resources on Mesoamerican Barrier Reef and beyond. Whale sharks appeared to use a strategy of locally constrained movement behaviour as seen with juvenile lemon sharks (Gruber *et al.*, 1988) and scalloped hammerheads (Klimley *et al.*, 1988) mixed with large-scale movements often seen in humpback whales (Baker *et al.*, 1986; Darling & Cerchio, 1993) or bluefin tuna (Block *et al.*, 2001). The use of home ranges or discrete activity spaces to describe whale shark constrained habitat use is incompatible with this study's results. Even based on the data available, whale sharks do not appear to maintain distinct diel activity spaces or home ranges as recorded with other species of shark such as juvenile lemon sharks whose home ranges are well defined and positively correlated with body size (Gruber *et al.*, 1988; Morrissey & Gruber, 1993). Although some whale sharks ranged widely and were transient at all sites monitored, others demonstrate a form of meso-scale site fidelity as termed by Holland *et al.* (1999) and showed regional fidelity to the Gulf of Honduras and the spawning site of Gladden Spit. As such, whale sharks qualify as possessing "ocean-sized habitats" a term now used to describe the activity spaces of a few highly mobile species ranging throughout oceans that include albatross, turtles, bluefin tuna and whales (Mills & Carlton, 1997; Hyrenbach *et al.*, 2000; Norse *et al.*, in press)

If the suggested rapid increase in home range or activity space size in relation to modest increases in body size exists in larger shark species than the lemon shark (Morrissey & Gruber, 1993), then a mature whale shark > 9 m TL could theoretically possess an activity space over 1,000 km^2, an area which easily encompasses the Mesoamerican Barrier Reef. Instead of displaying trans-oceanic migrations as recorded by Eckert and Stewart (2001), whale sharks sighted at Gladden may circulate throughout the Mesoamerican Reef area or the Caribbean basin, moving from one seasonally productive patch to another on an annual cycle or longer. Following the peak aggregations of whale sharks at Gladden Spit in April and May, peak sightings of whale sharks in other areas of the Caribbean take place in June to September north of Holbox on the Yucatan Peninsula (M.C. Garcia, pers. comm. 2000), July to September in the Upper Gulf of Mexico at the Flower Gardens Banks National Marine Sanctuary (E. Hickerson, pers. comm. 2001), October to December near the southern coast of Cuba (F. Pina, pers. comm. 2000), and December to February off the north coasts of the Bay Islands in Honduras (D. Afzal & A. Antoniou, pers. comm. 2001). Migrations encompassing several sites during an annual cycle are not unusual. Wildebeest in the Serengeti Park, Tanzania, move over several hundred kilometres from a site in the southeast to the northwest and subsequently the northeast, timed in relation to rainfall and resource availability (Dingle, 1996).

Differences in movement behaviour and habitat use among conspecifics have also been recorded by Sundstrom *et al.* (2001) for lemon sharks in the Bahamas and by McKibben and Nelson (1986) for grey reef sharks in a lag0on at Enewetak Atoll, occasionally taking the form of ontogenetic partitioning. Lemon sharks in the Bimini Lagoon segregate according to size with juveniles occupying a smaller shallow part of the lagoon and adults utilising a different and larger part of the lagoon (Gruber *el al.* 1988). Similar partitioning appears to take place at Gladden Spit where larger whale sharks, many of adult size, were observed offshore over waters >2000 m deep, and with predominantly juvenile males being sighted on the fringes of the barrier reef and at the Gladden Spit spawning aggregation.

Whale sharks have been found to range along coastal areas following the bathymetric contours of the reef fore-edge (Gunn *et al.*, 1999) (Graham, unpublished data). Underwater and boat-based observations coupled with spot-checks using a boat-based acoustic receiver indicate that whale sharks patrol the northern section of the Gladden Spit promontory displaying behaviour akin to commuting during the spawning aggregation period from the North Gladden receiver (no. 5) to the spawning aggregation site on the tip. This behaviour has been noted elsewhere in relation to high prey density. Gunn *et al.* (1999) acoustically recorded two sharks patrolling along the coast in Ningaloo during the plankton blooms and Graham (unpublished data) recorded two sharks moving back and forth off the south-east of Mahé in the Seychelles during a peak of planktonic productivity. Unlike Australia or the Seychelles, Gladden Spit's spawning aggregation site provided a focus for patterns of whale shark movement during spawning periods. With the acquired knowledge of late afternoon fish spawning, whale sharks may be seeking other prey such as pelagic baitfish, jellyfish and plankton along the fore-reef during other times of the day. This movement is similar to the patrolling behaviour observed in several species of predatory shark in relation to food availability including the white shark patrolling the waters near the seal colony in the Farallon islands (Goldman & Anderson, 1999).

Movements of whale sharks away from the Gladden Spit spawning aggregation site following cessation of spawning indicated that their distribution and timing of movements were strongly influenced by prey availability. All food types that the whale shark fed on showed high variability in temporal persistence. Snapper spawn is available from March through June, jellyfish such as *Linuche unguiculata* often bloom from April to May (pers. obs.), plankton density increases at Gladden Spit from March through July and possibly beyond as noted from samples taken and a decrease in visibility during this period, and the movements of schools of small pelagic baitfish are not yet characterised. Such low habitat persistence favours movements that track available prey, a strategy that has been quantitatively demonstrated for basking sharks in the Atlantic (Sims & Quayle, 1998; Sims *et al.*, 2003) and has been apparently adopted by whale sharks (primarily juvenile males) along the Mesoamerican Barrier Reef. Based on repeated sightings and anecdotal reports from fishers made on a regular basis of greatly reduced water visibility due to plankton abundance, three sites other than Gladden Spit appear to possess high seasonal abundances of prey along the Mesoamerican Barrier Reef: the north-east tip of the Yucatan Peninsula above Isla Contoy and the coastal community of Holbox (P. Ramirez, pers. comm. 2002) (Merino, 1997), south-southeast of the Sapodilla Cayes and the northeast coast of Utila, in the Bay Islands of Honduras (D Afzal, pers. comm. 2001).

When dispersal is blind, i.e., the shark moves into unfamiliar territory and does not know if and when it will encounter a patch of food, sensory skills can enable it to pick up the scent of prey or detect environmental conditions associated with previous prey encounters. The release of dimethylsulfide (DMS) produced by zooplankton grazing on phytoplankton, particularly in open-ocean environments (Dacey & Wakeham, 1986) may provide a key sensory cue that orients whale sharks towards dense and abundant patches of zooplankton. Sims and Quayle (1998) suggested that DMS may provide the chemical cue that helps basking sharks to orient towards abundant patches of food. DMS is a proven attractant of long-distance foraging procellariiform seabirds such as the cape petrel (*Daption capensis*) and the southern giant petrel (*Macronectes giganticus*) (Nevitt *et al.*, 1995; Nevitt, 1999). Additionally DMS is often concentrated in areas of upwelling or physical features such as seamounts (Nevitt, 1999). It is possible that reef promontories provide a similar concentrating effect.

When dispersing from a feeding site, whale sharks on the Mesoamerican Barrier Reef appeared to use a mixed strategy that includes exploratory ranging and highly directed movements. Exploratory movements were supported by long intervals between visitations at receivers. During these periods of ranging it was highly likely that whale sharks fed on small bait fish corralled by schools of tuna, events frequently observed on the Belize reef and recorded worldwide (Hoffman *et al.*, 1981; Arnborm & Papastavrou, 1988; Colman, 1997). Directed movements by whale sharks indicated that prey is patchily distributed throughout the Belize and Mesoamerican reefs and that spawn is recognized as a spatio-temporally reliable food source. Areas of high prey abundance could also serve to focus reproduction aggregations in mature individuals, although this is not the reason for the feeding aggregation at Gladden Spit. Sims *et al.* (2000) noted that fronts of abundant zooplankton served as aggregating sites for courting basking sharks off the southeast coast of the UK.

Repeat visitation to sites with high seasonal food abundance coupled with the strong directionality of movement and coincident timing with a seasonal food source (e.g. Gladden Spit's snapper spawn) suggests that whale sharks have developed memory maps that incorporate navigational cues that direct and time their movements to known patchy and ephemeral food sources and possibly even to reproductive grounds. How whale sharks identify new patch locations is not yet known but may be based on a combination of exploratory ranging coupled with oscillatory dives (See Chapter 5 on diving behaviour) in search of vertically stratified chemical odours revealing the presence of prey, a tactic suggested for blue sharks (Carey & Scharold, 1990).

Spatial learning and the existence of memory maps is documented for a range of animals (Nevitt, 1999; Fischer *et al.*, 2001; Salo & Rosengren, 2001). Memory maps must display plasticity to incorporate changes in prey location. Although the precise mechanism of how the maps are created and maintained is not fully known, in fish, spatial learning and memory appear to have a neurological basis controlled by the telencephalon, the part of the brain that interprets sensory impulses, motor function, smell and touch (Lopez *et al.*, 2000). Successful foraging on patches of abundant food can be incorporated into such memory maps and repeated successes will strengthen the maps. Specific characteristics of an abundant patch in a marine environment such as temperature, currents, odour and geomagnetic positioning memorized from past feeding experiences may help to identify new patches.

Sims and Quayle (1998) revealed that basking sharks (*C. maximus*) are indicators of areas of high productivity as they selectively target front-induced concentrations of zooplankton. It appears that whale sharks target similar zooplankton aggregations in the tropics, as Wolanski and Hamner (1988) observed concentrated in reef passages at the Great Barrier Reef's Ribbon Reefs. Therefore, identification of water-mass boundaries (fronts) using tools such as geostationary satellites (Legeckis *et al.*, 2002) could prove a rapid means of identifying areas likely to yield high abundances of whale sharks and other planktivorous megafauna. Yet large-scale shifts in abundances of predictable prey can alter predictable migration routes or patterns of visitation. It is thought therefore that the decline in basking sharks off the West coast of Ireland between 1949 and 1975 may have been partly due to a distributional shift induced by a reduction in their primary prey (copepods), and not entirely due to fisheries overexploitation (Sims & Reid, 2002). Although a combination of the two factors probably led to the dramatic decrease in abundance sighted off the coast of Ireland. Humpback whales (*Megaptera novaeangliae*) displayed distributional shifts from the Georges Bank to Stellwagen Bank and Great South Channel from 1970 to the mid-1990s, induced by fisheries overexploitation and subsequent collapse of the herring populations, their primary prey (Weinrich *et al.*, 1997). Environmental variability can trigger these changes in distribution and abundance and promote low feeding success. Shifts of up to 4,000 km in large masses of warm oligotrophic water by the El Niño Southern Oscillation (ENSO) are responsible for the accompanying large-scale alterations in the distribution of skipjack tuna (*Katsuwonus pelamis*) in the western Pacific Ocean (Lehodey *et al.*, 1997). El Niño-like events have also been known to cause changes in migratory routes and increased time spent foraging by sperm whales (*Physeter macrocephalus*) (Whitehead, 1996) and increasing sea-surface temperatures triggered an increase in gray whale mortality off the Pacific east coast (Le Boeuf *et al.*, 2001). Wilson *et al.* (2001) discovered that fluctuations in the Southern Oscillation Index (a measure of the difference in atmospheric pressure between Tahiti in the South Pacific and Australia), coastal water temperatures and the strength of the Leeuwin Current are linked to the number of whale shark sighted off Ningaloo Reef. Although whale shark sightings per unit effort increased and decreased between 1998 and 2002 at Gladden Spit (see Chapter 7), it was not possible in this study to determine if climatic shifts such as the 1998 El Niño event affected the abundance and distributions of whale sharks or their prey. The timing of whale shark movements in relation to specific areas of prey abundance is discussed in detail in Chapter 3.

It is not known if whale sharks can withstand long periods of time without feeding as documented in sperm whales (Whitehead, 1996), and thus reach broadly spaced patches of food. However, their large liver and their thick, lipid-filled skin (see Chapter 5 and Gudger 1915) may mimic the marine mammals' blubber layer and provide them with a source of energy throughout periods of fasting when faced with low prey abundances as they range or migrate.

4.4.2 Rates of movement

Whale sharks revealed a range of point-to-point rates of movement (RM) along the Mesoamerican Barrier Reef. Speeds appear to be highest when distances measured were shortest and when linked to arrival at a known food source. RM do not necessarily represent through-the water swimming speed because the impact of animal meander rate, current speeds and direction are unknown but nonetheless give a good estimation of a shark's swimming capabilities. Compared to a range of shark species, predatory and planktivorous, whale sharks have proven relatively rapid despite their ectothermy with documented RMs of 0.02-0.41 BL s^{-1} (Table 4.3). A relatively small 4.2 m TL juvenile male shark swam at a mean point-to-point speed of 1.75 m s^{-1} (0.41 BL s^{-1}) for 5.6 hours and sustained a mean RM of 1.2 m s^{-1} for 13.3 hrs. Gunn *et al.* (1999) recorded similar RMs with a 6.0 m TL male whale shark tracked at Ningaloo Reef for 25 hours that ranged from 0.1-1.8 m s^{-1} for a mean RM of 0.8 m s^{-1} (0.13 BL s^{-1}). Over a much longer period of time, Eckert and Stewart (2001) tracked a 15.0 m TL shark for nearly three years as it crossed the Pacific and recorded a mean travel rate of 0.33 m s^{-1}. This is close to the RM recorded for the much smaller (7.0 TL) whale shark tagged at Gladden and resighted near Cancún that moved at a mean rate of 0.26 m s^{-1} over the course of ~23 days. The optimal swimming speed for whale sharks is not known but most sharks are unable to cruise faster than 1 BL s^{-1} (Weihs, 1973). A note of caution if and when comparing rates of movement between sharks: apart from the effect of currents on shark swimming speeds, RMs are also affected by the time-scale during which they are taken. Rates of movement measured over short periods will incorporate fewer meanders (if any) and therefore better represent a shark's true speed through the water than RMs measured over longer times periods.

Other planktivorous sharks that also show high RM include basking sharks that were recorded at a mean rate of 0.85 m s^{-1} while filter-feeding on zooplankton fronts off the SW coast of England (Sims, 1999). However, basking sharks have been found to move faster at 1.15 ± 0.03 m s^{-1} while cruising (Sims, 2000) but the tracks taken were relatively short term and may indicate rapid movement between patches of food. By comparison, Nelson *et al.* (1997) determined that a megamouth shark (*Megachasma pelagios*) tracked for 50.5 h moved at an average estimated speed of 0.49 m s^{-1}. Extension.

Ectothermic predatory sharks appear to swim at speeds resembling those of ectothermic planktivorous sharks. Additionally, endothermy can confer speed advantage to sharks, with endothermic lamnids recording higher RM than ectothermic

Table 4.3: Rates of movement for eight species of large shark. RM = rate of movement; BL = body lengths.

Species	Total length (cm)	Mean RM (km h^{-1})	Mean RM (m s^{-1})	Mean RM (BL s^{-1})	Max RM (m s^{-1})	Reference
Prionace glauca	-	1.5 ± 0.61	0.42 ± 0.17	-	-	Carey and Scharold 1990
	-	4.8	1.33	-	-	Sciarrotta and Nelson 1977
	-	-	0.6	0.4	2.5	Klimley *et al.* 2002
	-	-	0.3	0.2	0.6	Klimley *et al.* 2002
Rhincodon typus	1500	1.2	0.33	0.02	-	Eckert and Stewart 2001
	500-600			0.12-0.14		Gunn *et al.* 1999
	700	4.3	0.26	0.04	-	Graham *et al.*
	420	6.3	1.75	0.41	-	Graham *et al.*
Isurus oxyrhynchus	120	-	0.9	0.8	7.8	Klimley *et al.* 2002
	142	-	1.2	0.8	9.1	Klimley *et al.* 2002
	135	-	0.7	0.5	2.0	Klimley *et al.* 2002
Galeocerdo cuvier	-	3.9	-	0.29	-	Holland *et al.* 1999
Carcharodon carcharias	-	3.2 km h^{-1}	0.88	-	-	Strong *et al.* 1992
	-	3.2	0.88	-	-	Carey *et al.* 1992
	-	2.3	0.64	-	-	Goldman *et al.* 1999
	152		0.8	0.5	1.3	Klimley *et al.* 2002
Cetorhinus maximus	400	3.9	1.08	-	-	Sims 1999
Megachasma pelagios	-	1.78	0.49	0.10	-	Nelson *et al.* 1997
Sphyrna lewini	-	?	?	1.4	-	Lowe 2001
Negaprion brevirostris	210	-	0.69	0.33	-	Gruber *et al.* 1988
	164		0.64 ± 0.12			

carcharinids(Carey & Scharold, 1990; Graham *et al.*, 1990; Klimley *et al.*, 2002). Carey and Scharold (1990) tracked 13 blue sharks (*P. glauca*), an ectotherm, and found an average RM of 0.42 m s^{-1} outside of currents. For the white shark, Strong *et al.* (1992) found mean rates of movement of 3.2 km h^{-1} (0.88 m s^{-1}) and Goldman and Anderson (1999) record a RM of 2.3 km h^{-1} (0.64 m s^{-1}) taken over the course of 4-9 days of acoustic tracking at 1-min intervals. Makos (*Isurus oxyrhynchus*) display similar RM with a range of 0.7-9.1 m s^{-1} recorded during tracking ranging from 1230 h to 3810 h off the La Jolla Canyon in California (Klimley *et al.*, 2002). As ectotherms, whale sharks are likely to modify their position in the water column to swim at physiologically efficient speeds. Makos and white sharks show behavioural preferences for swimming in warmer waters that enable the high RM recorded (Klimley *et al.*, 2002).

In general, sharks display diel differences in rates of movement with greater RM recorded at night than during the day for hammerheads (Holland *et al.*, 1993), blue sharks (Sciarrotta & Nelson, 1977), and grey reef sharks (McKibben & Nelson, 1986). Although it was not possible to accurately determine diel differences in RM for whale sharks on the Mesoamerican Barrier Reef during the course of this study, Gunn *et al.* (1999) noted a slight increase in the movement rate in whale sharks at night at Ningaloo Reef. The megamouth shark tracked for 50.5 hrs by Nelson *et al.* (1997) showed no significant diel differences in RM.

4.4.3 Diel and seasonal patterns of movement

Whale sharks at Gladden undertook a range of diel movements that were seasonally cued in relation to food availability. Results from acoustic receivers in the Gladden Spit Marine Reserve indicate that whale sharks moved onto the reef slope during the day and engaged in patrolling, behaviours also noted by Gunn *et al.* (1999) in Western Australia's Ningaloo Reef and in the Seychelles (Graham, unpublished data). In the afternoon, the sharks moved towards the reef-fish spawning site leaving the site following the cessation of spawning. Whale shark visitation also predominated during the day at the North Gladden receiver (4.2 km to the north of the spawn site, also located on the reef shelf). Whale sharks were not moving much by either receiver during the night, indicating that they may have been moving to other areas of the reef, but most probably offshore. This was further supported by satellite tag depth data detailed in Chapter 5. Looking specifically at the depth data for shark S4, swimming took place primarily between 50 and 200 m, beyond the depth of the fore-reef shelf where the fish spawning took place. Whale sharks may have ranged to the south and southeast in the fall and winter based on visitation at receivers 1-3 (Figure 4.7) and numerous winter sightings in the waters north of the Bay Islands of Honduras (D. Afzal, pers. comm. 2001). This could explain the lack of visitation at Gladden Spit during the months of November through February. Although it was not possible to characterise whale shark short-term movements during the course of this study, Sciarotta and Nelson (1977) noted very similar seasonally-modulated diel patterns of movement with blue sharks off the coast of Santa Catalina Island in California. At night, sharks moved near shore and offshore during the day from March through June and remained predominantly offshore the rest of the year.

4.4.4 Orientation

Whale sharks appear to have highly developed sensory and orientation skills based on the directionality and rates of movement recorded during movements to the Yucatan Peninsula, to Honduras and back and forth from Glover's Atoll. Strong orientation skills would help a whale shark to make directed movements and minimize energy expenditure while moving from one patch of dense, abundant food to another. These feats often take place in the oligotrophic environment that characterises tropical waters (Lalli & Parsons, 1997). Although food availability at Glover's is not known, the tip of the Yucatan Peninsula supports a well-documented coastal upwelling and associated plankton abundance between June and September (Merino, 1997). Many whale sharks have been sighted surface feeding in that area during those months (M. Garcia, pers. comm. 2000; P. Remolina, pers. comm. 2001).

Endogenous circadian or circalunar clocks synchronised by an external cue such as light may provide the timing framework for whale shark movement as observed in several species of teleost fish and elasmobranchs (Finstad & Nelson, 1975; Boujard, 1995; Sanchez-Vazquez *et al.*, 1995; Heilman & Spieler, 1999; Cummings & Morgan, 2001) (see Chapter 5). Although whale sharks are observed to orient to bathymetry during movements (Gunn *et al.*, 1999) (Graham, unpublished data and pers. obs.), they may also possess true navigation ability that enables them to move to sites without the reference of familiar landmarks such as the sea-floor or sea-slope or chemical and auditory cues provided by nearby coral reefs. They may navigate using some or all of these cues in parallel or in series to reflect ambient conditions. Whale sharks swim within the top 10 m almost every day and therefore may use polarised light, moon light and at deeper depths sunlight, as observed in a study of lemon sharks movement (Gruber *et al.*, 1988). They also perform a range of oscillatory and deep dives that may represent searches for prey, looking for the sea-floor or slope, or could provide them with greater orientation with respect to the Earth's dipole field, a strategy potentially used by blue sharks and scalloped hammerheads (Carey & Scharold, 1990; Klimley *et al.*, 2002) (see Chapter 5 for more detail on diving patterns).

Whale sharks have been recorded on all functioning receivers deployed on the barrier fore-reef shelves indicating that they could be displaying topotaxis, orienting themselves using landmarks such as the bathymetry of the barrier reef slope. However, their movements to atolls indicated that they were not using the forereef slopes to navigate by, as they were only picked up at promontory sites. Many species of sharks are capable of highly directed swimming regardless of visual or tactile cues and that sensitivity to fluctuations in the Earth's geomagnetic field may be an important cue used to orient themselves. Kalmijn (1982) demonstrated that sharks can sense changes in the surrounding electrical field and orient themselves accordingly. Although mechanisms for orienting or navigating using the Earth's magnetic field are not fully understood in sharks, it appears as though they use their ampullae of Lorenzini to measure kinetic electric fields (Bleckmann & Hoffman, 1999) rather than possess magnetite located in the brain and discovered in a range of animals including teleosts (Walker, 1984), marine mammals (Zoeger *et al.*, 1981), and invertebrates (Boles & Lohmann, 2003). Scalloped hammerhead sharks move at night along pathways with little geographic variation between the El Bajo Espiritu Santo seamount and Las Animas Island located 20 km apart in Baja California (Klimley, 1993). The paths occurred most often between maxima and minima in the geomagnetic field leading Klimley (1993) to speculate that the sharks oriented themselves according to distortions in the magnetic field created by the two seamounts. Additionally, sharks may navigate using a bi-coordinate map enabling movement in directions other than in a strictly north-south direction. Holland *et al.* (1999) noted highly directed south-easterly movements of tiger sharks (*Galeocerdo cuvier*) from the island of Oahu in Hawaii to their feeding grounds on Penguin Banks, 35 km away, and Carey and Scharold (1990) noted that blue sharks were capable of sustaining a directed southeast heading away at night from the shelf platform of Santa Catalina Island, California. However, studies on green turtles (*Chelonia mydas*) revealed that this species is not heavily dependent on a magnetic compass to orient itself. A small magnet was placed on the study animals to disrupt any magnetic sense and these were able to orient to the Brazilian coast with as much success as the control animals (Papi *et al.*, 2000).

The impact of currents on patterns of movement of whale sharks cannot be estimated in this study. However, large-scale currents in the region run from east to west-northwest based on the repeated tracks of YOTO drifters[3]. For movements north, whale sharks may swim offshore beyond the atolls to capitalize on the west-northwest flowing current. When returning south, they could avoid swimming counter-current by keeping inside the atolls and close to the barrier reef. Currents could further help to orient them during their migrations as documented with several species of fish (Arnold, 1981; Montgomery *et al.*, 1997) such as the bluefin tuna that frequently move north with the warm water of the Gulf Stream to feed in northern mid-Atlantic (Block *et al.*, 2001). Six detached and surface-floating satellite tags tracked for 15-20 days each during different periods of the year either moved inshore from the barrier reef or circulated in the Gulf of Honduras (Figure 4.6). Although short-term, these results support the existence of a gyre in the Gulf of Honduras counter to the prevailing east-west current (Heyman & Kjerfve, 2001) that may exist year-round and concentrate plankton. Such a gyre may explain the numerous sightings by fishers and boat captains of whale sharks feeding year-round in the region of the southern barrier reef and the Bay Islands of Honduras.

4.4.5 Social behaviour during movements

Several species of shark display a spectrum of social behaviours ranging from agonistic displays and territorial exclusion in white sharks (Klimley, 1996; Klimley *et al.*, 1996b) and lemon sharks (Gruber *et al.*, 1988), to courtship in basking sharks (Sims *et al.*, 2000) and nurse sharks (*Ginglimostoma cirratum*) (Pratt & Carrier, 2001). Repeated observations of feeding whale sharks revealed little social interaction while feeding at Gladden or elsewhere. Group foraging is apparent in whale sharks that aggregate opportunistically to feed on dense and abundant yet patchy food sources at different sites worldwide (Taylor, 1996; Clark & Nelson, 1997; Colman, 1997; Graham, 2001; Heyman *et al.*, 2001). However, whale sharks appeared to possess a mixed feeding strategy that involved solitary and group foraging apparently modulated by the degree of clumping or dispersal of prey. In Belize and outside of the Gladden Spit aggregation, whale sharks were often encountered feeding individually and occasionally in small groups. The underlying rationale for the use of one type of foraging behaviour over another is demonstrated by the walleye pollock (*Theragra chalcogramma*). When

[3] For the specific YOTO drifter tracks recorded in the Western Caribbean go to: http://drifters.doe.gov/data.html.

acclimatized to widely dispersed zooplankton, juvenile walleye pollock were observed under laboratory conditions to forage individually. Yet, when food was clumped in patches pollock usually forage in groups and respond to food discovery cues (local enhancement) by other individuals by aggregating to feed (Ryer & Olla, 1995). Group foraging may therefore be an evolutionarily successful strategy to increase prey encounter rates in clumped and patchy prey (Clark & Mangel, 1986). Whale sharks may have responded to local enhancement while feeding on the spawn at Gladden. Discovery of new patches and active surface-feeding behaviour commonly polarized the movement of other sharks towards the new patches and away from dissipating patches, often located 50-100m away. Alternatively, whale sharks could have been orienting themselves up prey gradients using area-restricted search behaviour as Sims and Quayle (1998) observed with basking sharks feeding on copepods off the south-west coast of Britain. It was not possible to determine in this study if either or both of these prey-searching mechanisms was used.

Based on departure records from Gladden Spit, whale sharks did not appear to school when moving from one site to the next as noted with scalloped hammerheads (Klimley *et al.*, 1988), lemon sharks (*N. brevirostris*) (Gruber *et al.*, 1988; Morrissey & Gruber, 1993) and grey reef sharks (McKibben & Nelson, 1986). Such disparate movements may in fact be to a whale shark's benefit to ensure that they encounter sufficient prey in an area of low abundance. Rapid prey depletion and even death from starvation can result from the congregations of large numbers of predators, a suggested cause for the high mortality of gray whales feeding on low abundances of amphipods in 1999 in the eastern Pacific (Le Boeuf *et al.*, 2001). Similarly, lemon sharks appear to maximize the likelihood of prey recovery by only utilizing a proportion of their daily home range (Morrissey & Gruber, 1993).

The majority of sharks identified in Belize were juvenile males pointing to segregation by sex and size (see more on population structure in Chapter 2). These data are not unique to Belize or to whale sharks. A similar pattern of juvenile-dominated population structure and possible sexual segregation exists with whale sharks in Seychelles (Graham, unpublished data) and Ningaloo Reef, Western Australia (Taylor, 1994; Colman, 1997; Stevens *et al.*, 1998). Such segregation may come about due to behavioural differences between sexes, uneven sex ratios in the population visiting Gladden Spit, and/or increased feeding efficiency on spawn of smaller sharks compared to larger sharks. Few records exist of females and mature whale sharks on the Belize Barrier Reef indicating that sampling at Gladden only captured a section of the overall population. Only six females were sighted in five years and large, mature animals were generally sighted outside the spawning aggregation time and/or in the tuna feeding aggregations. Segregated movement based on size and sex is recorded for several other species of sharks including scalloped hammerheads (Klimley, 1987) and white sharks (Goldman & Anderson, 1999). Although the majority of whale shark movements recorded in this study were linked to seasonal food availability, adult whale shark movements in the region may also be geared towards reproduction (see Chapter 2).

4.4.6 Movement in relation to the network of marine reserves and the implications for the conservation of large migratory fish

Over the course of 15 years (c. 1987), Belize has established a network of 12 marine reserves along its barrier reef and coastal areas. This study revealed broad-scale patterns of movement by whale sharks throughout the Belize Barrier Reef and temporary residence or transience in at least six of these marine reserves (Hol Chan, Half Moon Caye, Glover's Reef Atoll, Gladden Spit, Laughing Bird Caye Faro, Sapodilla Cayes). Fisher sightings of whale sharks in Xcalak (in Yucatan, north of the Belize border) possibly feeding on the spawn of white margate (*Haemulon album*), indicate that the sharks may also be visiting Belize's northernmost marine reserve Bacalar Chico[4]. This is another barrier reef promontory that previously supported a thriving multi-species reef fish spawning aggregation. They are further sighted at the Isla Contoy National Park and the Banco Chinchorro Marine Reserve in Mexico's Yucatan Peninsula.

Tracking the movements of large pelagic fish such as whale sharks could help to identify areas of high productivity and associated schools of commercially important species. Improvements in tag design, transmission modalities and satellite reception can only help to improve data collection and knowledge of movement behaviour. In Belize and along the Mesoamerican Barrier Reef, it is hoped that using satellite location-only tags will help to chart daily or weekly movements of whale sharks and possibly reveal the sites and timing of undiscovered fish spawning aggregations or other seasonally predictable occurrences of dense patches of food. These technologies might also reveal meso-scale home ranges, migratory corridors and reproduction sites.

Large highly migratory pelagic fish defy many of the established means of protection for marine species. Whale sharks in particular are now recorded as ranging throughout the territorial waters of over 120 countries. Their patterns of movement

[4] Two receivers installed successively at Bacalar Chico's spawning aggregation site disappeared before any data downloads could be made.

between these states have only been investigated in six countries. Although some of their diving and feeding behaviour mimics that of large marine mammals, whether they possess regularly used migratory paths similar to those documented for baleen whales is as yet unknown. Conservation measures require a combination of strategies that include site-specific protection coupled with international treaties that protect them throughout their range. Specifically this would include marine reserves sited at known areas of vulnerability, e.g., feeding, reproduction, and/or nursery sites (Norse *et al.*, in press). To facilitate protected areas management, these sites preferably need to be spatially discrete, i.e. seamounts, reef promontories. Gladden Spit and Ningaloo Reef (Western Australia) are the only two marine reserves worldwide that currently protect whale sharks in known feeding areas. Yet, simply siting marine reserves in areas of known high productivity such as seasonal fronts or even spawning aggregations may be inadequate as these may shift beyond reserve borders. Therefore a new generation of open-ocean marine reserves might be needed to protect preferred temporary habitats created by the confluence of optimal environmental factors and an abundance of food (Mills & Carlton, 1997; Hyrenbach *et al.*, 2000; Norse *et al.*, in press). Reserves are not sufficient though. Conservation of highly migratory animals such as the whale shark can only be achieved through a combination of coastal and open-ocean protected areas linked to regional accords and binding and enforceable international agreements such as the Convention on Migratory Species and the Convention on the International Trade for Endangered Species. In the Caribbean basin specifically, continued research into whale shark patterns of movement using acoustic and satellite telemetry could help to identify and characterize other sites of importance during a whale shark, the linkages between these areas, and the causes and timing of movements. These data could provide the basis for a regional network linking critical habitats and spatio-temporally abundant patches of food important for the protection of whale sharks and other migratory species utilizing the same resources.

4.5 References

Alava M. N. R., Dolumbalo E. R. Z., Yaptinchay A. A. & Trono R. B. 2002. Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In: *Elasmobranch Biodiversity Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997*. (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 132-147. Sabah, Malaysia. IUCN, Gland, Switzerland.

Arnborm T. & Papastavrou V. 1988. Fish in association with whale sharks *Rhiniodon typus* near the Galapagos Islands *Noticias de Galapagos*, pp 13-15.

Arnold G. P. 1981. Movement of fish in relation to water currents. In: *Animal Migration*. (Aidley D. J. ed.), pp 55-79. Cambridge. Cambridge University Press.

Baker C. S., Herman L. M., Perry A., Lawton W. S., Straley J. M., Wolman A. A., Kaufman G. D., Winn H. E., Hall J. D., Reinke J. M. & Ostman J. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Marine Ecology Progress Series*. **31**: 105-119.

Beckley L. E., Cliff G., Smale M. J. & Compagno L. J. V. 1997. Recent strandings and sightings of whale sharks in South Africa. *Environmental Biology of Fishes*. **50** (3): 343-348.

Bleckmann H. & Hoffman M. H. 1999. Special senses. In: *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes*. (Hamlett W. C. ed.), pp 300-328. Baltimore, Maryland 21218-4363. The Johns Hopkins University Press.

Block B. A. 2000. Mattanza - Love and death in the Sea of Sicily. *Science*. **289** (5481): 876-877.

Block B. A., Dewar H., Blackwell S. B., Williams T. D., Prince E. D., Farwell C. J., Boustany A., Teo S. L. H., Seitz A., Walli A. & Fudge D. 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science*. **293** (5533): 1310-1314.

Boles L. C. & Lohmann K. J. 2003. True navigation and magnetic maps in spiny lobsters. *Nature*. **421**: 60-63.

Boujard T. 1995. Diel rhythms of feeding activity in the European catfish, *Silurus glanis*. *Physiology & Behavior*. **58** (4): 641-645.

Boustany A. M., Davis S. F., Pyle P., Anderson S. D., Le Boeuf B. J. & Block B. A. 2002. Satellite tagging: expanded niche for white sharks. *Nature*. **415** (6867): 35-36.

Carey F. G. & Scharold J. V. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*. **106**: 329-342.

Chen C.-T., Liu K.-M. & Joung S.-J. 1996. Preliminary report on Taiwan's whale shark fishery. In: Fowler S. L., Reed T. M. & Dipper F. A. (eds.) *Elasmobranch Biodiversity, Conservation and Management*. The IUCN Species Survival Commission, Sabah, Malaysia, July 1997, pp 162-167.

Clark C. W. & Mangel M. 1986. The evolutionary advantages of group foraging. *Theoretical Population Biology*. **30**: 45-75.

Clark E. & Nelson D. R. 1997. Young whale sharks, Rhincodon typus, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes*. **50**: 63-73.

Colman J. G. 1997. A review of the biology and ecology of the whale shark. *Journal of Fish Biology*. **51** (6): 1219-1234.

COP12. 2002. Proposal for inclusion of whale sharks on Appendix II - Proponents India and Philippines. CITES. 24 pp.

Cummings S. M. & Morgan E. 2001. Time-keeping system of the eel pout, *Zoarces viviparus*. *Chronobiology International*. **18**: 27-46.

Dacey J. W. H. & Wakeham S. G. 1986. Oceanic dimethylsulphide: production during zooplankton grazing on phytoplankton. *Science*. **233**: 1314-1316.

Dacke M., Nilsson D. E., Warrant E. J., Blest A. D., Land M. F. & O'Carroll D. C. 1999. Built-in polarizers form part of a compass organ in spiders. *Nature*. **401**: 470-473.

Darling J. D. & Cerchio S. 1993. Movement of a humpback whale (*Megaptera-novaeangliae*) between Japan and Hawaii. *Marine Mammal Science*. **9** (1): 84-89.

Dingle H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, New York. 474 pp.

Dittman A. H. & Quinn T. P. 1996. Homing in Pacific salmon: mechanisms and ecological basis. *Experimental Biology*. **199** (1): 83-91.

Domeier M. L. & Colin P. L. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science*. **60** (3): 698-726.

Eckert S. A., Dolar L. L., Kooyman G. L., Perrin W. & Rahman R. A. 2002. Movements of whale sharks (*Rhincodon typus*) in South-East Asian waters as determined by satellite telemetry. *Journal of Zoology*. **257**: 111-115.

Eckert S. A. & Stewart B. S. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environmental Biology of Fishes*. **60** (1-3): 299-308.

Finstad W. O. & Nelson D. R. 1975. Circadian activity rhythm in the horn shark *Heterodontus francisci*: effect of light intensity. *Bulletin of the Southern California Acadamy of Sciences*. **74**: 20-26.

Fischer J. H., Freake M. J., Borland S. C. & Philips J. B. 2001. Evidence for the use of magnetic map information by an amphibian. *Animal Behaviour*. **62**: 1-10.

Fowler S. L. 2000. Whale sharks *Rhincodon typus* policy research and scoping study. The Nature Conservation Bureau. UK. 27 pp.

Goldman K. J. & Anderson S. D. 1999. Space utilization and swimming depths of white sharks, *Carcharodon carcharias*, at the south Farallon Islands, central California. *Environmental Biology of Fishes*. **56**: 351-364.

Graham J. B., Dewar H., Lai N. C., Lowell W. R. & Arce S. M. 1990. Aspects of shark swimming performance determined using a large water tunnel. *Journal of Experimental Biology*. **151**: 175-192.

Graham R. T. 2001. Technical Report - Whale Shark Research Project. MCSS. Mahé, Seychelles. 20 pp.

Graves J. E., Luckhurst B. E. & Prince E. D. 2002. An evaluation of pop-up satellite tag technology for estimating post release survival of blue marlin (*Makaira nigricans*) from a recreational fishery. *Fishery Bulletin*. **100**: 134-142.

Gruber S. H., Nelson D. R. & Morrissey J. F. 1988. Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian Lagoon. *Bulletin of Marine Science*. **43** (1): 61-76.

Gunn J. S., Stevens J. D., Davis T. L. O. & Norman B. M. 1999. Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Marine Biology*. **135**: 553-559.

Hanfee F. 2001. Gentle Giants of the Sea: A report on trade in whale shark off the Gujarat coast. TRAFFIC-India/WWF-India. 38 pp.

Harcourt R. G., Bradshaw C. J. A., Dickson K. & Davis L. S. 2002. Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology-Progress Series*. **227**: 11-24.

Hays G. C., Dray M., Quaife T., Smyth T. J., Mironnet N. C., Luschi P., Papi F. & Barnsley M. J. 2001. Movements of migrating green turtles in relation to AVHRR derived sea surface temperature. *International Journal of Remote Sensing*. **22** (8): 1403-1411.

Heide-Jorgensen M. P. & Dietz R. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. *Canadian Journal of Zoology*. **73** (11): 2120-2132.

Heilman M. J. & Spieler R. E. 1999. The daily feeding rhythm to demand feeders and the effects of timed meal-feeding on the growth of juvenile Florida pompano, *Trachinotus carolinus*. *Aquaculture*. **180** (1-2): 53-64.

Heyman W. & Kjerfve B. 2001. The Gulf of Honduras. In: *Coastal Marine Ecosystems of Latin America*, pp 1-27. Heidelburg. Springer-Verlag .

Heyman W. D., Graham R. T., Kjerfve B. & Johannes R. E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology-Progress Series*. **215**: 275-282.

Hill R. 1994. Theory of geolocation by light levels. In: *Elephant Seals: Population Ecology, Behaviour and Physiology*. (LeBoeuf B. J. & Laws R. M. eds.), pp 227-236. Berkeley. University of California Press.

Hoffman W., Fritts T. H. & Reynolds R. P. 1981. Whale sharks associated with fish schools off South Texas. *Northeast Gulf Science*. **5** (1): 55-57.

Holland K. N., Wetherbee B. M., Lowe C. G. & Meyer C. G. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Marine Biology*. **134**: 665-673.

Holland K. N., Wetherbee B. M., Peterson J. D. & Lowe C. G. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia*. **1993** (2): 495-502.

Hughes G. R., Luschi P., Mencacci R. & Papi F. 1998. The 7000-km oceanic journey of a leatherback turtle tracked by satellite. *Journal of Experimental Marine Biology and Ecology*. **229** (2): 209-217.

Huntingford F. 1984. *The Study of Animal Behaviour*. Chapman and Hall Ltd, London. 411 pp.

Hyrenbach K. D., Forney K. A. & Dayton P. K. 2000. Marine protected areas and ocean basin management. *Aquatic Conservation-Marine and Freshwater Ecosystems*. **10** (6): 437-458.

Kalmijn A. J. 1982. Electric and magnetic field detection in elasmobranchs. *Science*. **218** (26): 916-918.

Klimley A. P. 1987. The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes*. **18**: 122-133.

Klimley A. P. 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology*. **117** (1): 1-22.

Klimley A. P. 1996. Residency patterns of white sharks at the South Farallon Islands, California. In: *Great White Sharks: The Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. A. eds.), pp 365-374. San Diego, California. Academic Press, Inc.

Klimley A. P., Anderson S. D., Pyle P. & Henderson R. P. 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia*. **1992** (3): 680-690.

Klimley A. P., Beavers S. C., Curtis T. H. & Jorgensen S. J. 2002. Movements and swimming behaviour of three species of sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*. **63**: 117-135.

Klimley A. P., Butler S. B., Nelson D. R. & Stull A. T. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *Journal of Fish Biology*. **33**: 751-761.

Klimley A. P. & Nelson D. R. 1984. Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. *Behavioral Ecology and Sociobiology*. **15** (1): 45-54.

Klimley A. P., Pyle P. & Anderson S. D. 1996a. The behaviour of white sharks and their pinniped prey during predatory attack. In: *Great White Sharks: The Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. A. eds.), pp 175-192. San Diego, California. Academic Press.

Klimley A. P., Pyle P. & Anderson S. D. 1996b. Tail slap and breach: agonistic displays among white sharks? In: *Great White Sharks: The Biology of Carcharodon carcharias*. (Klimley A. P. & Ainley D. A. eds.), pp 241-256. San Diego. Academic Press.

Kohler N. E., Casey J. G. & Turner P. A. 1998. NMFS Cooperative shark tagging program, 1962-93: An atlas of shark tag and recapture data. *Marine Fisheries Review*. **60** (2): 1-87.

Lalli C. M. & Parsons T. R. 1997. *Biological Oceanography: An Introduction*. Butterworth-Heineman, Oxford. 314 pp.

Le Boeuf B. J., H. Perez-Cortes M., J. Urban R., Mate B. R. & F. Ollervides U. 2001. High gray whale mortality and low recruitment in 1999: potential causes and implications. *Journal of Cetacean Resource Management*. **2** (2): 85-99.

Legeckis R., Brown C. W. & Chang P. S. 2002. Geostationary satellites reveal motions of ocean surface fronts. *Journal of Marine Systems*. **37** (1-3): 3-15.

Lehodey P., Bertignac M., Hampton J., Lewis A. & Picaut J. 1997. El Niño Southern Oscillation and tuna in the western Pacific. *Nature.* **389**: 715-718.

Lohmann K. J., Cain S. D., Dodge S. A. & Lohmann C. M. F. 2001. Regional magnetic fields as navigational markers for sea turtles. *Science.* **294** (5541): 364-366.

Lopez J. C., Broglio C., Rodriguez F., Thinus-Blanc C. & Salas C. 2000. Reversal learning deficit in a spatial task but not in a cued one after telencephalic ablation in goldfish. *Behavioural Brain Research.* **109** (1): 91-98.

Loyacano H. A., Chappel J. A. & Gauthreaux S. A. 1977. Sun-compass orientation in largemouth bass, *Mocropterus salmoides. Transactions of the American Fisheries Society.* **106**: 77-79.

Mate B., Rossbach K. A., Nieukirk S. L., Wells R. S., Irvine A. B., Scott M. D. & Read A. J. 1995. Satellite-monitored movements and dive behaviour of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science.* **11** (4): 452-463.

McKibben J. N. & Nelson D. R. 1986. Patterns of movement and grouping of grey reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bulletin of Marine Science.* **38** (1): 89-110.

Merino M. 1997. Upwelling on the Yucatan Shelf: hydrographic evidence. *Journal of Marine Systems.* **13** (1-4): 101-121.

Mills C. E. & Carlton J. T. 1997. Rationale for a system of international reserves for the open ocean. *Conservation Biology.* **12** (1): 244-247.

Montgomery J. C., Baker C. F. & Carton A. G. 1997. The lateral line can mediate rheotaxis in fish. *Nature.* **389**: 960-963.

Montgomery J. C. & Walker M. M. 2001. Orientation and navigation in elasmobranchs: which way forward? *Environmental Biology of Fishes.* **60**: 109-116.

Morrissey J. F. & Gruber S. H. 1993. Home range of juvenile lemon shark, *Negaprion brevirostris. Copeia.* **1993** (2): 425-434.

Mouritsen H. 2001. Navigation in birds and other animals. *Image and Vision Computing.* **19** (11): 713-731.

Nelson D. R., McKibben J. N., Strong W. R., Lowe C. G., Sisneros J. A., Schroeder D. M. & Lavenberg R. J. 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes.* **49**: 389-399.

Nevitt B. A., Veit R. R. & Kareiva P. 1995. Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds. *Nature.* **376**: 680-682.

Nevitt G. 1999. Foraging by seabirds on an olfactory landscape. *American Scientist.* **87**: 46-53.

Norse E. A., Roberts C. M., Soule M. E., Crowder L. B. & Safina C. in press. Marine reserves for large pelagic species:

Papi F., Luschi P., Akesson S., Capogrossi S. & G. H. 2000. Opcn-sca migration of magnetically disturbed sea turtles. *The Journal of Experimental Biology.* **203**: 3435-3443.

Pardini A. T., Jones C. S., Noble L. R., Kreiser B., Marlcolm H., Bruce B. D., Stevens J. D., Cliff G., Scholl M. C., Francis M., Duffy C. A. & Martin A. P. 2001. Sex-biased dispersal of great white sharks. *Nature.* **412**: 139-140.

Pratt H. L. & Carrier J. C. 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum. Environmental Biology of Fishes.* **60**: 157-188.

Priede I. G. 1984. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote-sensing. *Fisheries Research.* **2** (3): 201-216.

Romanov E. V. 2002. Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. *Fishery Bulletin.* **100** (1): 90-105.

Ryer C. H. & Olla B. L. 1995. Influences of food distribution on fish foraging behaviour. *Animal Behaviour.* **49**: 411-418.

Salo O. & Rosengren R. 2001. Memory of location and site recognition in the ant *Formica uralensis* (Hymenoptera: Formicidae). *Ethology.* **107**: 737-752.

Sanchez-Vazquez F. J., Zamora S. & Madrid J. A. 1995. Light-dark and food restriction cycles in sea bass: effect of conflicting zeitgebers on demand-feeding rhythms. *Physiology & Behavior.* **58** (4): 705-714.

Sciarrotta T. C. & Nelson D. R. 1977. Diel behaviour of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. *Fishery Bulletin.* **75** (3): 519-528.

Seitz A., Wilson D. & Nielsen J. L. 2002. Testing pop-up satellite tags as a tool for identifying critical habitat for Pacific halibut (*Hippoglossus stenolepsis*) in the Gulf of Alaska. USGS. Anchorage, Alaska. 43 pp.

Sims D. W. 1999. Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife edge? *Proceedings of the Royal Society of London Series B-Biological Sciences.* **266**: 1437-1443.

Sims D. W. 2000. Filter-feeding and cruising swimming speeds of basking sharks compared with optimal models: they filter-feed slower than predicted for their size. *Journal of Experimental Marine Biology and Ecology.* **249** (1): 65-76.

Sims D. W., Fox A. M. & Merrett D. A. 1997. Basking shark occurrence off south-west England in relation to zooplankton abundance. *Journal of Fish Biology*. **51** (2): 436-440.

Sims D. W. & Quayle V. A. 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature*. **393**: 460-464.

Sims D. W. & Reid P. C. 2002. Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland). *Fisheries Oceanography*. **11** (1): 59-63.

Sims D. W., Southall E. J., Quayle V. A. & Fox A. M. 2000. Annual social behaviour of basking sharks associated with coastal front areas. *Proceedings of the Royal Society of London Series B-Biological Sciences*. **267**: 1897-1904.

Sims D. W., Southall E. J., Richardson A. J., Reid P. C. & Metcalfe J. D. 2003. Seasonal movements and behaviour of basing sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series*. **248**: 187-196.

Stevens J. D., Norman B. M., Gunn J. S. & Davis T. L. O. 1998. Movement and behavioural patterns of whale sharks at Ningaloo Reef: the implications for tourism. National Ecotourism Final Report: Application Ref. No. 30051. CSIRO Marine Research. 35 pp.

Strong W. R., Murphy R. C., Bruce B. D. & Nelson D. R. 1992. Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: A preliminary report. *Australian Journal of Marine and Freshwater Research*. **43**: 13-20.

Sundstrom L. F., Gruber S. H., Clermont S. M., Correia J. P. S., Marignac J. R. C. D., Morrissey J. F., Lowrance C., Thomassen L. & Oliveira M. T. 2001. Review of elasmobranch behavioral studies using telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes*. **60**: 225-250.

Taylor J. G. 1994. *Whale Sharks, the Giants of Ningaloo Reef*. Angus & Robertson, Sydney.

Taylor J. G. 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*. **47** (4): 637-642.

Walker M. M. 1984. Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. *Science*. **155**: 673-679.

Walker M. M., Diebel C. E., Haugh C. V., Panhurst P. M., Montgomery J. C. & Green C. R. 1997. Structure and function of the vertebrate magnetic sense. *Nature*. **390**: 371-376.

Weihs D. 1973. Optimal fish cruising speed. *Nature*. **245**: 48-50.

Weinrich M., Martin M., Griffiths R., Bove J. & Schilling M. 1997. A shift in distribution of humpback whales, *Megaptera novaeangliae*, in response to prey in the southern Gulf of Maine. *Fishery Bulletin*. **95**: 826-836.

Welch D. W. & Eveson J. P. 1999. An assessment of light-based geoposition estimates from archival tags. *Canadian Journal of Fisheries and Aquatic Sciences*. **56**: 1317-1327.

Whitehead H. 1996. Variation in the feeding success of sperm whales: temporal scale, spatial scale and relationship to migration. *Journal of Animal Ecology*. **65** (4): 429-438.

Wilson S. G., Taylor J. G. & Pearce A. F. 2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/Southern Oscillation. *Environmental Biology of Fishes*. **61** (1): 1-11.

Winn H. E., Salmon M. & Roberts N. 1964. Sun-orientation by parrot fishes. *Ethology*. **21**: 798-812.

Wolanski E. & Hamner W. M. 1988. Topographically controlled fronts in the ocean and their biological influence. *Science*. **241**: 177-181.

Wolfson F. H. 1986. Occurrences of the whale shark, *Rhincodon typus*, Smith. In: Uyeno T. & et. al. (eds) *Indo -Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*. Ichthyological Society of Japan, Tokyo, pp 208-226.

Zoeger J., Dunn J. R. & Fuller M. 1981. Magnetic material in the head of the common Pacific dolphin. *Science*. **213**: 892-894.

Chapter 5. Patterns of whale shark diving over variable time scales

Abstract

Whale sharks are proving more physiologically robust and closer to marine mammals in their diving behaviour than previously thought. Using satellite pop-off archival tags, the diving patterns of whale sharks over different time scales and in relation to a predictable food source, the seasonal spawn of aggregating snappers, was investigated. Satellite tags deployed over periods of 14 days to 206 days provided dive data on four male whale sharks. All four recorded dives of over 1000 m to depths with temperatures of less than 8.5^{0}C, with one shark (S4) withstanding ambient water temperatures below 4.35^{0}C with possible dives to below 1500 m. All sharks displayed diel oscillatory diving behaviour, with shallow diving taking place at night and deeper dives taking place during the day. Similar to marine mammals, whale shark ascents are significantly faster than descents during directed dives over 500 m. The recovery of a satellite tag from a shark (S4) with 206 days of archived data on depth and temperature logged every 60 seconds provided an unprecedented fine-scale dive data for a shark. Dive data from S4 displayed clear periodicities at 45 minutes, 8 hours, 24 hours and 29 days indicating the possible existence of free-running endogenous ultradian, circadian and circalunar rhythms.

5.1 Introduction

Understanding patterns of diving in sharks provides insights into the processes that regulate their foraging behaviour throughout the water column. Deep diving imposes many physiological stresses on an organism including increased hydrostatic pressure, decreased light and temperature that the organism must counteract with physiological or behavioural mechanisms (Boyd, 1997; Willmer *et al.*, 2000).

Many difficulties exist in studying the diving behaviour of large pelagic marine fish. Researchers have gleaned most insights through the use of acoustic tracking (Sciarrotta & Nelson, 1977; Carey & Scharold, 1990; Nelson *et al.*, 1997; Gunn *et al.*, 1999). However, this method is only feasible over the short-term and is both labour- and cost-intensive. To elucidate longer term or seasonal diving patterns, researcher-independent methods are required. Recently developed pop-up satellite archival tags that record the study animal's ambient environmental parameters have proved key in revealing diel and seasonal diving patterns of marine species long after researchers have released the study animal. Although most of these tags have been deployed on marine mammals and turtles (Le Boeuf *et al.*, 1988; Delong & Stewart, 1991; Mate *et al.*, 1995; Hochscheid *et al.*, 1999; Hooker & Baird, 1999; Bekby & Bjorge, 2000; Hays *et al.*, 2000), the decline of stocks of commercially-important species of teleost fish such as tuna and billfish have prompted the use of these fisheries-independent monitoring techniques to reveal patterns of movement (Block *et al.*, 1998; Lutcavage *et al.*, 1999; Block *et al.*, 2001; Marcinek *et al.*, 2001; Graves *et al.*, 2002).

Only three studies have yielded diving data for shark species based on the use of satellite tags, including basking sharks (*Cetorhinus maximus*) (Sims *et al.*, 2003), white sharks (*Carcharodon carcharias*) (Boustany *et al.*, 2002) and whale sharks (*Rhindocodon typus*) (Eckert & Stewart, 2001). Previous research on shark diving behaviour has relied on acoustic telemetry (Klimley & Nelson, 1984; Klimley *et al.*, 1988; Carey & Scharold, 1990; Holland *et al.*, 1993; Klimley, 1993; Nelson *et al.*, 1997; Gunn *et al.*, 1999; Sundstrom *et al.*, 2001; Klimley *et al.*, 2002). Results indicate that several species of shark make brief oscillatory or 'yo-yo' dives interspersed with less frequent deep dives (Carey & Scharold, 1990; Nelson *et al.*, 1997; Eckert & Stewart, 2001; Klimley *et al.*, 2002). Patterns of locomotory activity and diving are thought to be regulated by circadian rhythms (Finstad & Nelson, 1975), which may be synchronized by light (Carey & Scharold, 1990; Nelson *et al.*, 1997).

Very little is known about whale shark diving behaviour in particular. Whale sharks are coastal-pelagic planktivores distributed throughout the world's tropical seas (Gudger, 1915; Colman, 1997). Measuring up to 18 m in length (Chen, unpublished data), whale sharks are able to feed opportunistically on a range of small nekton including many species of zooplankton (Gudger, 1915), copepods (Clark & Nelson, 1997), small fish and squid (Colman, 1997), and fish eggs (Heyman *et al.*, 2001) (see Chapter 1 for more information on whale sharks). Two studies using acoustic telemetry and satellite tags respectively have yielded data on their diving patterns indicating that they are a shallow epipelagic species that spend the majority of their time in water around 28^0C (Gunn *et al.*, 1999; Eckert & Stewart, 2001).

The objectives of this study were to investigate the behaviour and rhythmicity of whale shark diving in the Western Caribbean using data from pop-up satellite archival tags deployed between 2000 and 2001.

5.2 Materials and methods

5.2.1 Study area

A full description and map of the site is given in Chapter 1, and a satellite photo of the research region is noted in Figure 5.1. The present study ran from 23 April 2000 to 28 March 2002 and is based on the analysis of depth, temperature and irradiance data acquired following deployment of 11 satellite archival pop-off tags deployed on nine whale sharks.

5.2.2 Satellite archival pop-off tags

Eleven satellite archival pop-off tags (Wildlife Computers, Redmond, Washington) were deployed on nine whale sharks at Gladden Spit during 2000 and 2001. Sat-tags record depth as pressure, light levels as irradiance, and temperature in degrees Celsius every 60 seconds (user-set intervals) (Figures 5.2a & 5.2c). Tags have a maximum depth reading capability of 979.5 m and are pressure tested to 1,500 m. Settings for all satellite tags deployed at Gladden Spit are listed in Tables 5.1 and 5.2. Tags were rigged up and deployed from the boat using a pole-spear in the same manner as marker and acoustic tags noted in Chapters 2 and 3. Deployment times varied with each tag and ranged between 14-249 days (Table 5.3).

Table 5.1: Satellite tag sensor settings and resolution for deployed satellite pop-off archival tags.

Sensor	Setting	Resolution
Depth	-20 m to 99.5 m	1 m
	100 m to 199.5 m	2 m
	200 m to 299.5 m	4 m
	300 m to 499.5 m	8 m
	500 m to 979.5 m	16 m
Temperature	-40 ^{o}C to 60 ^{o}C	0.5 ^{o}C
	0 ^{o}C to 37.45 ^{o}C	0.15 ^{o}C
Light levels	0 to 225 Ir	1 Ir †

† Light level is measured as irradiance at a wavelength of 550nm. The sensor measures from 5 x 10–12 W.cm^{-2} to 5 x 10^{-2} W.cm^{-2} in logarithmic units. Dawn and dusk events can be discriminated at depths up to 300m in clear water conditions (Source: Wildlife Computers pat-tag manual).

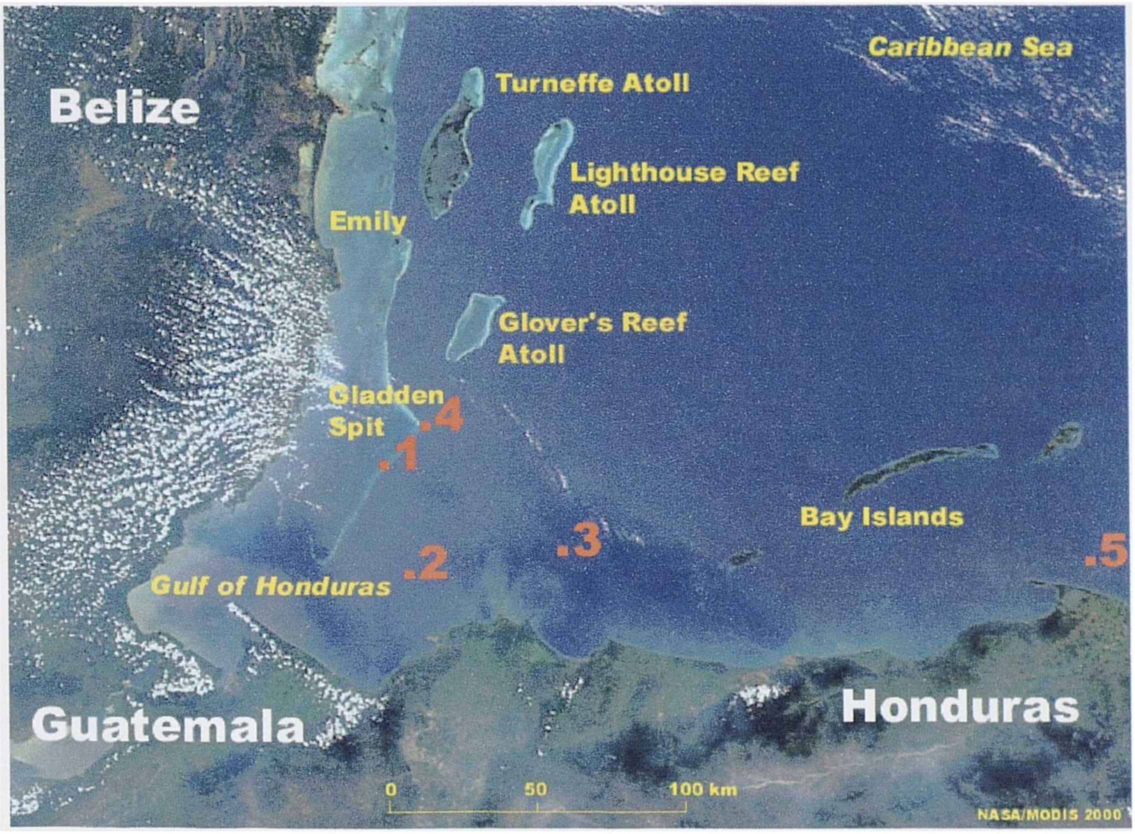
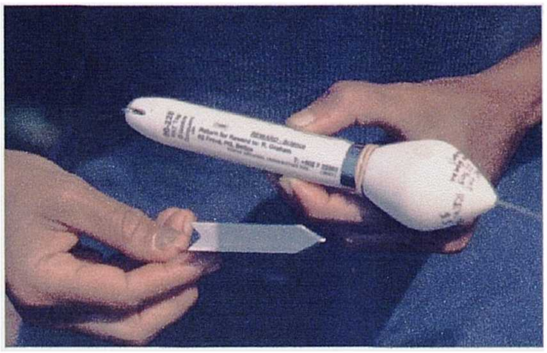
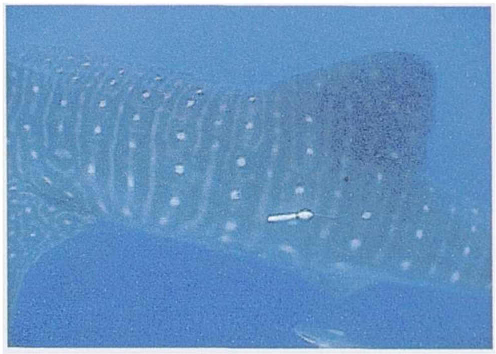


Figure 5.1: Detachment locations for four satellite pop-off tags (S1-3 and S5) and removal from shark (S4) between 2000 and 2001. All deployments took place at Gladden Spit at the S4 retrieval site (base photo courtesy of NASA/MODIS 2000).



(a)



(b)

(c)

(d)

Figure 5.2: (a) Photograph of a satellite tag and old-style titanium dart before deployment (subsequently dart was changed to a lighter version) and (b) deployed on the shark; (c) Fouled satellite tag on whale shark S4 one year after deployment, and (d) after direct retrieval from the shark following pop-off malfunction.

Table 5.2: Resolution for temperature and pressure settings for all satellite-tag three-hour data summaries.

Summaries	1	2	3	4	5	6	7	8	9	10	11	12
Depth (m)	0	10	50	100	150	250	350	450	550	650	750	979.5
Temp. (^{0}C)	5	7.5	10	12.5	15	17.5	20	22.5	25	27.5	30	60

All tags were tested for functioning pressure, temperature and light sensors both by the manufacturer and in the field using the Wildlife Computers PAT-Host software.

To facilitate transmission of data to polar-orbiting Argos system satellites following detachment, tags averaged the 60-second archival data into 3-hour summaries. Once detached, sat-tags floated to the surface, and the data were transmitted to the Argos satellite in 32-byte messages. Location data were set as priority transmissions for the first three days following detachment. The tags had sufficient battery power to transmit up to 20 days and enable a full download of data summaries. Subsequent to detachment of the tags, Argos satellites record locations of the drifting tags by measuring the Doppler shift in the tag's signal frequency. Argos assigns a location class to each fix (Quality 3, 2, 1, 0, A, B, Z) with 3 being the highest quality data representing location accuracy of less than 150 m from the tag. Argos determines the transmission's location quality by the number of messages received per tag, the angle between the satellite and the tag, and transmission stability. The Argos Service Processing Centre in Largo (Maryland, USA) process data initially according to the requirements of the project (large marine animal platform, transmission repeat rate of 45 seconds). Data are then sent to the user by email for pasting into software provided by Wildlife Computers which sorts the individual records into minimum and maximum temperatures per three-hour summary, into average and maximum depths for each three-hour summary, and calculates estimated longitude from irradiance data.

5.2.3 Analyses

Depth data for tagged whale sharks denoted S1-4 were analysed for maximum depth and minimum temperature attained per shark per 3-hr data summary and per day. Data were further analysed for the percentage of time spent per day at different depths and percentage time at depth according to the time of day. Diel, lunar and seasonal diving patterns were analysed based on the summary data of tags S1-4 and the full archival 60s interval data from S4. "Day" was calculated based on the time from sunrise to sunset in Belize (data obtained from the Belize's hydrometeorological organisation).

Table 5.3: Summary of satellite tag deployment and detachment for 11 whale sharks. All deployments took place at Gladden Spit at 16°30'N, 87°57'W.

Sat-tag Number	Marker tag	Acoustic tag	Sat tag	Size (m)*	Sex	Original duration of deployment (days)	Deploy date and location	Pop-up date	Pop-up Latitude	Pop-up longitude	Max depth (m)	Max Water Temp ^{0}C	Min Water Temp ^{0}C
S1	M044		27610	5.5	JM	14	23-4-00	7-5-00	16.38	88.05	>980	>30.0	<7.5
S2	M045		27611	3.6	JM	40	23-4-00	2-6-00	16.04	87.98	>980	28.6	<7.5
S3	M075		27989	9.7	MM	188	11-4-01	15-10-01	16.11	87.52	>980	30.6	<7.5
S4 *	M043		27989	6.7	JM	248	11-4-01	Cut off	16.30	87.57	>980	30.8	4.35
S5 **	M043		27609	6.7	JM	14	21-4-00	6-5-00	15.92	86.05	>650	>30.0	<12.5
S6 ***	M048		27865	5.5	?	105	25-4-00	8-8-00	15.99	87.95	NA	NA	NA
S7 ***	M048		27866	5.5	?	40	25-4-00	12-6-00	16.45	88.01	NA	NA	NA
S8 +			27988	5.2	JM	127	16-3-01	31-7-01	?	NA	NA	NA	NA
S9 +	M073	A8	27987	6.7	JM	187	11-4-01	30-6-01	?	NA	NA	NA	NA
S10 +	M070		28961	5.2	JM	163	11-4-01	-	?	NA	NA	NA	NA
S11 ++	M080		28962	5.5	?	249	10-5-01	3-7-01	16.22	88.88	NA	NA	NA

* Tag was recovered directly from the shark in March 2002; ** Tag provided pop-off location and an incomplete set of data only; *** Tag fell off prematurely, sank to the sea-floor but popped off on time and reported data; + Tag failed to report position and data; ++ Tag reported position but failed to report data. NA = Data not available.

Data were analysed using the statistical package SPSS and tested for normality using Kolmogorov-Smirnov. Normal data were analysed using parametric tests and non-normal results were analysed using non-parametric tests.

In collaboration with Jim Smart (University of York), dive data were analysed using the Fast Fourier Transform (FFT) technique within the software MATLAB to identify any periodic signals in diving depths. Smart states: "Frequency domain analysis provides an immediate means of appraising the periodic content of the time-series data stream, but does not present underlying temporal relationships in a readily accessible manner. Frequency domain analysis could immediately identify the presence of, for example, a daily or hourly cycle in depth variation within the overall pattern of movement of the fish, but would not necessarily identify whether such periodicity was only present during only the first three months of monitoring or occurred sporadically over the whole monitoring period."

All depth data for S4 over 206 days (252,429 data points) were presented as frequencies in 50, 5 and 0.25 cycles per day representing periods of time from > 24 h to < 45 min. Dives at and over 500 m lasting 5 minutes or more (includes descents and ascents) were classified as deep dives due to S4's distinctive mode of behaviour of diving in a very directed manner at and following this depth (n = 49, 1074 data points). Diving data were also segregated into two time periods: dive data recorded during the fish spawning season and outside of the spawning period.

It was not possible to objectively discriminate between spectral peaks so the criteria of >50% of magnitude of the surrounding spectral pattern noise was used to highlight peaks representing dive periodicities. To determine if deep dives had any effect on the remaining dive behaviour of S4, deep dives were removed from the data set and repositioned randomly throughout the < 499 m shallower water dive data recorded for 206 days. The repositioning algorithm prevented overwriting of one deep dive with another during reinsertion. The algorithm ran 100 iterations with the 252,429 data points. A FFT frequency spectrum was produced for each iteration and averaged. 99.9% confidence intervals about the mean magnitude of each spectral component were calculated from the standard error of the mean for each spectral component.

5.3 Results

5.3.1 Tag recovery and performance

In total 11 satellite tags were deployed within the Gladden Spit Marine Reserve between 2000 and 2001. Six tags detached to provide pop-off locations (Table 5.3). Two sharks were double tagged with satellite tags to assess tag-shed rates, one with tags S4 and S5 and the second shark with tags S8 and S9. Four tags detached within 100 km of Gladden Spit (nos. S1, S2, S3 and S11). Tag S5 detached 214 km SE of Gladden Spit off the north coast of Honduras, and tag S4 was retrieved directly from the shark on 28 March 2002 (Figure 5.1). Six tags released at the pre-programmed date but only four (S1-4) provided usable data on the diving behaviour of whale sharks and their timing relative to the snapper spawning aggregation periods. S6 and S7 fell off the same shark prematurely and sank to the sea-floor weighted down by their darts. S6 malfunctioned but S7 recorded the ambient temperature at 450 m for 40 days before detaching at the pre-programmed time from the dart, then surfaced and transmitted data. S8-S10 released prematurely and provided no position or data. S11 provided locations only. S4 never reported back.

Tag malfunction was clarified following the retrieval of S4. Tag S4 was found still attached to a whale shark that returned in March 2002. The tag was heavily fouled (Figure 5.2c & 5.2d) and clipped off by a research associate diver (D. Castellanos) and sent back to the manufacturers to check the malfunction. The tag-maker subsequently found that the tag's pin detachment mechanism had malfunctioned but the tag contained a full set of archival and summary data. The tag provided a minute-by-minute view of the whale shark's diving behaviour and ambient temperature over the course of 206 days at sea from 11 April to October 4 2001. No archival memory to store fine-scale data was left after this date. Programmed to detach on 15 December 2001, the tag compiled 3-hr summary data until 25 November 2001 until the memory was filled. However, these data can only be considered usable until the 31 October. This is because analysis of the archived data further yielded a clue to the tag's pop-off malfunction. On 31 October 2001, the whale shark dived to over 1,000 m according to the depth data and the tag ceased to record depth and temperature accurately, i.e., showing continuous recording of a single temperature and depth, which contradict whale shark diving behaviour. The manufacturers noted that the pressure and temperature sensors were broken, possibly caused by a dive to beyond the 1,500 m rated depth limit of the tag

(Roger Hill, pers. comm. 2002). It is highly plausible that the other non-reporting or prematurely released tags were attached to sharks that dived beyond tag limits.

Sat-tags transmitted usable data in three formats, the 3-hr depth and temperature summary data (PDT) and the "time at depth" and "time at temperature" summaries (percentage of time at predetermined ranges of depths or temperatures). Successful PDT data retrieval from sat-tags reached 34.2%. This includes data from the retrieved tag S4 and tag S7 that fell off their shark five days after tagging but transmitted data recorded during deployment. If only data from the four tags that transmitted data after popping-off are assessed (S1-S3, S7), success drops to 22.7%. There is a clear decay in percentage of usable data with length of deployment (Figure 5.3). S4 is discussed separately since it was retrieved directly from the shark. However, tags often provided more data in the "time at depth" and "time at temperature summaries" (percentage of time at predetermined ranges of depths or temperatures) than in the PDT data that combines both. S1 with a 14-day deployment produced 46.3% usable PDT data with 50 usable 3-hr data summaries out of a possible total of 108. S2 was deployed for 40 days for a possible total of 308 transmitted summaries: 61 summaries or 19.8% PDT data were transmitted. S3 was deployed for 188 days with 1492 possible summaries, and 94 summaries or 6.3% usable data was retrieved. S4 was originally deployed for 249 days for a possible total of 1980 3-hr summaries. Due to the direct retrieval of this tag from the shark following the tag malfunction, 1587 summaries were considered usable representing 80.2% of PDT data. S7 transmitted 56 out of a possible 308 3-hr summaries to yield 18.2% usable data. Longitudinal data derived from recorded light levels for tags S3 and S4 are discussed in Chapter 4.

5.3.2 Diving behaviour

All four sharks (S1-S4) displayed a range of diving behaviours based on recorded depths and time spent at depth. All sharks dived to beyond 1000 m (Table 5.3). To determine at what depths S1-S4 spent the majority of time (0-50 m; 50-250 m; 250-550 m; 550-1000 m; >1000 m), minutes at depth were compared and illustrated in Figures 5.4 and 5.5 as percentage time at depth. S1, S3 and S4 spent the greatest proportion of their time in 50-250 m (Kruskal-Wallis test: df = 4; χ^2 = 320.2; p < 001) with S4's longer-term deployment revealing a mean depth of 58 m ± 44 m SD, indicating that they are primarily epipelagic. However S3 and S4 display a bimodal pattern of spending more time at 0-50 m and 250-1000 m during the day as compared to 50-250 m at night (20:00-4:59) (Figure 5.4). Although S4's temperature data indicated that it was able to

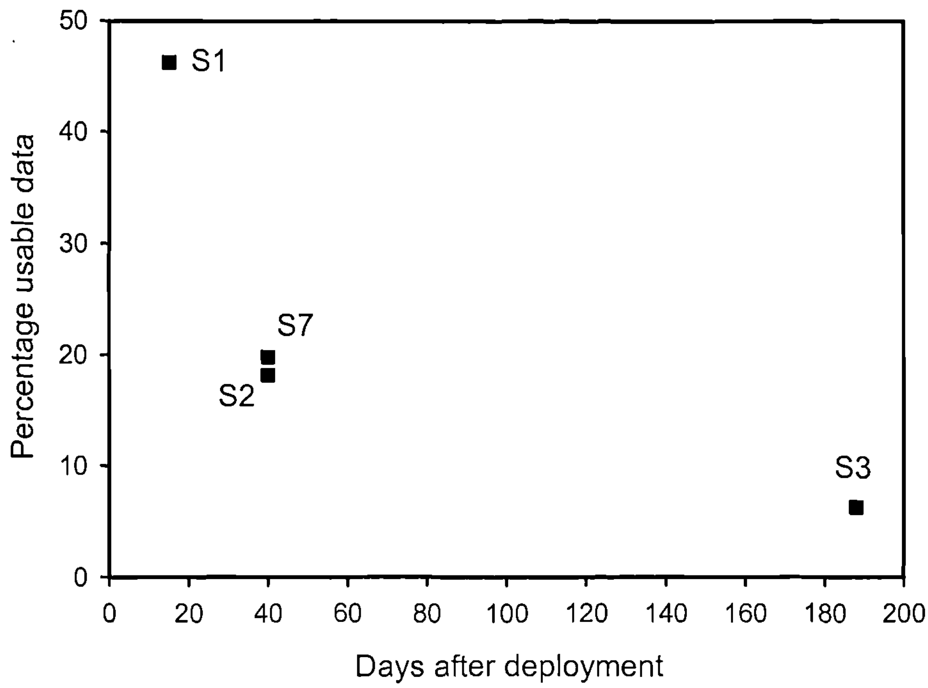


Figure 5.3: Percentage of usable data received from 4 satellite tags (S1-3, S7) deployed between 2000 and 2001. Data are based on 3 hr PDT summaries compiled by the tags and transmitted following pop-off.

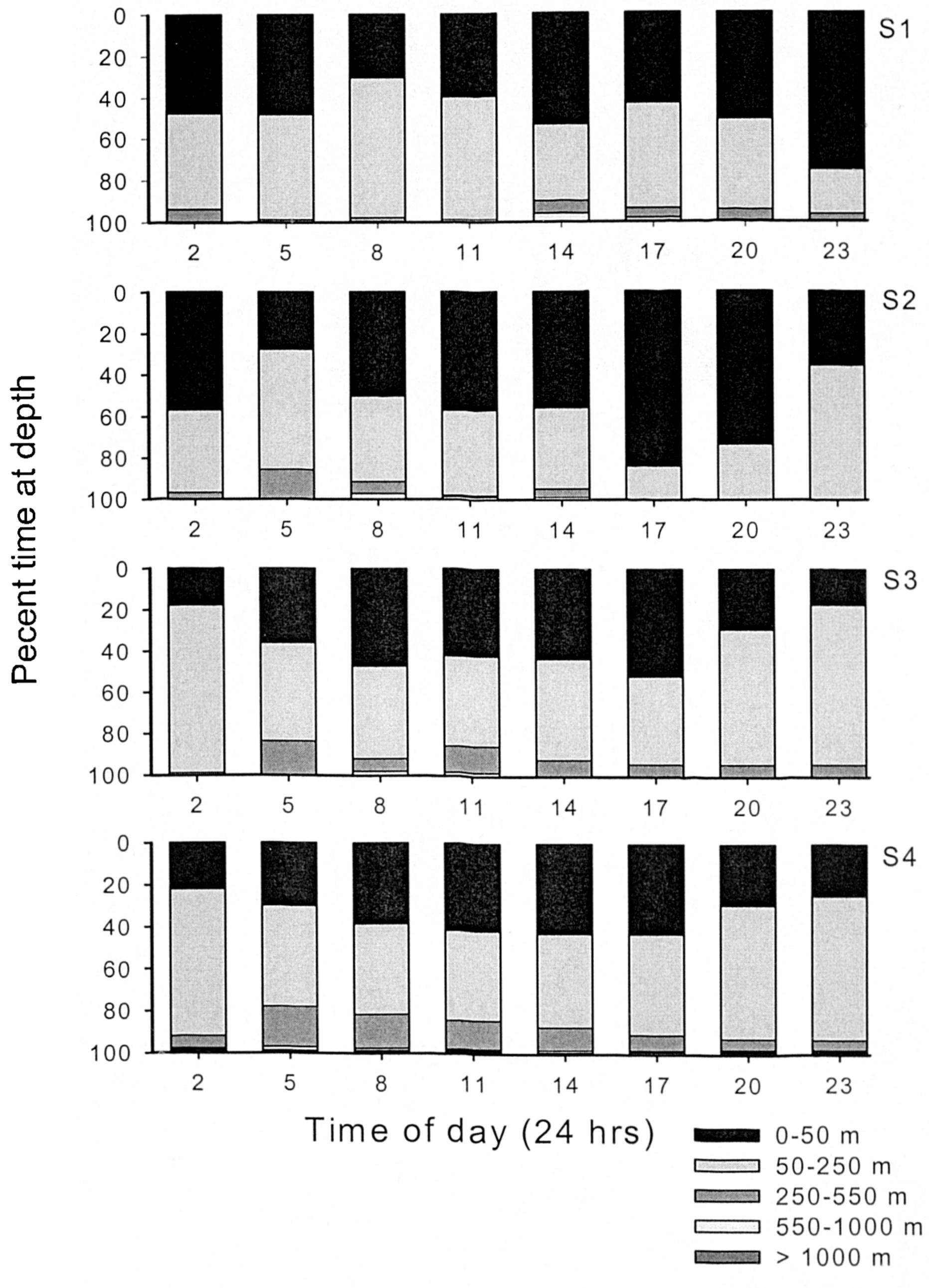


Figure 5.4: Percentage of time at each depth for all tag deployment days recorded by the satellite for S1-4. Each stacked bar represents a mean of all minutes spent at specific depth composites for each 3-hour summary shown. The hours are based on a 24 hr clock and represent local time in Belize when 180-minute data summaries were compiled during 8 periods of the day.

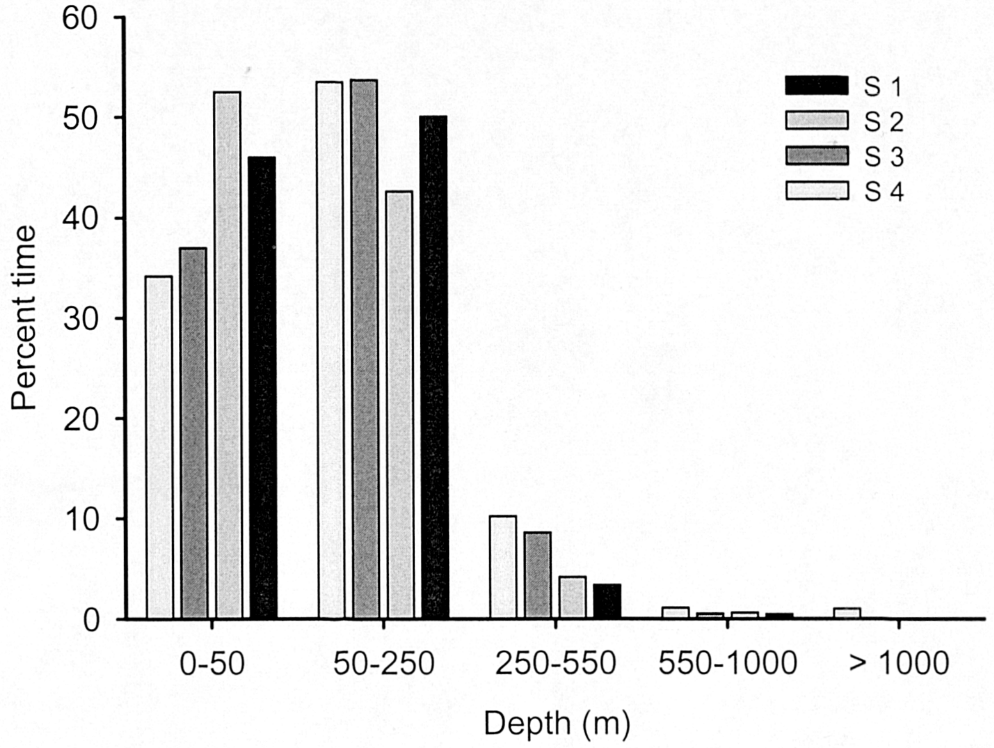


Figure 5.5: Percent time spent by S1-4 at 5 depth composites during the deployment of their respective satellite-tags.

tolerate a temperature range of 26.4^{0}C (range 4.35^{0}C to 30.75^{0}C), S1-S4 spent over 80% of their time in waters warmer than 25^{0}C (Figures 5.6 and 5.7) which indicates that they are spending the majority of their time above 100 m. Occasional forays at depth are brief and as such are not well represented in the cooler temperatures. Mean temperature at 30 m at the Gladden Spit snapper spawning site was 27.7^{0}C ± 0.91 SD (measured between 2 January 2002 and 19 March 2003). S4's complete data set enabled a detailed characterisation of its diving behaviour during the 206-day deployment. S4 displayed a range of diving behaviours (Figure 5.8a) including oscillatory or yo-yo diving and directed deep dives. In Figure 5.8b the dawn and dusk depth-changing transitions highlight a clear diel behavioural pattern swimming deeper during the day and shallower at night. Finer scale diving detail is displayed in Figures 5.9 and 5.10 with two 24 h periods coinciding with 21 May and 14 September 2001. The shark initiated deeper dives with the onset of day and ascended to the shallows at dusk. The regular oscillatory diving pattern at night rarely exceeded depths of 200 m. Day dives and oscillations display a steep vertical profile whereas night dives often plateau for periods of up to an hour.

While diving to depths of less than 500 m, S4 primarily displayed ranging behaviour at depth, mixed with frequent shallow oscillatory dives. However, in dives over 500 m S4 displayed the hallmarks of a deep excursion with a steep profile of descent and ascent. As a result, these dives are considered deep-directed dives and treated separately from dives less than 500 m. S4 took significantly longer to descend than ascend to the surface when diving over 500 m (Wilcoxon paired ranks test: $Z = -2.32$; $p < 0.05$) (Figure 5.11). In all S4's dives over 500 m ($n = 49$), the mean period of descent of 38.8 minutes (range 8-111 min ± 27.6 SD) was almost one and half times as slow as the mean period of ascent of 29.3 minutes (range 11-92 min ± 15.3 SD).

In the six deep dives over 980 m undertaken over the course of 206 days (dates in 2001: 29-5; 1-7; 25-7; 28-7; 31-7; 14-9), ascents were twice as fast as descents as reflected in Figure 5.12 (descent: range 38-98, $\bar{X}$: 52.9 min ± 22.2 SD) (ascent: range 32-72, $\bar{X}$: 29.7 min ± 15.3 SD) (Wilcoxon paired ranks test: $z = -1.992$; $p < 0.05$). The fastest ascent recorded from dives beyond 980 m ($n = 6$) to the surface was 32 minutes, 25.5 m min^{-1} or 3.8 body-lengths minute ^{1} (BL min^{-1}) or 0.06 BL second^{-1} (BL s^{-1}) for the 6.7 m shark. Mean descent period for all dives over 980 m was 61 minutes or 16.1 m min^{-1} (2.4 BL min^{-1}, 0.04 BL s^{-1}) and mean ascent was 41.5 minutes or 23.6 m min^{-1} (3.5 BL min^{-1}, 0.06 BL s^{-1}).

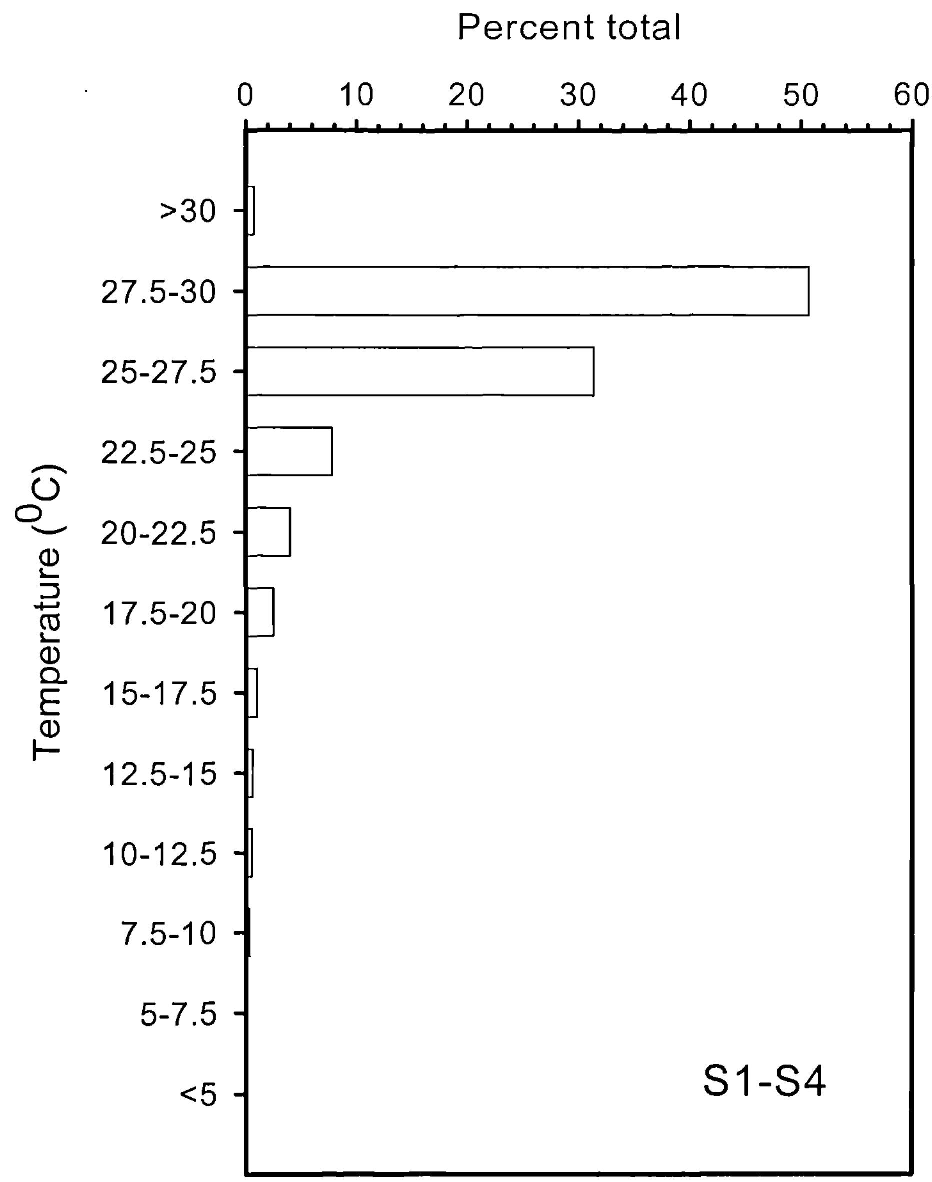


Figure 5.6: Percentage of time at each temperature (^{0}C) recorded during deployment for four whale sharks tagged with satellite tags S1-S4 (n = 1777).

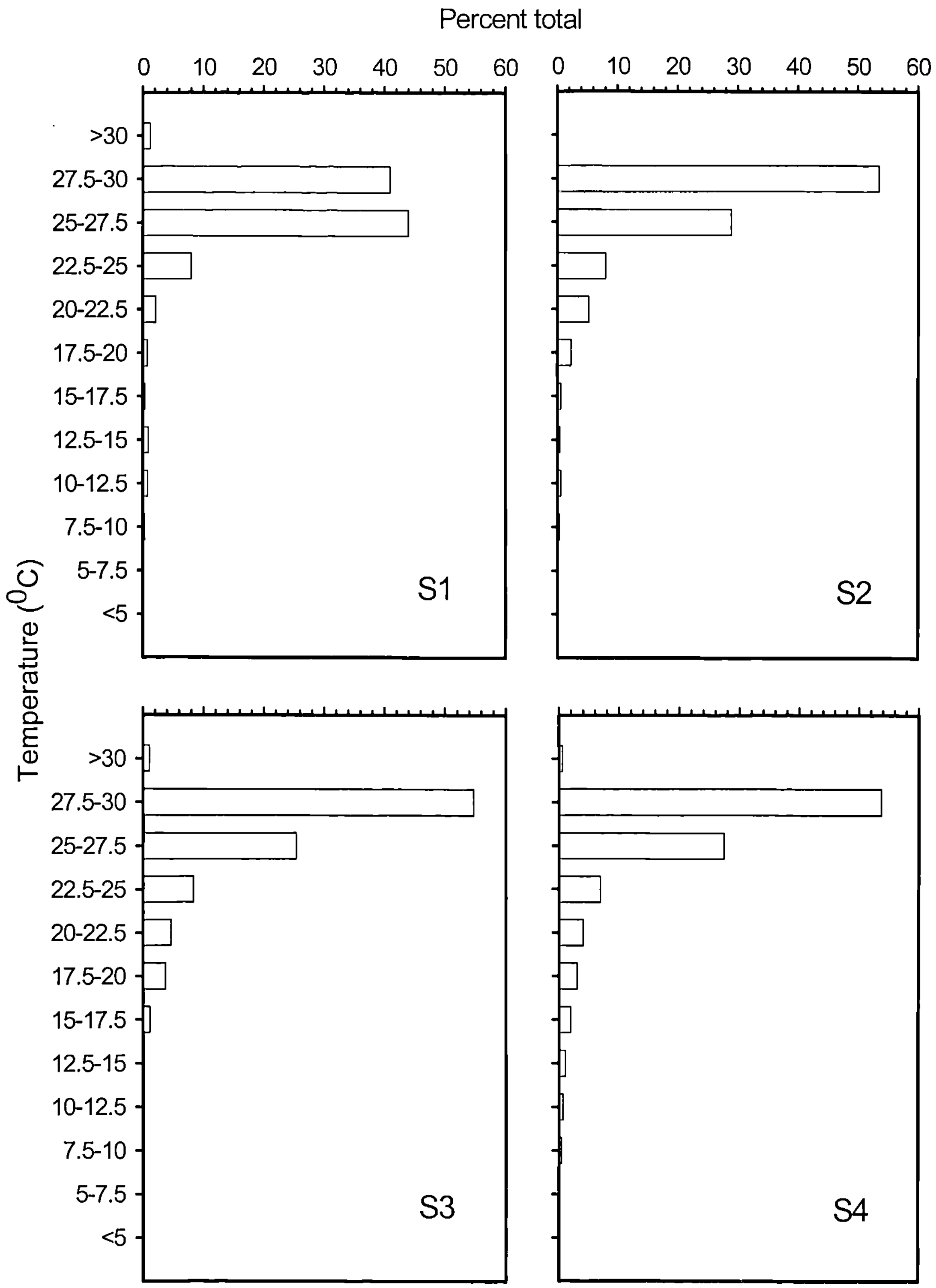


Figure 5.7: Percentage of time at each temperature summary (^{0}C) recorded during deployment for four whale sharks tagged with satellite tags S1 (n = 54), S2 (n= 47), S3 (n= 79) and S4 (n = 1597).

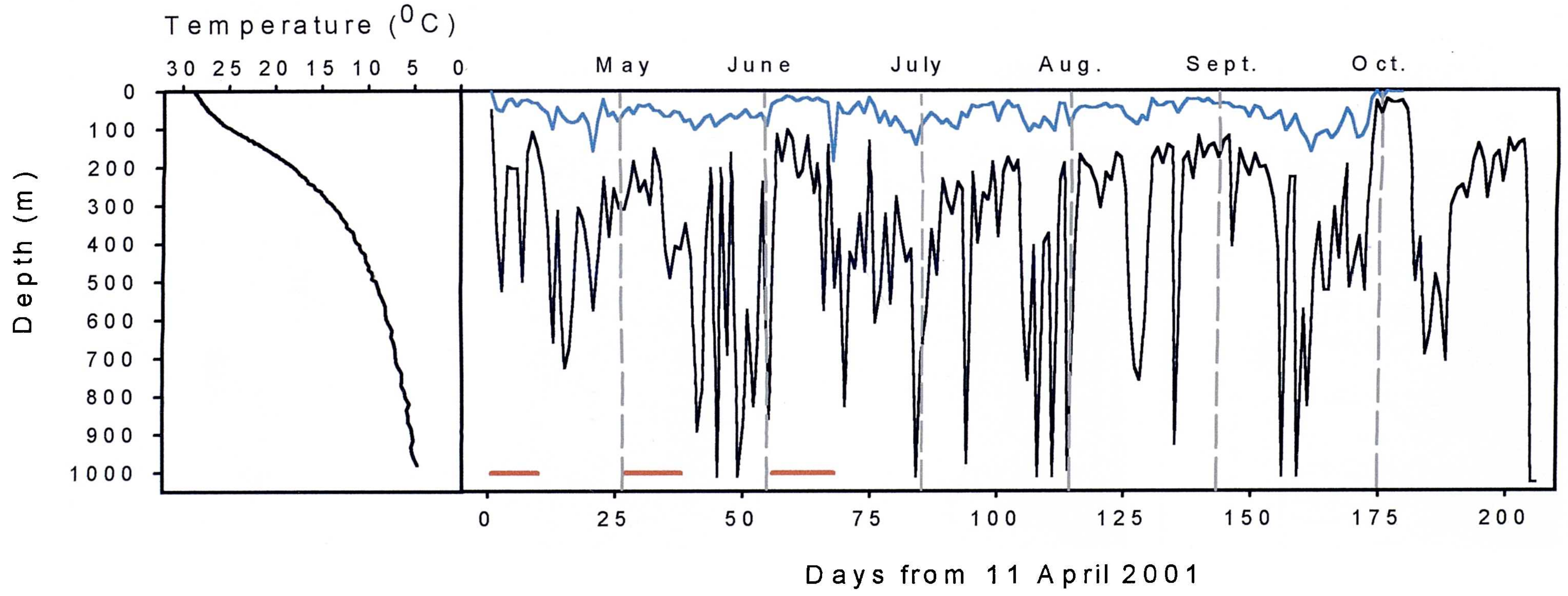


Figure 5.8a: Maximum (black) and mean (blue) daily depth of a juvenile male whale shark (S4) in the Western Caribbean. Mean depths are calculated for each day from all the pressure measurements at 60-s intervals. Maximum depth is the single deepest depth recorded in the 24-hour period. Tag was collected from the shark and archival data shown dates from 11 April to 4 October 2001. Summary data with maximum depths were recorded until 31 October 2001. Deep diving to over 900 m relaxes during the peak snapper spawning-period of April, May and June (represented by red lines), during and following the period indicated by the gray hashed lines which represent the full moon.

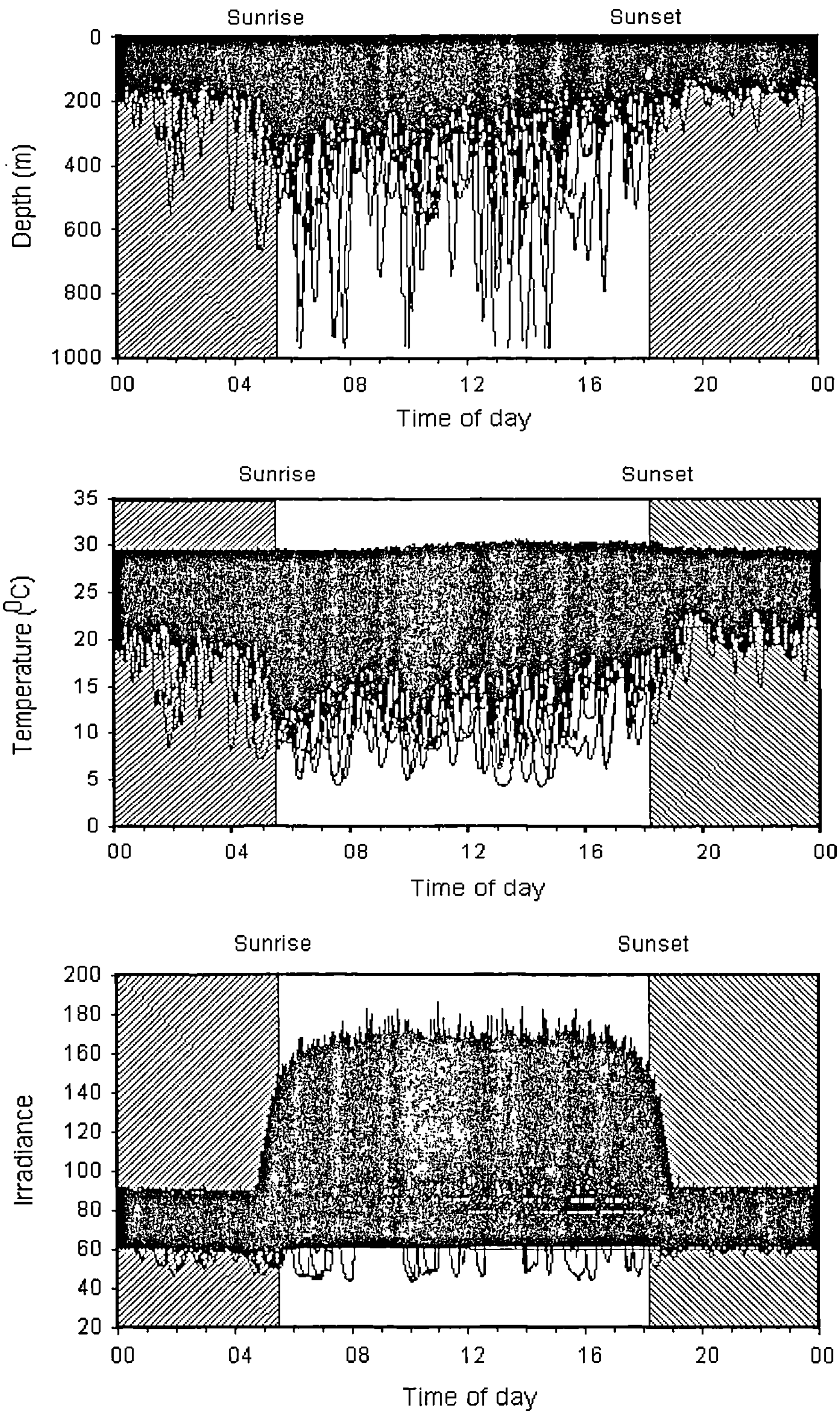


Figure 5.8b: All dive, temperature and irradiance satellite-tag data collected every 60s for 206 days for whale shark S4. Data are superimposed in a 24 hr period (Belize local time) and shaded areas coincide with nighttime. Sunrise and sunset are based on mean values for the 206-day period.

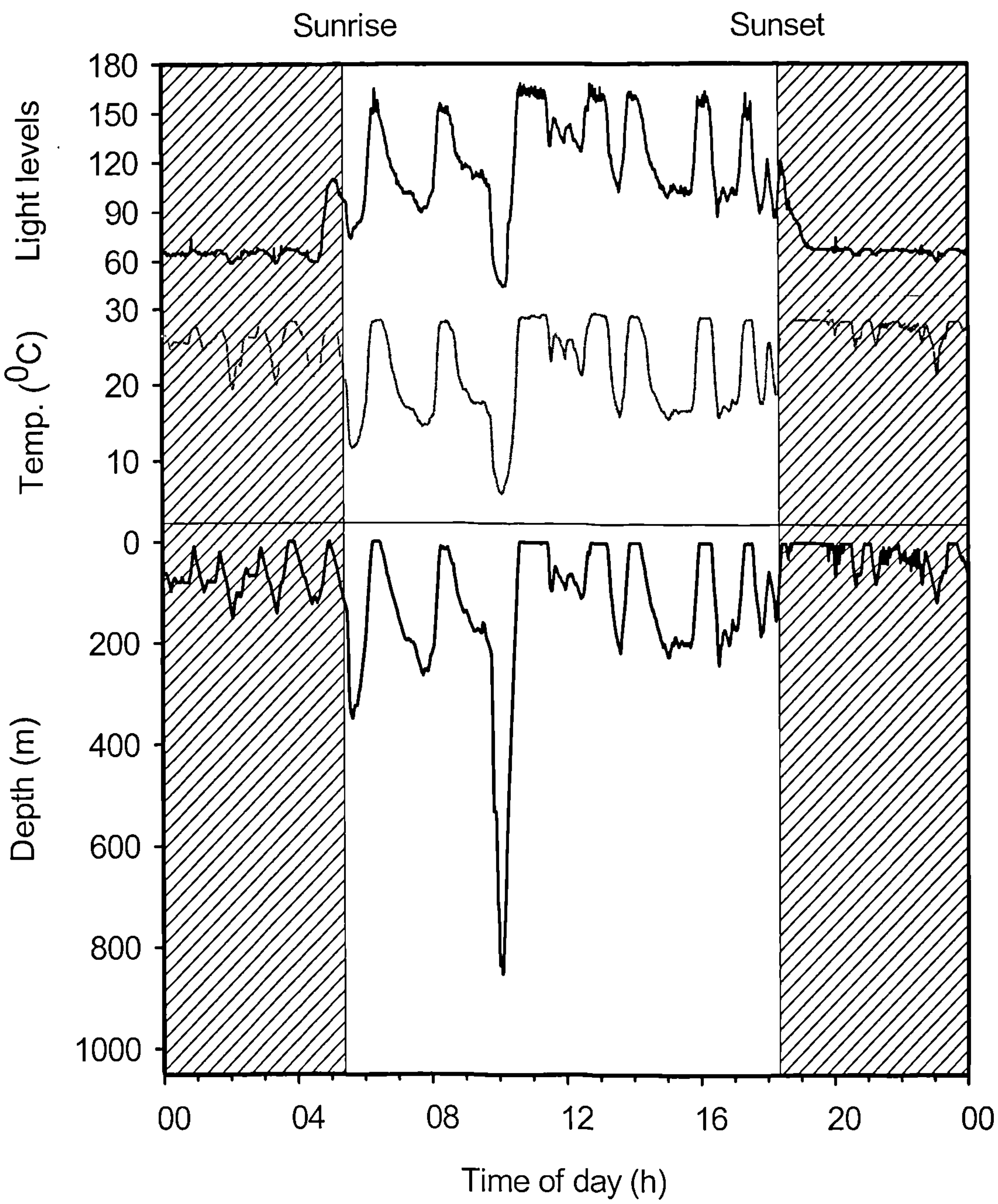


Figure 5.9: Diving profile with recorded ambient temperature and light levels over a 24-hour period for whale shark S4 on 21 May 2001. This date falls within the snapper spawning-season between monthly peak snapper spawning events at 15 days after the May full moon.

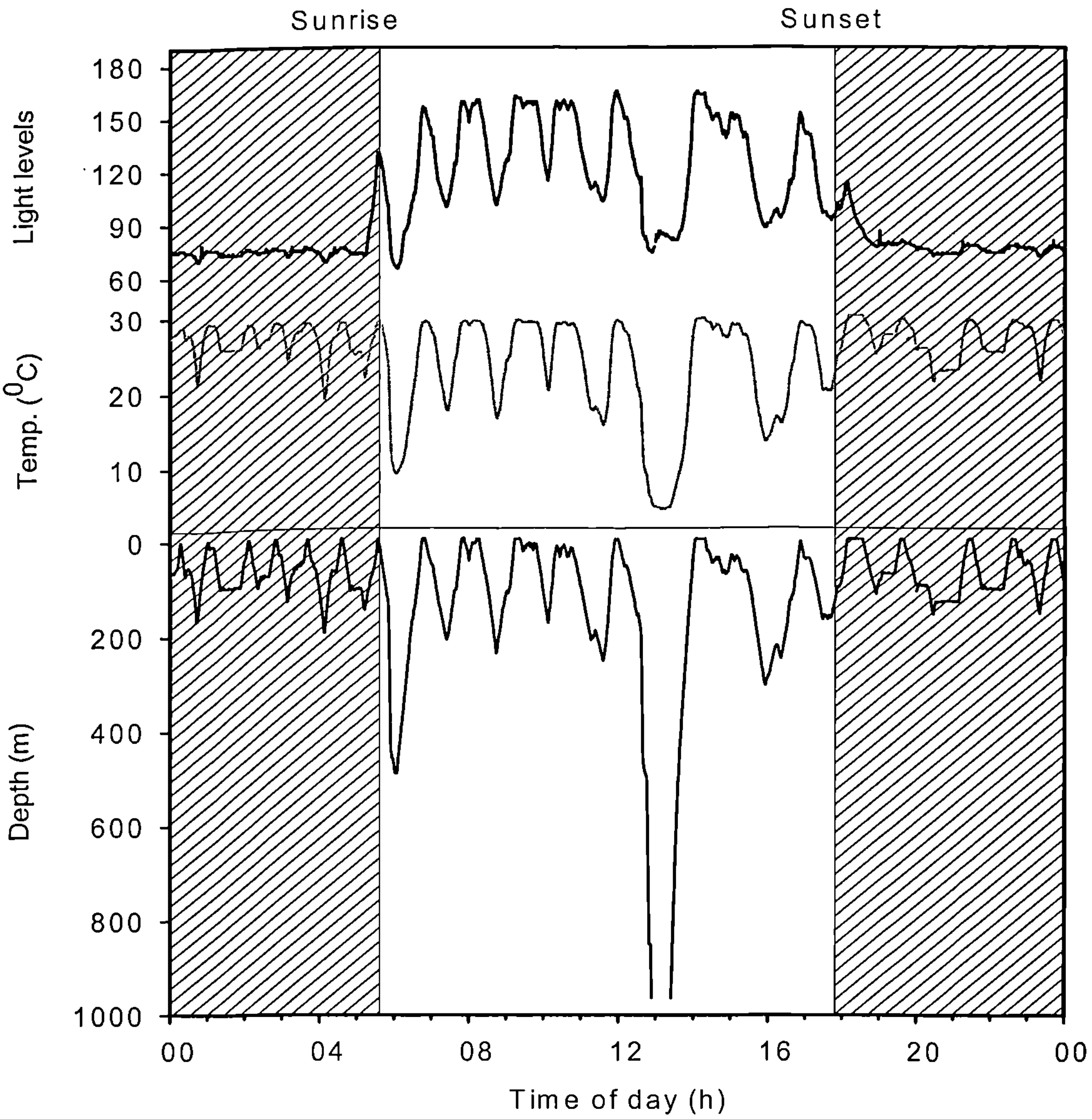


Figure 5.10: Diving profile with recorded ambient temperature and light levels over a 24-hour period for whale shark S4 on 14 September 2001. This date falls outside of the peak snapper spawning-season, 13 days after the September full moon. The tail of the deep dive is not included as no depths are recorded with precision beyond 980 m.

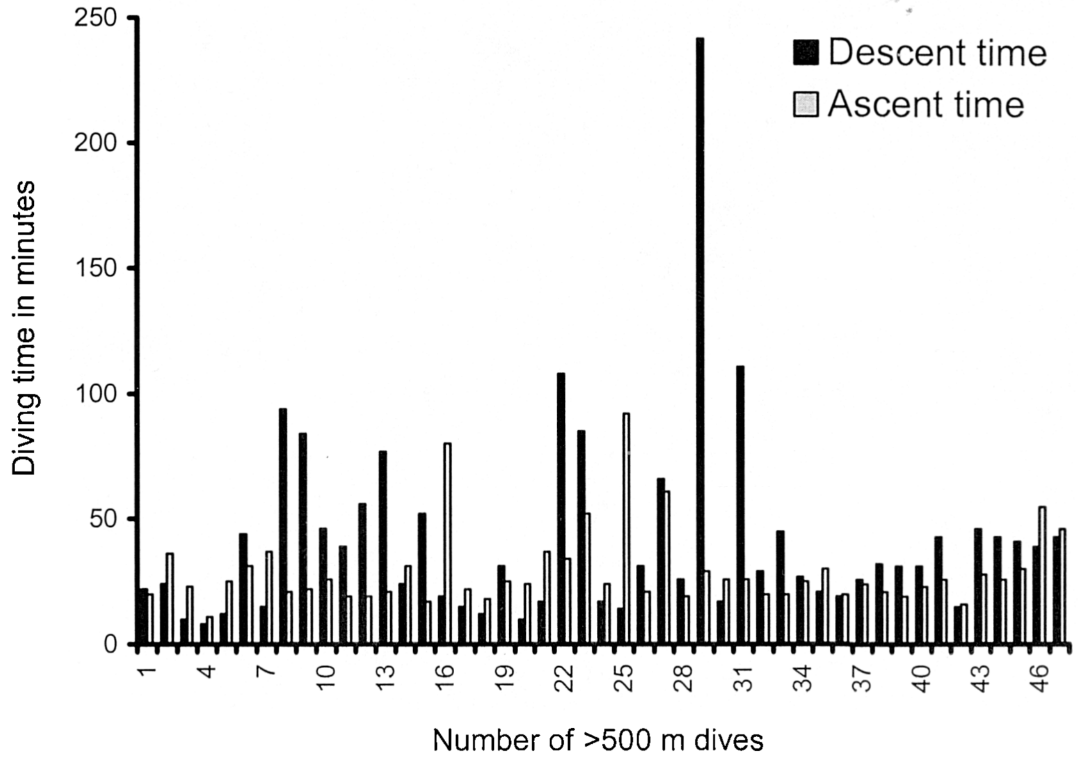


Figure 5.11: Minutes taken by whale shark S4 to descend and ascend to depths equal to or over 500 m over the course of 177 days from 11 April to 4 October 2001 (n = 47; $p < 0.05$).

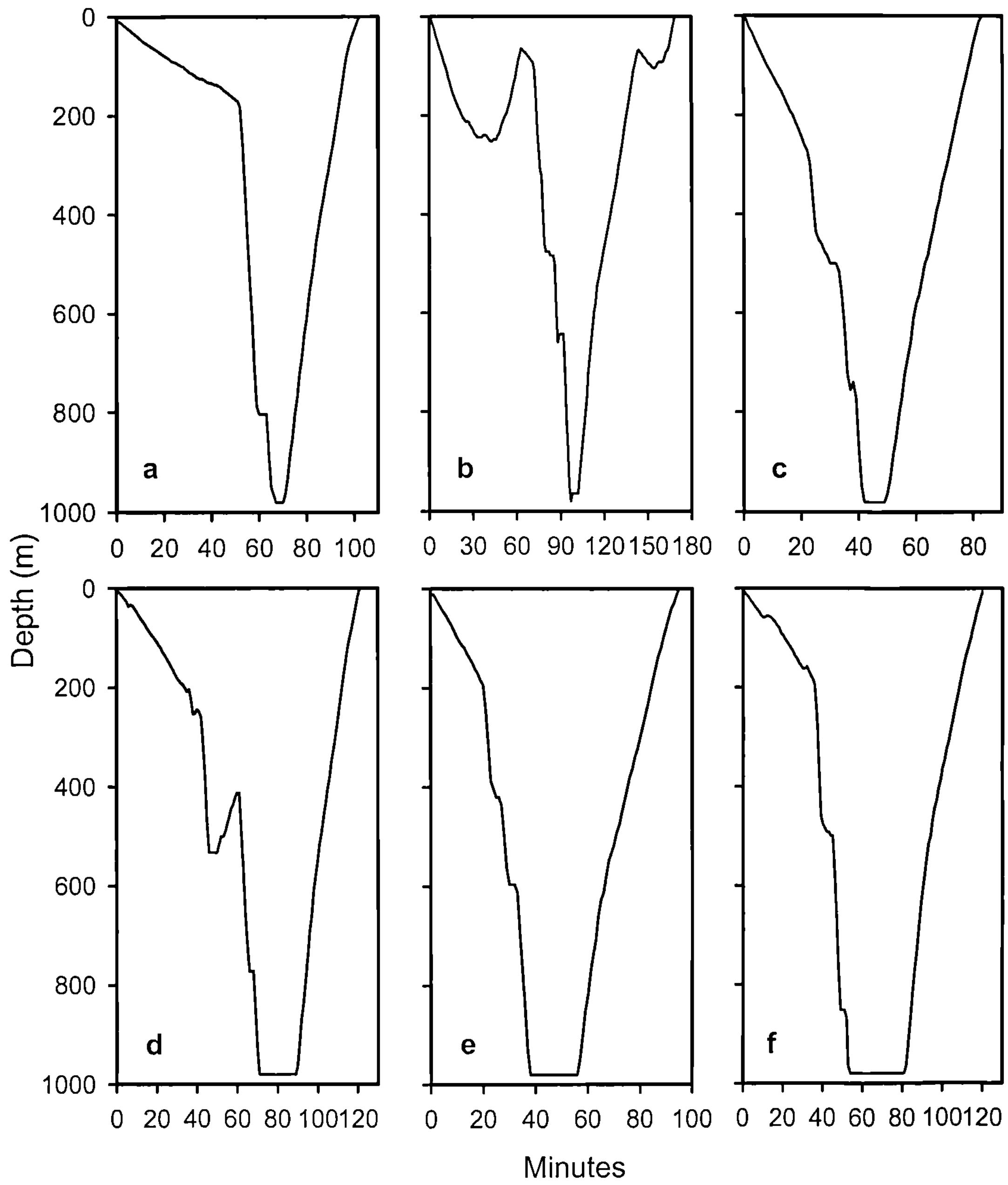


Figure 5.12: Diving profiles for six dives >979.5 m in whale shark S4 over the course of the 206 day tag deployment. a) 29-5-01, b) 1-7-01, c) 25-7-01, d) 28-7-01, e) 31-7-01, f) 14-9-01.

S4 spent a mean of 13.2 min per dive at depths >980 m (range 1-28 min ± 10.5 SD). Mean minimum temperature recorded during dives over 980 m was 4.65^{0}C (range 4.35-5.4^{0}C ± 0.27^{0}C SD) and mean maximum temperature prior to the dives was 29.05^{0}C ± 0.53^{0}C SD. Time at depth for the final deep dive recorded on 30 October 2001 cannot be determined due to tag malfunction during and following the dive. However, if S4 dived beyond 1500 m, at the fastest rate of descent and ascent for a dive over 980 m, it would have remained deeper than 1000 m for 46.5 minutes at a mean temperature < 4.65^{0}C. S4 made all dives beyond 980 m during the day between 06:12-14:19 h local time. Four >980 m dives were made during the first quarter moon (29-5; 1-7; 28-7; 31-7), one late in new moon (25-7), and one between the last quarter moon and new moon (14-9). The final dive made on October 30th fell within the last quarter moon. Three of the dives were made within 6 days of each other (25-31 July).

Based on percentage time at depth data generated by the satellite tag, S4 did not bask on the surface every day yet remained relatively shallow and swam at a mean depth of 58.0 m throughout the 6-month period. Temperatures in the upper water column (0-50 m) ranged from 16.2^{0}C-30.8^{0}C, mean minimum temperature of 27.9^{0}C ± 1.2^{0}C SD. The longest period S4 spent submerged was from 1-8 June 2001 for a total of about 180 h or 7.5 days at depths below 10 m. These dates span the last part of the first quarter moon and the beginning of the full moon. Climatic events may affect surface visitation pattern for whale sharks. S4 swam at the surface every day three days prior to the arrival of Category 4 Hurricane Iris at 20:00 h on 8 October 2001. Once the shark dived it did not revisit the surface for over 48 hours and remained at a minimum depth below 10 m from midnight to 03:00 h, 9 October. After this time it resumed periodic surface visits for the following 4 days. It is probable that the shark was not in the path of the hurricane but may have been affected by the storm surge or the regional drop in barometric pressure.

5.3.3 Diel diving patterns

Several shark species display differences in day versus night diving patterns (Carey & Scharold, 1990; Klimley *et al.*, 2002). To test whether whale sharks displayed the same behaviour, diving depths attained during night and day were compared. Sharks S1-4 dived significantly deeper during the day (3-hr data summaries: $n = 905$) than at night ($n = 887$) (Mann-Whitney U test: $z = -8.460$; $p < 0.001$). Finer detail variations in diving depth throughout the 24 h period are represented in Figure 5.4. The 3-hr data summaries each began at 02:00, 05:00, 08:00, 11:00, 14:00, 17:00, 20:00, and 23:00 local Belize time. Not all days of deployment provided usable data due to data dropout during transmission.

5.3.4 Seasonal diving behaviour

Since 1999, researchers, fishermen and tour operators have noted that fewer sharks were sighted in the two-week period following the cessation of snapper spawning that roughly coincides with the new moon and first quarter moons of April to June as compared to the full moon and last quarter moon periods (R. Graham, E. Cuevas, E. Leslie, and G. Eiley, pers. obs). To determine whether whale sharks modulate their diving behaviour in relation to snapper spawning and the lunar phase, maximum dive depths for S1-4 were compared within spawning and non-spawning periods. Peak snapper spawning periods from 9 March through 21 June 2001 are based on cumulative underwater observations of snapper spawning periodicity (see Chapter 6) and indicated by the hashed lines in Figures 5.13-5.16. Dive depths during the full moon (FM) and last quarter moon (LQM) phases were compared to depths recorded during the new moon (NM) and first quarter moon (FQM) phases. These periods coincide with the onset and duration of snapper spawning and the cessation of spawning respectively. Data for S1-3 are summarised in figures 5.13-5.16 and a few days of data were lost during transmission to the satellite following detachment. S3 and S4 recorded depth data from April to October, four months beyond the peak snapper spawning-season of April through June.

Between April and June 2000 and 2001, S1-3 remained relatively shallow, above 200 m, during the full moon (FM) and last quarter moon (LQM) when the snappers spawn. S4's data indicate that the shark made several dives over 200 m during the same period (Figures 5.10a and 5.16). Regardless, between April to 21 June 2001, S1-4 dived significantly deeper in the new moon and first quarter moon periods once spawning was no longer occurring (Wilcoxon's test; $z = -4.089$; $p < 0.001$) and spent longer at depth (Figures 5.17-5.18). Following the peak snapper spawning season from July 2001 onwards, there was no significant difference in maximum depths reached for S3 and S4 during the full moon and new moon periods (Paired samples t-test; $t(73) = -0.026$; $p = 0.979$). The magnitude of differences in the means was very small (eta squared = 0.00001) indicating that the shark's diving behaviour is linked to timing of snapper spawning but is probably not directly influenced by the lunar phase outside of the spawning season. Although the sat-tag's light data does not allow for accurate georeferencing of tagged sharks throughout deployment periods, S1-S2 were resighted

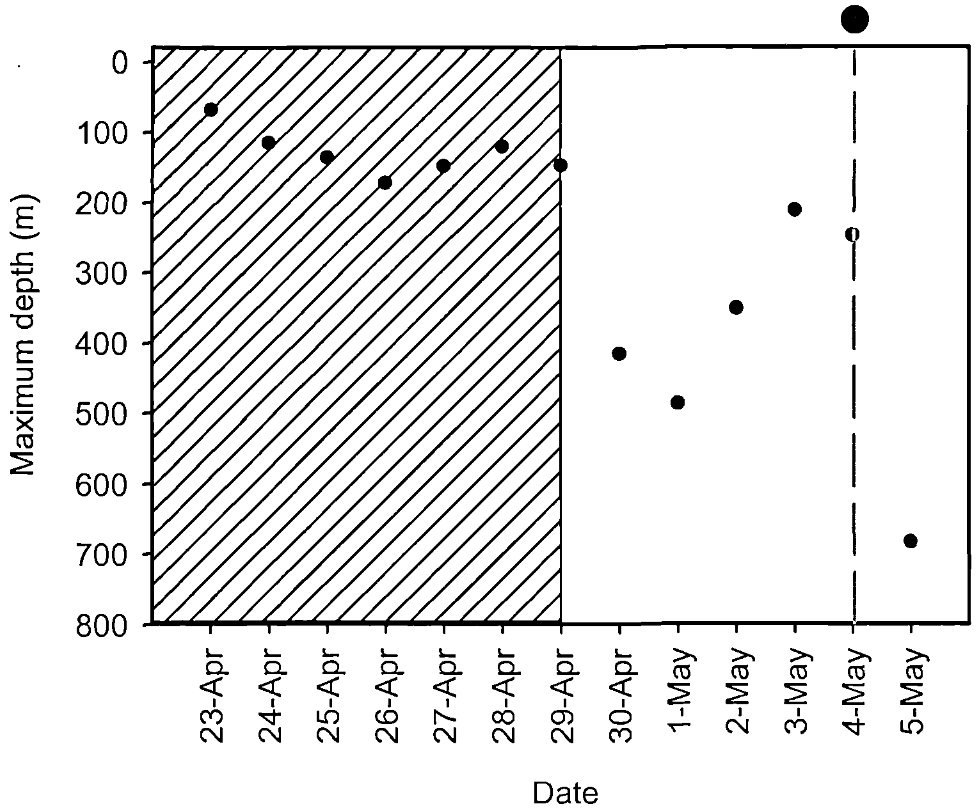


Figure 5.13: Maximum depths registered per diving day by whale shark S1 during the 15 days of satellite tag deployment from 23 April to 5 May 2000. The gray line indicates the transition to a new lunar phase where ●= New moon. The satellite did not receive all days of data transmitted. The hatched area represents the snapper spawning period.

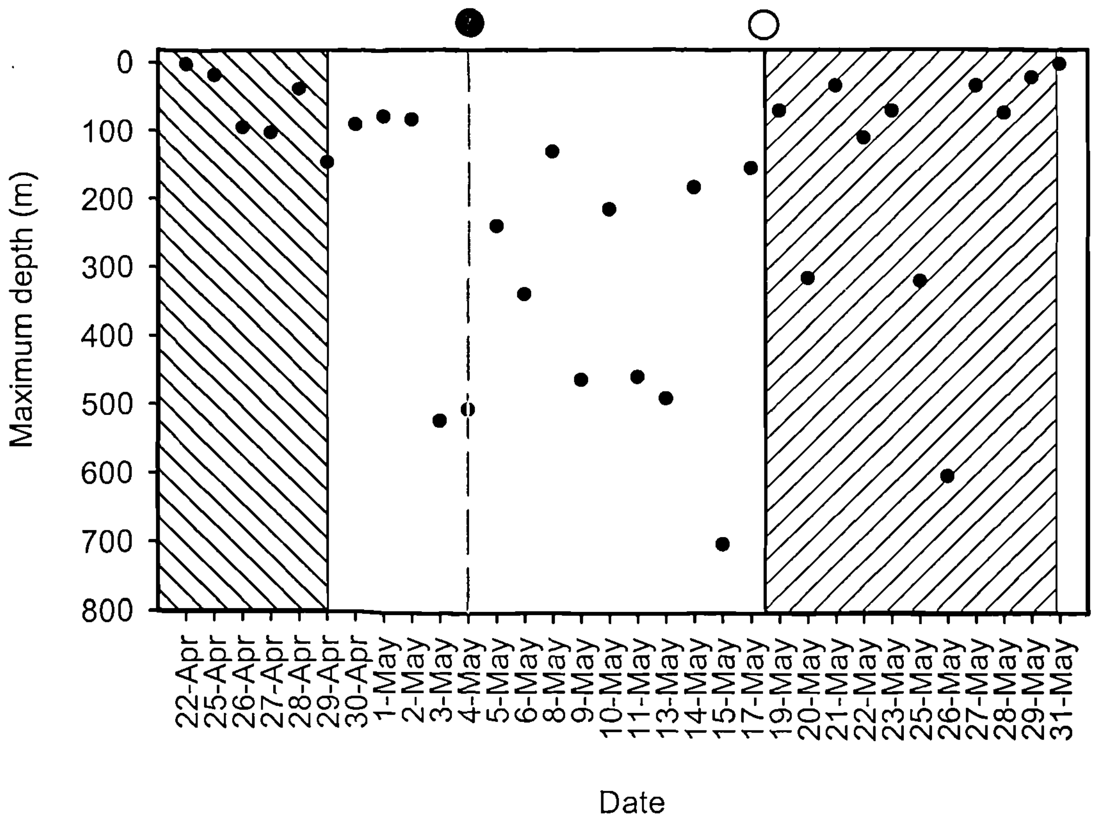


Figure 5.14: Maximum depths registered per diving day by whale shark S2 during the 40 days of satellite tag deployment. The gray and black lines indicates transitions to a new lunar phase where ●= New moon; ○ = Full moon. The satellite did not receive all days of data transmitted; hence several days are omitted from the graph. The hatched area represents the snapper spawning period.

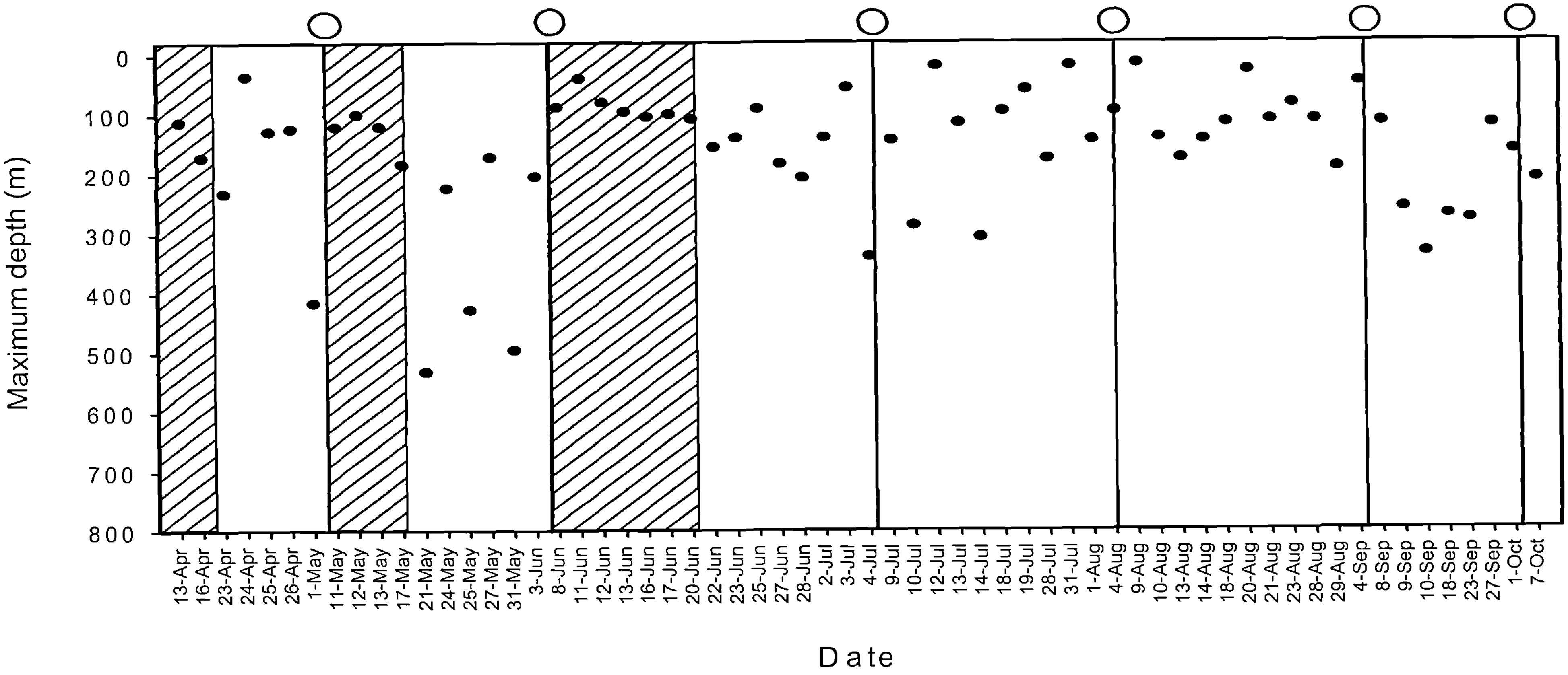


Figure 5.15: Maximum depths registered per diving day by whale shark S3 during the 188 days of satellite tag deployment. Not all days of data were transmitted. The black line indicates the transition to a new lunar phase where ○ = Full moon. The shaded areas represent peak snapper spawning periods. The satellite did not receive all days of data transmitted; hence several days are omitted from the graph and some months have more data than others.

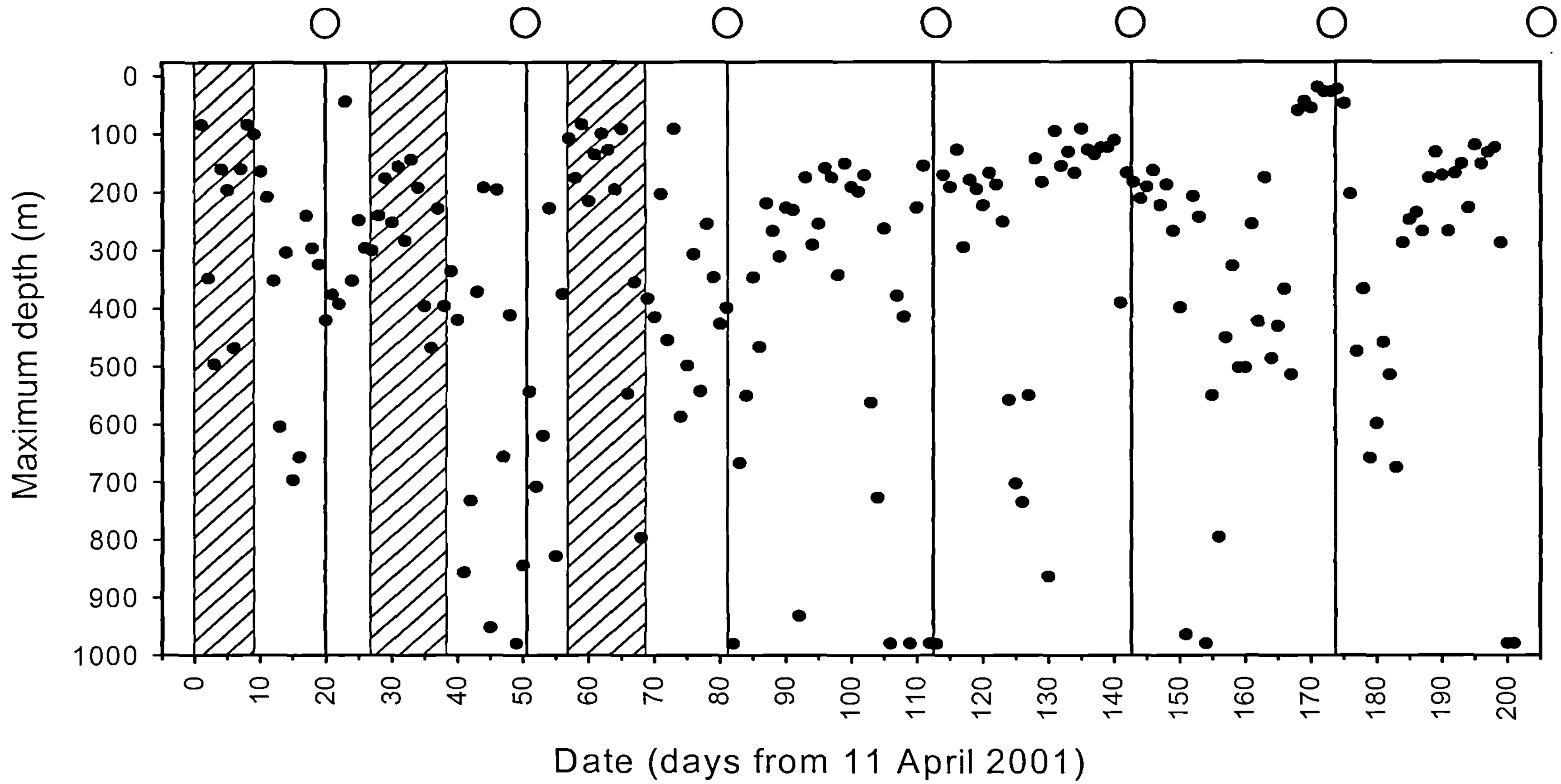


Figure 5.16: Maximum depths registered per diving day by whale shark S4 during the 206 days of functional satellite tag deployment. The black line indicates the transition to a new lunar phase where ○ = Full moon. The hatched areas represent peak snapper spawning periods.

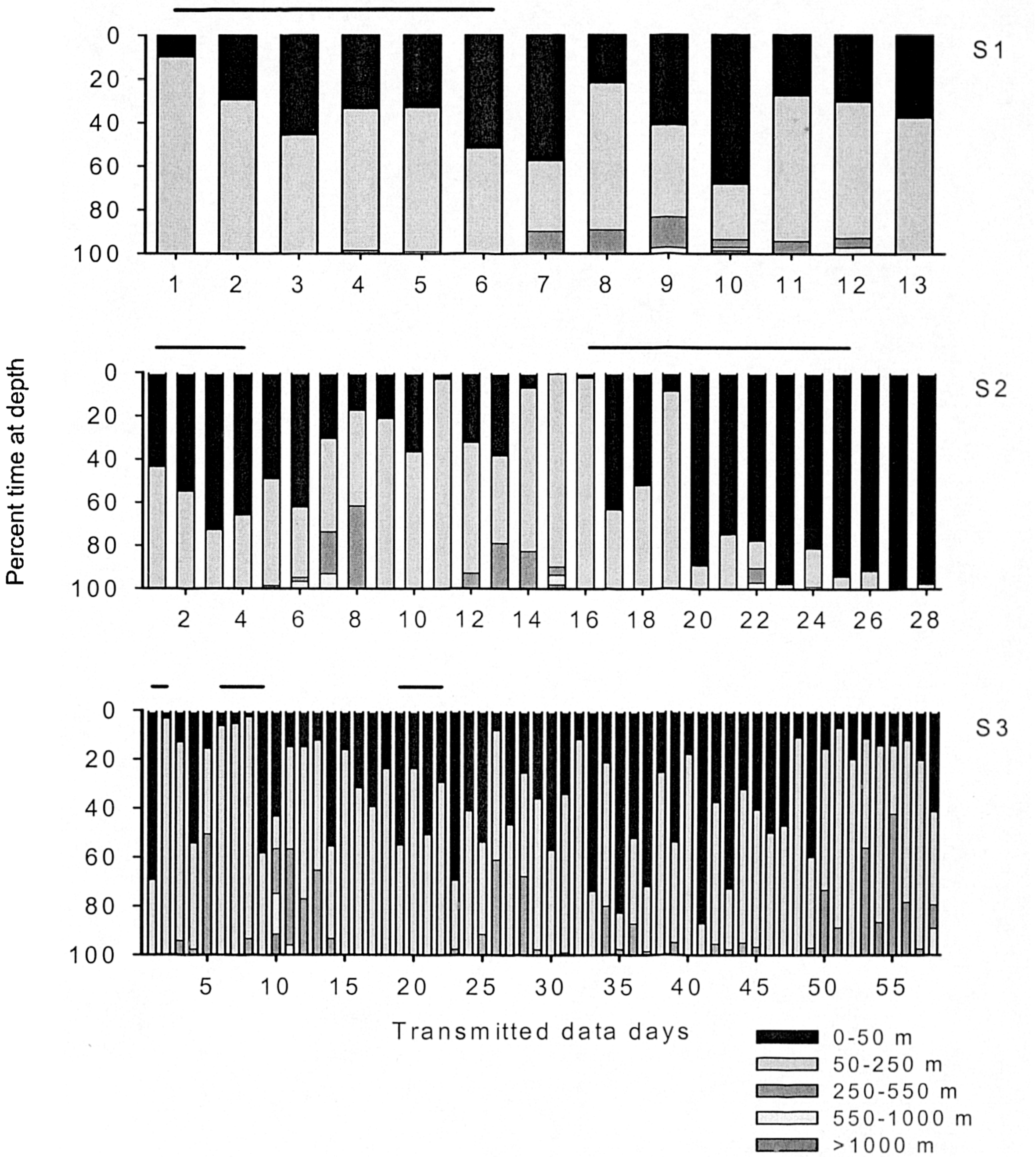


Figure 5.17: Percentage of time spent at each depth for all tag deployment days recorded for whale sharks S1-3. Each stacked bar represents a mean of all minutes spent at specific depth composites for each day shown. Black horizontal lines above each graph indicate peak spawning periods for cubera and dog snappers.

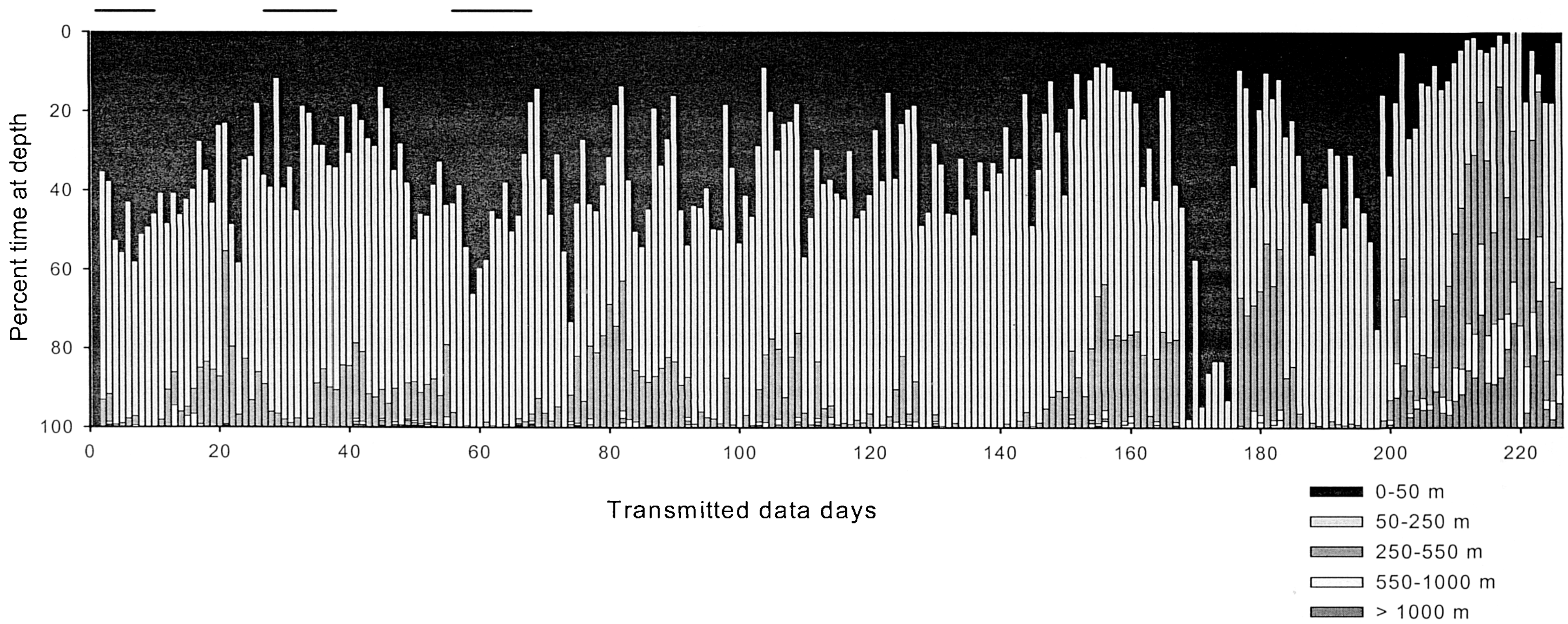


Figure 5.18: Percentage of time spent at each depth for all tag deployment days recorded for whale shark S4. Each stacked bar represents a mean of all minutes spent at specific depth composites for each day shown. Black horizontal lines above the graph indicate the peak spawning periods for cubera and dog snappers.

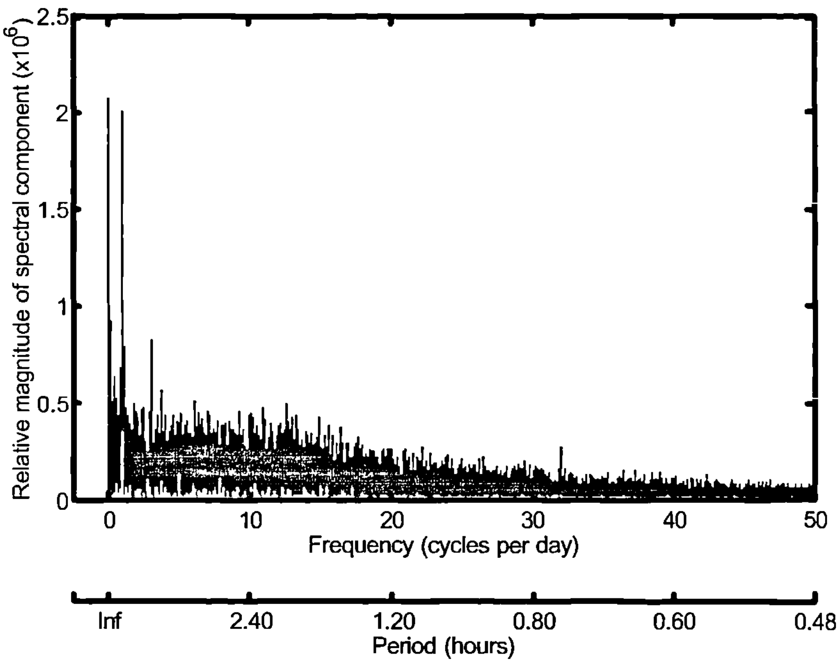
in the May and snapper spawning moon of 2000 and S3-S4 were resighted during the May and June spawning moons in 2001. S4 was resighted again during the March, April and May spawning moons of 2002. This places the sharks on the spawning grounds when they display a relaxation of deep diving and further indicates that diving behaviour is modulated by the spawning events.

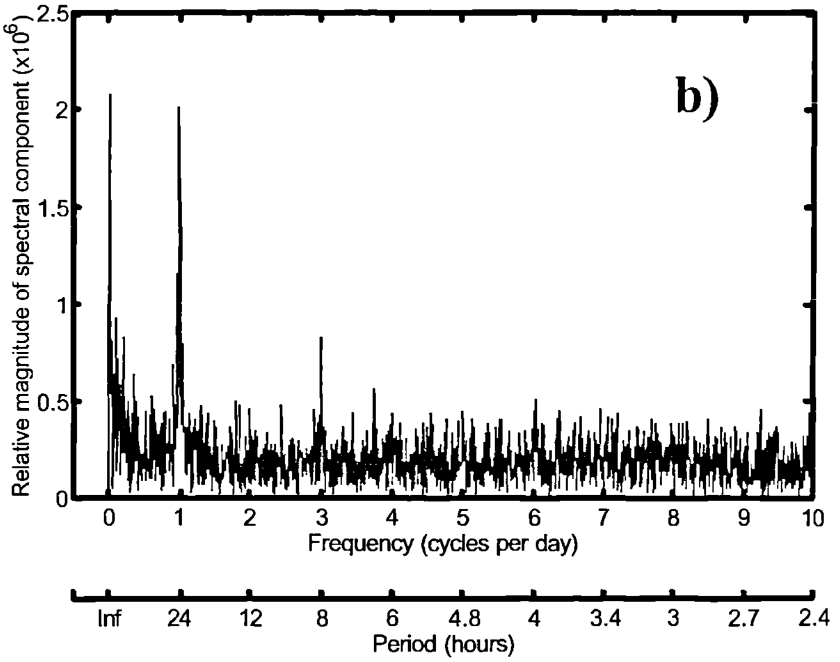
Whale sharks behaved similarly when diving: sharks S2-S4 dived deep between snapper spawning moons they returned to the surface to target the spawn. Whale sharks appeared to forage in the deep and near other promontory sites outside of snapper spawning periods at Gladden. At least 15 sharks tagged with acoustic tags were registered at receivers located at other sites along the reef e.g., in the Sapodillas and Turneffe between moons (See Chapter 4 on patterns of movement). S3 and S4 displayed a range of east-west movements, many of which placed them over the deep waters of the Cayman Trench, thus enabling deep dives (see Chapter 4).

5.3.5 Rhythmicity

Analysis of S4's 206-day time-series of depth data using the Fast Fourier Transform method revealed several circadian and ultradian patterns related to whale shark diving behaviour. Figures 5.19a-c represent all data collected every 60 s for 206 days (252,429 data points) with (a-b) representing 50 and 5 cycles recorded per day. "1" represented a 24 h cycle and each cycle afterwards representing a fraction of the 24 hour day e.g. 24/32 cycles = 45 minutes). Although these peaks could not be objectively defined, they showed a relative magnitude increase of at least 50% over the nearby surrounding pattern noise, and are highlighted at 0, 1, 3 and 32 cycles per day. These represent a periodicity in S4's diving behaviour over periods of time greater than 24 h, every 24 h, every 8 h and every 45 minutes respectively. Part of the 8 h signal coincides with the creation of the FFT square wave signal and is therefore slightly attenuated. However the signal's strength indicates periodicity above and beyond the creation of a square wave and should therefore be included. The ultradian 45 min rhythm does not contribute to signal formation and is considered a true rhythm. Spectral components over 24 h clearly noted in (c) coincide with periods of 29 days, 35 days and 58 days.

S4's diving behaviour is not random, all spectral components outside of the 99.9% confidence interval can be interpreted as non random diving. Figure 5.20 a-c reveal that only the >24 h and the 24 h periodicities remained strong with a 50% greater magnitude over the surrounding pattern, despite the random repositioning of deep dives in the data set. This indicates that the 45 minute and 8 h periodicities in diving behaviour were


Relative magnitude of spectral component (x10^6)
Frequency (cycles per day)
Period (hours)
Inf 2.40 1.20 0.80 0.60 0.48


b)
Relative magnitude of spectral component (x10^6)
Frequency (cycles per day)
Period (hours)
Inf 24 12 8 6 4.8 4 3.4 3 2.7 2.4

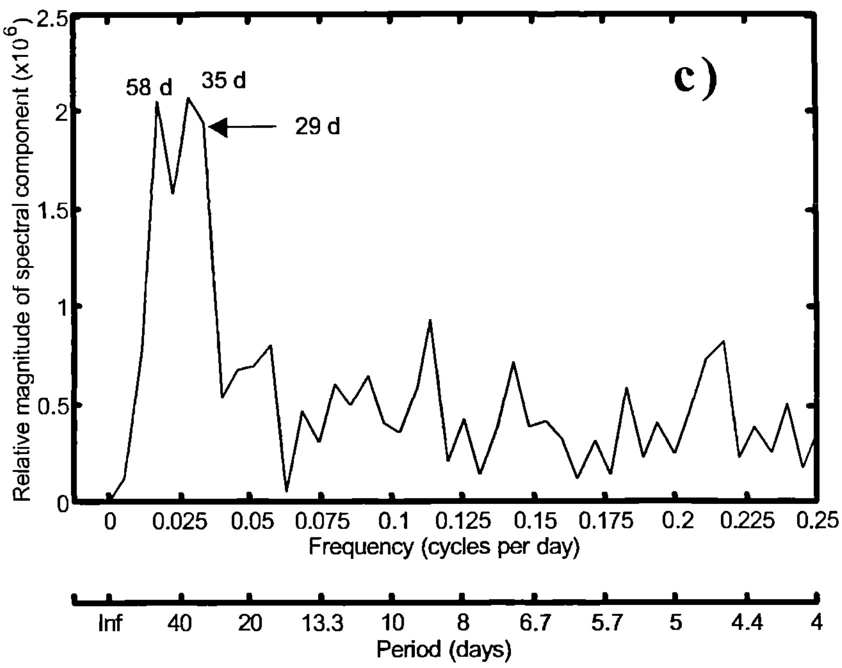
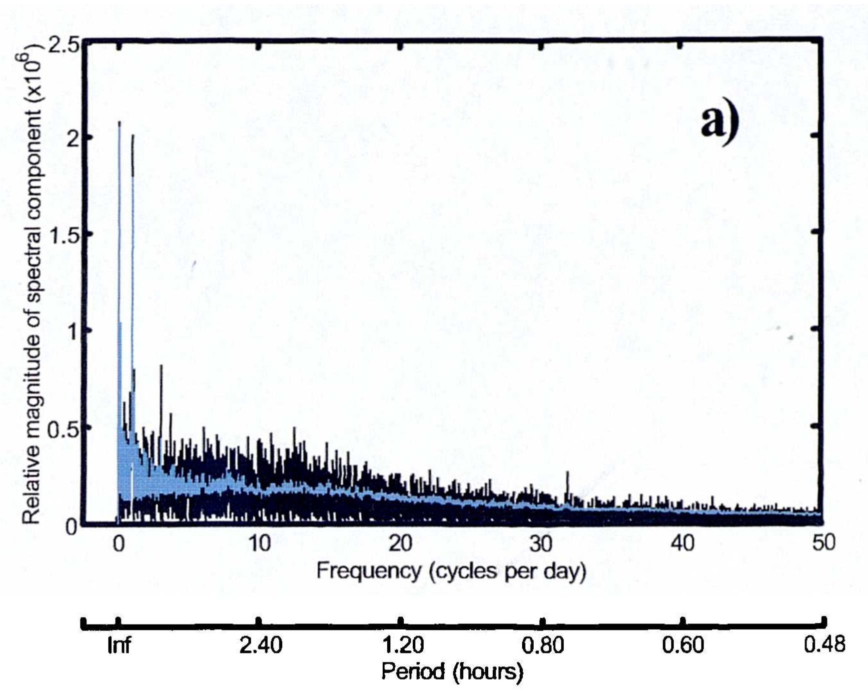
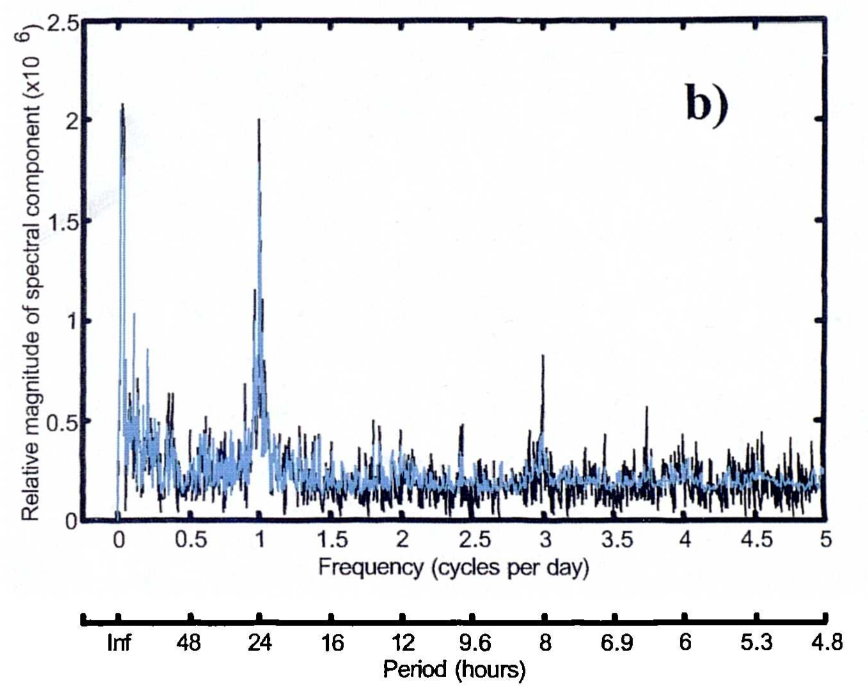


Figure 5.19 a-c: Fast Fourier Transform analysis of whale shark S4 diving periodicity producing a frequency spectrum of all dive data recorded every 60 seconds for 6 months (252,429 data points). a) represents spectral components with a frequencies up to 50 cycles per day or infinity to 0.48 hrs; b) same data at a frequencies resolution of 5 cycles per day or infinity to 4.8 hrs; c) same data at a frequencies resolution of 0.25 cycles per day or infinity to 4 days. Relative magnitude of frequencies coinciding with 58, 35 and 29-day periodicities are identified on the graph.


a)
Relative magnitude of spectral component (x10^6)
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50
Frequency (cycles per day)
Inf
2.40
1.20
0.80
0.60
0.48
Period (hours)


b)
Relative magnitude of spectral component (x10^6)
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
Frequency (cycles per day)
Inf
48
24
16
12
9.6
8
6.9
6
5.3
4.8
Period (hours)

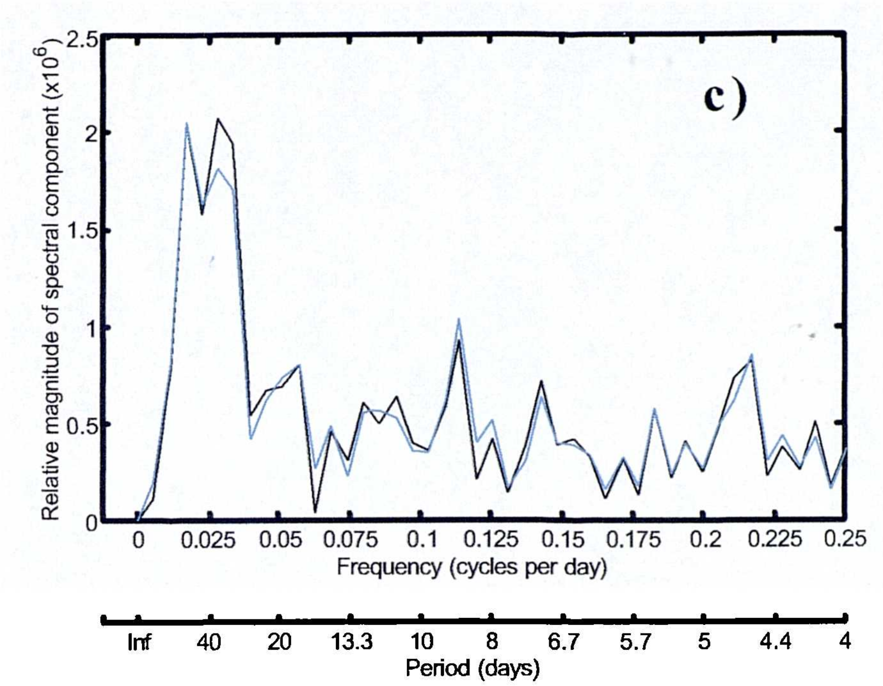


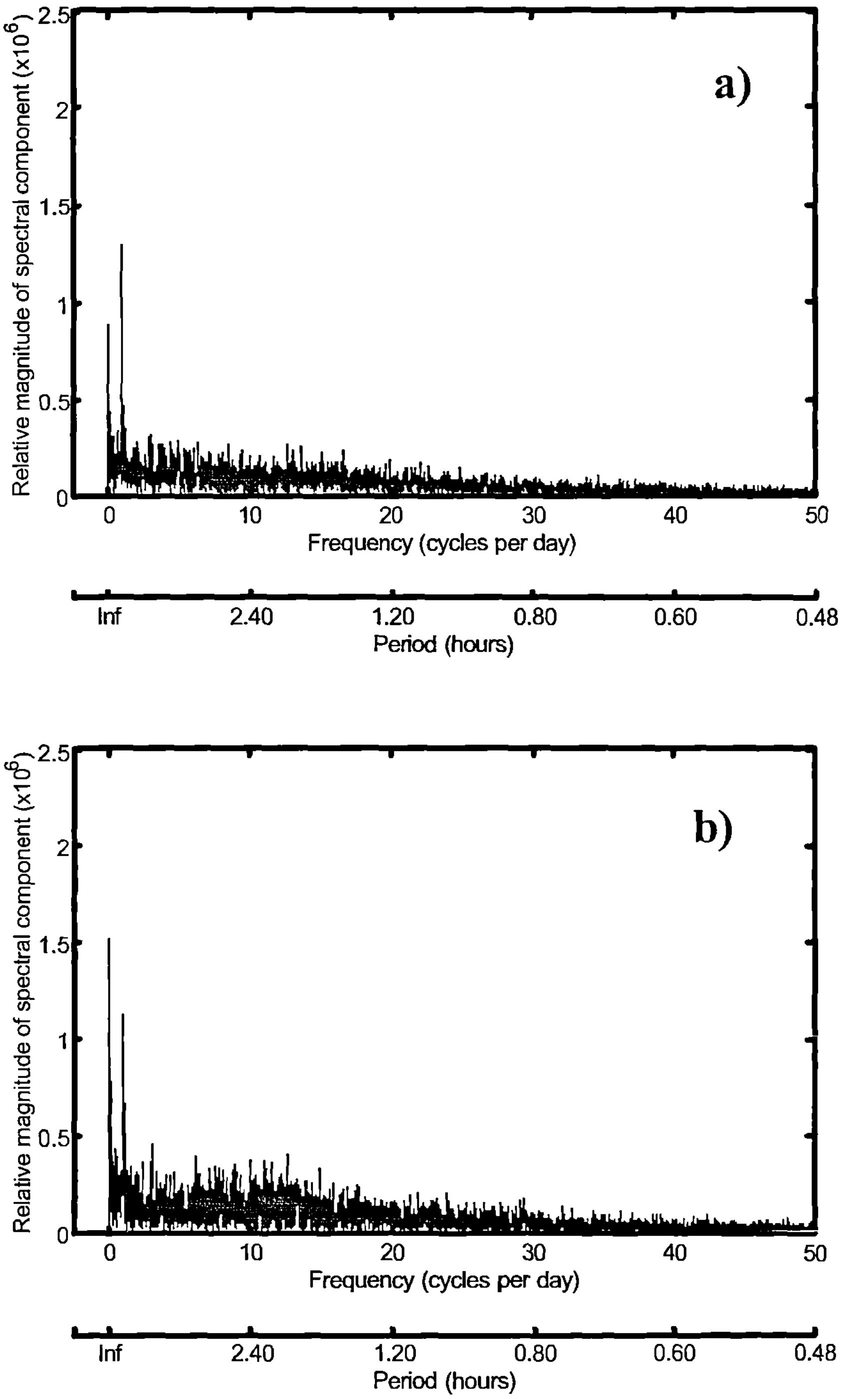
Figure 5.20 a-c: Upper 99.9% confidence interval (blue) spectral component magnitudes from 100 repeats of randomised deep dive notch repositioning overlaid on the frequency spectrum of he observed depth data (black). a) 50 cycles per day; b) the same data with a resolution of 5 cycles per day; c) the same data with a resolution of 0.25 cycles per day.

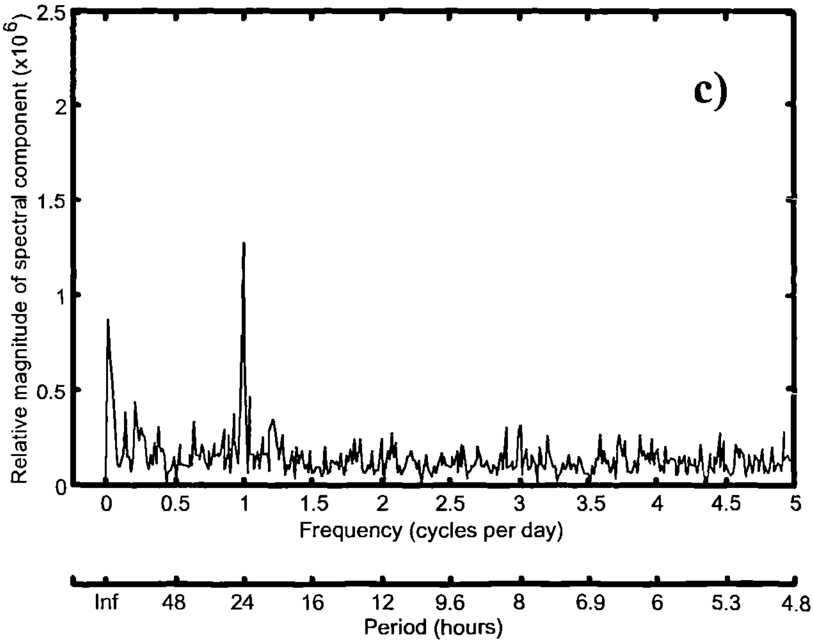
Figures 5.21 a-f: Fast Fourier Transform time series analysis of S4 diving periodicity for all dive data recorded every 60 seconds for 6 months encompassing the periods within and outside the Gladden Spit peak snapper spawning season.

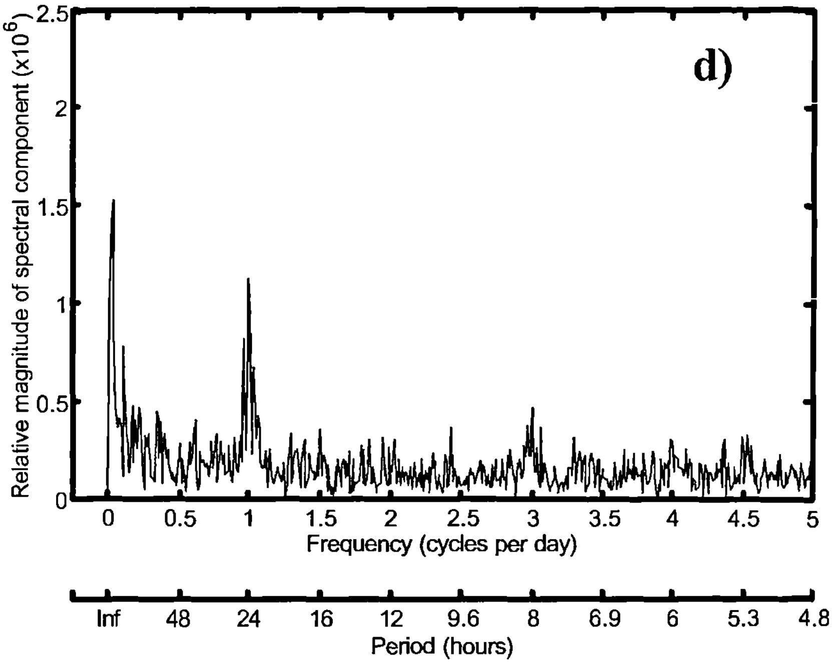
a: Diving periodicity during Gladden Spit peak snapper spawning season March-June 2001, 50 cycles a day; **b:** Diving periodicity outside of Gladden Spit peak snapper spawning season from July through October 2001, 50 cycles a day.

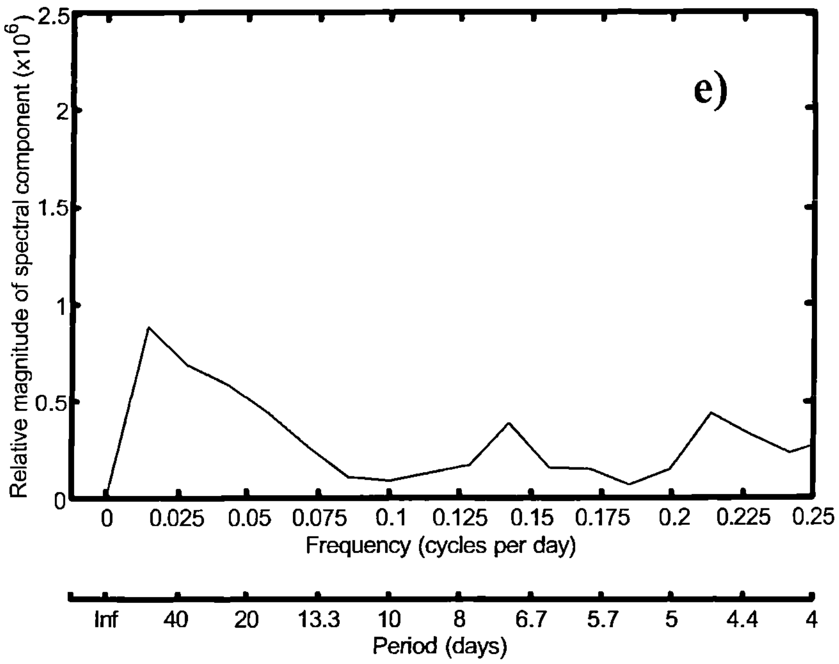
c: Diving periodicity during Gladden Spit peak snapper spawning season March-June 2001, 5 cycles a day; **d:** Diving periodicity outside of Gladden Spit peak snapper spawning season from July through October 2001, 5 cycles a day.

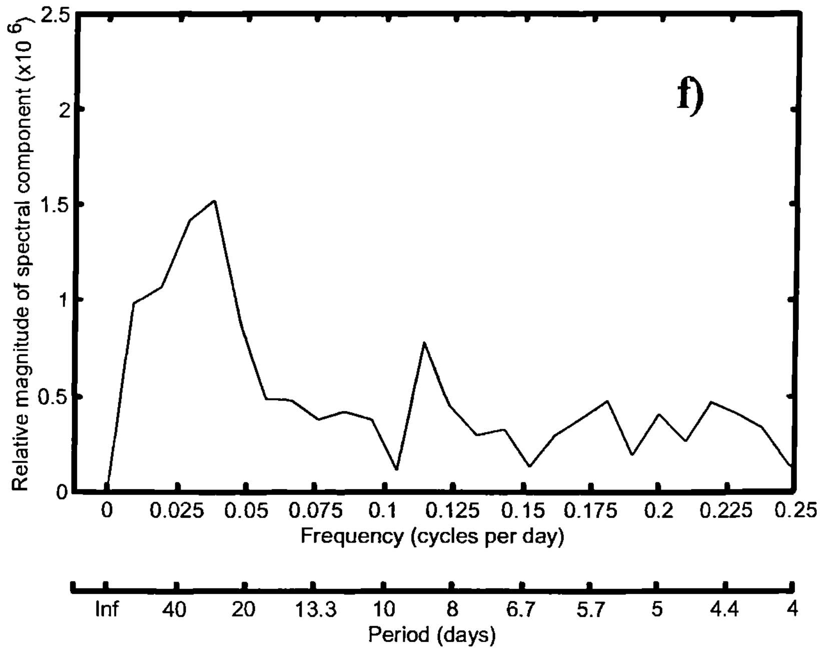
e: Diving periodicity during Gladden Spit peak snapper spawning season March-June 2001, 0.25 cycles a day; **f:** Diving periodicity outside of Gladden Spit peak snapper spawning season from July through October 2001, 0.25 cycles a day.


a)
Relative magnitude of spectral component (x10^6)
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50
Frequency (cycles per day)
Inf
2.40
1.20
0.80
0.60
0.48
Period (hours)
b)
Relative magnitude of spectral component (x10^6)
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50
Frequency (cycles per day)
Inf
2.40
1.20
0.80
0.60
0.48
Period (hours)


c)
Relative magnitude of spectral component (x10^6)
2.5
2
1.5
1
0.5
0
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5 5
Frequency (cycles per day)
Inf 48 24 16 12 9.6 8 6.9 6 5.3 4.8
Period (hours)


d)
Relative magnitude of spectral component (x10^6)
2.5
2
1.5
1
0.5
0
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5 5
Frequency (cycles per day)
Inf 48 24 16 12 9.6 8 6.9 6 5.3 4.8
Period (hours)


e)
Relative magnitude of spectral component (x10^6)
0
0.5
1
1.5
2
2.5
0 0.025 0.05 0.075 0.1 0.125 0.15 0.175 0.2 0.225 0.25
Frequency (cycles per day)
Inf 40 20 13.3 10 8 6.7 5.7 5 4.4 4
Period (days)


f)
Relative magnitude of spectral component (x10 ^{6})
0
0.5
1
1.5
2
2.5
0 0.025 0.05 0.075 0.1 0.125 0.15 0.175 0.2 0.225 0.25
Frequency (cycles per day)
Inf 40 20 13.3 10 8 6.7 5.7 5 4.4 4
Period (days)

strongly related to deep diving behaviour. It is unlikely that the 29-day coincides with a deep diving excursion recorded 6 times over the course of 206 days as three of the dives occurred within six days. Examination of 24 h slices of S4's data (all data in 5.10b and Figures 5.11 and 5.12) reveals a daily deep diving pattern, usually undertaken close to the middle of the day. The spectral component representing thc ultradian rhythms of 8 h and 45 min are not as strong as the circadian rhythms but impossible to ignore nonetheless. Data analysis does not reveal a clear behaviour pattern undertaken every 8 h but it is linked to deep diving behaviour. The 45 min pattern may coincide with the shark's pattern of undertaking an apparently exploratory dive before committing itself to a deeper dive over 500 m.

Differences in patterns of diving behaviour exist within and outside the peak snapper spawning-period of April through June 2001 (Figures 5.21 a-f). In all raw and averaged data, the 29-day and 24 h rhythms remain strong within and outside the snapper spawning seasons. The frequency of 29-day diving behaviour differs markedly within and beyond the spawning season in Figure 5.21 c-f where S4 displays a spectral magnitude of ~0.8 for the 29-day cycles within the spawning moons, and a magnitude of 1.3-1.5 outside of the spawning season. Periodicities of less than 24 h, or ultradian periods, do not appear to be more pronounced outside of the peak snapper season (Figure 5.21 a-f). Data analyses revealed that the spectral magnitude of the circadian periodicity (24 h) is stronger within the spawning season than outside it.

5.4 Discussion

5.4.1 Diving behaviour

Several studies on shark diving behaviour have revealed a multiplicity of patterns (Sciarrotta & Nelson, 1977; Klimley *et al.*, 1988; Carey & Scharold, 1990; Goldman & Anderson, 1999; Gunn *et al.*, 1999; Boustany *et al.*, 2002; Klimley *et al.*, 2002). This study reveals that whale sharks are superlative divers among elasmobranchs, diving deeper and withstanding greater temperature changes than previously recorded for any shark species. Although primarily epipelagic in nature, it is clear from these findings that whale sharks spend time in mesopelagic and bathypelagic regions. They exhibit a range of diel and seasonal diving behaviours, several of which are linked to a predictable food source. This study's results have provided new insights into the whale sharks' physiological capabilities while diving at depth.

Whale sharks make repeated shallow oscillatory dives within the mixed layer interspersed with regular deeper dives performed in the day. The regular vertical oscillations are similar to those displayed by whale sharks in other locations and several other species of shark. A whale shark tagged with an archival tag off the Western Coast of Australia by Gunn *et al.* (1999) displayed hallmarks of oscillatory diving behaviour during its 21 h track. Sims *et al.* (2003) revealed that basking sharks make frequent dives throughout the water column while possibly searching for prey, with one shark making a deep dive over 750 m. Mako (*Isurus oxyrhinchus*) and blue sharks (*Prionace glauca*) were recorded making repeated oscillatory dives, also to possibly locate horizontally stratified odour trails and subsequently prey (Carey and Scharold 1990).

The reasons for oscillatory dives are not clear since sharks do not need to surface repeatedly to breathe. As ectotherms, whale sharks may be displaying behavioural thermoregulation. Carey and Scharold (1990) and Klimley *et al.* (2002) suggest that short shallow dives serve a thermoregulatory function in blue sharks, makos and white sharks. Small, precise, oscillatory dives are made to forage and warm up since the thermal gradient is very steep, particularly in the first 250 m changing from 28^0C to 16^0C. Since whale sharks S1-S4 spent over 80% of their time in waters warmer than 25^0C, dives may also represent a means of cooling body temperatures if overheating occurred. There may be a strong physiological basis for such precise thermoregulatory behaviour. Brown (2003) has shown that shark ampullae may possibly respond to temperature changes smaller than 0.001^0C perhaps providing a mechanism by which sharks are able to closely follow temperature gradients.

A broad range of marine animals dive to deep depths. Marine mammals that make regular vertical migrations in excess of 500 m include sperm whales (*Physeter macrocephalus)* (Papastavrou *et al.*, 1989) and northern elephant seals (*Mirounga angustirostris*) (Le Boeuf *et al.*, 1988), and in fish Atlantic bluefin tuna (*Thunnus thynnus thynnus*) (Block *et al.*, 2001), blue sharks (Carey & Scharold, 1990), white sharks (Boustany *et al.*, 2002), basking sharks (Sims *et al.*, 2003), pygmy sharks (*Europtomicrus bispinatus*) (Willmer *et al.*, 2000) and cookie-cutter sharks (*Isistius brasiliensis*)(Le Boeuf *et al.*, 1987). All four whale sharks tagged in Belize recorded deep dives to beyond 1000 m. During its 206-day deployment, S4 displayed repeated dives to over 1000m and a possible final tag-breaking dive of over 1500 m. It further tolerated a range of temperature while diving of 26.4^0C (range 30.75^0C to 4.35^0C).

Depths attained by whale sharks S1-S4 are further supported by results from whale sharks tagged in the Seychelles where one shark was recorded diving to 785 m

(Graham, unpublished data). In contrast, Eckert and Stewart's (2001) four sat-tagged whale sharks with deployments in the Gulf of California (ranging from 28 to 1144 days) spent the majority of time in the upper 10 m with about 1 % of time at 240 m or deeper. However, similar to S1-S4, the four sharks spent the majority of their time in 28^{0}C waters. Carey and Scharold (1990) found that ectothermic blue sharks dive regularly to 200 and 400 m with occasional deeper forays to 620 m and can withstand a 19^{0}C change in temperature. Boustany *et al.* (2002) discovered that endothermic white sharks can dive to 650-680 m, and tolerate temperature changes of 21.2^{0}C. Atlantic bluefin tuna surpass only slightly the whale shark's temperature tolerance with a recorded range of 27.8^{0}C (Block *et al.*, 2001), yet tuna are also considered endothermic and are able to maintain their body temperature above ambient levels (Altringham & Block, 1997). Basking sharks were previously thought to remain shallow while feeding and hibernate during winter months, descending to deeper cooler waters and shedding their gill rakers. Sims *et al.* (2003) have since found that basking sharks do not hibernate but are capable of making deep dives to between 750-1000 m possibly in search of dense patches of zooplankton.

Diving may serve several functions: 1) to prey on a previously detected food source at depth, 2) to enable the detection of horizontally stratified scents, 3) to minimize energy expenditure while swimming, 4) to navigate, and 5) to thermoregulate.

Olfaction is particularly acute in sharks, helping them to identify and target prey (Bleckmann & Hoffman, 1999). Coupled with oscillatory and deep dives, a keenolfacotry sense could help sharks to detect horizontally stratified odours in the water column (Carey & Scharold, 1990; Boustany *et al.*, 2002; Klimley *et al.*, 2002). It is possible that the whale sharks' pattern of evening oscillations highlight a process of "overshooting" an odoriferous layer that betrays the target prey, and the brief ascent corrects the diving behaviour to reach the layer of food. Regular dives may enable whale sharks to hunt for food at depth. Zooplankton appears to form a primary component of a whale shark's diet (Clark & Nelson 1997; Colman 1997; Graham, unpublished data) (see trophic analysis in Chapter 3). Many species of mesozooplankton are vertical migrators that live at depth during the day forming a "deep scattering layer" and ascend to the shallows at night (Koppelmann & Weikert, 1997; Vinogradov, 1997; Onsrud & Kaartvedt, 1998; Chou *et al.*, 1999). In the 24 h dive profiles, whale sharks exhibited a recurring diving pattern after sunset: a dive to 120-150 m followed immediately by a slight ascent and directed horizontal movement lasting several minutes to over an hour before ascending again and repeating the behaviour at a shallower depth. Although the presence of a deep scattering layer consisting of dense patches of zooplankton could not be determined during the course of this study, whale sharks displayed characteristic behaviour of an organism that is following the layer as it ascends at night in the water column. A similar pattern was detected in the acoustically tracked megamouth (*Megachasma pelagios*) off California (Nelson *et al.*, 1997).

Minimizing energy while swimming appears to drive some of the diving behaviour in several species of fish. Weihs (1973) suggested that to minimize energy while swimming, fish could use a glide on descents and active stroking approach on the ascents. In Belize, whale sharks have frequently been observed in a gliding descent from the surface to beyond 75 m and power stroking in the ascent. In deep dives to over 500 m, whale sharks descend one and half times as slowly as they ascend indicating the possible use of this strategy. However, the angles of descent in dives to over 1000 m noted in Figure 5.12 indicate possible active strokes, and negate the energy saving "gliding" strategy. Using the "Crittercam" video attached to tiger sharks in Australia, Heithaus *et al.* (2002) discovered that individuals actively swam during descents nullifying the theory of minimizing energy expenditure while gliding.

Several species of marine vertebrates and invertebrates have been shown to possess a magnetic compass and orient to the north-south bands of magnetisation and the numerous anomalies that constitute the earth's magnetic field (Zoeger *et al.*, 1981; Kalmijn, 1982; Walker, 1984; Walker *et al.*, 1997; Sandberg *et al.*, 2000; Fischer *et al.*, 2001; Lohmann *et al.*, 2001; Boles & Lohmann, 2003). Sharks are no exception and may orient using small anomalies in the earth's magnetic field (Kalmijn, 1982). Hammerheads swimming between two seamounts in the Gulf of California appear to orient themselves according to the magnetic topography and use oscillatory dives to distinguish local magnetic gradients from the main field (Klimley, 1993). These "landmark" anomalies increase in intensity with increasing depth (Klimley *et al.*, 2002) and could benefit migratory species capable of deep diving, such as the whale shark.

Although cooler temperatures at depth may constrain dive time at depth, whale sharks move back and forth across a range of temperatures (e.g., the thermocline) and possibly to thermoregulate and/or forage for food. No thermocline was detected offshore from Gladden Spit following multiple casts of a Conductivity/Temperature/Depth Instrument (CTD) in the first 200 m of the water column (Bjorn Kjerfve, pers. comm. 2003). Yet, the composite temperature profile recorded for S4 in waters in the Gulf of Honduras (Figure 5.8a) may indicate the presence of a thermocline around 250m when the curve steepens and temperatures cool more rapidly. Carey and Scharold (1990) believe that numerous transitions from the mixed layer through the thermocline by blue sharks are a form of behavioural thermoregulation and/or a search for food.

Heat conservation strategies are demonstrated in a range of teleost fish and sharks including tuna (Altringham & Block, 1997), alopiids (Carey & Robinson, 1981), and blue sharks (Carey & Scharold, 1990), yet have not been demonstrated for whale sharks or other orectolobiforms (Jeff Carrier, pers. comm. 2003). Whale shark S4 demonstrated that it could remain deeper than 1000m in waters cooler than 4.35^0C for at least 28 minutes. If S4 dived to over 1500m, it would have spent over 45 minutes in cold waters. In both situations heat conservation strategies would be necessary to offset cooling of body tissues. As such, whale sharks may retain heat passively through their thick skin and body mass. Whale shark epidermis covers a thick layer of subcutaneous fat that has been measured as 148 mm and 98 mm thick along the dorsal and abdominal areas respectively (Silas, 1986). High lipid levels in the subcutaneous layer were confirmed during the analysis of Nitrogen and Carbon stable isotopes (see Chapter 3). This thick layer would presumably provide insulation in colder waters by slowing core temperature decline over time.

As obligate air-breathers, marine mammals need varying periods of post deep-dive recovery (Le Boeuf *et al.*, 1988; Hooker & Baird, 1999; Le Boeuf *et al.*, 2000). Although fish do not require air, other factors such as low temperature or dissolved oxygen levels may require post-deep dive recovery time. Whale shark S4 interspersed its three dives to depths of over 1000m with at least 2.5 days between 25 and 31 July 2001. Although it is not possible to determine if ascents to warmer more oxygen rich waters constitute a form of recovery, whale sharks S1-S4 did not dive more frequently over 1000m than once every 2.5 days. With S4 however, all dives to over 1000 m were preceded with a dive to over 400 m only several hours before. Deep dives were also often followed by another >400 m dive indicating that S4 did not necessarily need to ascend immediately to warm surface water in between and following deep dives. The precursor medium depth dive might serve as an orientating dive before embarking on the deeper descent.

It is worth noting that all four sharks displayed no immediate changes in behaviour following surface-based tagging unlike that recorded for blue sharks (Sciarrotta & Nelson, 1977; Carey & Scharold, 1990), makos and white sharks (Klimley *et al.*, 2002). Tagging can also provoke increases in swimming speed (Sundstrom & Gruber, 1997) or departure from the tagging area (Klimley *et al.*, 1988). Whale sharks are not obligate daily surface-swimmers. In Ningaloo Reef, Western Australia, the longest time a whale shark spent away from the surface was 40 minutes but the tracking was relatively short; up to 26 h (Gunn *et al.*, 1999). S1-S4 summary data indicates that whale sharks swim at the surface every day. However, archival data indicates that S4 recorded nearly 8 days below 10 m depth, revealing the drawbacks of only using summary data in satellite pop-up tags.

5.4.2 Constraints of deep diving

Diving deep imposes numerous constraints on all marine animals. These include a lack of dissolved oxygen, decreased temperatures, increased hydrostatic pressure, and lack of light. It is possible that whale sharks go into oxygen debt while making excursions beyond 500 m, hence the directed and relatively brief nature of dives made beyond this depth. Global composites for dissolved oxygen levels in the tropics (Figure 5.22) indicate that levels drop precipitously from ~4.0 ml/l to < 1.0 ml/l close to 500 m at latitudes 15^{0}00'N-18^{0}00'N (encompassing the Mesoamerican Barrier Reef region). This coincides with the depth at which S4 begins dedicated deep dives with steep profiles and minimal recorded bottom time. Levels only increase again to ~4.0 ml/l at 1800 m depth[1]. In fish species, movement with respect to an oxygen minima/maxima layer has been proposed for swordfish *Xiphias gladius* and bigeye tuna, *Thunnus obesus* (Carey & Robinson, 1981; Holland *et al.*, 1992), although this has not been demonstrated definitively. Papastavrou *et al.* (1989) noted that sperm whale dives made in the Galapagos area in 1985 appeared to coincide with the oxygen minimum layer (~420 m) at that time. Papastavrou *et al.* (1989) suggested that an oxygen minimum layer can concentrate prey that are attempting to avoid predation, and renders respiring prey easier to catch due to low oxygen levels. These may provide some of the reasons for why whale sharks may dive in search of prey near to 500 m off the Mesoamerican Barrier Reef.

Deep diving leads to increased hydrostatic pressure that affects fishes in similar ways to marine mammals. Whale sharks are making descents and ascents beyond 1000 m (possibly beyond 1500 m), subjecting their bodies and metabolism to the rigours of over 100 atmospheres of hydrostatic pressure. The pygmy shark is known to regularly range to 1500 m in search of prey and teleost fish species have been recorded at depths of 7000 m (Willmer *et al.*, 2000). These abilities indicate that fish have undergone a

[1] Mapped from the global marine data set from the National Oceanographic Data Center's interactive web page http://iridl.ldeo.columbia.edu/SOURCES/NOAA/ NODC/WOA98/.

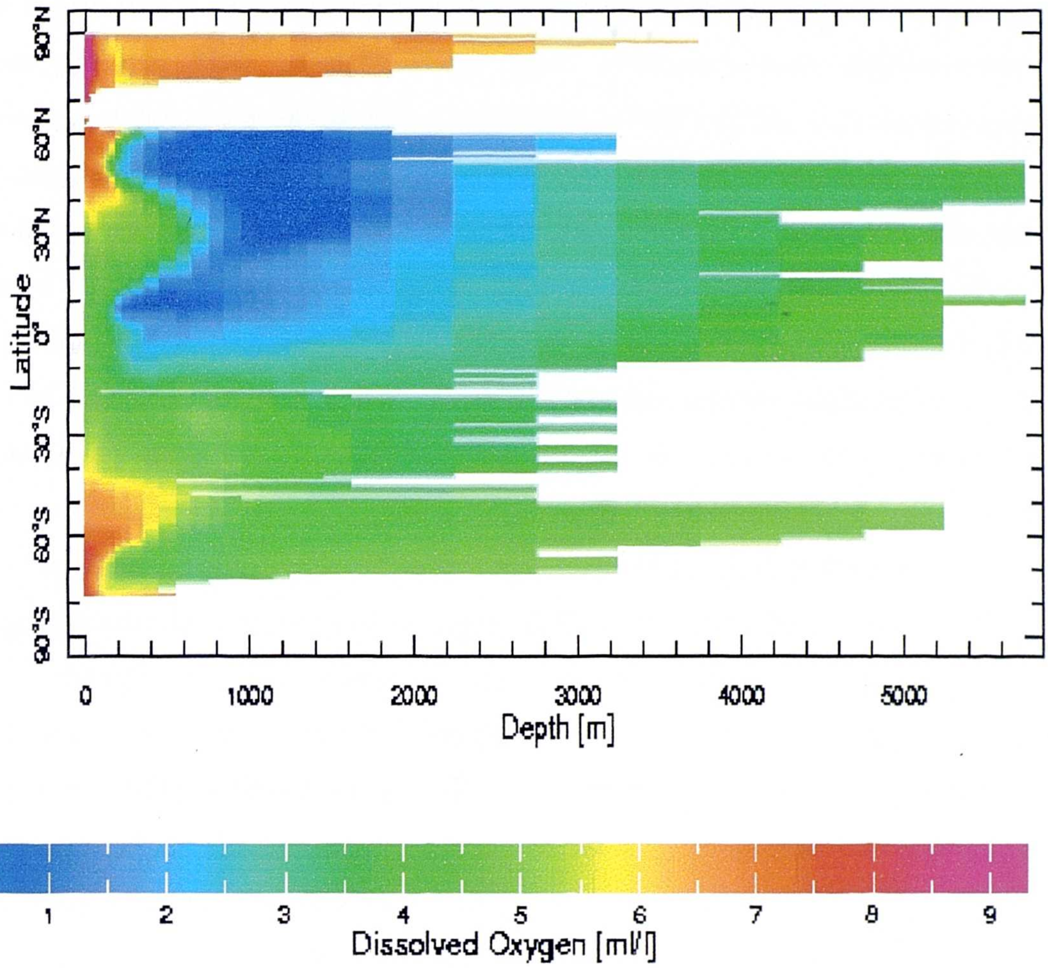


Figure 5.22: Global levels of dissolved oxygen ml/l (figure reproduced from NOAA/NODC World Ocean Atlas 1998).

range of adaptations to cope with pressure. Although information on the impact of pressure on fish is sparse, increased compression is known to impact the neurological system (termed high pressure neurological syndrome) with shallow-water fish displaying symptoms at about 100 atmospheres or 1000 m that include uncoordinated movements, seizures and irreversible immobility (Willmer *et al.*, 2000; Sebert, 2002). However, many species of deep-dwelling fish are among the oldest vertebrates and have adapted to cope with the physiological demands of increased pressure (Cailliet *et al.*, 2001). One adaptation noted is the increased levels of trimethylamine-*N*-oxide (TMAO) in deep dwelling as compared to shallow gadiform teleosts (Gillette *et al.*, 1997). TMAO is an important osmotic solute that is also found in sharks and helps them to counteract the macromolecular effects of urea and osmoconform to the surrounding seawater. TMAO helps to protect protein structure and function at depth and may confer added buoyancy to elasmobranchs (Yancey & Somero, 1980; Gillette *et al.*, 1997).

Although whale shark metabolic rates (rate of oxygen consumption) are unknown, sharks are considered to have low metabolic rates compared to teleost fishes (Brett & Blackburn, 1978; Bushnell *et al.*, 1989). As relatively slow-moving planktivorous ectotherms, whale sharks may have lowered rates in comparison to their lamnid or carcharinid cousins. Metabolic rate decreases with lower temperatures and oxygen availability limits the maximum potential size of a marine organism (Chapelle & Peck, 1999). This would explain why deep-dwelling fish (below 100 m) have dramatically lower oxygen consumption rates than species inhabiting the upper 100 m of the water column (Willmer *et al.*, 2000). Consequently, a lowered metabolism in whale sharks would benefit them during their daily deep dives. In many respects, vertical migrators such as whale sharks can be grouped with permanent deep residents (Willmer *et al.*, 2000).

These same constraints to diving deep and bottom-time may also provide cues that enable whale sharks to regulate their diving depth. Hydrostatic pressure was recently found to modulate the movements for dogfish, *Scyliorhinus canicula*, through simulated changes hydrostatic pressure in the vestibular II hair cells (Fraser & Shelmerdine, 2002). Although a lack of light is not necessarily a constraint to deep diving, changes in light levels are important cues and entrainers of locomotor activity in a range of fish and shark species (Finstad & Nelson, 1975; Carey & Scharold, 1990; Nelson *et al.*, 1997; Cummings & Morgan, 2001) and regulate diving activity in megamouth sharks (Nelson *et al.*, 1997) and blue sharks (Carey & Scharold, 1990).

5.4.3 Rhythmicity

Ultradian and circadian periodicity

The Fast Fourier Transform (FFT) method can help to reveal patterns of periodicity in time-series data by indicating the magnitude of a repeated activity over time. Although clear patterns can represent rhythmic behaviour, it is not always possible to determine why an animal is acting in a rhythmic manner. In this study, whale sharks revealed a strong non-random circadian periodicity to their diving behaviour that appeared to be rhythmic. The FFT analysis revealed the first indication of a free-running circadian rhythm (24 h) correlated with diving behaviour in a free-ranging shark. S4 also displayed rhythmic diving behaviour that coincided with periodicities of 45 min, 8 h, and 29, 35 and 58 days. These periodicities were highlighted as their signal magnitude represented approximately a 50% increase or greater over the surrounding spectra. S4's 45 min ultradian rhythm is remarkably precise and appears to be correlated with deep diving behaviour as it disappeared following the random repositioning of deep dives within the data set. Visual scanning of the data set showed that S4 often undertook a dive inferior to 500 m of about 45 minutes before embarking on a deeper dive of longer duration. Additionally when the data were segregated and analysed according to whether they fell within the snapper spawning-season or beyond, the ultradian rhythms disappeared. The 8 h periodicity was also correlated with deep diving behaviour as it was greatly reduced when the deep dives were randomly repositioned throughout the dive data.

The 24 h rhythm in S4's diving occurred irrespective of the presence or absence of deep dives in the data set. This non-random pattern may be linked to the diel vertical migrations of zooplankton that usually aggregate near the surface by night and descend to deeper depths during the day (Folt & Burns, 1999). Diel vertical migration of zooplankton or changes of light level during twilight periods may therefore modulate whale shark diving behaviour leading to patterns of shallow dives at night and deeper dives recorded during the day. Depth change events were very distinct and always encompassed sunset and sunrise. This similarity in behaviour was recorded for the four tagged male sharks. Consequently, sex-based differences in whale shark diving behaviour cannot be determined from this study. Several other studies on diel diving behaviour have revealed similar patterns across a range of shark species. Gunn *et al.* (1999) found that four whale sharks tracked at Ningaloo Reef spent more time close to the surface at night than during the day. A 4.9 m megamouth tracked for 50.5 h showed that the shark stayed shallow at night above 25 m and went deeper 120-166 m during the day (Nelson *et al.*, 1997). Nelson *et al.* (1997) also determined that the shark's chosen depth was largely determined by light level.

Rhythmic feeding behaviour and patterns of activity have been documented for a range of fish and shark species (Finstad & Nelson, 1975; Naylor, 1985; Boujard, 1995; Sanchez-Vazquez *et al.*, 1995; Heilman & Spieler, 1999). Many of the circadian rhythms discovered to date in fish are linked to feeding behaviour, e.g. pompanos (*Trachinotus carolinus*) (Heilman & Spieler, 1999), catfish (*Silurus glanis*) (Boujard, 1995), and European sea bass (*Dicentrarchus labrax*) (Boujard *et al.*, 2000). Sanchez-Vazquez *et al.* (1995) showed that food-demand rhythms in nocturnal and diurnal sea bass are modulated by periodic food availability under a constant light regime. However, an endogenous rhythm unrelated to food availability may be responsible for changes in feedings patterns from nocturnal to diurnal in some fish (Sanchez-Vazquez *et al.*, 1995).

Because the sharks are diving deeper during the day, often beyond 200 m, they must be swimming offshore beyond the fore-reef shelf. This was further supported by the periodic lack of daytime visitation by acoustically tagged sharks at the Gladden Spit acoustic receiver during the snapper spawning-season (Chapter 3). The 24 h periodicity may coincide with a peak in diving depth and may be synchronized by light. Several species of fish display a 24 h ± 4 h circadian rhythm of locomotor activity, and different rhythms may exist in synchrony as seen with the inter-tidal blennies (*Zoarces viviparus*) that display ultradian tidally-synchronized peaks in locomotion and 24 h spikes in activity (Cummings & Morgan, 2001). Although many shark species such as the blue shark are considered nocturnal (Sciarrotta & Nelson, 1977), Finstad and Nelson (1975) noted that horn sharks (*Heterodontus francisci*) displayed light-triggered onset of activity under natural and laboratory conditions. Bonnethead sharks (*Sphyrna tiburo*) also display a diurnal peak in activity recorded in the late afternoon (Sciarrotta & Nelson, 1977). Whale sharks appear to be diurnal and nocturnal feeders based on day-time observations (Taylor, 1996; Clark & Nelson, 1997; Gunn *et al.*, 1999; Heyman *et al.*, 2001) and night-time sightings (Gunn *et al.*, 1999).

It is not clear what activity the whale shark is undertaking during any of the periodicities recorded and must be further investigated. Furthermore, it was not possible in this study to determine whether the rhythms detected through whale shark diving periodicity were endogenous or entrained solely by external cues such as light levels.

Circalunar and seasonal periodicity

Whale shark diving patterns were seasonal. Within the snapper spawning season, from March to July, the increased spectral magnitude of the 24 h or circadian periodicity recorded in S4's diving may have been due to S4 cueing its diving behaviour with the vertical movements and spawning of the aggregating snappers in addition to following vertically migrating zooplankton. During the peak 14-day snapper spawning periods that took place during the full moon and last quarter moon periods from March to July, whale sharks relaxed deep-diving behaviour. Shallow oscillatory swimming during this period enabled whale sharks to remain close to the fish spawning aggregations while searching for other possible food items. This restricted searching behaviour was also recorded for whale sharks in Ningaloo Reef, Australia by Gunn *et al.* (1999) in relation to zooplankton blooms. Seasonality in diving has been noted in other species of marine animals. Carey and Scharold (1990) noted that blue sharks displayed seasonal diving patterns and relaxed deep diving behaviour in May, June and July. Similarly, dive depths varied seasonally in elephant seals in relation to food type and availability (Delong & Stewart, 1991) and inter-tidal blennies showed seasonal variations in the persistence of circatidal swimming (Cummings & Morgan, 2001).

Following the cessation of snapper spawning at Gladden Spit, whale sharks dispersed and incorporated deeper dives into their diving behaviour. This could explain why tour-guides and fishers rarely saw the whale sharks near the Gladden Spit spawning grounds outside of spawning periods. Deep dives to over 2000 m were possible next to the Gladden promontory where the fore-reef rapidly drops into the southern end of the Cayman Trench. During this period whale sharks may have been targeting food at depth similar to the behaviour displayed by blue sharks feeding on *Alloposus mollis* octopods during forays to over 250 m (Carey and Scharold 1990).

The stronger spectral magnitude coinciding with the 29-day diving periodicity recorded outside of the snapper spawning-season may correlate with the shark's need to forage more actively throughout the water column in search of food once the snappers had ceased spawning. These data are further supported by the increase in deep dives made by whale sharks and movement away from Gladden Spit and past other acoustic receivers along the barrier reef between and beyond spawning moons (see Chapter 4 on patterns of movement). The whale shark circalunar endogenous rhythm may also aid in navigation. Lohmann and Willows (1987) demonstrated that magnetic orientation can be cued by the lunar phase in nudibranchs and light intensities equivalent to moonlight have been demonstrated as sufficient to entrain circalunar rhythms in *Carcinus* crabs (Naylor, 1985).

5.5 Conclusions

Results from this study indicate that whale sharks are physiologically much more resistant to diving stresses and closer in diving behaviour to marine mammals than previously thought. Previously considered solely epipelagic, whale sharks are able to tolerate a broad range of temperatures and hydrostatic pressures and oxygen depauperate zones during their frequent dives. Diving patterns appear to be regulated by ultradian, circadian and circa-lunar rhythms. Several of these rhythms are free-running and endogenous and appear to be synchronized by light whereas the ultradian rhythm appears to be cued by food availability. However, additional tagging with archival pop-up tags of the broader population is needed to reveal more on whale shark diving locations and behaviour, particularly for females and mature sharks, and by world region. Characterisation of the oxygen minima/maxima layer and locations and behaviour of the zooplankton deep scattering layers will help to better understand the factors that regulate whale shark diving behaviour. As diving appears to be an essential component of whale shark behaviour it should be incorporated into any strategies for whale shark conservation.

5.6 References

Altringham J. D. & Block B. A. 1997. Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *Journal of Experimental Biology*. **200** (20): 2617-2627.

Bekby T. & Bjorge A. 2000. Diving behaviour of harbour seal *Phoca vitulina* pups from nursing to independent feeding. *Journal of Sea Research*. **44** (3-4): 267-275.

Bleckmann H. & Hoffman M. H. 1999. Special senses. In: *Sharks, Skates, and Rays: The Biology of Elasmobranch Fishes*. (Hamlett W. C. ed.), pp 300-328. Baltimore, Maryland 21218-4363. The Johns Hopkins University Press.

Block B. A., Dewar H., Blackwell S. B., Williams T. D., Prince E. D., Farwell C. J., Boustany A., Teo S. L. H., Seitz A., Walli A. & Fudge D. 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science*. **293** (5533): 1310-1314.

Block B. A., Dewar H., Farwell C. & Prince E. D. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proceedings of the National Academy of Sciences of the United States of America*. **95** (16): 9384-9389.

Boles L. C. & Lohmann K. J. 2003. True navigation and magnetic maps in spiny lobsters. *Nature*. **421**: 60-63.

Boujard T. 1995. Diel rhythms of feeding activity in the European catfish, *Silurus glanis*. *Physiology & Behavior*. **58** (4): 641-645.

Boujard T., Gelineau A., Corraze G., Kaushik S., Gasset E., Coves D. & Dutto G. 2000. Effect of dietary lipid content on circadian rhythm of feeding activity in European sea bass. *Physiology & Behavior*. **68** (5): 683-689.

Boustany A. M., Davis S. F., Pyle P., Anderson S. D., Le Boeuf B. J. & Block B. A. 2002. Satellite tagging: expanded niche for white sharks. *Nature*. **415** (6867): 35-36.

Boyd I. L. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology & Evolution*. **12** (6): 213-217.

Brett J. R. & Blackburn J. M. 1978. Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. *Journal of Fisheries Research Bd. Can.* **35**: 816-821.

Brown B. R. 2003. Sensing temperature without ion channels. *Nature*. **421**: 495.

Bushnell P. G., Lutz P. L. & Gruber S. H. 1989. The metabolic rate of an active tropical elasmobranch, the lemon shark (*Negaprion brevirostris*). *Experimental Biology*. **48**: 279-283.

Cailliet G. M., Andrews A. H., Burton E. J., Watters D. L., Kline D. E. & Graham L. A. F.-. 2001. Age Determination and validation studies of marine fishes: do deep-dwellers live longer? *Experimental Gerontology*. **36**: 739-764.

Carey F. G. & Robinson B. H. 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fishery Bulletin*. **79**: 277-292.

Carey F. G. & Scharold J. V. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*. **106**: 329-342.

Chapelle G. & Peck L. S. 1999. Polar gigantism dictated by oxygen availability. *Nature*. **399**: 114-115.

Chou S.-C., Lee M.-A. & Lee K.-T. 1999. Diel vertical movement of the deep scattering layer on the continental slope of I-Lan Bay, Taiwan. *Fisheries Science*. **65** (5): 694-699.

Clark E. & Nelson D. R. 1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes*. **50** (1): 63-73.

Colman J. G. 1997. A review of the biology and ecology of the whale shark. *Journal of Fish Biology*. **51** (6): 1219-1234.

Cummings S. M. & Morgan E. 2001. Time-keeping system of the eel pout, *Zoarces viviparus*. *Chronobiology International*. **18**: 27-46.

Delong R. L. & Stewart B. S. 1991. Diving patterns of northern elephant seal bulls. *Marine Mammal Science*. **7(4)**: 369-384.

Eckert S. A. & Stewart B. S. 2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico, and the north Pacific Ocean. *Environmental Biology of Fishes*. **60** (1-3): 299-308.

Finstad W. O. & Nelson D. R. 1975. Circadian activity rhythm in the horn shark *Heterodontus francisci*: effect of light intensity. *Bulletin of the Southern California Academy of Science*.**74**: 20-26.

Fischer J. H., Freake M. J., Borland S. C. & Philips J. B. 2001. Evidence for the use of magnetic map information by an amphibian. *Animal Behaviour*. **62**: 1-10.

Folt C. L. & Burns C. W. 1999. Biological drivers of zooplankton patchiness. *Trends in Ecology & Evolution*. **14** (8): 300-305.

Fraser P. J. & Shelmerdine R. L. 2002. Dogfish hair cells sense hydrostatic pressure. *Nature*. **415**: 495-496.

Gillette M. B., Suko J. R., Santoso F. O. & Yancey P. H. 1997. Elevated levels of trimethylamine oxide in muscles of deep-sea gadiform teleosts: a high-pressure adaptation? *The Journal of Experimental Zoology*. **279**: 386-391.

Goldman K. J. & Anderson S. D. 1999. Space utilization and swimming depths of white sharks, *Carcharodon carcharias*, at the south Farallon Islands, central California. *Environmental Biology of Fishes*. **56**: 351-364.

Graves J. E., Luckhurst B. E. & Prince E. D. 2002. An evaluation of pop-up satellite tag technology for estimating post release survival of blue marlin (*Makaira nigricans*) from a recreational fishery. *Fishery Bulletin*. **100**: 134-142.

Gudger E. W. 1915. Natural history of the whale shark, *Rhineodon typus* Smith. *Zoologica*. **1** (19): 345-389.

Gunn J. S., Stevens J. D., Davis T. L. O. & Norman B. M. 1999. Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Marine Biology*. **135**: 553-559.

Hays G. C., Adams C. R., Broderick A. C., Godley B. J., Lucas D. J., Metcalfe J. D. & Prior A. A. 2000. The diving behaviour of green turtles at Ascension Island. *Animal Behaviour*. **59**: 577-586.

Heilman M. J. & Spieler R. E. 1999. The daily feeding rhythm to demand feeders and the effects of timed meal-feeding on the growth of juvenile Florida pompano, *Trachinotus carolinus*. *Aquaculture*. **180** (1-2): 53-64.

Heithaus M. R., Dill L. M., Marshall G. J. & Buhleier B. 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology*. **140** (2): 237-248.

Heyman W. D., Graham R. T., Kjerfve B. & Johannes R. E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology-Progress Series*. **215**: 275-282.

Hochscheid S., Godley B. J., Broderick A. C. & Wilson R. P. 1999. Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Marine Ecology-Progress Series*. **185**: 101-112.

Holland K., Brill R. W., Chang R. K. C., Sibert J. R. & Fournier D. A. 1992. Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature*. **358**: 410-411.

Holland K. N., Wetherbee B. M., Peterson J. D. & Lowe C. G. 1993. Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia*. **1993** (2): 495-502.

Hooker S. K. & Baird R. W. 1999. Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proceedings of the Royal Society of London Series B-Biological Sciences*. **266** (1420): 671-676.

Kalmijn A. J. 1982. Electric and magnetic field detection in elasmobranchs. *Science*. **218** (26): 916-918.

Klimley A. P. 1993. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biology*. **117** (1): 1-22.

Klimley A. P., Beavers S. C., Curtis T. H. & Jorgensen S. J. 2002. Movements and swimming behaviour of three species of sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*. **63**: 117-135.

Klimley A. P., Butler S. B., Nelson D. R. & Stull A. T. 1988. Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *Journal of Fish Biology*. **33**: 751-761.

Klimley A. P. & Nelson D. R. 1984. Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. *Behavioral Ecology and Sociobiology.* **15** (1): 45-54.

Koppelmann R. & Weikert H. 1997. Deep Arabian Sea mesozooplankton distribution. Intermonsoon, October 1995. *Marine Biology.* **129**: 549-560.

Le Boeuf B. J., Costa D. P., Huntley A. C. & Feldkamp S. D. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris. Canadian Journal of Zoology.* **66** (2): 446-458.

Le Boeuf B. J., Crockers D. E., Grayson J., Gedamke J., Webb P. M., Blackwell S. B. & Costa D. P. 2000. Respiration and heart rate at the surface between dives in northern elephant seals. *Journal of Experimental Biology.* **203** (21): 3265-3274.

Le Boeuf B. J., McCosker J. E. & Hewitt J. E. 1987. Crater wounds on northern elephant seals: the cookiecutter shark strikes again. *Fisheries Bulletin.* **85** (2): 387-392.

Lohmann K. J., Cain S. D., Dodge S. A. & Lohmann C. M. F. 2001. Regional magnetic fields as navigational markers for sea turtles. *Science.* **294** (5541): 364-366.

Lohmann K. J. & Willows A. O. 1987. Lunar-modulated geomagnetic orientation by a marine mollusk. *Science.* **235**: 3331-3334.

Lutcavage M. E., Brill R. W., Skomal G. B., Chase B. C. & Howey P. W. 1999. Results of pop-up satellite tagging of spawning size class fish in the gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries Aquatic Science.* **56**: 173-177.

Marcinek D. J., Blackwell S. B., Dewar H., Freund E. V., Farwell C., Dau D., Seitz A. C. & Block B. A. 2001. Depth and muscle temperature of Pacific bluefin tuna examined with acoustic and pop-up satellite archival tags. *Marine Biology.* **138** (4): 869-885.

Mate B., Rossbach K. A., Nieukirk S. L., Wells R. S., Irvine A. B., Scott M. D. & Read A. J. 1995. Satellite-monitored movements and dive behaviour of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science.* **11** (4): 452-463.

Naylor E. 1985. Tidally rhythmic behaviour of marine animals. *Symposium of the Society for Experimental Biology.* **39**: 63-93.

Nelson D. R., McKibben J. N., Strong W. R., Lowe C. G., Sisneros J. A., Schroeder D. M. & Lavenberg R. J. 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes*. **49**: 389-399.

Onsrud M. S. R. & Kaartvedt S. 1998. Diel vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. *Marine Ecology Progress Series*. **171**: 199-208.

Papastavrou V., Smith S. C. & Whitehead H. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Canadian Journal of Zoology*. **67**: 839-846.

Sanchez-Vazquez F. J., Zamora S. & Madrid J. A. 1995. Light-dark and food restriction cycles in sea bass: effect of conflicting zeitgebers on demand-feeding rhythms. *Physiology & Behavior*. **58** (4): 705-714.

Sandberg R., Backman H., Moore F. R. & Lohmus M. 2000. Magnetic information calibrates celestial cues during migration. *Animal Behaviour*. **60**: 453-462.

Sciarrotta T. C. & Nelson D. R. 1977. Diel behaviour of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. *Fishery Bulletin*. **75** (3): 519-528.

Sebert P. 2002. Fish at high pressure: a hundred year history. *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*. **131**: 575-585.

Silas E. G. 1986. The whale shark (*Rhiniodon typus* Smith) in Indian coastal waters: is the species endangered or vulnerable? *Marine Fisheries Information Service*. **66**: 1-38.

Sims D. W., Southall E. J., Richardson A. J., Reid P. C. & Metcalfe J. D. 2003. Seasonal movements and behaviour of basing sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series*. **248**: 187-196.

Sundstrom L. F. & Gruber S. H. 1997. Using speed sensing transmitters to model the bioenergetics of subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. *Hydrobiologia*. **271/272**: 241-247.

Sundstrom L. F., Gruber S. H., Clermont S. M., Correia J. P. S., Marignac J. R. C. d., Morrissey J. F., Lowrance C., Thomassen L. & Oliveira M. T. 2001. Review of elasmobranch behavioral studies using telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes*. **60**: 225-250.

Taylor J. G. 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*. **47** (4): 637-642.

Vinogradov M. E. 1997. Some problems of vertical distribution of meso- and macroplankton in the ocean. *Advances in Marine Biology*. **32**: 1-92.

Walker M. M. 1984. Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. *Science*. **155**: 673-679.

Walker M. M., Diebel C. E., Haugh C. V., Panhurst P. M., Montgomery J. C. & Green C. R. 1997. Structure and function of the vertebrate magnetic sense. *Nature*. **390**: 371-376.

Weihs D. 1973. Mechanically efficient swimming techniques for fish with negative buoyancy. *Journal of Marine Research*. **31**: 194-209.

Willmer P., Stone G. & Johnston I. 2000. *Environmental Physiology of Animals*. Blackwell Science Ltd, London. 644 pp.

Yancey P. H. & Somero G. N. 1980. Methylamine osmoregulatory compounds in elasmobranch fishes reverse usea inhibition of enzymes. *Journal of Experimental Zoology*. **212**: 205-213.

Zoeger J., Dunn J. R. & Fuller M. 1981. Magnetic material in the head of the common Pacific dolphin. *Science*. 213: 892-894.

Appendix 5.A

Satellite tag performance

Satellite pop-off tags are the best fisheries- and sightings-independent technology we have to assess large fish behaviour. Tags deployed in Belize have provided new and exceptional insights into whale shark diving behaviour. Unfortunately satellite pop-off tags must endure the rigours of the marine environment that accounts for the failure of some tags to report data. To date, satellite archival pop-off tags performance when deployed on marine fish has been variable. Knowledge of tag success rates help to improve tag design. In this study, the success rate reached 55% with 6 out of 11 tags providing usable data. There is no clear definition for what constitutes a "successful" tag as researchers consider that any data is better than no data. This study's success rate is similar to that observed in a whale shark study in the Seychelles (Graham, unpublished data), a white shark (*Carcharodon carcharias*) study conducted by a highly experienced white shark tagging team based in California (Chuck Farwell, pers. comm. 2001) and surpasses the success rates of a white shark study in South Africa (R. Bonfil, pers. comm. 2002). Tag success rates appear significantly higher for Block *et al.* (2001) who noted data acquisition from 90% of pop-off satellite tags deployed on Atlantic bluefin tuna. However, when data from the four performing tags (S1-S4) are assessed, there is a clear decay in percentage of usable data with length of deployment. This would indicate that shorter period deployments are advisable to generate the maximum data when conducting studies with tight budgets.

Physical damage may cause the greatest numbers of tag failures. Predators or associated commensal species may impact tags while they are attached to their hosts (M. Braun, pers. comm. 2002), damaging the tag structure or impacting transmission through damage to the antenna (Graham, pers. obs.). Pressure is another culprit. Of two tags that never reported after their release date, S4 had to be clipped off the returning shark a year after it was deployed and was heavily fouled (Figure 5.2). The manufacturer considered that the pop-off mechanism had been damaged when the shark apparently dived beyond the tag depth limit of 1500 m. Dives beyond 1500 m may account for the remaining poorly transmitting or non-reporting satellite tags. Transmission errors and obstruction of transmission can also account for lack of data. S5 may have washed up on the north coast of Honduras after detachment. This would account for its initial location transmission followed by sporadic but generally few data transmitted. However, the manufacturers now provide a guillotine device that releases tags when the animal dives to beyond 1,500 m, hopefully reducing tag mortality in future studies. These devices were not available during this study.

Finding a satellite tag full of data is a windfall in pelagic fish research providing exceptional new insights into patterns of diving behaviour and in the case of the whale shark, further insights into its physiology. Sims retrieved two tags following detachment from basking sharks that are providing new insights into the species' diving behaviour (D. Sims, pers. comm. 2002) and Block retrieved 49 archival tags (out of 279 or 18%) from Atlantic bluefin tuna (Block *et al.*, 2001). Despite notices of cash rewards posted in fisheries offices and tourist centres, only one tag was ever recovered after having washed up on a beach. Unfortunately, the tag was subsequently lost before it could be returned.

Chapter 6. Characterising the mutton snapper (*Lutjanus analis* Cuvier, 1828) spawning aggregation fishery at Gladden Spit, Belize

Abstract

The predictable sites and timing of reef fish spawning aggregations have made them an easy target for fisheries worldwide and more recently targets for the conservation of fish stocks. Scientific information on the decline of reef fish spawning aggregations, particularly snapper (Lutjanidae) aggregations in tropical countries is sparse. In Belize, fishers once fished thirteen seasonal spawning aggregations, primarily for grouper species. Following extirpation of most of these aggregations, the mutton snapper (*Lutjanus analis* (Cuvier)) spawning aggregation fishery at Gladden Spit remains the last commercially fished in Belize. Analysis of inter-seasonal catch, effort and yield of this small-scale fishery revealed a significant 58.5% decline in catch per unit effort (CPUE) and a decrease of 22% in mean landings per fisher between 2000 and 2002. Over the same period the mean number of fishers increased by 27% and boats by 25% and these were accompanied by a significant 34% increase in the mean time spent fishing. Mean mutton snapper fork-length in catches decreased by 4.2%. The fishery's worth was estimated at US$35,497 in 2002. Gladden Spit also harbours a dense and predictable aggregation of whale sharks (*Rhincodon typus*) that feed on the spawn of cubera and dog snappers (*L. cyanopterus* and *L. jocu*). Fishers believe that the sharks also feed on the spawn of mutton snappers and are responsible for the decline in catches. Results indicate that the Gladden Spit mutton snapper population is primarily impacted by the fishery and is unsustainable even at the current level of small-scale artisanal fishing. These findings mirror trends noted in numerous historical extirpations of other spawning aggregations in Belize and worldwide. As such, the precautionary principle should be applied, whereby this and other spawning aggregations should be fully protected to ensure the health and survival of remaining spawning fish stocks.

6.1 Introduction

Fish that aggregate to reproduce at predictable times and sites are particularly vulnerable to capture (Johannes, 1978; Sadovy, 1996; Domeier & Colin, 1997).

Consequently, worldwide interest is turning towards the conservation of fish spawning aggregations as a means of stemming the decline in fish stocks (Bohnsack, 1989; Sadovy, 1994; Johannes, 1998; Beets & Friedlander, 1999; Sala *et al.*, 2001; Sadovy & Cheung, 2003). Fishing spawning aggregations has been a favoured solution to feeding growing populations, and maximising gains while minimising fishing costs, particularly in tropical countries. Yet, targeting spawning aggregations is a short-term and unsustainable solution to satisfying the increasing demand for fish products.

Historical and documented evidence from several tropical countries point to local, regional and worldwide patterns of over-exploited and even extirpated spawning aggregations of reef fish (Johannes, 1978; Sadovy, 1992, 1993, 1994; Domeier & Colin, 1997; Salem, 1999; Sala *et al.*, 2001). Mass migrations of fish to spawning aggregation sites may also be targeted and vulnerable to extirpation, as has been documented by the dramatic decline in landings of the Gulf of California's totoaba (*Totoaba macdonaldi*) from half to one million kilograms in 1930 to very low numbers currently (Cisneros-Mata *et al.*, 1995; Roberts & Hawkins, 1999). Extirpation of lane snappers (*L. synagris*) and the serial exploitation and depletion of other snapper species has been recorded in Cuba (Claro, 1991). Craig (1966) recorded the unsustainable fishery for mutton snappers migrating past Long Caye in Belize towards spawning aggregation sites (Craig, 1966).

Families of reef fish known to aggregate in large numbers to spawn include the Serranidae, Lutjanidae, Caesionidae, Mugilidae, Mullidae, Scaridae, Siganidae (Claro, 1981; Munro, 1983; Sadovy, 1996; Domeier & Colin, 1997) Balistidae, Ostraciidae and Carangidae (Graham, unpublished data). Studies that document the chronology of exploitation and systematic decline of a spawning aggregation are sparse. In Egypt, Salem (1999) studied a spawning aggregation fishery for *Lethrinus nebulosus* that has been intensively fished for over 20 years and has led to a decline of 50% in catch per unit effort over five years. In the Caribbean, several spawning aggregations of Nassau grouper (*Epinephelus striatus*) identified in the Dominican Republic, Bermuda, Bahamas and the US Virgin Islands were extirpated within a few years of being heavily fished (Colin, 1992; Sadovy, 1992, 1993). In the absence of documented catch statistics, much of the historical and anecdotal information provided by fishers on spawning aggregations has become an invaluable benchmark to manage and measure the health of a fishery (Johannes, 1998). Most information on spawning aggregation declines stems from historical accounts of previous abundance by fishers (Olsen & Place, 1979;

Johannes, 1998; Sadovy & Cheung, 2003), several of which were observed in the Caribbean (Olsen & Place, 1979; Paz & Grimshaw, 2001; Sala *et al.*, 2001).

In Belize at least 13 spawning aggregation sites for grouper are documented yet only four support spawning aggregations that number over 50 individuals, none of which are considered commercially viable fishing sites (Paz & Grimshaw, 2001). The most famous spawning aggregation fishery in Belize targeted the Nassau groupers at Caye Glory. Craig (1966) documented an estimated 300 fishing boats and official catch statistics recorded an estimated 32,328 kg of grouper landed from Caye Glory in the 1963 spawning season; considered by Craig an underestimate of true landings. By 1965, the fishery was already perceived in decline by older fishers (Craig, 1966) and in 1985, the site was no longer considered commercially viable (Paz & Grimshaw, 2001).

Spawning aggregations may not rebuild once they have been extirpated. If a large proportion of mature adults are removed from the population, then recruitment failure can ensue (Sadovy, 1996), particularly if populations consist of long-lived fish (over 25 years) such as groupers and snappers (Allen, 1985; Sadovy & Ecklund, 1999; Burton, 2002). Preliminary evidence is not encouraging: populations have not recovered in several formerly successful fisheries based on spawning aggregations including the cod fisheries of Newfoundland and New England (Haedrich & Barnes, 1997; Lawson & Rose, 2000), several sites in the Caribbean (Sadovy & Ecklund, 1999), and the Belize-based Caye Glory grouper fishery (Paz & Grimshaw, 2001) even after years of respite from intensive large-scale fishing. An underwater fish census undertaken at Caye Glory in December 2001 and January 2002, the peak Nassau grouper spawning months, revealed four groupers in December and about 150 in January. These results indicate that after 16 years the spawning population, which once numbered in the thousands, had not rebuilt and was still no longer commercially viable.

Snapper spawning migrations and aggregations have also been targeted and extirpated by fisheries (Craig, 1966; Claro *et al.*, 2001). In Belize, mutton snappers (*Lutjanus analis* (Cuvier, 1828)) form the basis of the only remaining commercial fishery on a spawning aggregation. Mutton snappers are a reef-associated pan-Caribbean species with high commercial fisheries value (Claro, 1981; Bortone & Williams, 1986). Maturing at an approximate fork length of 50 cm and an age of 5 years (Claro *et al.*, 2001) mutton snappers are highly fecund. One individual weighing 4.7 kg and measuring 61 cm was recorded as producing 3.8 million eggs (Claro, 1981). Using the von Bertalanffy 'back calculation' technique, mutton snappers were recently found to reach at least 29 years of age (Burton, 2002). Mutton snapper feed on a range of smaller fish and invertebrates (Druzhinin, 1970; Claro, 1981; Sierra, 1996), and occupy a range of habitats throughout its life cycle. Mutton snappers utilise inshore mangroves and sea grass beds when young and move to fore-reef areas when adult (Claro, 1981; Claro *et al.*, 2001; García-Cagide *et al.*, 2001). Like all Lutjanids, mutton snappers are gonochoristic (sex does not change within a life-cycle), transient group spawners whose spawning aggregation behaviour is entrained by a lunar rhythm (Wicklund, 1969; Munro *et al.*, 1973; Claro, 1981). The spawning season is protracted from March to August-September (Claro, 1981). Like several other group spawning reef fish species, mutton snappers migrate from inshore reef areas and aggregate to spawn at fore reef sites, using promontories or other areas of high relief to spawn (Johannes, 1978; Claro, 1991; Carter & Perrine, 1994; García-Cagide *et al.*, 2001).

Little is known about the reproductive behaviour of Lutjanidae in the wild (Claro, 1981; Claro, 1983; Carter & Perrine, 1994) compared to numerous studies that document grouper reproductive behaviour and the associated fisheries (Munro *et al.*, 1973; Colin, 1977; Johannes, 1978; Colin, 1982; Moyer *et al.*, 1983; Colin & Clavijo, 1988; Johannes, 1988; Shapiro *et al.*, 1993; Russ & Alcala, 1994; Aguilar Perera & Aguilar Davila, 1996; Zeller, 1998; Beets & Friedlander, 1999; Sala *et al.*, 2001; Rhodes & Sadovy, 2002). Only three species of lutjanids, *Lutjanus synagris*, *L. cyanopterus* and *L. jocu* have ever been documented to spawn (Wicklund, 1969; Heyman *et al.*, 2001). Documented declines of artisanal and commercial fisheries on snapper spawning aggregations are equally sparse (Claro, 1991; Domeier *et al.*, 1996; Claro *et al.*, 2001).

In Belize, mutton snapper are primarily caught in fore-reef areas during the spawning aggregation period of March through June using hook and line (handline), the second most important method of reef fishing for artisanal fishers in the Caribbean after traps (Munro, 1983). Handlining is one of the most benign forms of fishing in terms of low impacts on habitats relative to dredging, trawling and gill netting and is considered the most appropriate form of fishing for predatory fish in reef areas (Munro, 1983; Dalzell, 1996). Yet, handlining is an effective means of selecting for predatory fish. Additionally, handlining can exert strong pressures on fish stocks when these aggregate to spawn (Craig, 1969; Olsen & Place, 1979) through rapid removal of a high percentage of the spawning stock in a short time (Sala *et al.*, 2001; Rhodes & Sadovy, 2002). The removal of larger more fecund fish can create a sex-bias in the remaining population and impact recruitment (Sadovy, 1996). As a result, protective measures have been implemented in several countries in an attempt to minimize or eliminate fishery impacts on vulnerable spawning fish.

Protection of spawning aggregations has taken many forms from seasonal closures, harvest bans, gear bans and site closures (Bohnsack, 1989). Many of these regulations have been ineffective at stemming the decline in adult fish populations and are often easily circumvented (Rhodes & Sadovy, 2002). However, permanent site closures or no-take marine reserves have become the recent focus of most efforts to protect spawning stocks worldwide (Roberts, 1994, 1997; Roberts, 1998; Sala *et al.*, 2002) as they provide the additional benefit of preserving spawning habitats (Salem, 1999). Riley's Hump in Florida's Dry Tortugas was declared a no-take marine reserve in 2001 following the commercial extirpation of the once productive mutton snapper spawning aggregation fishery (Domeier *et al.*, 1996). Similarly, the Belize Government recently declared a seasonal ban on fishing of Nassau grouper from December to March and the protection of 11 of the 13 known reef fish spawning aggregation sites located along the Belize Barrier Reef. However, Gladden Spit is not included in the 11 fully protected sites.

The mutton snapper fishing season at Gladden Spit also coincides with the whale shark tourism season. Whale sharks aggregate seasonally at Gladden to feed on the spawn of cubera and dog snappers (Heyman *et al.,* 2001). They have not been observed to feed on spawn of mutton snappers. Nonetheless, fishers have perceived whale sharks as competitors for the same resource and a direct threat to the fishery. Additionally, the close proximity of tour and fishing boats at the fish spawning and whale shark aggregation site has led to conflicts between fishermen and dive operators during the fishing moon over geographic rights and the relative economic importance of both activities.

The objective of this study was to characterise the status of the mutton snapper spawning aggregation fishery at Gladden Spit and derive recent morphological and fisheries information for its management and conservation. According to a range of studies, fishing on reef fish spawning aggregations leads to decreases in mean fish size and abundance over a short time prompting regulatory measures (Sadovy, 1994; Claro *et al.*, 2001). In this study, the fishing effort and yield are specifically assessed, as well as changes in fish size frequency in catches from 2000-2002 to determine if fishing is impacting the spawning aggregation. Additionally, this study attempted to determine whether fishers were competing directly with whale sharks (*Rhincodon typus*) for mutton snapper spawn. To best characterize this fishery, a combination of empirical data and anecdotal information was used, where anecdotal information was gleaned from observations and semi-structured interviews with fishers. Results are discussed in the context of historical fishing efforts at Gladden Spit and current spawning aggregation conservation strategies employed in Belize.

6.2 Methods

6.2.1 Study site

The study focused on Gladden Spit, a near 90^0 bend in the Belize Barrier Reef located ~46 km from the mainland, and ~42 km east of the town of Placencia at 16^035'N 88^000'W (Figure 6.1). A full description of the study site with maps can be found in Chapter 1.

Gladden Spit hosts over 25 species of fish that seasonally aggregate at the tip to spawn (Graham, unpublished data) according to observed courtship and or spawning behaviour and based on criteria listed by Domeier and Colin (1997). A dedicated fishery exists for at least nine of these species (Graham, unpublished data), seven of which are fished legally by Belizeans and two fished illegally by non-Belizeans. The mutton snappers aggregate to spawn on the northern edge and tip of the promontory near G1 on Figure 6.2. Gladden Spit was declared a marine reserve on 18 May 2000. However, at the time of this study, there were no restrictions on time or area of fishing, providing fishers held a valid Belizean fishing and boat license.

6.2.2 Fishing survey

Much of the information gleaned on fishing at Gladden Spit comes primarily from 12 boat captains who kindly shared their knowledge. They provided information on the history and seasonality of fishing at Gladden Spit, methods, costs, constraints and alternatives. Fishers were informally surveyed at the fishing and landings sites, while visiting Placencia, or in their homes, in addition to observing daily routines at the fishing site or on Buttonwood Caye. Located ~6.8 km NW of Gladden Spit's northern most fishing site, Rocky Point, Placencia-based fishers have traditionally used Buttonwood Caye as a fishing base camp, spending about two weeks of every month from March to June at this location to land and gut their catch before taking it into Placencia. Questions asked included the seasonality of fishing, its costs and opportunities and recorded gear type, boat type and engine type, location of fishing, and timing of fishing. Women rarely fish at Gladden Spit and few are involved in fish

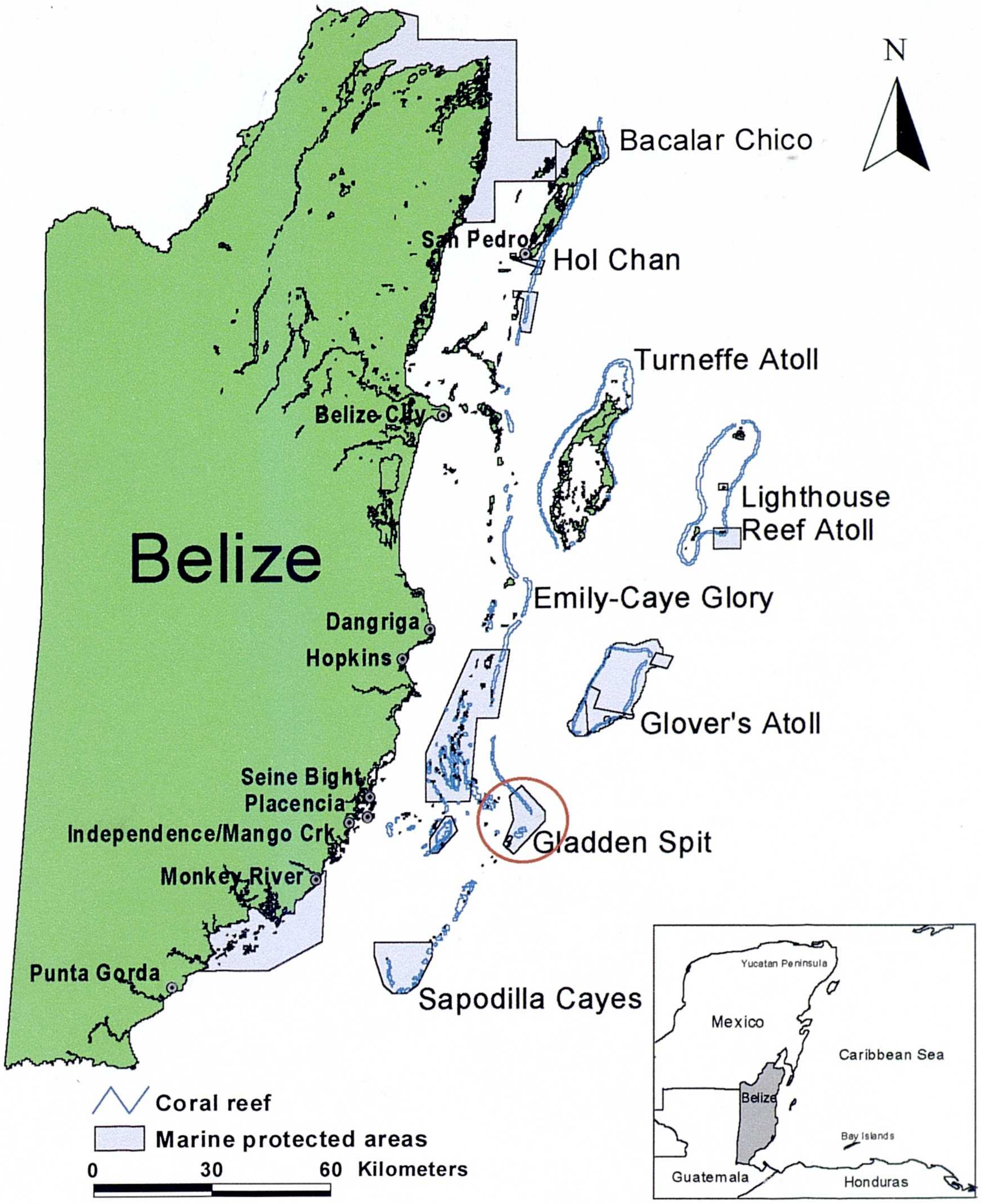


Figure 6.1: Map of Belize and its marine protected areas (Base map kindly provided by Belize's Coastal Zone Management Authority (CZMA)).

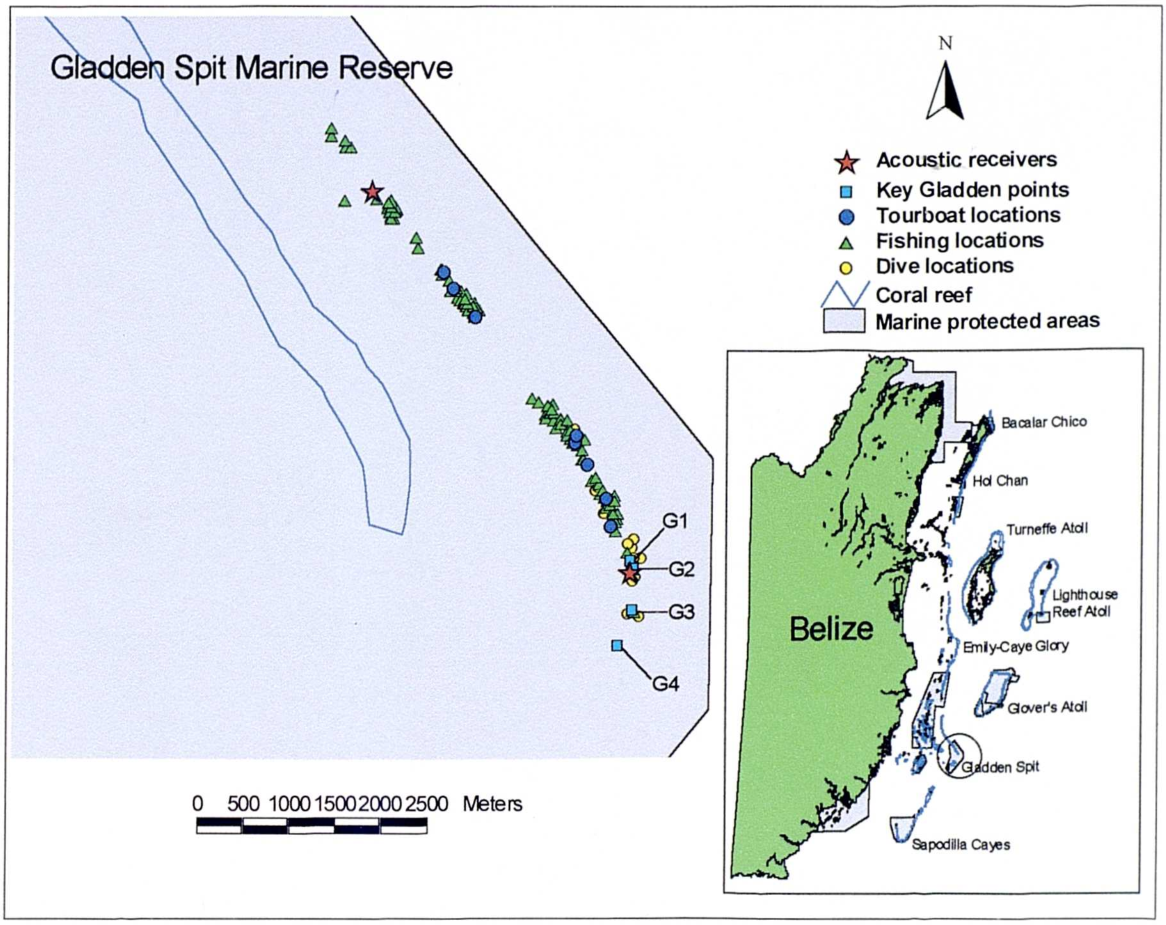


Figure 6.2: Location of fishing boats and tour boats within the Gladden Spit Marine Reserve. Locations were recorded primarily in 2001 and 2002 during the peak mutton snapper spawning aggregation period of March–June 2001 and 2002. G1 = Nassau groupers aggregation site; G2 = acoustic receiver, the site where cubera and dog snapper spawning often starts and continues until G3; G4 = southernmost point reached at which point no fish or spawning are observed. The dive locations indicate main entry points for the visual transects run daily during the snapper spawning-season (Base map kindly provided by CZMA).

preparation and therefore do not play a direct major role in the Gladden fishery *per se*. As a result, women's perspectives have not been included in this chapter.

6.2.3 The mutton snapper fishery

The most intensive fishing at Gladden Spit takes place yearly during the mutton snapper spawning aggregation period. This usually spans three lunar months for a period of 10-16 days just before and following the full moon periods of March to June with peaks in catches during the April and May full moons. Periodicity of the mutton snapper fishery varies annually. If the moons fall in the second half of the month, March is included as a mutton snapper fishing month and June is not fished because it interferes with lobster fishing. The lobster fishery legally opens on June 15 and takes economic precedence over the mutton snapper fishery. If the moon falls early in the month, March is more likely to yield yellowtail snapper (*Ocyurus chrysurus*) and June will be fished for mutton snapper before the lobster season begins.

6.2.4 Fleet size

The locally-based Placencia and Mango Creek Fishermen's Cooperatives provided total fisher numbers in the stakeholder communities. To estimate the percentage of fishermen and boats using the Gladden Spit Marine Reserve, the number of boats sighted daily at Gladden were counted over the course of 7-14 days following each full moon from March to June in 2000 to 2002. As part of the daily observational dives undertaken to survey fish and whale sharks, single or multiple transits past the fishermen's boats were made to record the number of boats and fishers, port of origin, boat size, engine size, and fishing position (in Universal Transverse Mercator, UTM, using a Garmin 12 GPS) for subsequent mapping. These visits also provided the opportunity to discuss fishing progress, time spent fishing, any impediments or other issues that fishermen were dealing with, and gave us an estimated time for heading back to Buttonwood Caye for landings data recording. Boat counts ceased when catch per unit effort decreased and fishermen finally left the area towards the end of spawning. The decrease in mutton fishing activity usually coincided with an observed decrease in spawning aggregation sizes, a cessation of spawning in cubera and dog snappers and a decrease in the number of whale sharks sighted.

6.2.5 Landings and catch per unit effort

Weather permitting, fishing took place daily during the snapper aggregation season and lasted up to 16 days during recorded fishing moons. Fishing often started 2-3 days before the full moon to 1-14 days after the full moon. Fishers whose landings were recorded were based on Buttonwood Caye, located 6.5-11.5 km from the fishing grounds on the outer reef (Figure 6.2). Fisher distribution along the 4.2 km stretch of the forereef at Gladden Spit varied within and among days. To maximise catch and "find the best fishing location", fishers usually moved from one site to another along the same reef stretch at least once during the day. They usually left Buttonwood Caye for the fishing area at 5:00-5:30 h and returned to the caye to off-load and gut their catches twice daily, once between 11:30-12:30 h and between 17:00 h and 18:30 h. Because travel time was standardized amongst all fishers based at Buttonwood Caye, fishing effort included travel to and from the fishing site, and time to anchor and bait the hooks. Effort did not include the search for bait and gutting the catch. Fishers based at Buttonwood Caye navigated through a narrow channel in the reef crest to minimize distance travelled. We collected all landings data on Buttonwood Caye. Fishers were not required to keep catch and effort records for the Belize Department of Fisheries but kindly and readily cooperated in our collection of landings data.

To assess potential changes in population abundances, landings and catch per unit effort (CPUE) data were recorded with the Department of Fisheries during each fishing moon using standardized forms (Appendix 6.A and 6.B). To determine if mean fish size and weight changed over time, fork length (FL) was measured to the nearest 0.5 cm and weighed whole fish to the nearest 0.23 kg or 0.5 lbs. I recorded landings in pounds in 2000 and 2001 and pounds and kilograms in 2002. Values were converted to kilos and grams during analysis. Mutton snapper gonads were removed and weighed to the nearest 20 g. Whole fish and gonad weights helped to ascertain length at first maturity and gonad index. Gonads were classified into four categories of development according to external appearance: I) Immature, small transparent, undeveloped gonads with no vascularization; II) Mature, vascularization of the ovaries and visible eggs; III) Running ripe, highly vascularized with mostly hydrated eggs visible; IV) Spent, most or all hydrated eggs released, ovary sac collapsed. If there was any uncertainty as to whether a female was at Stage II or Stage III, the fisher was asked if he would eat the roe. Only mature roe is considered a delicacy and a "No" response indicated that the roe was hydrated and therefore deemed a Stage III.

CPUE calculations were based on kilogram (kg) caught per man-hour fished, whereby each boat was identified under its captain's name with the number of fishers and the time spent fishing recorded and cross-checked with on-site visits to the fishing grounds. Not all landings could be recorded, particularly when all boats arrived at the same time on Buttonwood Caye and catches were high. Estimates of total mutton snapper landings for Gladden Spit and their value are based on the data recorded from the number of fishers and boats recorded at the site and from fishers and landings taken at Buttonwood Caye. Mutton snappers are sold gutted. Therefore, the scalar of 1.25 from Heyman and Graham (2000) was used to calculate the weight of gutted fish in total landings, and estimate a total value for the gutted catch. Bycatch was counted and weighed when possible, all species landed were noted to provide an incidence of bycatch per species and per family.

6.2.6 Underwater surveys

To assess mutton snapper school abundance underwater, the mutton snapper aggregation site was surveyed once or twice daily using SCUBA, during the moons of March through June in 2000-2002, weather permitting. Most fish species displaying signs of spawning behaviour (Domeier & Colin, 1997), were observed distributed along the reef slope over a distance of 500 m from north to south from a point termed "Grouper Rock" at G1 (Chapter 2, Figure 2.4.). This is where the Nassau grouper, black grouper (*Mycteroperca bonaci*), yellowfin grouper (*M. venenosa*) and tiger grouper (*M. tigris*) are seen to aggregate in December-February, to G2 where cubera and dog snappers are most often found to spawn (Figure 2.2). The majority of surveys began close to 150 m north of G2, where an acoustic receiver was moored, and continued southward towards G3 along the fore-reef above its steeply sloping edge (130-150ft deep). A team of 2-6 divers dived close to 09:30 and again at 16:45 with dives lasting between 15 and 60 minutes depending on conditions. In May 2002, the fish were dispersed along the reef and often seen travelling north and/or offshore during the day. Survey dives were therefore initiated between G2 and 2km northward often cued by the presence of acoustically-tagged whale sharks detected by the VR60 boat-based acoustic receiver (see Chapter 3).

On each dive, all species of commercial importance and those demersal species aggregating or behaving in a manner indicating readiness to spawn (Domeier & Colin, 1997) were recorded. Spawning-related behaviours included unusually large numbers of conspecific fish aggregated in a small area, chasing, coloration changes, nuzzling and false rises. False rises occurred when an aggregation of several hundred fish would suddenly rapidly rise up in the water column while displaying chasing and nuzzling behaviour without a release of gametes. When possible, digital images were taken of spawning events or courtship behaviour with a digital stills camera or an underwater video camera (Appendix 6.C). Abundances were estimated through direct counts when the number was small and using volumetrically-derived estimates when the school numbered over 200 fish. This method involved estimating the volume occupied by 10, 50, 100 and 500 fish and then extrapolating out to the three dimensional school. Several counts were confirmed by reviewing digital video of aggregating schools.

At random times during the peak moons, GPS point locations of all boat types located at the fishing site were recorded and points plotted on ArcView software (ESRI Corp.). This helped to assess distribution of fisher and tour boats on the spawning grounds within the context of the marine reserve boundaries and whale shark observation sites.

6.3 Results

6.3.1 Fisher provenance and fishing activity

Traditionally, most fishers fishing Gladden Spit come from five communities that lie 42-80 km away: Monkey River, Placencia, Independence and Mango Creek, Seine Bight, and Hopkins. In 2000, these communities totalled 4,416 inhabitants (CSO, 2000, 2001). At least 43 fishers or 1% of the stakeholder population are registered as full-time producers with the local fishing cooperatives in Mango Creek and Placencia. Most of the fishers registered at the cooperatives are boat captains and less than half (~21) fish the mutton snapper spawning aggregation, often filling their boats with part-time or non cooperative-registered fishers. These figures vary as dedicated fisher activity waxes and wanes in the light of other economic opportunities that arise.

Fishers at Gladden Spit fish either on the outer reef (Figure 6.2) for snappers and groupers, and/or inside the reef area for invertebrates such as spiny lobster *Panulirus argus* and queen conch *Strombus gigas*. Their fisheries target six species of seasonally spawning fish, all of which belong to the families Lutjanidae and Serranidae (Table 6.1). Only a proportion of the mutton snapper fishery catches from Gladden Spit are monitored by the Fisheries Department during the spawning aggregation period from March through May. The Fisheries Department make spot checks on conch and lobster harvests, but catch records are primarily gleaned from produce deposited with the fishing cooperatives.

Semi-structured interviews with 13 local active boat captains representing 30 fishers belonging to one of two local fishing cooperatives (Placencia or Mango Creek) and one retired captain revealed that the Gladden Spit mutton snapper spawning

Table 6.0: Summary information from semi-structured interviews with 13 boat captains that fished the Gladden Spit snapper spawning aggregation." —" indicates that no alternatives were mentioned or respondent did not know.

Boat Captain	Total no. of fishers represented	Years old	Estimated no. of years fishing	Residence	Current economic alternatives	Decline in catch compared to 10 yrs ago? Yes/No	Decline in fish size compared to 10 yrs ago? Yes/No
1	3	40-50	30	Placencia	Hospitality, small business	Y	Y
2	2	60-70	45	Placencia	—	Y	Y
3	2	40-50	30	Monkey River	Guiding (whale shark, fly and recreational fishing), hospitality, research	Y	Y
4	2	30-40	25	Independence	Guiding (snorkel, whale shark, terrestrial, flyfishing and recreational fishing), research	Y	—
5	1	40-50	30	Placencia	Boat captain, small business	Y	Y
6	3	60-70	50	Placencia	Hospitality, small business	Y	Y
7	3	50-60	47	Monkey River	Boat captain, research	Y	Y
8	2	20-30	12	Placencia	Guiding (snorkel, whale shark, kayak, rec-fishing)	Y	Y
9	2	50-60	30	Mango Creek	—	Y	Y
10	3	40-50	30	Mango Creek	Fish reseller	Y	—
11	1	60-70	50	Placencia	Employee of cooperative	Y	Y
12	3	40-50	35	Placencia	Watchman	Y	Y
13	3	30-40	20	Placencia	Employee of cooperative	Y	—
	Σ 30		$\overline{X}$ 33.2, SD11.5				

Table 6.1: Seasonality of the targeted fisheries at Gladden Spit.

Fishing months	Species caught (common names)	Scientific names
November-March	Red hind	*Epinephelus guttatus*
	Black grouper	*Mycteroperca bonaci*
	Yellowfin grouper	*Mycteroperca venenosa*
	Tiger grouper	*Mycteroperca tigris*
	Nassau grouper	*Epinephelus striatus*
February-April	Yellowtail snapper	*Ocyurus chrysurus*
March-June	Mutton snapper	*Lutjanus analis*
July-November	Lobster	*Panulirus argus*
October-June	Conch	*Strombus gigas*

aggregation has been fished since the late 1800s. At least 39% of captains were 40-50 years old with 23 % aged 60 and above (Table 6.0). The captains had been fishing for an average of 33.2 years ± 11.5 SD. Approximately 92 fishermen from the five stakeholder communities were recorded fishing the Gladden Spit mutton snapper aggregation over the study period from 2000 to 2002. Fishers working from Buttonwood Caye represented 37-62% of fishermen observed at the site from 2000-2002. The highest number of fishers recorded on the fishing grounds in any one day during the study period was 38. Although fishers belong to several families, one family counting at least nine active fishers dominates fishing at Gladden Spit in terms of time spent on the fishing grounds, overall catch and knowledge of the area.

Fishermen at Gladden Spit use hook and line (handline) to fish mutton snapper. Monofilament lines are fitted with 1-3 hooks per fisher and weighted with pieces of steel rebar and baited with sprat (*Mugil* spp.), bonito (*Sarda sarda*), or conch (*Strombus gigas*). To attract fish to the area fishers sometimes fill a conch shell with rotting conch and other bait and drop it over the side, termed a "scent-up". Fishers from Monkey River, Placencia and Independence use primarily fibreglass skiffs of 7.0 m (23 ft) fitted with a two-stroke 40 or 60 horsepower engine. New, these cost about US$ 7,000 in 2002. Several fishermen from Hopkins use a combination of motorized fibreglass skiffs and traditional wood dories outfitted with 40 horsepower engines. The costs of fishing, particularly at Gladden, a distant site, have increased over time, increasing pressures on the mutton snapper spawning aggregation as fishers attempt to break even. As a result, there has been a decrease in the number of fishers from Hopkins from 2000 to 2002. This community is located further away (51 km) from Gladden's northern-most part of the fishing grounds and does not possess the tourism wealth of Placencia. As gasoline prices increased over the past 4 years from about US$ 2.6 per gallon to US$ 3.5 per gallon, at least five boat captains have purchased the more expensive yet more environmentally friendly four-stroke engines. These require 50% less gasoline to run the same distance and are quiet, a bonus for the fishers who double as tour-guides (the 50 hp is considered the equivalent to the 60 hp two-stroke but costs almost twice as much as a two-stroke). There are additional savings because lubricant (US$ 3.00) does not have to be added to the gasoline. Two captains mentioned that they made up the price of their new four-stroke due to savings in gas in one lobster season (7 months).

6.3.2 Preparation and marketing

Historically, fishers gutted and corned their fish near Gladden Spit (salting it for preservation) and transported it back to the mainland after a week or two. With the ready-availability of ice over the past 10 years either from the cooperatives and/or intermediaries who purchase the fish on site at Gladden Spit, corning is rarely practiced anymore for the Belizean market. Ice is not cheap: filling a 92-gallon ice-chest costs between US$ 5-7.8 and lasts only 2-3 days. Strategies for replenishing supplies and ice have included selling directly to an intermediary with a large ice-laden boat located next to the barrier reef or working as groups and pooling product which is taken back to the mainland by a few of the fishers while those remaining continue to fish at Gladden. Two fishing cooperatives provided competing prices for snapper (US$ 2.75 $kilo^{-1}$ gutted fish), and following the loss of the non-competitive intermediary, fishers in 2002 sold their catch directly to the cooperatives. Roe sold for US$ 6.6 $kilo^{-1}$. The costs of the 6-hr roundtrip journey of about 80 km that includes offloading the catch, weighing, and resupplying as opposed to selling on site are outweighed by the better price given per pound by the cooperatives. All fishers must hold a valid fishing license (US$ 12.5 per year) and captains must licence their boats (US$ 12.5 per year).

Gladden fishers traditionally work cooperatively in small groups, with two to four fishers per boat. Groups may include only members of a family or based on partnerships between recognized successful fishers. Many such fishing partnerships span years and yield high catches. Working cooperatively has many advantages: safety is increased as Gladden can be very rough, catch per boat is increased, and costs are shared. The disadvantage of sharing the profits is usually outweighed by the advantages, although several fishers traditionally fish alone. Fishers interviewed estimated the cost of fishing at Gladden for a moon (about 14 days) at about US$ 275-325 per person in 2001 and 2002. This included gas, engine lubricant, fishing gears, food, ice and occasionally a tarp or containers. All fishers gut their own fish and when the catch is taken to the intermediary or the cooperative, half of the profits go to the captain to cover boat and engine costs and the remainder is shared between the remaining fishers after the trip costs have been covered. The fixed costs for a full mutton snapper fishing season (three moons) at Gladden Spit run an estimated US$ 900 per fisher.

6.3.3 Fleet Size

A difference was recorded in the mean daily number of fishing boats at Gladden during the snapper season based on a mean of 5.8 ± 3.17 SD boats in 2000, 5.2 ± 2.35 SD boats in 2001 and 7.5 ± 3.98 SD boats per day in 2002 (One-way between groups Anova: df = 2; $F_{(2,84)} = 3.87$; $p < 0.05$) (Figures 6.3 and 6.4). A post hoc comparison of boat numbers revealed a significant increase from 2001 to 2002 (Tukey HSD, $p < 0.05$). However, the mean number of fishers per boat did not differ between years with 2.3 ± 0.94 SD fishers per boat in 2000 to 2.4 ± 0.66 SD fishers recorded per boat in 2002 (Kruskal-Wallis test; n = 431; df = 2; $\chi^2 = 2.24$; $p = 0.327$) (Figure 6.4). Due to boat size there is an upper limit on the number of fishers that can be accommodated with the ice and catch (Figure 6.5). Although 4 to 5 fishers are occasionally observed fishing from the same 7.0 m or 7.5 m skiff, they are not usually those seen fishing regularly at Gladden and are not considered the high-yield fishers.

Interviews with the boat captains and five former fishermen turned tour-operators indicated that the number of boats and fishers was substantially greater 10-15 years ago (before 1992). Several mentioned the density of boats at the fishing site whereby a verbal message could easily be sent from boat to boat from a location close to G1 (Figure 6.2) to 4.2 km away close to Rocky Point (location of the northern acoustic receiver). When asked for specific numbers, five fishers estimated over 200 fishers in 60 to 80 boats or more. All those interviewed emphasised that the number of boats and fishers had decreased significantly compared to 10-15 years previously. Two of the patriarch fishers working at Gladden Spit since the mid-1900s noted that in the 50s to 70s, many fishers were still using sailing dories to reach the fishing grounds. The transition to powered fibreglass skiffs was slow as fishers first outfitted their wooden dories with 15 hp engines. Due to safety constraints of fishing outside the barrier reef with a sailing dory, by default the aggregation was often not fished for several days during the peak season. Despite the decrease in total number of boats and fishers as compared to 15 years ago, interviewed fishers perceived a decline in the amount of fish landed and a decrease in fish size. However, several fishers felt strongly that the snapper

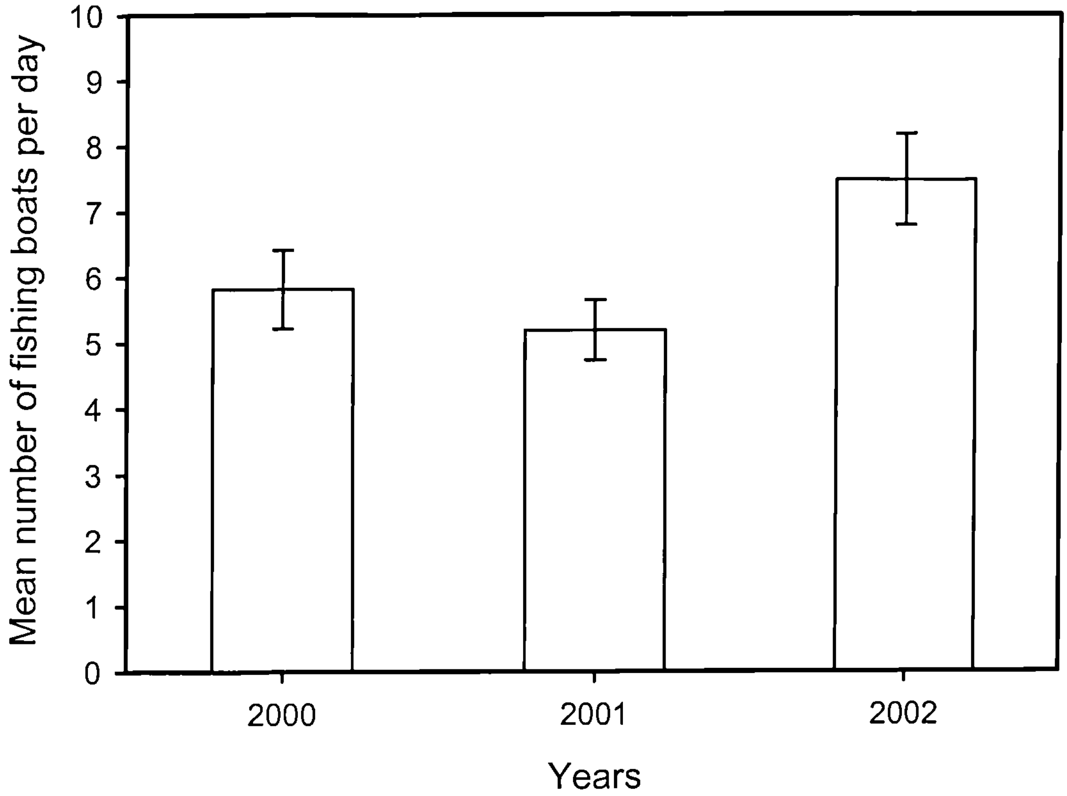


Figure 6.3: Mean number of fishing boats fishing the mutton snapper fishery during the peak mutton snapper spawning aggregation period at Gladden Spit between 2000 and 2002. Error bars represent ± SE.

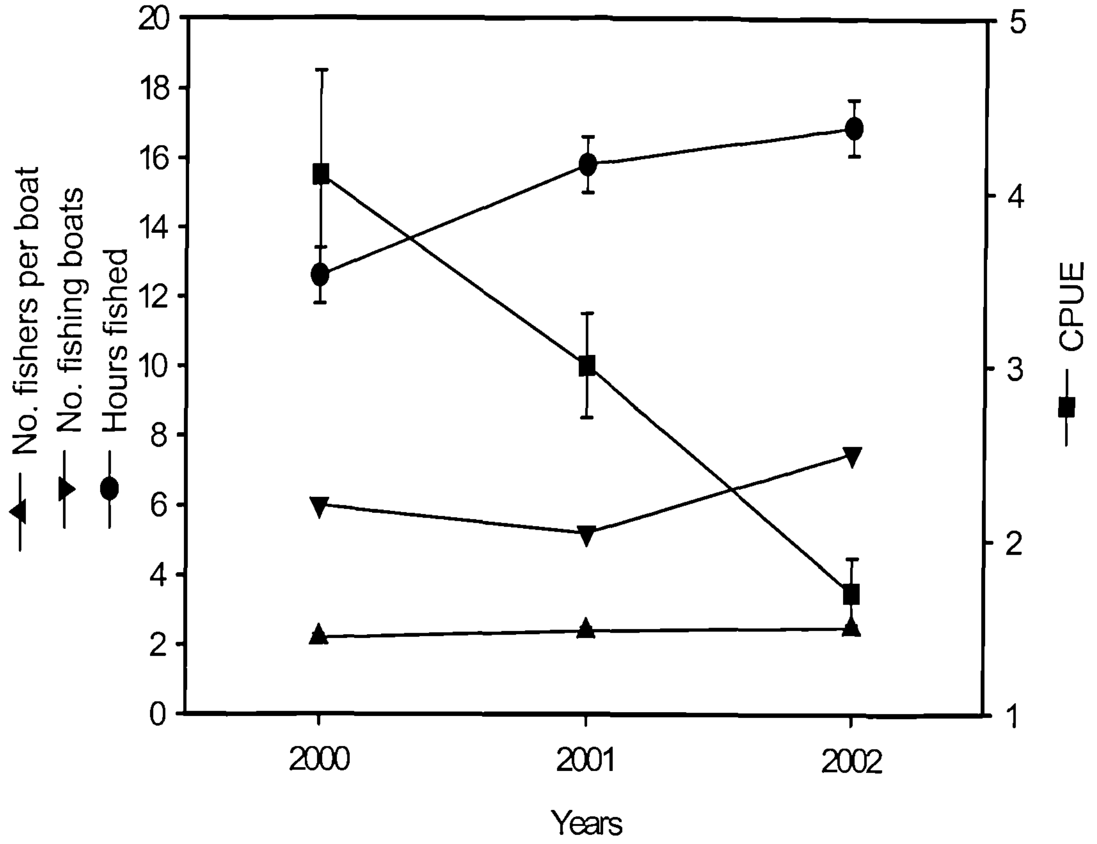


Figure 6.4: Mean numbers of fishers per boat, hours fished per boat, fishing boats and catch per unit effort in kg per man-hour fished for the mutton snapper fishery at Gladden Spit for 2000-2002. Error bars show ± SE.

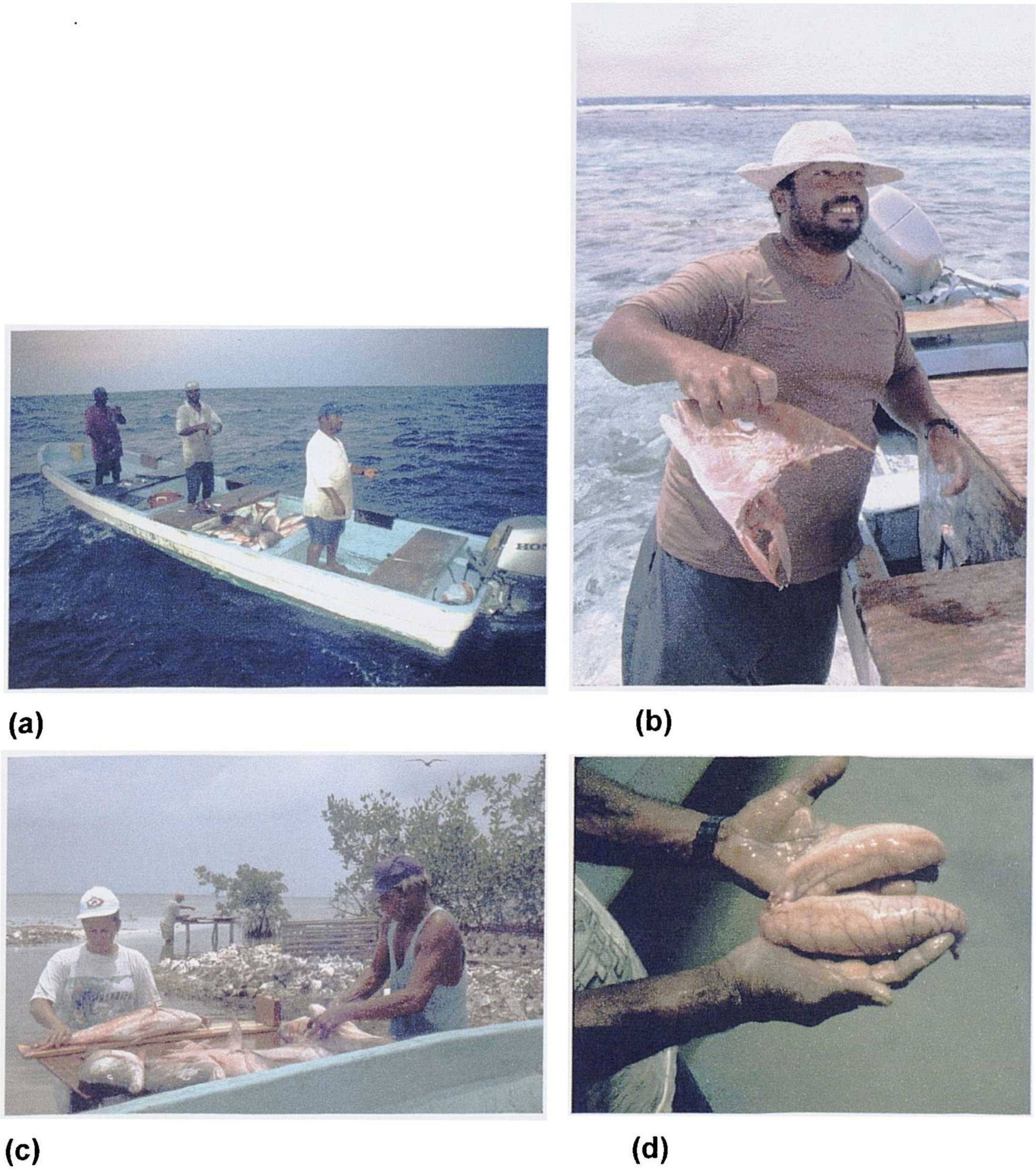


Figure 6.5 a-d: Images of the mutton snapper fishery at Gladden Spit. (a) Traditional handline fishing at the Gladden Spit spawning aggregation site; (b) Snapper loss due to shark predation; (c) Taking landings data for the snapper spawning aggregation fishery at Buttonwood Caye; (d) Hydrated mutton snapper roe.

aggregation could not be extirpated because they use handlines as opposed to traps and snappers are plentiful. Belizean fishers blame catch decline on the fish moving away, on the increase in number of tourists, on illegal fishers from Guatemala and Honduras and on oophagous whale sharks.

Fishers from Guatemala and Honduras illegally fish the seasonal aggregation, albeit primarily at night to avoid detection from the Belize Defence Force and the Department of Fisheries. Honduran fishers fish out of similar 7.0 m fibreglass skiffs, often outfitted with twin engines that enable them to run the 74 km of open sea between Puerto Cortés/Omoa and Gladden Spit in two to three hours. A minimum of 13 illegal boats were sighted at one time in 2001 waiting to fish the aggregation site, each carried between two and three fishermen, for an estimated 26-39 additional fishermen using the site. Mutton snapper are not known to "bite" at night so it is thought that they are not impacting that spawning aggregation. However, cubera and dog snappers readily take bait at night following spawning at dusk. Honduran bait preference differs from Belizean fishermen. Illegal fishermen were recorded at Gladden catching bonito for bait and those caught by enforcement patrols have been found with frozen bonito as their bait of choice. The use of this bait may have led to the observed increase in predatory sharks at Gladden Spit, consisting primarily of bull sharks (*Carcharhinus leucas*), with occasional observations of silky sharks (*C. falciformis*) and Caribbean reef sharks (*C. perezi*) that have proved a nuisance to Belizean fishermen and decreased their catch (Figure 6.5).

6.3.4 Catch size-composition

A total of 5167 fish were included in the catch and size analysis between 2000 and 2002 (Figure 6.6a). The maximum fork length (FL) recorded for a mutton snapper was 91 cm (female) and minimum was 18 cm FL (male). These, and ten other individuals accounting for 0.2% of the sampled population were removed as outliers during statistical analyses leaving a sample total of 5155 fish for all analyses other than the length-weight relationship. Figure 6.6b indicates that the majority of fish recruit into the spawning population when above 30 cm FL and mass increased exponentially with increasing length. The ratio of captured females ($n = 2387$) to males ($n = 2768$) was 1:1.12 indicating little evidence of sex-dependent selectivity of fishing. All mutton snapper morphometric data were tested for normality using the Kolmogorov-Smirnov test and the distribution was found to be non-normal and so non-parametric tests were employed. Although size distributions for mature individuals of both sexes

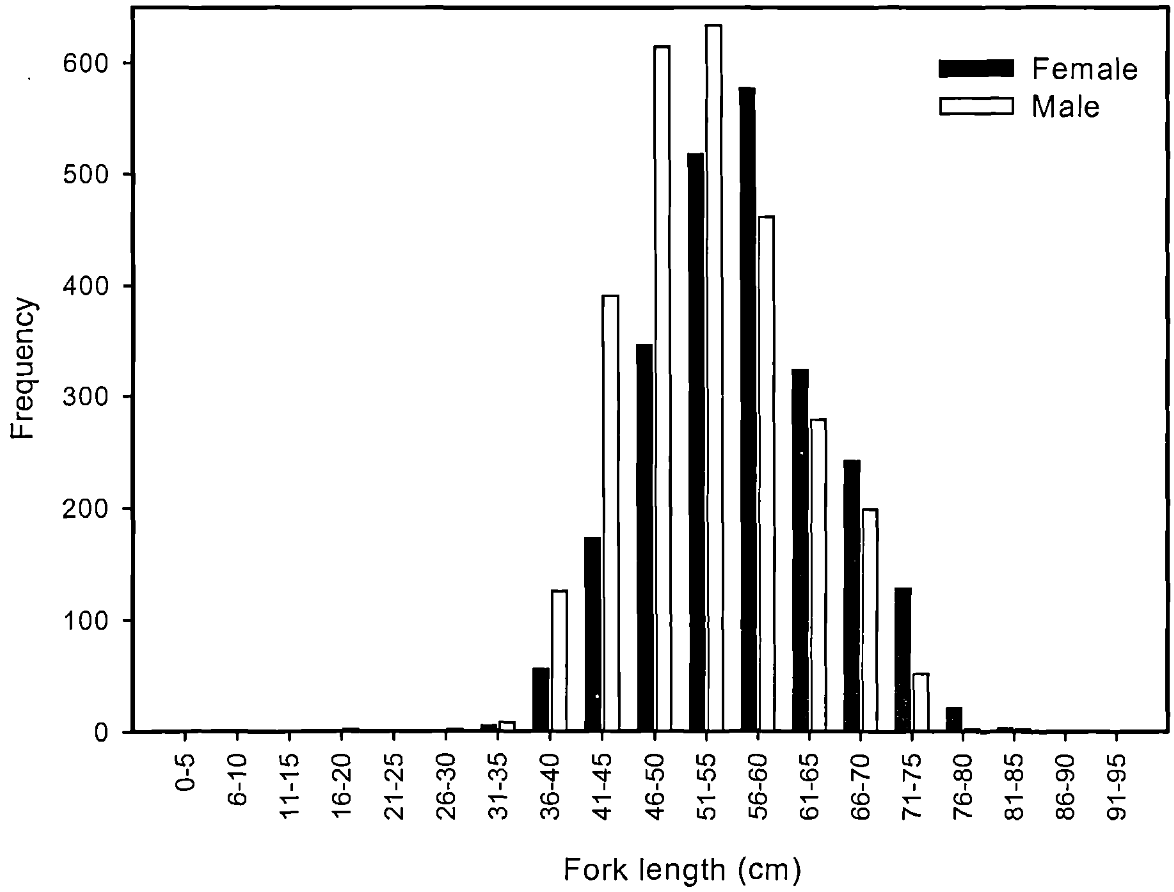


Figure 6.6a: The length frequency distributions of *L. analis* females and males (n = 5155) from the seasonal fishery at Gladden Spit between 2000 and 2002.

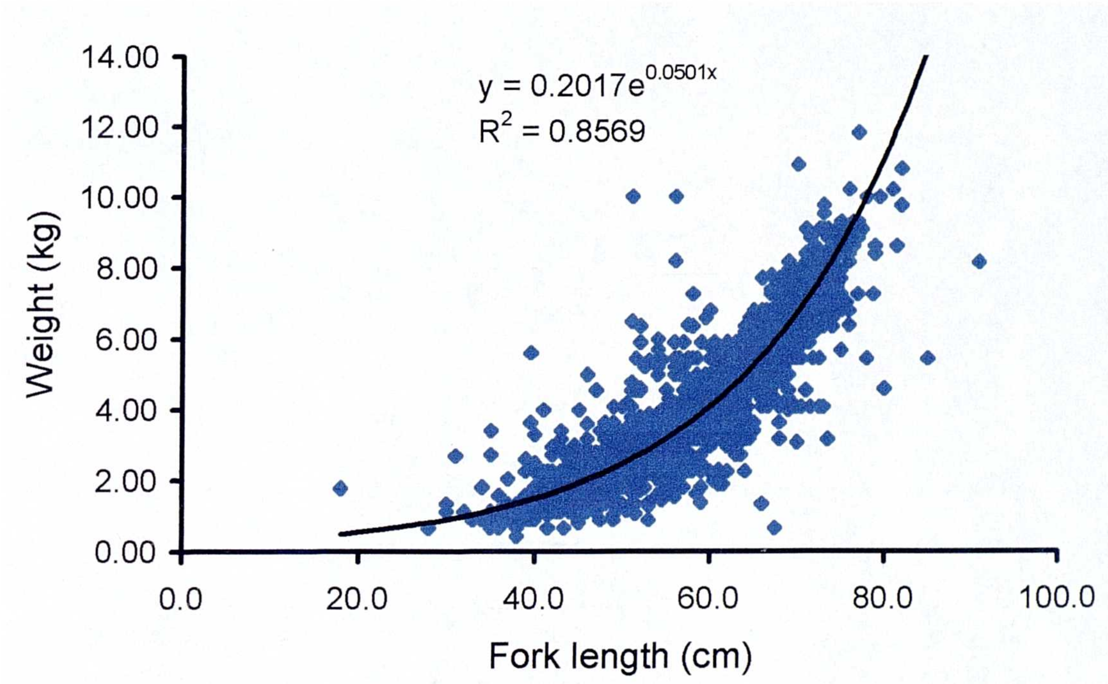


Figure 6.6b: Length-weight relationship for *Lutjanus analis* from the Gladden Spit spawning aggregation fishery (n = 5167).

overlapped, females (mean = 56.6 cm ± 8.4 cm SD FL, n = 2387, range = 33-78 cm FL) were significantly larger than males (mean = 53.2 cm ± 8.24 cm SD FL, n = 2768, range = 31-78 cm) (Mann-Whitney U test; n = 5,155; $p < 0.001$).

To determine whether fishing pressure affected mutton snapper size, differences in mutton snapper fork length were analysed from 2000 to 2002. Peak size frequency for combined male and female mutton snappers in 2000 was 56-60 cm FL cm, shifting to 51-55 cm FL in 2002 (Figure 6.7) suggesting that larger fish are more vulnerable to capture. This was further supported by a difference in mutton snapper fork length (FL) recorded between 2000 and 2002 (Kruskal-Wallis test: n = 5155: $\chi^2 = 134.85$; df = 2; $p < 0.001$), with a decline noted from 57.2 cm in 2000 to 53.5 cm in 2001, rising slightly in 2002 to 54.8 cm (Figure 6.8). The decreased FL over the three-year period was reflected equally between both sexes (Figure 6.9) further supporting the lack of sex-bias in landings.

Over 80% of macroscopically observed gonads sampled from female mutton snappers caught at Gladden fell within the development stages of late maturation (stage II) or running ripe (stage III) (Figure 6.10a). Mean gonadosomatic indices (GSI) for female mutton snappers landed in 2001 and 2002 were 4.07 ± 0.14 SE (n = 438) and 3.88 ± 0.08 SE (n = 837) respectively. Mean monthly GSI indicates a rise in female gonad weight as a percentage of total weight as spawning progresses from April to June (Figure 6.10b) with the exception of April 2001 that showed a relatively high GSI of 6.93 ± 1.0 SE. Figures 6.11a and 6.11b show a weak relationship between gonad weight and fork length in female and male mutton snappers measured.

6.3.5 Catch and effort

Between 2000 and 2002, 18,552 kg of mutton snapper were caught at Gladden Spit (Table 6.2). This figure represents all mutton snappers landed at Buttonwood Caye for which we have fully recorded information on sex, weight and size. A total of 255 fish of both sexes and all sizes were excluded from these calculations due to gaps in the records caused by broken scales. Based on the number of boats and fishers counted at the fishing site, 18,552 kg represents 44.8% of all mutton snapper caught at Gladden Spit worth an average of US$ 1,382 per fisher per season or US$ 4,145 per fisher over the three seasons. Only a portion of the fishermen's landings could be sampled due to restrictions in team sampling size and because several fishers returned to Placencia or other ports after fishing and their catches could not be recorded. Estimated total

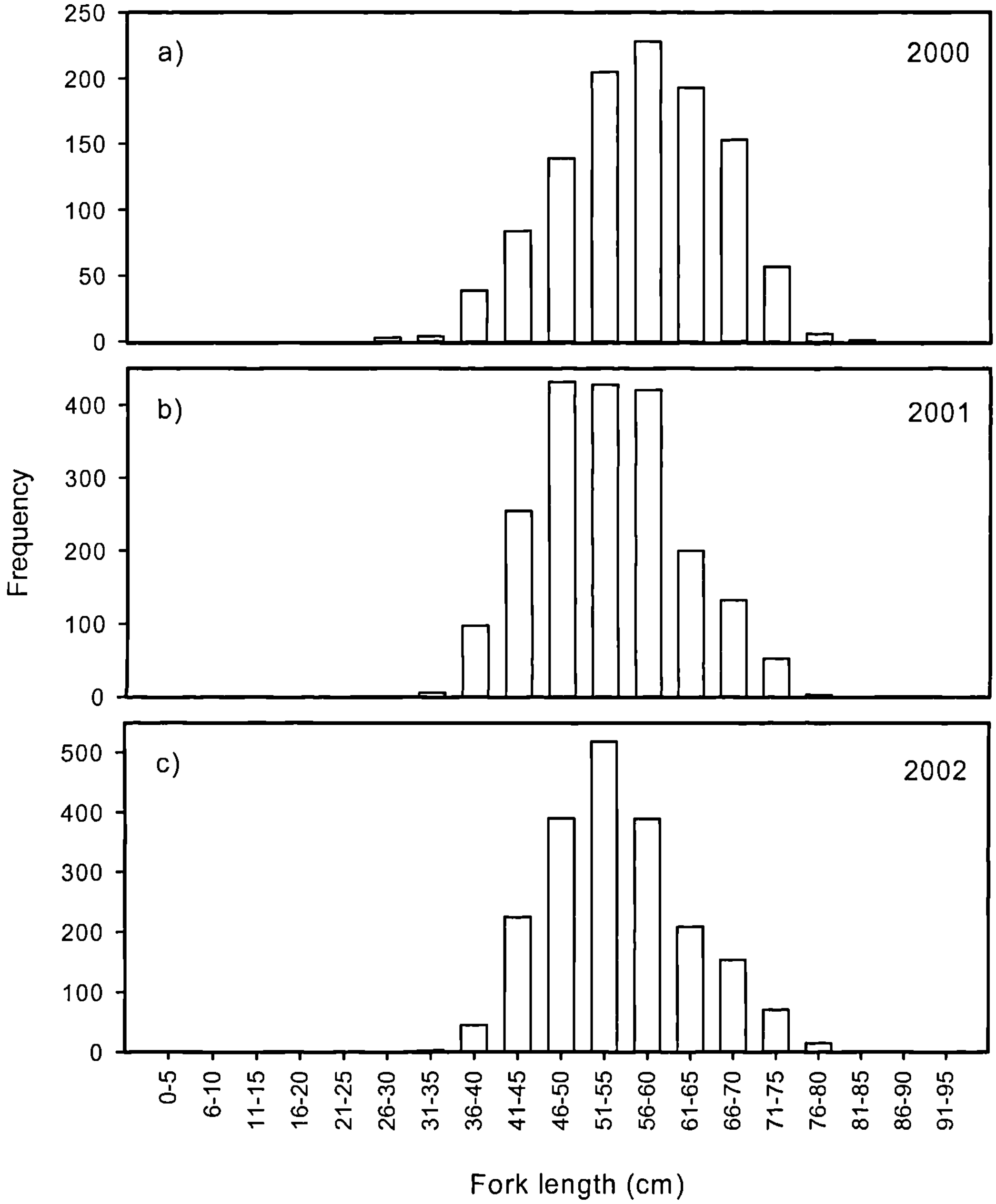


Figure 6.7: The length-frequency distributions of *L. analis* per fork length category from the seasonal fishery at Gladden Spit in a) 2000 (n = 1105), b) 2001 (n = 2029); and c) 2002 (n = 2021).

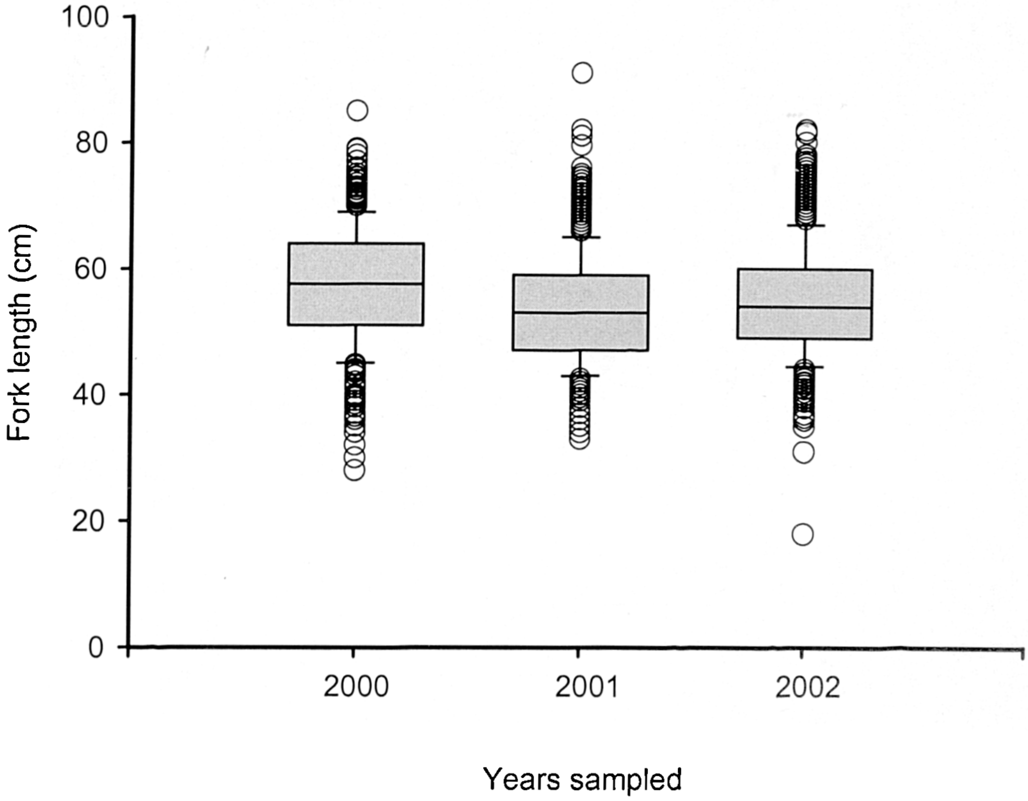


Figure 6.8: Difference in median fork length size of *L. analis* from the seasonal fishery at Gladden Spit between 2000 and 2002 (n = 5155) ± SD.

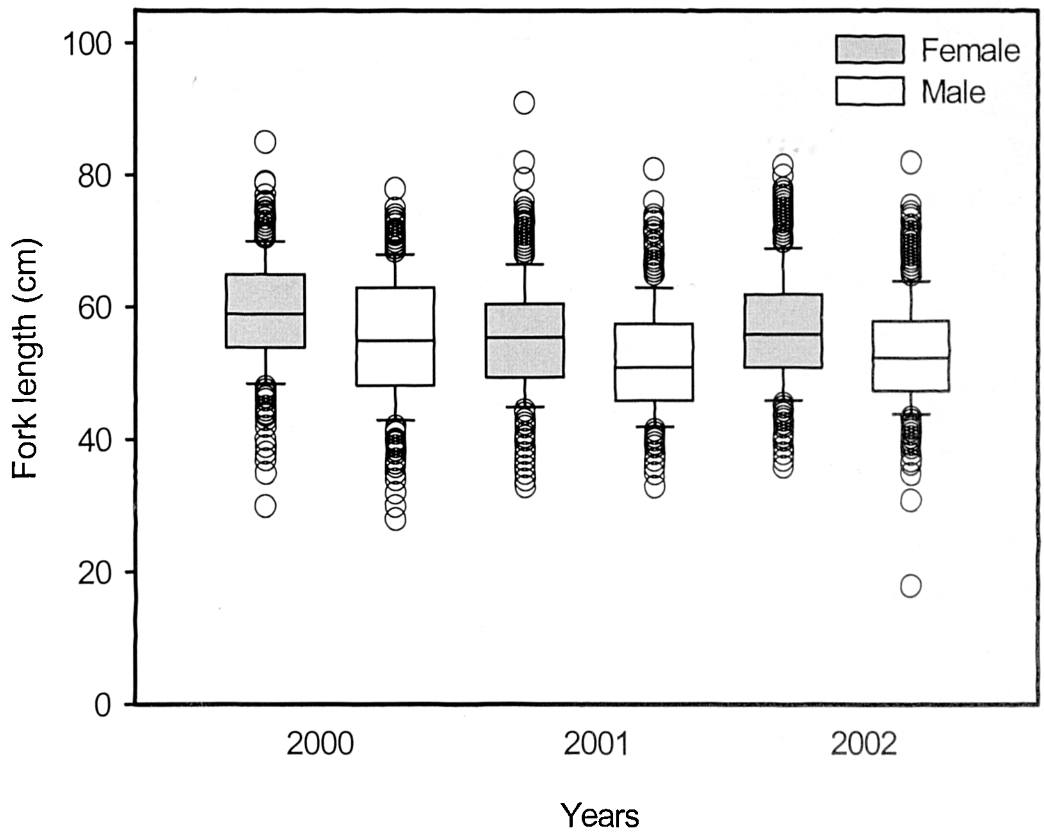


Figure 6.9: Difference in median fork length size of female (F) and male (M) *L. analis* from the seasonal fishery at Gladden Spit from 2000 to 2002 ± SD.

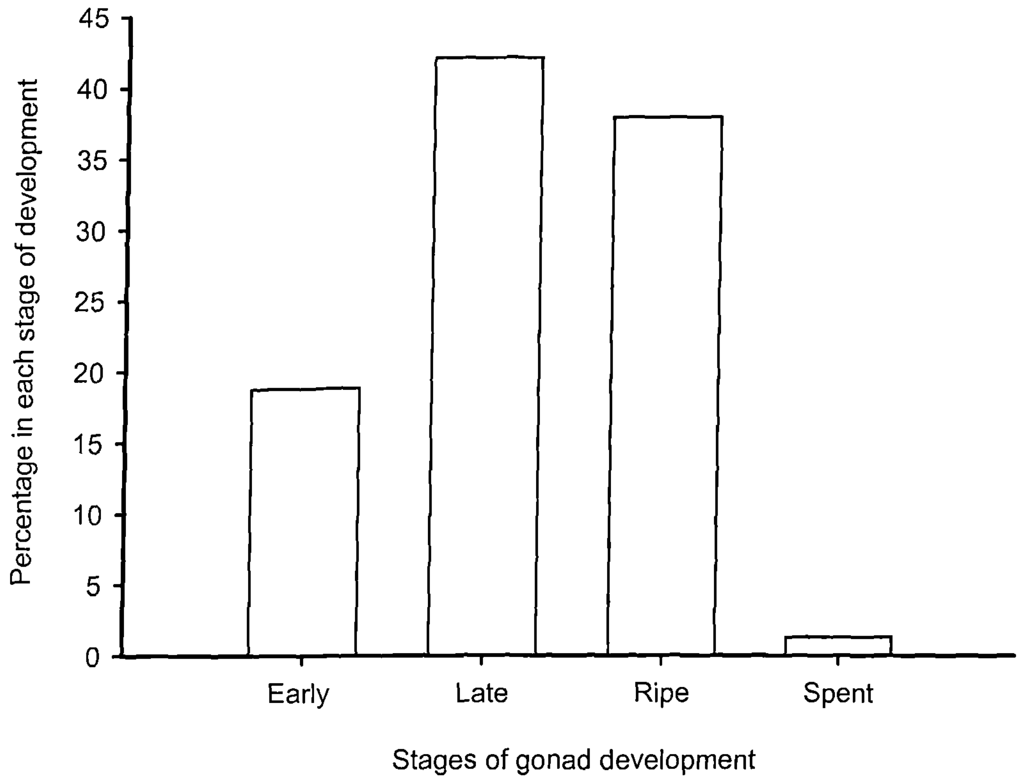


Figure 6.10a: Percentage of landed mutton snapper in each of the four stages of reproductive development for female muttons snappers (n = 1727) during the peak spawning period from 2001-2002.

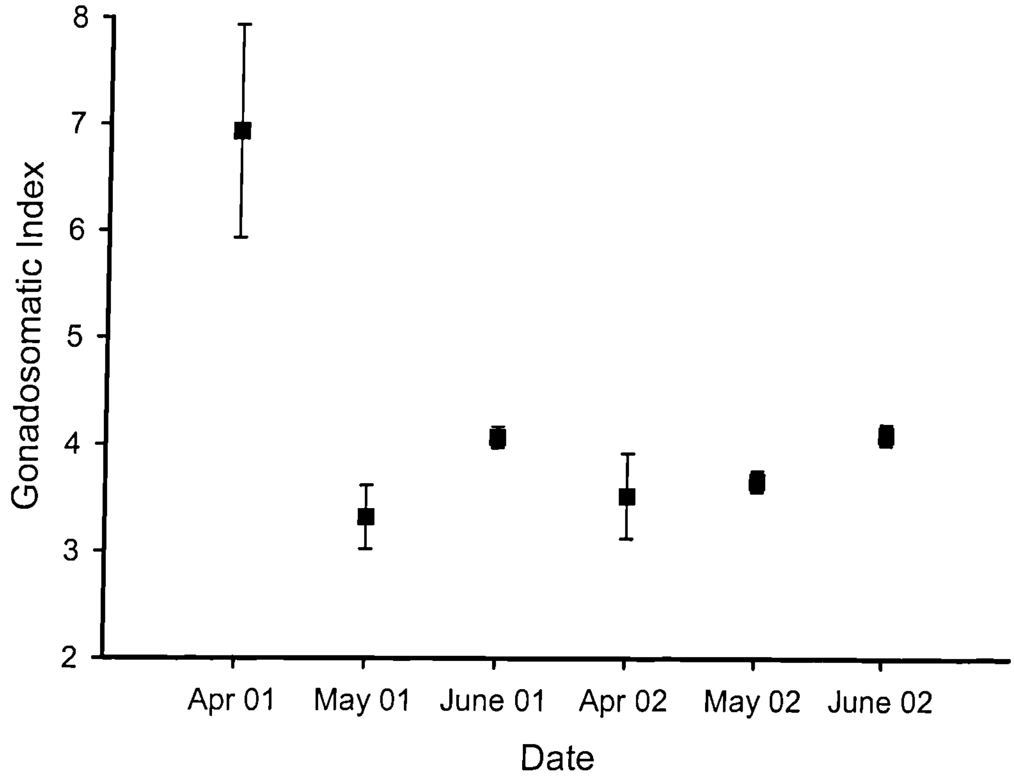


Figure 6.10b: Changes in mean monthly gonadosomatic indices between 2001 and 2002 for the mutton snapper fishery at Gladden Spit.

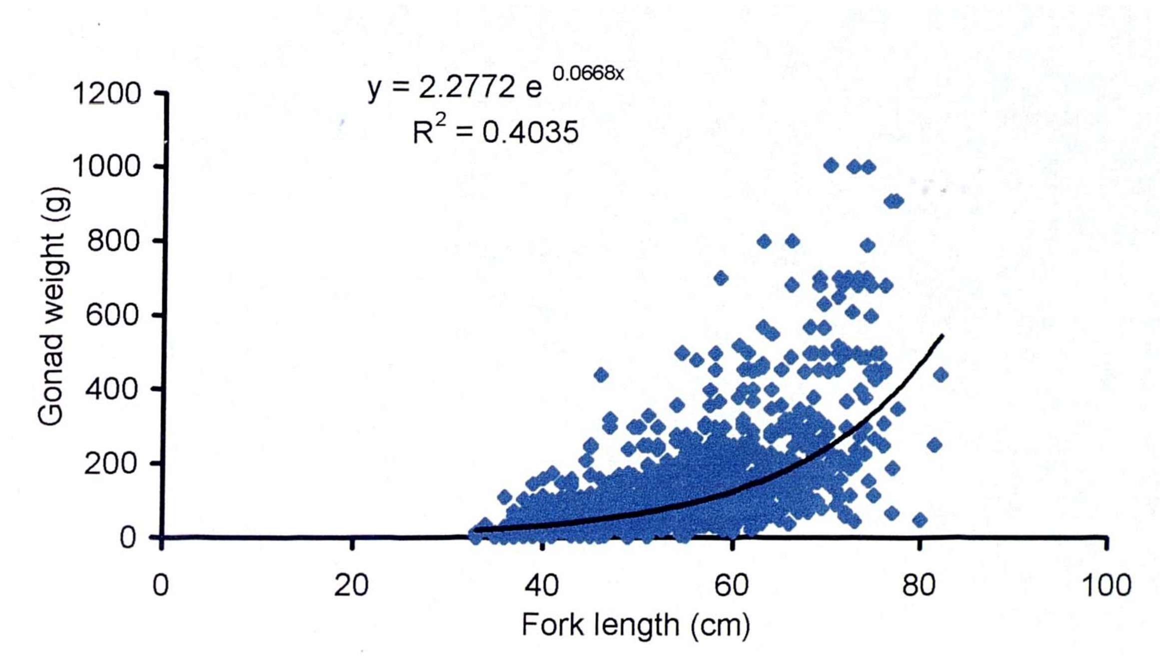


Figure 6.11a: Fork length versus gonad weight for female *L. analis* landed from the seasonal fishery at Gladden Spit between 2001 and 2002 (n = 1668).

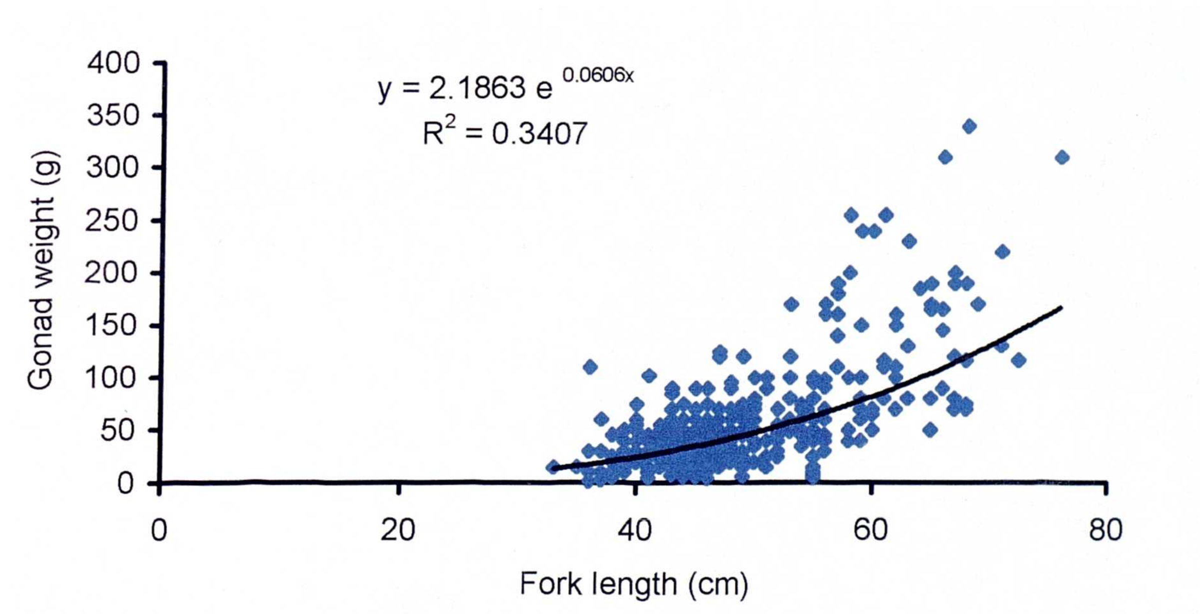


Figure 6.11b: Fork length versus gonad weight for male *L. analis* landed from the seasonal fishery at Gladden Spit between 2001 and 2002 (n = 393).

Table 6.2: Summary of catch and value for the mutton snapper aggregation fishery based on landings recorded per fishers and boats sampled on Buttonwood Caye. These figures represent a large proportion of all fishers and boats fishing the mutton snapper spawning aggregation yearly.

Year	Total no. of boats sampled	No of days sampled	Total no. of fisher-days	Total landings recorded - whole fish (kg)	Mean landings whole fish per fisher per day (kg)	Mean landings gutted fish per fisher (whole kg/1.25)	Total value of landings (gutted in US$)*	Value of landings per fisher per day (gutted in US$)*	Value of landings per fisher (US$) during sample period
2000	62	18	131	5093	38.9	31.1	11205	85.53	1539.62
2001	84	16	200	7184	35.9	28.7	15805	79.03	1264.48
2002	98	24	247	6275	25.4	20.3	13805	55.89	1341.36
Total	244	58	578	18552	33.4**	26.7**	40815	73.48**	4145.46

* Figures assume an exchange of 2BZ = 1US and a 2002 price of BZ$5.5 per kg or US$2.75 per kg of gutted mutton snapper from 2000-2002. A 1.25 scalar is used to transform the whole snapper weights to gutted weights. ** Mean values used.

landings of mutton snapper during the peak fishing season at Gladden Spit from 2000-2002 reached 41,429 kg (Table 6.3). This figure is calculated from the mean catch in kg per fisher per day between 2000-2002 multiplied by the total number of fishers and days fished between 2000 and 2002. The Placencia Cooperative's final figures for 2001 are 2,265 kg for whole fish (gutted) and 2,982 kg for fillet (representing over 6,000 kg in whole fish). The Mango Creek cooperative only began to receive snapper in mid 2001 and its estimated purchase of gutted mutton and yellowtail snapper from fishers in 2002 ranged between 6,818 kg and 9,091 kg. The mutton snapper fishery yielded an estimated 9,224 kg in 2001 and 12,908 kg in 2002. These figures indicate that the seasonal mutton snapper spawning aggregation fishery largely contributes to the annual finfish fishery recorded by the two cooperatives. The Central Statistical Office in Belize (2001) records 50,000 kg of finfish landed. Based on estimates from Table 6.3, approximately 22% of these national landings comprised mutton snappers caught at Gladden's spawning aggregation.

Despite a historical decrease in the number of boats and fishers at Gladden Spit, testing for differences in CPUE between 2000 and 2002 indicated catches declined from 4.1 kg to 1.7 kg per man-hour fished in only three years (Kruskal-Wallis test: n = 244; df = 2; $\chi^2 = 25.23$; $p < 0.001$). The mean catch per boat differed significantly with a decline noted from 82.1 kg to 64. 0 kg (Kruskal-Wallis test: n = 244; df = 2; $\chi^2 = 7.67$; $p < 0.05$) (Table 6.4) while fishing differed significantly with an increase from 12.6 to 16.9 hours fished per boat per day (Kruskal-Wallis test: n = 244; df = 2; $\chi^2 = 14.07$; $p < 0.001$) (Figure 6.4).

Although inter-seasonal CPUE declined, intra-seasonal CPUE increased significantly between April and May in 2000 (Mann-Whitney U test; n = 62; $p < 0.001$) and March and June 2002 (Kruskal-Wallis test: n = 98; df = 2; $\chi^2 = 30.85$; $p < 0.001$) (Figure 6.12). There was no significant difference in CPUE between April and June 2001 (Kruskal-Wallis test: n = 84; df = 2; $\chi^2 = 4.60$; $p = 0.101$). Consequently, peak spawning aggregation moons for mutton snapper appear to be May and June. Interviewed fishers noted that when they fish mutton in June, catches are often excellent but the weather is unpredictable and often very rough.

6.3.6 Bycatch

Although handlining can be a very targeted means of fishing mutton snapper in a spawning aggregation, other species are also caught in the process (Figure 6.13). These may not be considered true bycatch since many of the fish species are kept and

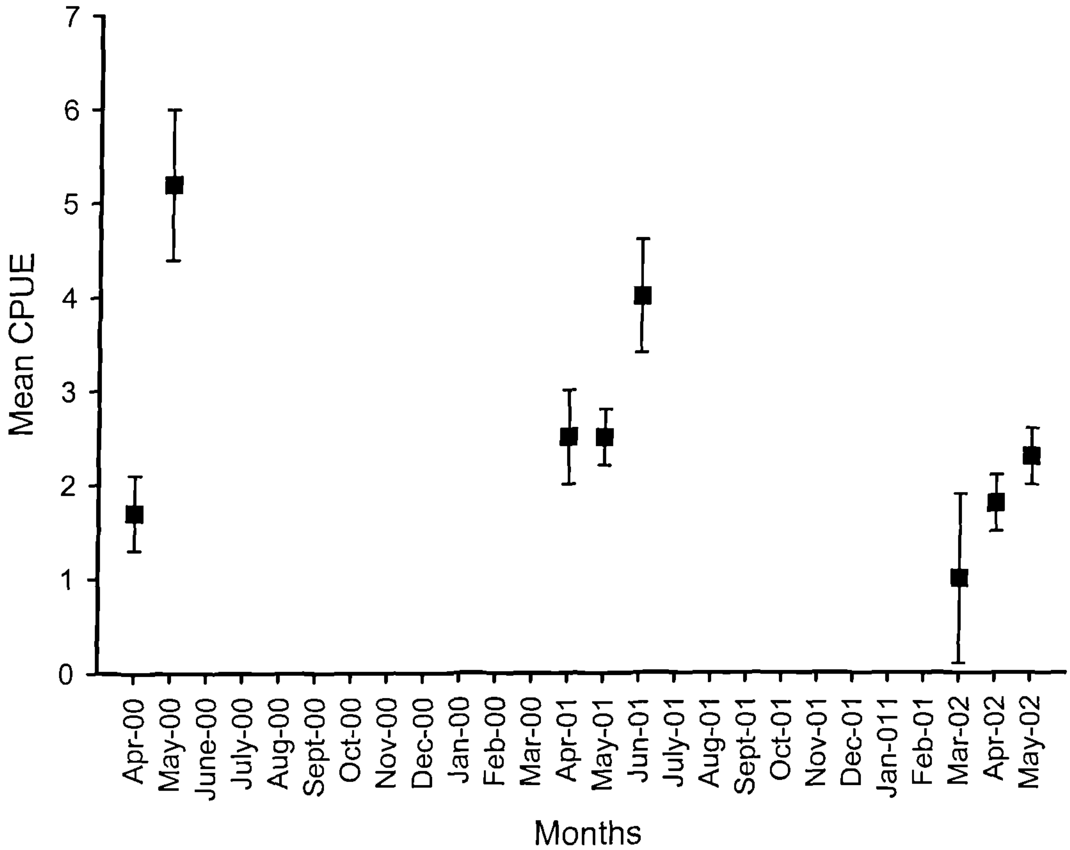


Figure 6.12: Mean catch per unit effort ± SE for the mutton snapper fishery at Gladden Spit for the study's eight sample months during 2000-2002.

Table 6.3: Summary of estimated catch and value of mutton snapper aggregation fishery for all boats and fishers recorded at Gladden Spit. The total number of fishers recorded fishing the Gladden Spit from 2000 to 2002 is based on daily boat and fisher counts during the peak mutton snapper fishing period. Estimated total landings in kg and US$ are based on mean landings recorded at Buttonwood Caye for a proportion of the fishers fishing Gladden Spit mutton snapper spawning aggregation.

Year	Total no. of boat-days recorded at Gladden	Total no. of estimated fisher-days	Total landings whole fish (kg)	Total landings gutted fish (whole kg/1.25)	Value of landings per season (US$)*
2000	163	354	13764	11011	30280
2001	135	321	11530	9224	25366
2002	247	635	16135	12908	35497
Total	545	1,310	41429	33143	91143

* Figures assume an exchange of 2BZ = 1US and a 2002 price of BZ$5.5 per kg or US$2.75 per kg of gutted mutton snapper from 2000-2002. A 1.25 scalar is used to transform the whole snapper weights to gutted weights.

Table 6.4: Summary of key effort and catch details for the hook and line mutton snapper fishery at Gladden Spit during the full moon periods of 8 months from 2000 to 2002.

Month	N (total)	CPUE kg/man hour fished	SE	Hours fished/boat	SE	Catch/boat (kg)	SE	No. fishers/boat	SE
2000									
Apr-00	7	1.7	0.4	13.0	1.6	30.5	6.1	2.2	0.2
May-00	11	5.2	0.8	12.4	1.0	105.0	13.3	2.2	0.1
Mean	18	4.1	0.6	12.6	0.8	82.1	10.3	2.2	0.1
2001									
Apr-01	4	2.5	0.5	16.3	2.5	39.2	6.8	2.8	0.3
May-01	7	2.5	0.3	15.6	0.9	80.5	7.0	2.4	0.1
Jun-01	5	4.0	0.6	15.8	1.6	111.7	14.5	2.2	0.2
Mean	16	3.0	0.3	15.8	0.8	85.5	6.4	2.4	0.1
2002									
Mar-02	6	1.0	0.9	13.9	2.4	7.6	4.0	2.8	0.2
Apr-02	7	1.8	0.3	16.7	1.1	70.1	10.1	2.4	0.1
May-02	10	2.4	0.3	17.8	1.2	83.4	7.7	2.5	0.1
Mean	24	1.7	0.2	16.9	0.8	64.0	5.9	2.5	0.1
2000-2002 Mean	58	2.8	0.2	15.4	0.5	76.0	4.2	2.4	0.0

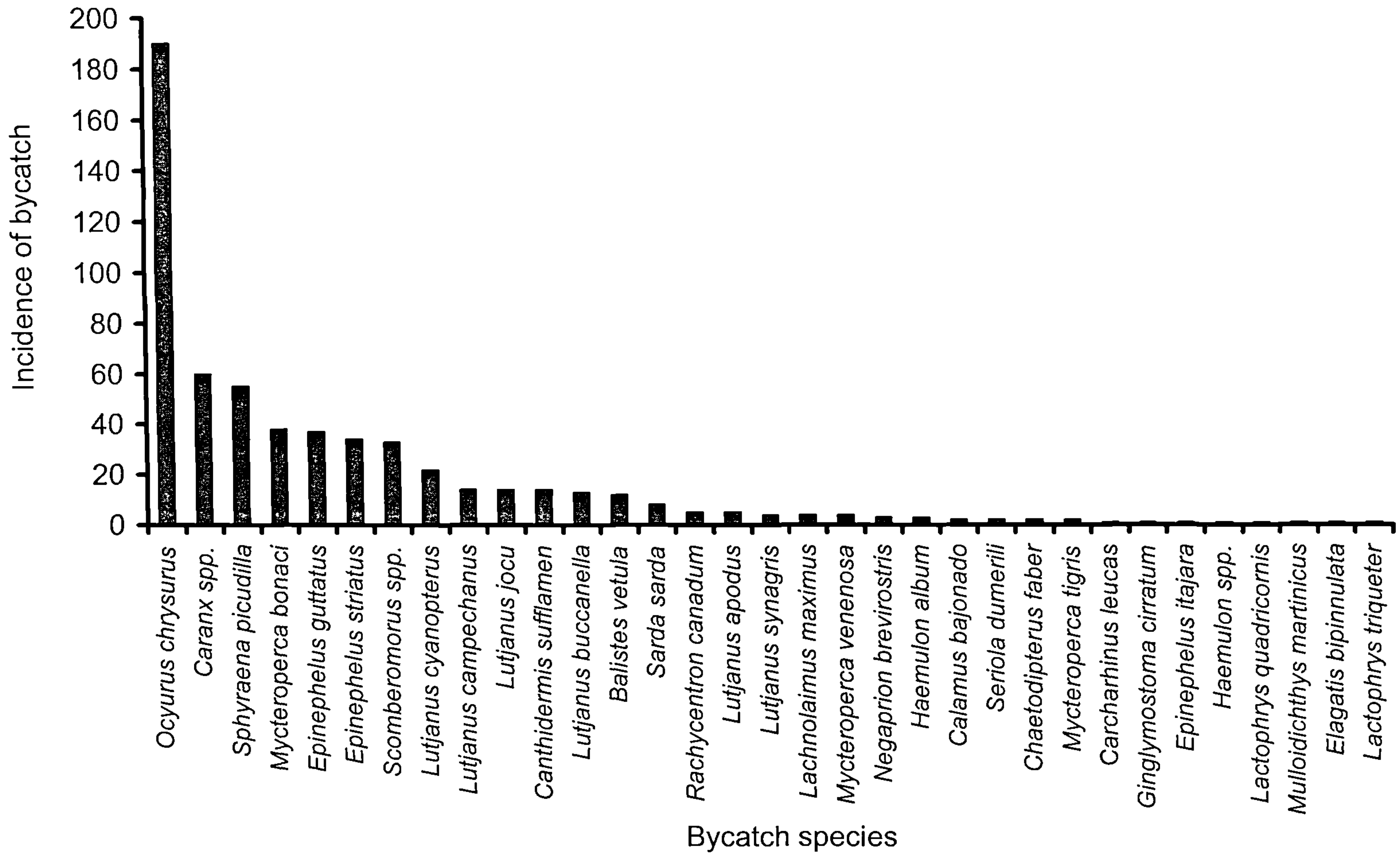


Figure 6.13: Incidence of bycatch by recorded species for the mutton snapper spawning aggregation fishery at Gladden Spit from 2000 to 2002.

consumed at home or traded locally. However, for the purpose of this study, they are considered bycatch of the mutton snapper fishery. Grouper are sold to restaurants or to the cooperative and fetch at least US$3.00 per pound of fillet. Yellowtail snapper dominated the mutton snapper fishery bycatch and was recorded in the landings of 190 boats surveyed from 2000 to 2002. No market existed for yellowtail snapper until March 2002 when despite a late March moon, a lack of mutton snapper landings and a catch abundance of yellowtail led both local fishing cooperatives to offer the equivalent of US$0.75 per pound of gutted whole yellowtail (as opposed to fillet). Two species of jack, the crevalle (*Caranx hippos*) and horse-eye jack (*Caranx latus*) were often not distinguished during record taking and therefore grouped together under "Jack" or *Caranx* spp., and were recorded in 60 boats surveyed. Other species caught included barracuda (*Sphyraena picudilla*) and several species of grouper (*Mycteroperca bonaci*, *M. venenosa*, *Epinephelus guttatus*, and *E. striatus*).

Due to the high representation of yellowtail snappers in bycatch, the lutjanid family representation in bycatch was more than twice that of the next most important family the serranids, followed by the families Carangidae and Sphyraenidae (Figure 6.14).

6.3.7 Underwater surveys

From 1999 to July 2002 presence versus absence and school size for 36 species that show signs of spawning at Gladden Spit were recorded (Table 6.5). These included direct observations of eleven species of reef fish spawning at Gladden Spit, including cubera and dog snappers, Atlantic spadefish (*Chaetodipterus faber*), permit (*Trachinotus falcatus*), yellow jack (*Caranx bartholomaei*), the French and grey angelfish (*Pomacanthus paru* and *P. arcuatus*), the smooth trunkfish and trunkfish (*Lactophrys triqueter* and *L. lagonus*), Creole wrasse (*Clepticus parrae*) and the hogfish (*Lachnolaimus maximus*) but never the mutton snapper. However, fully hydrated roe from landed mutton snapper from March to June each year indicate that the fish were within hours of spawning when caught (Colin, 1992).

Mutton snapper schools of 40 to over an estimated 4000 fish were recorded on 59 dives during the peak spawning period of March through June 1999 to 2002. School size may have been underestimated with larger schools as they were often loosely aggregated on the edge of the fore-reef, occupying depths from 30 m to over an

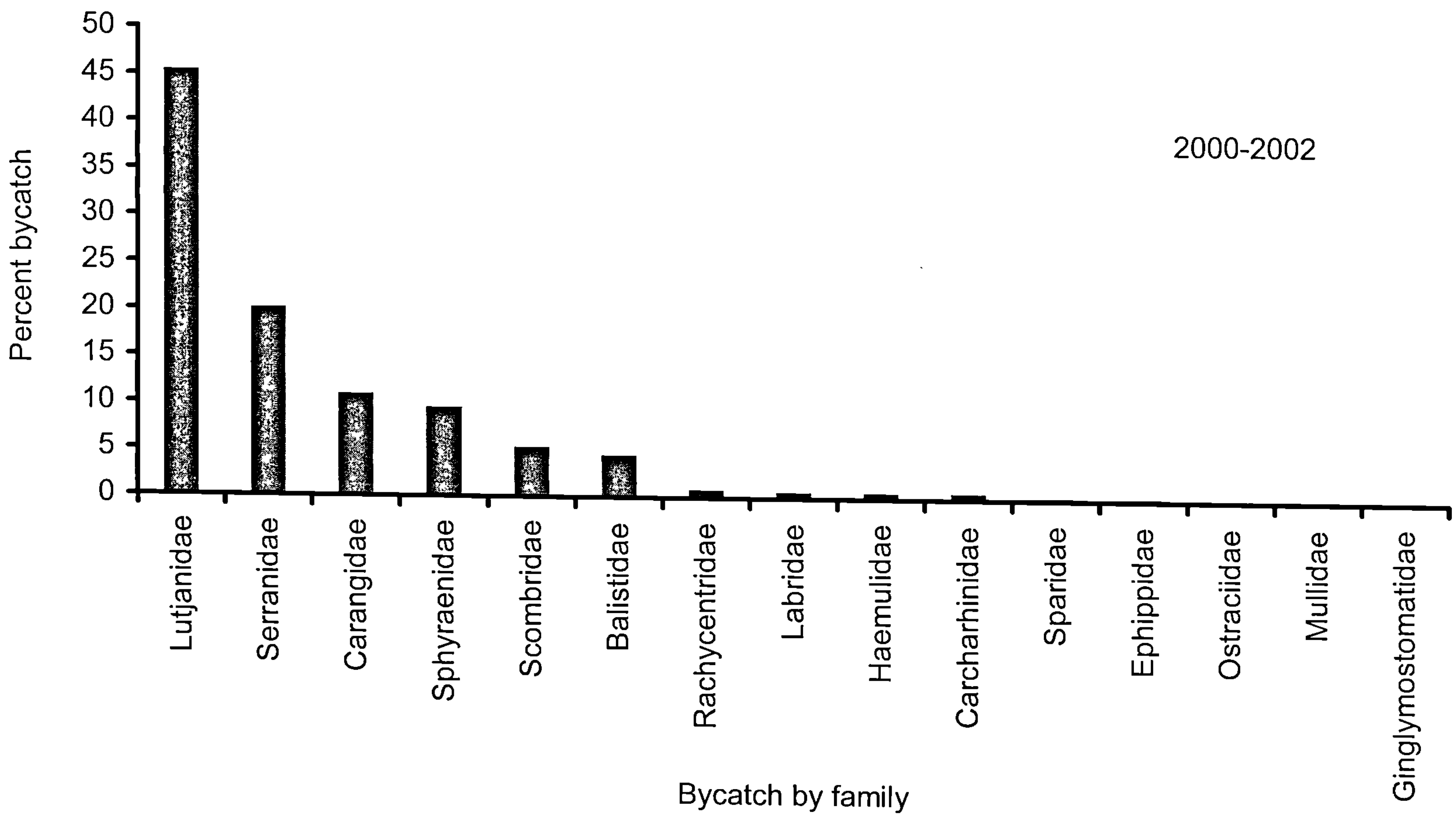


Figure 6.14: Percentage bycatch by family for the mutton snapper spawning aggregation fishery at Gladden Spit from 2000 to 2002.

Table 6.5: List of species of reef fish that appear to spawn at Gladden Spit according to criteria set out by Domeier and Colin (1997).

No.	Species	Common name	Spawning observed	Coloration changes observed	Courtship observed	Nesting observed	Unusual schooling or abundance observed	Hydrated roe	Targeted fishing (yes/no)
1	*Lutjanus analis*	Mutton snapper			X		X	X	Y – legal
2	*L.cyanopterus*	Cubera snapper	X	X	X		X	X	Y – illegal
3	*L. jocu*	Dog snapper	X	X	X		X	X	Y – illegal
4	*Ocyurus chrysurus*	Yellowtail snapper		X	X		X	X	Y – legal
5	*Trachinotus falcatus*	Permit	X	X	X		X		N
6	*Lactophrys triqueter*	Smooth trunkfish	X	X	X		X		N
7	*L. trigonus*	Trunkfish	X	X	X		X		N
8	*Diodon holocanthus*	Balloonfish ●	X		X		X		N
9	*Caranx hippos*	Crevalle jack		X	X		X		N
10	*Caranx latus*	Horseye jack	X	X	X		X		N
11	*Caranx bartholomaei*	Yellow jack	X	X	X		X		N
12	*Seriola dumerili*	Amberjack		X	X		X		N
13	*Caranx ruber*	Barjack		X	X		X		N
14	*Haemulon album*	White margate			X		X		N
15	*Calamus bajonado*	Jolthead porgy		X	X				N
16	*Epinephelus striatus*	Nassau grouper		X	X		X	X	Y – legal
17	*Mycteroperca bonaci*	Black grouper		X	X		X	X	Y – legal
18	*M. venenosa*	Yellowfin grouper		X	X			X	Y – legal
19	*M. tigris*	Tiger grouper		X	X			X	Y – legal
20	*E. guttatus*	Red Hind			X			X	Y – legal

No.	Species	Common name	Spawning observed	Coloration changes observed	Courtship observed	Nesting observed	Unusual schooling or abundance observed	Hydrated roe	Targeted fishing (yes/no)
21	*Pomacanthus paru*	French angelfish	X		X				N
22	*P. arcuatus*	Grey angelfish	X		X				N
23	*Canthidermis sufflamen*	Ocean triggerfish		X	X	X	X		N
24	*Balistes vetula*	Queen triggerfish			X		X		N
25	*Melichthys niger*	Black durgon			X		X		N
26	*Clepticus parrae*	Creole wrasse	X	X	X		X		N
27	*Chaetodipterus faber*	Atlantic spadefish	X	X	X		X		N
28	*Xanthichthys ringens*	Sargassum triggerfish			X		X		N
29	*Scomberomorus cavalla*	Kingfish					X	X	N
30	*Scomberomorus regalis*	Cero mackerel					X	X	N
31	*Sphyraena barracuda*	Barracuda					X	X	N
32	*Caranx crysos*	Blue runner					X		N
33	*Sarda sarda*	Bonito						X	N
34	*Thunnus atlanticus*	Blackfin tuna					X	X	N
35	*Lachnolaimus maximus*	Hogfish	X		X				N
36	*Makaira nigricans*	Blue marlin					X		Y – legal

Legal = fish species are primarily targeted and fished by Belizean fishers with a fishing permit. Illegal = the fish species are primarily targeted by fishers who do not hold a Belizean fishing permit and come from Guatemala or Honduras to fish at Gladden Spit.

- indicates a species only observed to spawn by survey colleague D. Castellanos.

estimated 65 m depth and at times spread over 500 m. Mutton snappers moved slowly against the low (under 1.0 m s^{-1}) prevailing current. When the water visibility was over 35 m, schools were sometimes sighted at over 70 m depth. Shy and rapidly dispersing when approached, mutton snappers were very infrequently observed in tight schools. The exception occurred in 2002, when more densely aggregated schools were observed on three occasions in the late afternoon close to 17:00 h. Within the more densely formed schools several individuals displayed signs of courtship whereby two to three individuals nuzzled the genital pore of another fish and several individuals were chased by others on the periphery of and inside the school. No colour changes were observed between the courting fish. In several instances where fishers caught mutton snappers with handlines touching at about 30 m depth, the fish were either patrolling the platform, possibly looking for the source of the bait smell or swam up to the reef platform from the deep beyond the reef edge. Schooling fish did not appear to break rank to bite the baits even when the schools were located close to the moored fishing boats.

Although the spawning behaviour of mutton snappers was not observed, over 147 instances of spawning in dog and cubera snappers were recorded. They were found to aggregate and spawn up to 14 days from 2 days before the full moon to twelve days after, primarily between March and June. Spawning aggregations can be huge: an estimated cubera aggregation reached 10,000 individuals on 21 May 2000 although the mean observed aggregation size for cuberas is 2,200 and for dogs is 1,500. Dog and cubera snappers also spawn in August and October, and dogs in December and January (Figure 6.15). Both species form tight aggregations with individuals displaying courtship behaviour such as nuzzling, twitching, pushing and colour morphing before rising up in the water column and releasing gametes. It is highly probable that mutton snappers spawn in the same manner as dogs and cuberas based on the recently observed behaviour of individuals in densely aggregated schools. Mutton snappers probably spawn after dusk and during the night or early morning based on the degree of egg hydration in the roe of landed females. This could explain why in five years of dive observations at the site I have never yet witnessed a single spawning event for this species.

6.3.8 Fishing versus tourism

The primary whale shark tourism site located at the northern reef edge and tip of Gladden Spit overlapped completely with the mutton snapper fishery site (Figure 6.2).

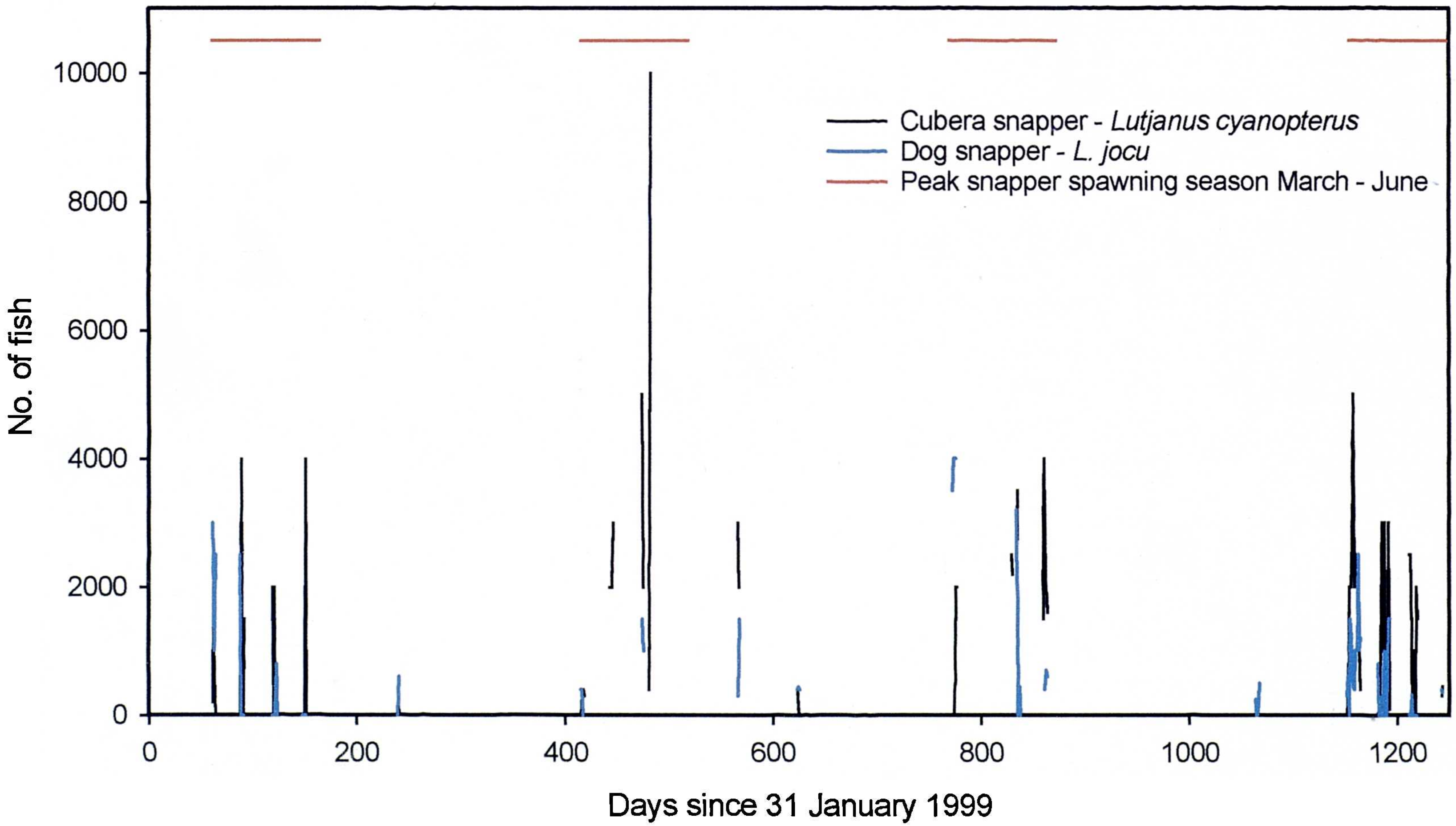


Figure 6.15: Periodicity of spawning in dog and cubera snappers (*Lutjanus jocu* and *L. cyanopterus*) at Gladden Spit from 31 January 1999 to 1 July 2002. The seasonal peak snapper spawning period from March to June is indicated by red horizontal bars.

The number of tour operators offering whale shark tours increased from 2 in 1998 to 18 in 2002 and the mean number of tourist boats arriving at Gladden during the snapper spawning aggregation season on a daily basis rose significantly from 3.2 in 2000 to 6.1 in 2002 (Kruskal-Wallis test: n = 83; df = 2; χ^2 = 11.478; $p < 0.05$). This was accompanied by a rise in the estimated number of tourists from 795 to 1668 visitors during the same period. This sudden increase in tourism usage of the traditional fishing site has led to conflict between fishers and tour operators. Divers visiting Gladden Spit to see whale sharks are blamed for "scaring away the fish" and considered one of the reasons for catch decline. Fishers are also worried about safety issues since divers are regularly observed diving under their boats and on several occasions have bumped into their lines or surfaced under or near their boats.

6.3.9 Economic alternatives to fishing the mutton snapper spawning aggregation

When interviewed, the 13 boat captains representing 30 fishers (Table 6.0) mentioned that they had been engaged in seven economic alternatives to fishing the Gladden Spit mutton snapper spawning aggregation including: boat captain, hospitality (running a hotel or guesthouse, restaurant), research assistant, small business owner (e.g. laundry, shop), watchman, employee of the fisheries cooperative, fish reseller, and guide (includes terrestrial guiding, snorkel guide, recreational fishing and flyfish guiding). Most economic alternatives cited (guiding, hospitality, boat captaining) were linked to the tourism industry. Three captains had made an almost complete recent transition from fishing the aggregation to tour-guiding, providing research support or hospitality. All five captains aged 50 or older were not interested in moving into the tourism industry and felt that the only alternative suitable for them would perhaps be related to boat captaining or fish-farming if this were developed. Four boat captains under 50 years old viewed tourism as easier and more lucrative work than spawning aggregation fishing. They were able to capitalise on their knowledge of the region and of the sea by focusing on lucrative and flexible forms of tourism such as fly-fishing, spin-casting and deep-sea trolling, kayak trips near the reef, and snorkelling. Additionally, interviews with five tour-operators who had previously fished at Gladden and moved into tourism from ten years ago onwards, cited tourism as an easier and more lucrative endeavour. Three of these former fishers are now involved in the dive industry with two each owning a dive shop.

6.4 Discussion

In this section, the mutton snapper spawning aggregation fishery at Gladden Spit is characterised in terms of catch, yield, fleet size and anecdotal data on fishers and the fishery. The decline in fish size and catch per unit effort from 2000 to 2002 indicate that the fishery is currently unsustainable even at its current historically low-levels. Within season increases in catch per unit effort indicate that June is potentially the peak spawning month for mutton snapper. The decline in mutton snapper catches and the increase in the yellowtail snapper catch in March 2002 could warn of a possible serial depletion of snapper species at Gladden.

Historically, reef fish spawning aggregations are targeted by fisheries due to their spatio-temporal predictability and high yields (Sadovy, 1994; Heyman & Graham, 2000). Over the past 50 years, spawning aggregations in Belize have provided much of the national annual fish landings (Thompson, 1944; Craig, 1969; CSO, 2001). An estimated 1.36–1.82 million kg of live fish were caught annually by 350-400 fishers between 1937-1944 (Thompson, 1944) and Craig (1969) estimated catches from the Caye Glory Nassau grouper spawning aggregation site at over 32,000 kg over two months in one spawning season. Deeming the fisheries underexploited in the then British Colony of British Honduras, Thompson (1944) suggested increasing fishing effort in general and promoted recreational fishing as a means of generating added income. Historically, grouper have been the preferred family of fish by both local and international consumers (Thompson, 1944; Craig, 1969), and this is particularly evident in Belize. However, due to a dramatic decline in grouper stocks in Belize, fishing pressure has shifted onto snappers, which are now considered the most important fish food source for coastal families.

The decline and extirpation of spawning aggregations of commercially important species of fish due to overexploitation has been documented in several areas worldwide (Smith, 1972; Olsen & Place, 1979; Fine, 1990; Shapiro *et al.*, 1993; Luckhurst, 1998; Bolden, 2000; Morris *et al.*, 2000; Rhodes & Sadovy, 2002) and locally in Belize (Craig, 1969; Paz & Grimshaw, 2001; Sala *et al.*, 2001). Most documented declines focus on serranids (Olsen & Place, 1979; Fine, 1990; Shapiro *et al.*, 1993; Luckhurst, 1998; Bolden, 2000; Morris *et al.*, 2000; Rhodes & Sadovy, 2002) with few examples from the Lutjanidae (Claro, 1991). Serial depletion of several spawning sites has occurred in Belize with the most notable extirpations taking place at Rocky Point, Caye Glory, Glover's Atoll and Rise and Fall Banks (Paz & Grimshaw, 2001). Gladden Spit remains the only commercially fished spawning aggregation on the Belize Barrier Reef.

Additionally, extirpation of one species can further lead to the serial depletion of other co-existing species that occupy a similar niche (Claro, 1991). The groupers and snappers are often linked together as a grouper-snapper complex because of their similar life histories and ecology (Beets & Friedlander, 1999; Lindeman *et al.*, 2000). Although both families arc highly fecund and relatively long-lived, snappers are perceived by local fishers in Belize to be more resistant to overexploitation than groupers because they do not enter traps as readily and are more dispersed throughout an area. Local fishers also perceive that snappers aggregate in much larger abundances than groupers, although schools of Nassau grouper have been historically estimated underwater at over 100,000 fish in the Bahamas (Smith, 1972). Huntsman and Schaaf (1994) noted that gonochoristic fish such as snappers will not be impacted as readily by the same level of fishing effort as protogynous fish, many of which are groupers. Yet, mutton snappers are intermittent or periodic spawners (Claro, 1981) that migrate large distances and often across several political borders towards spawning sites (Domeier & Colin, 1997), making them vulnerable to several fishing populations at several stages throughout their life-cycle. One mutton snapper tagged at Gladden Spit was recaptured over 570 km away in Akumal, Mexico, following the peak spawning-season (W. Heyman, pers. comm. 2001).

6.4.1 Catch size composition and yield

Mutton snappers caught at Gladden Spit were slightly larger than those landed from a spawning aggregation in Cuba where females measured 55.5 ± 1.5 cm and 50.7 ± 1.5 cm for males during a May moon. The largest fish caught at Gladden was a female of 91 cm FL, larger than the maximum length established by Mason and Manooch's 86.2 cm (1985) and Burton's 86.9 cm (2002). The change in catch composition from larger to smaller mutton snappers from 2000 to 2002 indicates that the fishery at Gladden Spit is impacting the population through the removal of larger individuals. Although there was a slight rise in size between 2001 and 2002, the overall pattern from 2000 to 2002 was one of significant decline in size. Removal of larger individuals can impact the reproductive fitness of a species as Bohnsack (1990) noted that larger fish produce an exponentially greater number of eggs than much smaller fish with a single 13 kg *L. campechanus* producing more eggs than 200 individuals weighing about 1 kg. Over-fishing of aggregations can change sex ratios, reduce genetic diversity (Kapuscinski & Philipp, 1988) and affect future spawning performance with the greatest impact noted for protogynous species through selective removal of larger individuals of a specific sex

(Colin, 1992, Johannes *et al.*, 1999). Compared to seining or trapping, hook and line fishing can select for larger predatory fish (Dalzell, 1996). The removal of larger more fecund fish has contributed to the extirpation of several spawning aggregations in Belize (Craig, 1969; Paz & Grimshaw, 2001; Sala *et al.* 2001) and worldwide (Olsen & la Place, 1979; Sadovy, 1994; Claro, 1991).

The small increase in gonadosomatic index (GSI) over two months in 2001 and the three months of recorded landings in 2002 indicate that the mutton snapper spawning peak at Gladden Spit is likely to take place in June or later, indicating that the spawning season is protracted and runs from March to July, if not later. This concords with findings by Claro (1981) where mutton snappers in Cuba show a range in GSI from 2.0 to 9.0 with an average of 4.0 and spawn from March to August-September and show peak GSI in May and June (Claro, 1981; García-Cagide *et al.*, 2001). The high GSI value for April 2001 appears erroneous and due to an unusually high number of fish with heavy roe (16%) in a small sample size for that month (n = 32).

In the absence of underwater count data, catch per unit effort is often used as a proxy for fish stock abundance (Gulland, 1969; Evans & Grainger, 2002). However, CPUE is not always considered an accurate indicator of abundance (Beverton & Holt, 1957) particularly if the CPUE increases or species undergoes changes in range with changes in abundance (Harley *et al.*, 2001). Although fishing gears and fisher distribution have not changed over the past 50 years, it appears that CPUE is not proportional to abundance estimates at Gladden Spit. When mutton snapper schools were encountered underwater, surveys yielded an estimated mean abundance of 2,400 fish with a peak abundance of 4,000 fish in May 2000. Yearly catch statistics surpass underwater survey estimates indicating that the visual surveys underestimated true population abundance. Nonetheless, these fisheries dependent and independent methods of assessing population abundance are likely to represent a fraction of the size of the mutton snapper spawning aggregation 15 or 50 years ago.

The decrease in the catch per fisher and per unit effort is significant. However, gross recorded landings between 2000 and 2002 increased which to some might indicate a still healthy population. Yet, total landings, like CPUE, do not necessarily represent true fish abundance. Variations in landings over short time scales may be based on environmental conditions affecting fish survival and the recruitment of juveniles, and differences in cohort sizes entering into the fished population. Increased landings may also be attributable to a "gold rush" effect. Following the news that the Gladden Spit spawning aggregation site was going to be closed, a rapid increase in the number of boats and fishers was recorded in 2002. Despite the increase in fishers, catch per unit effort decreased and pooled with the significant decrease in fish size over three years and the historical downward trend in catches, results suggests that the mutton snapper fishery at Gladden Spit is in decline.

6.4.2 Spawning site location

Reef fish appear to show behavioural adaptations to increase reproductive fitness (Johannes, 1978; Claro, 1981) and increase larval retention near spawning sites (Colin, 1992; Swearer *et al.,* 1999; Jones *et al.,* 1999). Promontories appear to be choice locations where many species of reef fish aggregate to spawn (Johannes, 1978; Colin, 1992; Claro, 1991; Paz & Grimshaw, 1991). This was particularly evident during underwater surveys of spawning aggregation of lutjanids where spawning was restricted to a 1 km stretch of the reef. Spawning was rarely observed underwater further north than G1 and no spawning of any species was ever sighted further south than G3 (Figure 6.2). Two hypotheses exist on the fate of spawn and larvae which include offshore transport championed by Johannes (1978) and a long-shore transport and recruitment (Colin, 1992; Swearer *et al.*, 1999). Increasing evidence from several locations indicate that reef fish larvae do not disperse as widely as previously thought indicating a high degree of self-recruitment (Jones *et al.*, 1999). Fertilised eggs spawned by cubera snappers aggregating at the same site as mutton snappers move with surface currents inshore from the Gladden Spit promontory (Heyman *et al.*, in prep). During rapid fish censuses in the shallow waters of mangrove cayes less than 10 km away from the Gladden Spit promontory small juvenile (< 10 cm) individuals of *L. analis*, *L. synagris*, *L. cyanopterus* and *L. jocu* were sighted, further indication that larvae spawned on the forereef may be settling inshore close to spawning grounds.

6.4.3 Is overfishing the cause of mutton snapper decline at Gladden Spit?

Other than the active day-time fishery for mutton snappers at Gladden, there are several species of fish that predate on the different life stages of muttons snapper. At least five species of oophagous fish have been observed to feed on the spawn of dog and cubera snappers and are seen to forage close to the spawning aggregations of mutton: Atlantic spadefish, yellowtail snapper, Barjack (*Caranx ruber*), Rainbow runner (*Elegatis bipinnulata*) and Blue runner (*Caranx crysos*). When spawning takes place, schools of these fish rise towards the spawn, ingesting the rising fertilised eggs. Predation on adult mutton snappers has not been observed, however bull sharks (*Carcharinus leucas*) and bottlenose dolphins (*Tursiops truncatus*) have been seen rushing into schools of horseye jacks, yellow jack, dog, cubera and mutton snapper. On three occasions dolphins were observed catching a fish (*L. jocu, C. latus* and *C. bartholomaei)* and then playing with it, often taking it to the surface for other dolphins to play with.

Fishers have blamed an apparent rise in the number of predatory sharks on the fishing grounds, primarily bull sharks, as one of the main reasons for the mutton snapper fishery decline. Olsen and LaPlace (1979) noted that fishers also believed that predatory sharks caused the demise of the red hind (*E. guttatus*) aggregation in 1976. Despite the relatively high catches recorded at Gladden Spit in 2000, several patriarch fishers noted that they had never lost so many fish to sharks previously. One of the most experienced fishers caught 47 mutton snapper and lost 43 to sharks on 18 May 2000. Fisher claims were validated when up to 8 bull sharks were observed circling under a fishing boat at a time in 2000 while diving.

On over 70% of all dives during the peak snapper spawning-season at least two bull sharks were sighted, usually patrolling the reef shelf under the fishing boats. It is possible that the sharks have learned to associate engine noise with food since the Nassau grouper spawning aggregation fishery at Caye Glory in the mid-1900s was heavily fished from non-motorised dories, hundreds of fish caught were dangled over the side of the boats and attacks by sharks were uncommon (Craig, 1969). Fishers believe the increase in predatory sharks is due to the choice of bait employed by illegal fishers working at night. Illegal fishers have been observed catching bonito at Gladden Spit at dusk and using it as bait at the fishing grounds, in effect chumming the waters. Sharks are known to associate discarded bycatch or bait with food (Corkeron, 1990). It is not known how many cubera snappers are lost to sharks during night fishing but any sharks caught would probably be kept as shark fins and meat are readily sold in Honduras. Although they impact the fishery, predatory sharks are also an attraction for divers, an increasingly important economic alternative to the fishery at Gladden Spit. To minimize the number of sharks targeting the legal fishery, it would be preferable to place a ban on night fishing and enable night patrols to take place on the outer reef.

Local fishers also blame whale sharks for the fishery's decline. Once they knew that the whale sharks aggregated at Gladden Spit to feed on the eggs of cubera and dog snappers (Heyman *et al.*, 2001) fishers assumed that whale sharks fed on the eggs of mutton snappers. Despite many attempts to observe muttons snapper spawn, none have been recorded spawning from 1998 to 2002. Whale sharks may feed on mutton snapper gametes if this species spawns in the same manner as cubera and dog snappers and release thick clouds of fertilised eggs. However, site fidelity studies detailed in Chapter 3 indicate that outside of the cubera and dog spawning-period at dusk, whale sharks display a significant decrease in activity near the spawning site during the hours that mutton snappers arc believed to spawn. Additionally, results from the trophic analysis of whale shark tissues and several of its prey including snapper eggs (see Chapter 3 and Appendix 3.1) indicate that the sharks are primarily feeding on zooplankton, organisms at a lower trophic level than eggs, and that eggs do not appear to form the primary component of the sharks' general diet.

Whale sharks are believed to live between 60 and 100 years (Pauly, 2002), if not longer. Even if whale sharks were feeding on mutton snapper eggs, it is highly probable that they have evolved to do so over thousands of years, long before fishers fished Gladden Spit. Egg dispersal post-spawning is rapid, with eggs drifting rapidly inshore (Heyman *et al.*, in prep). Fisher removal of each fecund mutton snapper with hydrated roe will impact the reproductive fitness of the population at a far greater rate by removing millions of eggs from potential spawning events and future recruits.

Media portrayal of Gladden Spit as a site where whale sharks can be seen predictably from March to June has led to a rapid rise in dive and snorkel tourism from 1998 to 2002. Fishers and tour-boats share the same 4.2 km stretch of reef (Figure 6.2) leading to conflict on several occasions. Ironically, many dive operators or divemasters are local members of the fishers' family. In several instances tourism income from divers and snorkelers benefits the entire family including the fishers. When diving at Gladden before 2000, avoidance behaviour by aggregating fish was rarely observed, particularly cubera and dog snappers. At times, cuberas were even slightly aggressive, making loud low-frequency sounds by reverberating their swim bladders. After 1999, our research team decided to hover on the periphery of the fish aggregations to minimize any modification or impact on pre-spawning behaviour. However, in 2002, our team of five divers noticed the change in aggregated fish behaviour between 2001 and 2002. Cuberas avoided approaching divers, moved off the reef edge and often dived deep to > 50 m and beyond the reach of recreational scuba divers. If divers did not move and hovered in the water away from the aggregation, the fish would often return to their previous positions. Divers heading directly into the aggregations appear to initiate avoidance behaviour. Avoidance behaviour is also evident with Nassau groupers, yellowfin and black groupers when approached on the spawning grounds. They move away from previously held positions and take refuge in a coral crevice if one exists nearby. Diving on spawning aggregations is advocated by some as a means of financing their conservation (Sala *et al.*, 2001). Yet, disruption to courting or spawning fish may cause fish stress and ultimately decrease their reproductive potential (Schreck *et al.*, 2001), and thus defeat the objective of conserving a spawning aggregation. Behavioural changes witnessed with an aggregation of fish that previously appeared impervious to disruption, highlight the need to implement the precautionary principle. Divers should not attempt to move directly into fish schools and should maintain at least 15 m away from fish spawning aggregations.

6.4.4 Habitat damage

Many studies exist that detail the importance of intact habitats for marine ecosystem function (Turner *et al.*, 1999). Yet few studies have focused on the quality of habitats that support spawning aggregations. Removal of structural complexity such as coral or rocky outcrops, vegetation or other organic features such as large sponges can impact fish communities by reducing available refuges from predation or critical nursery or spawning habitats (Turner *et al.*, 1999). The effect of continuous trawling for cod (*Gadus morhua*) on the Georges Bank off Newfoundland and ensuing loss of benthic complexity is thought to be one of the contributing factors to the collapse of cod stocks (Watling & Norse, 1998; Roberts & Sargant, 2002). Salem (1999) recorded habitat damage in the *Lethrinus nebulosa* spawning aggregation grounds in Ras Mohammed on Egypt's Sinai Peninsula caused by fishing boat anchors. Habitat damage in the Gladden Spit fishing and spawning grounds is primarily restricted to the fore reef and mainly caused by anchored fishing boats. Few recreational fishing or tour boats anchor in the fishing grounds during their time at Gladden Spit.

Fishers anchor daily or twice daily during the mutton snapper spawning-season on the Gladden Spit fishing grounds. Few sites show a high degree of habitat complexity in the spawning grounds. Some of the largest emergent structures such as barrel sponges (*Xestospongia muta*) and coral outcrops often serve as important organizing features for aggregating fish. including dog and cubera snappers, smooth trunkfish and spotted trunkfish (*Lactophrys bicaudalis*) and several species of grouper (*Epinephelus* and *Mycteroperca* spp). Anchors were found lodged in several corals along the fishing grounds with evidence of damage from attempts to retrieve the anchors. A minimum of 545 fishing boats was recorded on the fishing grounds during the mutton snapper fishery period or 1090 anchor drops if all fishermen moored at least twice daily. Anchors are set along the forereef at ~45-55m depth, the most productive fishing area for mutton snapper. Anchor set figures underestimate the true damages sustained by the reef through anchor damage as it does not include the number of times fishermen change their fishing spot during their morning or evening fishing period and it does not include the illegal fishers who moor at night. These figures are only for the mutton snapper fishing season and do not encompass the yellowtail snapper and grouper fishing seasons of November to March.

6.4.5 Economic alternatives

When interviewed, all 13 fishing captains noted a decline in the catch and 77% noted a decline in size of the landed fish over the past ten years. As the cost of fishing 46 km from the mainland increased due to a rise in the cost of gasoline, fishermen were increasingly turning to alternative occupations that often yielded more lucrative returns. The national and local increase in tourism has led to a demand in guides for recreational fishing, camping, snorkelling and scuba diving. Some of these activities are perceived as culturally incompatible for some fishermen, particularly those over 50 years old, who prefer to find income from building cabanas and hotels.

Fishermen working Gladden Spit noted that they engaged in at least seven economic alternatives, three of which (boat captaining, hospitality and guiding) are directly linked to tourism. This is mirrored by a larger survey conducted in 1998 with boat captains/fishers in Southern Belize that noted that tourism-related activities, especially recreational and/or flyfish guiding, were fast becoming the most lucrative and accepted economic alternative to subsistence fishing (Heyman & Graham, 2000). Friends of Nature, a marine conservation non-governmental organisation that co-manages the Gladden Spit Marine Reserve, has been actively tackling the issue of reducing pressures on the spawning aggregations and helping to orient traditional fishers towards economic alternatives. Fishers over 30 years old have been directed more to traditional guiding including recreational fishing and flyfishing and younger fishers, mainly under 30 years old have been trained to become divemasters. At least 43 individuals in both age groups were trained as whale shark tour guides between 2001 and April 2003.

However, interviewed boat captains noted that there would always be a demand for fresh fish from the local communities and this would continue to impose pressures on the spawning aggregations. Demand for fresh snapper in the five stakeholder communities Belize is rising with the increased tourism. Gladden Spit is perceived by fishers and tour operators alike as the primary site to supply the demand. Two captains further noted that additional pressures might come from beyond Belize's borders, as there is interest from Jamaica to import Gladden Spit yellowtail snapper. To meet the increasing demand for fresh fish, there has been recent interest from abroad and locally to raise mutton snapper in fish pens between the mainland and the barrier reef. However, the issue of feed composition and provenance for this predatory fish has not been resolved and the project is pending external funding.

Whale shark tourism is an economic trade-off only during the lucrative snapper-fishing season, and therefore does not provide a broader distribution of economic activities throughout the year. However, estimates of local revenue captured by visitors undertaking tours to the Gladden Spit and Silk Cayes Marine Reserve (GSSCMR) to see the sharks netted an estimated US$1.35 million in 2002 (Chapter 7) compared to the US$ 35,497 netted by the mutton snapper spawning aggregation fishery. Yet, only one of the boat captains interviewed had moved over to whale shark tourism in 2002. Comparably, communities formerly dependent on open-access small-scale fisheries in Baja California, Mexico, are now increasingly involved in whale watching ecotourism following dramatic declines in fish abundance. However, the open-access and unregulated nature of the lucrative whale watching industry is creating user conflicts over access rights and meanwhile has not discouraged fishing the depleted resource (Young, 1999). With restrictions on the number of boats and licensed whale shark tour-guides being discussed by the local marine reserve management body and its advisory board, it is unlikely that this will be an open-access economic alternative to the snapper fishery, as the fishery has been historically. Another lucrative and often stable form of employment over the medium-term is research. Again, available positions are few and this alternative primarily benefits fishers who own a boat or have been trained to dive.

6.4.7 Implications for management

The Gladden Spit Marine Reserve was created in the interest of protecting its unique spawning aggregations and seasonal congregation of whale sharks. However, none of the recommendations listed on the statutory instrument such as regulating the number of fishers and tour-operators at Gladden have been passed into law and both fishing and whale shark tourism remain unregulated. Part of the reason for lack of legal statutes to apply to these two economic activities rested in the fact that until recently the GSSCMR had no defined management body to implement and enforce regulations. The Department of Fisheries has ~290 km of coastline and reef including three offshore atolls to manage and did not have the resources to manage GSSCMR. Following the consolidation and capacity-building of Friends of Nature, the GSSCMR is now managed locally through a co-management agreement signed with the Department of Fisheries. Recent closure of 11 spawning aggregation sites throughout Belize to fishing and a seasonal ban on Nassau grouper fishing from December to March has added strength to efforts to manage and even halt fishing on the over-exploited spawning aggregations. Gladden Spit is one of two spawning aggregation sites that does not have a total ban imposed on fishing, issues that are currently being discussed between local fishers and the Friends of Nature. Interviewed fishers strongly supported some form of management of the fishery at Gladden Spit, but primarily focused on halting illegal fishing from Honduras and resolving conflict with tour-operators utilising the same space as the fishers as opposed to curtailing their own fishing effort.

Fishing pressure has also increased due additional opportunities for sales of marine products through the second fishing cooperative established in Mango Creek in spring 2001. Competing with the well-established Placencia Cooperative, Mango Creek, a subsidiary of the larger parent Belize-based Northern Cooperative, entices fishers with competitive prices for lobster, conch, mutton snapper, and several other species of finfish, and low-interest loans. Both fishing cooperatives set a precedent in March 2002 by offering to purchase whole yellowtail snapper, a commercially important species in the Caribbean that lives to at least 14 years (Johnson, 1983). This species was not previously bought for the national market, fished instead for local consumption. The 2002 March moon coincided with an abundance of yellowtail and according to fishers interviewed, a record low catch of mutton snappers. If mutton snapper stocks are further depleted, a change in fish assemblage structure and the mean trophic level of landings is probable as fishers "fish down the food web" (Pauly *et al.*, 1998). Serial depletion of other species such as the yellowtail snapper can be expected as Claro (1991) recorded in Cuba following the extirpation of the lane snapper fishery by 1978.

There is sufficient evidence, historical and empirical, local and global, to indicate that targeted fishing of fish spawning aggregations leads to extirpation of the fish stock. Fish that were once safe from fishing pressures through inaccessibility or bad weather, existed by default in marine protected areas. With the advent of all-weather ships, prolific use of ice, sonar technology and efficient fishing gears, coupled with increasing pressure driven by an ever-burgeoning population, these refugia no longer exist. Quotas, restrictions and other regulations are difficult to enforce in most countries, even more so in countries where the majority of reef fish spawning aggregations exist. Reviewing all traditional management strategies available for the conservation of spawning aggregations including seasonal closures (Sala *et al.*, 2001), quotas, traditional fishing permits, total harvest and use bans (Bohnsack, 1989), none have been found effective over the long term (Rhodes & Sadovy, 2002). These methods require resources to manage, monitor and enforce regulations that often simply do not exist, particularly in tropical countries. Although blanket solutions to stemming the decline of reef fish spawning aggregations are not always advocated (Rhodes & Sadovy, 2002) it appears that the relatively simple solution to protecting spatio-temporally vulnerable spawning aggregations stands out: use well-defined no-take marine reserves (Roberts, 1994, 1997; Roberts, 2000). In light of the numerous extirpations of spawning aggregations documented and their inability to recover over time, safeguarding the reproductive potential of fish during one of the most vulnerable periods in their lifecycle is now mandatory to stem the continued decline of global fish stocks.

6.5 References

Aguilar Perera A. & Aguilar Davila W. 1996. A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of Fishes*. **45** (4): 351-361.

Allen G. R. 1985. FAO Species catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. *FAO Fisheries Synopsis 125*. **6**: 208 pp.

Beets J. & Friedlander A. 1999. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the US Virgin Islands. *Environmental Biology of Fishes*. **55** (1-2): 91-98.

Beverton R. J. & Holt S. J. 1957. On the dynamics of exploited fish populations. *Fishery Investigations, Series 2*. **19**: 533.

Bohnsack J. A. 1989. Protection of grouper spawning aggregations. National Oceanic and Atmospheric Administration Coastal Resources Division CRD-88/89-06. Miami, Florida. 8 pp.

Bohnsack J. A. 1990. The potential of marine fishery reserves for reef fish management in the US southern Atlantic. NOAA Technical Memo. NMFS-SEFC 261. 40 pp.

Bolden S. K. 2000. Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to a spawning aggregation in the central Bahamas. *Fishery Bulletin*. **98** (3): 642-645.

Bortone S. A. & Williams J. L. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida). US Fish and

Wildlife Service Biological Report US Army Corps of Engineers, TR EL-82-4. 18 pp.

Burton M. L. 2002. Age, growth and mortality of mutton snapper, *Lutjanus analis*, from the east coast of Florida, with a brief discussion of management implications. *Fisheries Research*. **59** (1-2): 31-41.

Carter J. & Perrine D. 1994. A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces, Lutjanidae) in Belize, Central America. *Bulletin of Marine Science*. **55** (1): 228-234.

Cisneros-Mata M. A., Montemayor-Lopez G. & Roman-Rodriguez M. J. 1995. Life history and conservation of *Totoaba macdonaldi*. *Conservation Biology*. **9** (4): 806-814.

Claro R. 1981. Ecología y ciclo de vida del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma cubana. *Informacion Científica Técnica, Academia de Ciencias de Cuba*. **186**: 1-83.

Claro R. 1983. Dinámica estacional de algunos indicadores morfofisiológicos del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma cubana. *Reporte de Investigaciones del Instituto Oceanológico Academia de Ciencias de Cuba*. **22**: 1-14.

Claro R. 1991. Changes in fish assemblage structure by the effects of intense fisheries activities. *Tropical Ecology*. **32** (1): 36-46.

Claro R., Baisre J. A., Lindeman K. C. & García-Arteaga J. P. 2001. Cuban fisheries: historical trends and current status. In: *Ecology of the Marine Fishes of Cuba*. (Claro R., Lindeman K. C. & Parenti L. R. eds.), pp 194-219. Washington DC. Smithsonian Institution Press.

Colin P. L. 1977. Spawning of Western Atlantic surgeonfishes. National Geographic Society. 243-250 pp.

Colin P. L. 1982. Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae). **80** (4): 853-862.

Colin P. L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes*. **34**: 357-377.

Colin P. L. & Clavijo I. E. 1988. Spawning activity of fishes producing pelagic eggs on a shelf edge of coral reef, Southwestern Puerto Rico. *Bulletin of Marine Science*. **43** (2): 249-279.

Corkeron P. J. 1990. Aspects of the behavioural ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In: *The Bottlenose Dolphin*. (Leatherwood S. & Reeves R. R. eds.), pp 285-294. San Diego, CA. Academic Press.

Craig A. K. 1966. Geography of fishing in British Honduras and adjacent coastal waters. Technical Report 28. Coastal Studies Lab. Louisiana State University. 143 pp.

Craig A. K. 1969. The Grouper Fishery of Cay Glory, British Honduras. *The Grouper Fishery*. **59**: 252-263.

CSO. 2000. Belize Population Census 2000. Central Statistical Office. Belmopan, Belize.

CSO. 2001. Abstract of Statistics: 2000. Central Statistical Office. Belmopan, Belize.

Dalzell P. 1996. Catch rates, selectivity and yields of reef fishing. In: *Reef Fisheries*. (Polunin N. V. C. & Roberts C. M. eds.), pp 161-192. Chapman and Hall.

Domeier M. L. & Colin P. L. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science*. **60** (3): 698-726.

Domeier M. L., Koenig C. & Coleman F. 1996. Reproductive biology of the grey snapper (Lutjanidae: *Lutjanus griseus*) with notes on spawning for other western Atlantic lutjanids. In: *Biology, Fisheries and Culture of Tropical Snappers and Groupers*. (Arreguín-Sanchez F., Munro J. L., Balgos M. C. & D. P. eds.), pp 189-201. ICLARM conference Proceedings.

Druzhinin A. D. 1970. The range and biology of snappers (Fam. Lutjanidae). *Journal of Ichthyology*. **10** (6): 717-736.

Evans D. & Grainger R. 2002. Gathering data for resource monitoring and fisheries management. In: *Handbook of Fish Biology and Fisheries - Volume II: Fisheries*. (Hart P. J. B. & Reynolds J. D. eds.), pp 84-102. Oxford. Blackwell Science Ltd.

Fine J. C. 1990. Spawning aggregations of Nassau grouper in Honduras: Groupers in Love. *Sea Frontiers* (Jan/Feb): 42-45.

García-Cagide A., Claro R. & Koshelev B. V. 2001. Reproductive patterns of fishes of the Cuban shelf. In: *Ecology of the Marine Fishes of Cuba*. (Claro R., Lindeman K. C. & Parenti L. R. eds.), pp 73-114. Washington DC. Smithsonian Institution Press.

Gulland J. A. 1969. *Manual of methods for fish stock assessment: Part I Fish population analysis*. Food and Agriculture Organization of the United Nations, Rome.

Haedrich R. L. & Barnes S. M. 1997. Changes over time of the size structure in an exploited shelf fish community. *Fisheries Research*. **31** (3): 229-239.

Harley S. J., Myers R. A. & Dunn A. 2001. Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences*. **58**: 1760-1772.

Heyman W. D. & Graham R. T. (eds.). 2000. The Voice of the Fishermen of Southern Belize. Toledo Institute for Environment and Development, Belize. 44 pp.

Heyman W. D., Graham R. T., Kjerfve B. & Johannes R. E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology-Progress Series*. **215**: 275-282.

Heyman W. D., Kjerfve B., Graham R. T., Cuevas E. & Rhodes K. L. in prep. Characterizing spawning aggregations of cubera snappers, *Lutjanus cyanopterus* (Pisces: Lutjanidae) on the Belize Barrier Reef:

Huntsman G. R. & Schaaf W. E. 1994. Simulation of the impact of fishing on reproduction of a protogynous grouper, the graysby. *North American Journal of Fisheries Management*. **14**: 41-52.

Johannes R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes*. **3** (1): 65-84.

Johannes R. E. 1988. Spawning aggregation of the grouper, *Plectropomus areolatus* (Ruppel) in the Solomon Islands. *6th International Coral Reef Symposium*, Australia.

Johannes R. E. 1998. The case for data-less management: examples from tropical nearshore fisheries. *Trends in Ecology and Evolution*. **13** (6): 243-246.

Johnson A. G. 1983. Age and growth of yellowtail snapper from South Florida. *Transactions of the American Fisheries Society*. **112**: 173-177.

Jones G. P., Milicich M. J., Emslie M. J. & Lunow C. 1999. Self-recruitment in a coral reef fish population. *Nature*. **402**: 802-804.

Kapuscinski A. R. & Philipp D. P. 1988. Fisheries genetics: issues and priorities for research and policy development. *Fisheries Research*. **13** (4): 4-10.

Lawson G. L. & Rose G. A. 2000. Seasonal distribution and movements of coastal cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland. *Fisheries Research*. **49** (1): 61-75.

Lindeman K. C., Pugliese R., Waugh G. T. & Ault J. S. 2000. Developmental patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas. *Bulletin of Marine Science*. **66** (3): 929-956.

Luckhurst B. E. 1998. Site fidelity and return migration of tagged red hinds (*Epinephelus guttatus*) to a spawning aggregation site in Bermuda *50th Gulf and Caribbean Fisheries Institute*, Bermuda, pp 750-763.

Morris A. V., Roberts C. M. & Hawkins J. P. 2000. The threatened status of groupers (Epinephelinae). *Biodiversity and Conservation*. **9** (7): 919-942.

Moyer J. T., Thresher R. E. & Colin P. L. 1983. Courtship, spawning and inferred social organization of American angelfishes (Genera *Pomacanthus, Holacanthus and Centropyge; Pomacanthidae). Environmental Biology of Fishes*. **9** (1): 25-39.

Munro J. L. 1983. Coral reef fish and fisheries of the Caribbean Sea. In: *Caribbean Coral Reef Fishery Resources*. (Munro J. L. ed.), pp 1-9. Center Living Aquatic Resources Management (ICLARM).

Munro J. L., Guat V. C., Thompson R. & Reeson P. H. 1973. The spawning seasons of the Caribbean reef fishes. *Fisheries Ecology Research Project* (5): 69-84.

Olsen D. A. & Place J. A. L. 1979. A study of a Virgin Islands grouper fishery based on a breeding aggregation. *Current Caribbean Fisheries Research*. **31**: 130-144.

Pauly D. 2002. Growth and mortality of the basking shark *Cetorhinus maximus* and their implications for management of whale sharks *Rhincodon typus*. In: *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Worjkshop, Sabah, Malaysia, July 1997*. (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 199-208. Gland, Switzerland and Cambridge, UK. IUCN SSC Shark Specialist Group.

Pauly D., Christensen V., Dalsgaard J., Froese R. & Torres F. 1998. Fishing down marine food webs. *Science*. **279**: 860-863.

Paz M. & Grimshaw T. 2001. Working towards the sustainable management of Nassau groupers in Belize. Workshop report. GreenReef. Belize City. 93 pp.

Rhodes K. L. & Sadovy Y. 2002. Temporal and spatial trends in spawning aggregations of camouflage grouper *Epinephelus polyphekadion*, in Pohnpei, Micronesia. *Environmental Biology of Fishes*. **63**: 27-39.

Roberts C. M. 1994. Marine reserves: a brief guide for decision makers and users *Workshop on Coastal and Ocean Resources Management. NGO Islands Forum. UN Global Conference on the Sustainable Development of small Island Developing States.*, Barbados April 25- May 6, 1994.

Roberts C. M. 1997. No-take marine reserves: unlocking the potential for fisheries. In: *Marine Environmental Management: Review of Events in 1997 and Future Trends.* (Earl R. C. ed.), pp 127-132. Gloucester. Kempley.

Roberts C. M. 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries.* **23** (7): 16-19.

Roberts C. M. 2000. Selecting marine reserve locations: optimality versus opportunism. *Bulletin of Marine Science.* **66** (3): 581-592.

Roberts C. M. & Hawkins J. P. 1999. Extinction risk in the sea. *Trends in Ecology & Evolution.* **14** (6): 241-246.

Roberts C. M. & Sargant H. 2002. Fishery benefits of fully protected marine reserves: why habitat and behaviour are important. *Natural Resource Modeling.* **15** (4): 487-507.

Russ G. R. & Alcala A. C. 1994. Sumilon Island Reserve: 20 years of hopes and frustrations *Naga, the ICLARM Quarterly*, pp 8-12.

Sadovy Y. 1992. The case of the disappearing grouper: *Epinephelus striatus*, the Nassau grouper, in the Caribbean and Western Atlantic *45th annual meeting of the Gulf and Caribbean Fisheries institute, Merida, Mexico*, Merida, Mexico, pp 1-18.

Sadovy Y. 1993. The Nassau grouper, endangered or just unlucky? *Reef Encounter.* **13**: 10-12.

Sadovy Y. 1994. Grouper stocks of the Western Central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute.* **43**: 42-64.

Sadovy Y. 1996. Reproduction of reef fishery species. In: *Reef Fisheries.* (Polunin N. V. C. & Roberts C. M. eds.), pp 15-59. Chapman and Hall.

Sadovy Y. & Cheung W. L. 2003. Near extinction of a highly fecund fish: the one that nearly got away. *Fish and Fisheries.* **4**: 86-99.

Sadovy Y. & Ecklund A. M. 1999. Synopsis of biological data on the Nassau grouper *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA NOAA Technical Report NMFS 146. 65 pp.

Sala E., Aburto-Oropeza O., Paredes G., Parra I., Barrera J. C. & Dayton P. K. 2002. A general model for designing networks of marine reserves. *Science.* **298**: 1991-1993.

Sala E., Ballesteros E. & Starr R. M. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: Fishery management and conservation needs. *Fisheries.* **26** (10): 23-30.

Salem M. 1999. Management of fishing in the Ras Mohammed Nationa Park with special reference to the fishery for *Lethrinus nebulosus* (Forsskal, 1775). Doctorate. Biology, York. 272 pp.

Schreck C. B., Contreras-Sanchez W. & Fitzpatrick M. S. 2001. Effects of stress on fish reproduction, gamete quality , and progeny. *Aquaculture.* **197**: 3-24.

Shapiro D. Y., Sadovy Y. & McGehee M. A. 1993. Size, composition, and spatial structure of the annual spawning aggregation of the Red Hind, *Epinephelus guttatus* (Pisces, Serranidae). *Copeia* (2): 399-406.

Sierra L. M. 1996. Relaciones tróficas de los juveniles de cinco especies de pargos (Pisces: Lutjanidae) en Cuba. *Revista Biológica Tropical.* **44** (3): 499-507.

Smith C. L. 1972. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Transactions of the American Fisheries Society.* **101**: 257-261.

Swearer S. E., Caselle J. E., Lea D. W. & Warner R. R. 1999. Larval retention and recruitment in an island population of a coral reef fish. *Nature.* **402** (16): 799-802.

Thompson E. F. 1944. The fisheries of British Honduras. Development and Welfare in the West Indies 21. 32 pp.

Turner S. J., Thrush S. F., Hewitt J. E., Cummings V. J. & Funnell G. 1999. Fishing impacts and the degradation or loss of habitat structure. *Fisheries Management and Ecology.* **6** (5): 401-420.

Watling L. & Norse E., A. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conservation Biology.* **12** (6): 1180-1197.

Wicklund R. 1969. Observations on spawning of the lane snapper. *Underwater Naturalist.* **6** (2): 40.

Young E. H. 1999. Balancing conservation with development in small-scale fisheries: Is ecotourism an empty promise? *Human Ecology.* **27** (4): 581-620.

Zeller D. C. 1998. Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. *Marine Ecology Progress Series.* **162**: 253-263.

Appendix 6.A Mutton snapper fishery landings form

Mutton snapper Landings Field Form - Belize Recorder :_______ __ Page :___

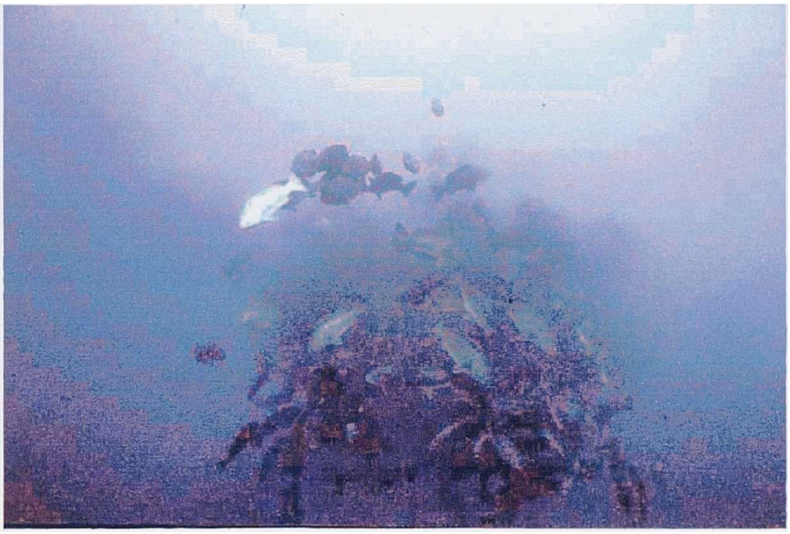
Date	Species	Wt (kg)	FL (cm)	Gonad wt (g)	Sex (M/F)	Maturity ED/LD/ RR/S	Fishers	Notes
20/5/02	Mutton	2.450	47	300	F	LD	Waga	Lost 40 snappers to sharks

Appendix 6.B Mutton snapper fishery CPUE form

CPUE Data – Mutton Spag fishery @ Gladden Spit 2002 Recorder:____________ Page:_____

Date	Boat Captain	Fishers per boat	Hours fished	Hooks on line	Total mutton (lbs)	Whole or gutted	No. of Mutton	Bycatch species	Total bycatch (lbs)	Total catch (lbs)

Appendix 6.C Spawning of aggregated snappers at Gladden Spit



Cubera snappers (*Lutjanus cyanopterus*) spawning in the late afternoon.

Dog snappers (*L. jocu*) spawning at a depth of 15 m.

Chapter 7. Whale shark tourism in the Gladden Spit and Silk Cayes Marine Reserve, Belize

Abstract

Whale shark encounter tourism is a lucrative and high profile activity that is growing rapidly worldwide, and particularly in Belize where sightings are seasonally predictable. Located on the Belize Barrier Reef, the Gladden Spit and Silk Cayes Marine Reserve forms the primary site for this wildlife tourism. Whale sharks congregate predictably in large numbers to feed on spawn produced by a seasonal aggregation of reproducing snappers. To provide information for management of this growing niche tourism, visitor counts to the marine reserve were conducted from 2000-2002 and questionnaire surveys conducted in 2001 and 2002. The number of operators running whale shark tours increased from 2 to 18 between 1997 and 2002, and tourists at the whale shark aggregation site increased by 64% between 2001 and 2002. Daily fees are being considered as a means of covering the reserve's operational and management costs. Surveys showed visitors were willing to pay a mean daily fee of US$ 9.62 in 2002 to visit the marine reserve and its fauna, representing only 64% of the proposed daily fee to visit the marine reserve. Willingness to pay is related to the presence of whale sharks and their overall satisfaction with their trip to Gladden Spit. During their trip to Belize, tourists spent a mean of US$1,777 ± 707 SD that rose to US$2,218 ± 1,804 SD in 2002. The reserve's five stakeholder communities captured 36% of expenditures in 2002 with mean visitor expenditure in the stakeholder communities of US$ 812 ± 999 SD. Whale shark tourism at the reserve is worth US$ 3.7 million for a six-week operating period in 2002 with US$ 1.35 million captured locally. Whale shark tourism can promote public and private support for shark and marine conservation both at the local and international levels. This study reveals that whale shark tourism generates employment and increases foreign currency earnings in Belize and is worth 39 times more than the spawning aggregation fishery that takes place at the same time of year. Yet, tourism is not the panacea for whale shark conservation and may not be able to underwrite marine reserve and conservation costs at Gladden Spit. Because tourism can impact its target resource, careful management and enforcement of regulations with the support of stakeholder communities is therefore required to ensure the sustainability of whale shark

tourism and the reef fish spawning aggregations that form the basis for predictable shark visitation at Gladden Spit.

7.1 Introduction

The increase in disposable income in developed countries and greater access to remote areas has led to a steep rise in coastal and marine ecotourism and its subsets of nature, adventure, and wildlife tourism (Miller, 1993). These forms of tourism provide excitement and rekindle links with nature (Orams, 1997; 2000; 2002). In particular, marine wildlife tourism is growing rapidly in popularity as the number of people who snorkel or who are certified to scuba dive grows yearly where current estimates indicate that there are over five million active divers worldwide (http://www.padi.com/english/common/padi/statistics). The increasing demand for close contact with nature (Richardson, 1998; Reynolds & Braithwaite, 2001), especially with large charismatic species (Orams, 2000; Vivanco, 2001; Orams, 2002) has fuelled lucrative industries such as whale-watching (Arnold & Birtles, 1993). Revenue from these activities has provided economic support for non-consumptive use of high-profile wildlife such as terrestrial predators, gorillas, whales, dolphins and sharks (Western, 1986; Davies, 1990; Barnes *et al.*, 1992; Butynski & Kalina, 1998; Anderson, 2002). However, wildlife tourism is not always the panacea of wildlife conservation as it can impact the targeted species (Olson *et al.*, 1997; Butynski & Kalina, 1998; Isaacs, 2000; Orams, 2000; 2002). A better understanding of the demands and pressures of wildlife tourism on target species can provide management and policy guidelines that help to avoid killing "the golden goose".

Shark diving in particular is a rapidly growing form of wildlife tourism that affords divers the opportunity to encounter sharks, either in the wild (Davis, 1998b; Anderson, 2002) or under a contrived setting where sharks are fed (Perrine, 1989; FFWCC, 2000). Its rise in popularity is timely as the need for shark conservation is underlined by recent evidence of rapid declines in shark populations both in the Atlantic (Baum *et al.*, 2003) and worldwide (Myers & Worm, 2003). Few sharks are more charismatic or sought after by snorkelers and divers than the whale shark. Documented encounters with whale sharks indicate that it ranges across at least 120 countries (COP12, 2002), but it remains elusive. Although the cryptic nature of a target species can make it more valuable and influence viewing capacity (Western, 1986), predictability of sightings is a mainstay of wildlife tourism.

Whale sharks are large, docile and relatively slow moving (an asset for shark encounter tourism), and will aggregate predictably, often on a seasonal basis, to feed (Clark & Nelson, 1997; Colman, 1997; Heyman *et al.*, 2001). As patterns of whale shark visitation at specific sites are gradually revealed (Taylor, 1996; Wilson *et al.*, 2001; Alava *et al.*, 2002) (see Chapter 3 on site fidelity), associated tourism has grown rapidly. Unlike many advertised commercial shark dives, viewing whale sharks does not involve baiting or feeding and is therefore closer to the unadulterated "wild" experience sought by visitors. Encounters with whale sharks are proving highly popular with snorkelers and divers as they provide the thrill of facing a shark with none of the dangers (Davis *et al.*, 1997; Davis, 1998a, 1998b; Walpole, 2001).

Anderson and Ahmed (1993) undertook a study on the shark watching tourism in the Maldives Islands in 1992, and found that on average, a single grey reef (*Carcharhinus amblyrhynchos*) shark was worth US$3,300 per year based on all the dives made at 35 shark-watching dive sites. Grey reef sharks live to be at least 18 years old, and hence could be worth over US$59,400. It was further estimated that tourism based on reef sharks in the Maldives was worth US$6.6 million in 1997, a figure that represented diving revenue alone and did not include accommodation, food and transport (Anderson & Ahmed, 1993). Whale shark tourism offers a valuable non-consumptive alternative to dedicated fisheries that threaten this species (COP12, 2002). At Ningaloo Reef, Western Australia, Davis (1998b) estimated tourism revenues at Aus$ 4.7 (US$ 3.1 million) for a two-month season in 1996 and was considered to be worth about Aus$ 12 million in 2002 (US$ 7.8 million) (CALM, pers. comm.). With at least 11 additional sites worldwide that boast of hosting predictable aggregations of whale sharks, (Mexico-two sites, Honduras, Belize, South Africa, Mozambique, Galapagos (Ecuador), Thailand, India, Seychelles, and Philippines), this tourism could be worth conservatively over US$ 30.0 million annually[1]. Several of these sites, such as Baja California, Mexico, Donsol in the Philippines, and Gladden Spit in Belize have seen rapid rises in tourism in recent years (Dowdell *et al.*, 2003) (M.C. Garcia, pers. comm.; J. Ketchum, pers. comm.; M. Alava, pers. comm.; this chapter). Additionally, three of these sites (Ningaloo Reef, Australia; Gladden Spit, Belize and Galapagos, Ecuador) are marine protected areas that can provide variable degrees of management for whale shark tourism.

[1] Estimating US$ 2 million per site per season based on a quarter of Australia's yearly revenue per site.

Tourism is rising in Belize with a 38% increase in arrivals from 134,298 in 1997 to 185,705 visitors in 2001 (BTB 2001). Tourism recently supplanted agriculture and fisheries as the primary source of income with an estimated revenue of US$145,701,000 at 2001 current prices for the tourism trade, restaurants and hotels versus US$ 114,193,000 for the primary activities of agriculture, forestry, fishing and mining combined (CSO, 2001). The majority of visitors considered marine life and activities the primary motivating factors for their visit to Belize: of the 186,719 tourists recorded entering Belize in 2000, over 60% visited the cayes and 44% visited the barrier reef (BTB, 2001). Much of the marine tourism is oriented towards the country's network of 12 marine protected areas (MPAs) located along the barrier reef and atolls. Support for MPAs is as key as these have been proven to protect habitat, and increase fish diversity, abundance and biomass (Roberts & Polunin, 1994; Roberts, 1995; Nowlis & Roberts, 1999; McClanahan & Mangi, 2000; Roberts *et al.*, 2001; Rudd & Tupper, 2002). Diversity and abundance of fish, and the presence of large fish are cited as important selling points to marine reserve visitors (Rudd & Tupper, 2002). MPAs and associated tourism also provide important economic benefits to local communities through employment opportunities, direct and indirect revenue (Dixon & Sherman, 1990; Dixon *et al.*, 1993; Vogt, 1996). However, tourism in marine reserves needs to be managed and regulated to avoid destruction of the resources on which it's based (Dixon & Hof, 1997).

In this context, whale shark tours represent a rapidly growing component of snorkel and dive tourism for Placencia and Gladden Spit's other four surrounding stakeholder communities. Gladden Spit, a promontory located in the southern half of the barrier reef was recognized on 18 May 2000 by the Government as a critical site hosting a dense seasonal aggregation of whale sharks and spawning aggregations of at least 25 species of reef fish and consequently declared a marine protected area. In seeking to manage the growing whale shark tourism, Friends of Nature (FON), a local non-governmental conservation group formerly known as Friends of Laughing Bird Caye, was chosen by Government to co-manage the Gladden Spit and the Silk Cayes Marine Reserve (GSSCMR, also referred to as the marine reserve) with the Department of Fisheries on 29 April 2002. FON developed a set of regulations for whale shark tourism (Appendix 7.A) and trained local fishermen and guides in whale shark and fish spawning aggregation biology and tourism. FON is also seeking to offset the costs of managing the reserve by levying a daily visitation fee, a strategy adopted by at least 24 other MPAs in the Caribbean (Green & Donnelly, 2003).

Information on the rapidly growing whale shark tourism and visitor's willingness to pay to visit Gladden Spit and contribute to the management of the site and its fauna will help the Belize Government, FON and local stakeholders to better manage and sustain this tourism and respond to the safety needs of both the fauna and tourists. To better understand the nature and plan for possible expansion of whale shark tourism, this study assessed 1) tourist visitation rates of the Gladden Spit and Silk Cayes Marine Reserve, 2) tourist demographics, perceptions, attitudes and management preferences of the reserve and its whale sharks, and 3) visitor willingness to pay for whale shark tours and protection of the reserve and its fauna and how this might offset marine reserve management costs. The management implications of these three aspects are discussed.

7.2 Methods

7.2.1 Study Site

A full description of the site is given in Chapter 1. This study focused primarily on the Gladden Spit promontory and the Gladden Spit and Silk Cayes Marine Reserve, Belize, as this is the most predictable whale shark aggregation site on the Belize Barrier Reef (Figures 1.4 and 7.1) (see Chapter 4 on movements). The peak whale shark season is defined as 12 days each month usually starting on the full moon, between March and June. Before March there are rarely any whale sharks sighted and after June whale shark sightings decrease and the weather is often too rough to take visitors out beyond the barrier reef.

7.2.2 Tour-operator survey

Tour operators offering whale shark tours were questioned in 2002 about their snorkel and dive charges for taking visitors to see whale sharks. Those tour-operators who only provided package rates were excluded. Rates for snorkelling included equipment and lunch, and dives included lunch. No marine reserve fee was levied from 2000 to 2002 but the rates included the country's obligatory 8% tourist tax.

7.2.3 Tourist boat visitation of the marine reserve

Data on tourist visitation and the number of tour boats engaging in whale shark tours from 1997 until 2002 were collected by questioning tour operators and noting who visited the

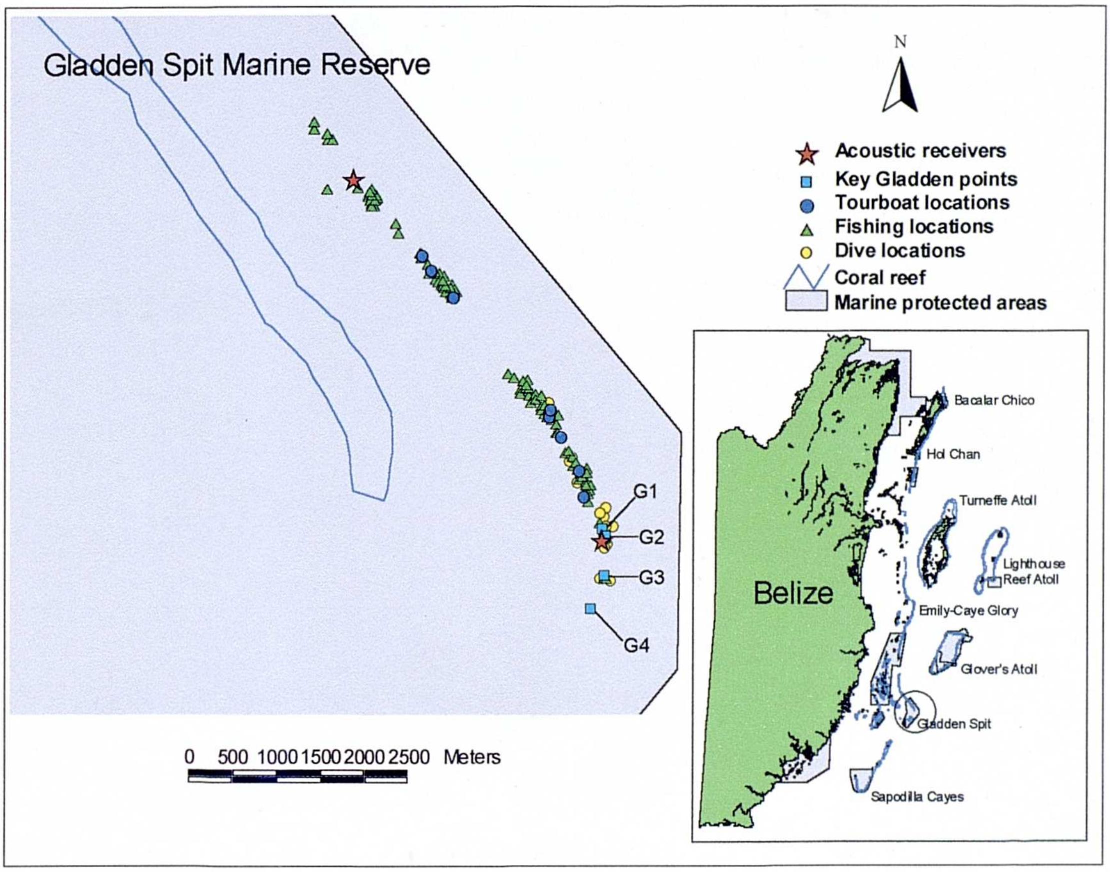


Figure 7.1: Location of tour-boats and fishing boats in the Gladden Spit and Silk Cayes Marine reserve in relation to the main whale shark and spawning aggregation site (G1-G3).

Gladden Spit and Silk Cayes Marine Reserve. Numbers of tourist boats and visitors using the Gladden Spit Marine Reserve were collected from 2000-2002. Information was recorded on log sheets and visitors and guides were counted for each boat. When a visitor count was not possible due to visitors diving or snorkelling or located far from the research boat, we identified the boat and estimated the minimum and maximum number of people. This minimum estimate was based either on the known minimum number of visitors the tour-operator would need to undertake a trip to Gladden Spit and the Silk Cayes and the maximum based on what the boat had either been seen to carry or could safely carry for its size. These figures were obtained during informal interviews with the tour-operators running trips to the site.

7.2.4 Visitor surveys

A pilot and a full-scale survey were administered to visitors to the reserve in 2001 and 2002 respectively to collect demographic, economic and experiential data on visitors who undertook trips to the marine reserve to see whale sharks during the peak aggregation season. Both questionnaires incorporated willingness to pay (WTP) questions within a contingent valuation survey to determine hypothetical increases in marine reserve fees, whale shark tour fees, and reduction in whale shark group size.

In 2001, the pilot survey used an open-ended question for the willingness to pay a daily fee to visit the reserve and its whale sharks. Based on the results of the first year, four bid amounts were set for the full survey in 2002, which used a closed ended response for its WTP question. Those questions that were identical in each survey were analysed together. Where response rates were perceived to be different between the two years, results were separated and compared. Copies of both surveys are presented in Appendix 7.B and 7.C.

Pilot visitor survey

A pilot survey was conducted from March through June 2001 (Appendix 7.B) and was comprised of 39 questions, including the three willingness-to-pay (WTP) questions noted below:

WTP Q1. Aimed at visitors who had encountered whale sharks preceded by four questions rating the encounter and questions on the group size:

Would you be willing to pay more to dive in a smaller group, making the experience more exclusive?

Yes		No

If yes, the visitor was asked how much more they would be willing to pay in increments of US$10 from $10-$50.

WTP Q2. An open-ended question aimed at visitors who were on a whale shark tour:

What is the most you would be prepared to pay for your daily Belize whale shark trip before you would decide not to go on the trip?

WTP Q3. An open-ended question aimed at visitors visiting the Gladden Spit and Silk Cayes Marine Reserve. The WTP question was preceded by three questions on marine reserves.

What daily entrance fee to Gladden Spit Marine Reserve would you be willing to pay in US$ to protect Gladden Spit, the Silk Cayes and its fauna including the large schools of fish and whale sharks?

$0		$1-5		$6-10		$11-15		$16+

A total of 92 dive and snorkel tourists were surveyed and completed the pilot survey, 69 on the Middle Silk Caye and 23 in Placencia, Punta Gorda and San Pedro. This represented approximately 13% of the observed number of visitors to the reserve during the peak snapper spawning aggregation period in 2001. Questionnaires were administered personally to each visitor. Tourist selection was not random: visitors who were visiting the reserve and who had already made at least one dive or snorkel looking for whale sharks on the reef were selected. Survey participants were further chosen based on their willingness to participate in the 20-minute survey.

Surveys administered on Middle Silk Caye took place usually during the middle of the day when tourists were lunching. Permission was sought from the tour-guide prior to asking tourists if they were willing to participate in the survey. Most often we would give a talk on whale sharks and the research conducted at Gladden Spit, and answer related questions from the tourists, which proved popular with visitors and tour-guides alike. Running surveys in Placencia proved very difficult, as there was little time before a tour during which to approach a participant. In addition, it was highly probable that the person had not taken the tour if approached in the morning. If approached in the evening, tourists showed low motivation to complete the survey, wishing instead to return to their hotels.

Full-scale visitor survey

The personal interview method was thorough but unfortunately missed many potential respondents. Several tour-guides did not stop at the Silk Cayes for lunch, opting to anchor inside the reef instead to minimize travel time and gasoline expenditures to the whale shark and fish aggregation site. It was not possible to administer surveys on the boats due to the length of the survey, lack of shelter and possible influence in answers by other visitors in close proximity. The full survey was expanded to encompass 75 questions regarding demographic information and visitor perceptions (Appendix 7.C). The full survey also assessed visitor willingness-to-pay (WTP) using a closed-ended question structured in the following way:

WTP Q3. Some divers and snorkelers feel that Gladden Spit and the Silk Cayes and its whale sharks and fish require additional management and protection by national and local organisations. These efforts will cost money and must be financed in some way (e.g., licence fees, higher diving-related expenses, taxes, etc.).

If additional management and protection meant that each visitor to the marine reserve would pay <bid amount> more per day, would you dive or snorkel with whale sharks and fish aggregations at Gladden Spit?

Yes No

The bid amounts of US$ 8, US$ 14, US$ 20 and US$ 30 per day based on responses from the pilot survey that indicated a strong willingness to pay at over US$ 6-10 per day to visit the marine reserve and help protect its fauna.

To increase the number of visitors sampled, an Internet-based survey was developed using a Web based company that provides the mechanisms to create and administer online surveys (www.surveymonkey.com). Visitors could answer the 75-question survey online and at their leisure once they had completed their trip. This approach proved rapid, as it only required gathering first and last names and email addresses from visitors at the site.

Once back on the mainland, all visitor information was typed into a spreadsheet and uploaded to the survey site and into the four surveys that represented the four WTP bid amounts. To randomise the selection of visitors into each survey, visitor names were randomly assigned a number from 1-4. All like numbers were grouped and entered into the lists for each respective survey/WTP bid amount. A request to fill out the questionnaire and link to the online survey was sent out in a standardized email using the researcher's email as a return address and contact point. Emails that no longer worked based on the receipt of non-deliverable message emails were crossed off the list after repeatedly trying to contact the visitor. Responses to the emails were monitored weekly through the online survey site. Visitors who did not fill out the questionnaire within a month of receiving the email were sent a second email asking for their collaboration in completing the survey. All visitors who completed the survey were sent thank you emails and an assurance that they would receive the results when these were ready if they had requested it while filling out the survey.

To speed up survey-response and spare visitors from having to answer sections that did not apply to them, the survey–site's option of editing logic for key questions was used. This allowed tourists who only dive to bypass all snorkelling questions or for those who did not encounter a whale shark to bypass the entire "whale shark encounter section".

Of the 415 visitors who agreed to participate in the full survey in 2002, 239 visitors filled out the survey, representing a response rate of 57.6% and approximately 21% of the observed number of visitors to the reserve in 2002.

7.2.5 Whale shark sightings

The maximum number of whale sharks sighted was tallied for each day during the peak whale shark season (period of 12 days after the full moon for three months from March through June). It was possible to differentiate between individual sharks based on spot patterns, scars and tags. An average number of sightings were generated per day and per year. Search effort was standardized throughout the days at Gladden Spit and the years with two trips and often two dives made per day to the Gladden Spit spawning aggregation area.

7.2.6 Analysis

Data from the pilot and full-scale surveys were analysed separately using descriptive statistics. Responses to questions common to both surveys were then pooled and analysed in the same manner. All data were tested for normality using the Kolmogorov-Smirnov tests and subsequently analysed using parametric techniques if normal and non-parametric techniques if non-normally distributed.

Four logistic regressions were run to determine which of ten variables influenced willingness to pay a daily fee to visit the reserve (see Table 7.7). Due to the small sample sizes obtained, categorical values were recoded with medians expressed for each category. Variables based on the degree of response, e.g., satisfaction with trip to Gladden or Belize, were recoded binomially (see coding on Table 7.7). Additionally, trip satisfaction to the marine reserve encompassed perception of service, levels of enjoyment, food quality, weather, sightings of whale sharks, group camaraderie, safety, diving or snorkelling comfort, tour operator professionalism and guide behaviour.

7.3 Results

7.3.1 Tour-operator survey

The number and geographic provenance of tour operators conducting whale sharks tours at Gladden Spit increased dramatically between 1997 and 2002 from 2 to 18 operators (Figure 7.2) with a doubling in the number of tour operators starting up whale shark tours in 2000. From 1997 to 2000, operators offering whale shark tours at Gladden Spit came from the marine reserve's five stakeholder communities (Placencia, Hopkins, Independence, Seine Bight and Monkey River) but by 2002, tour operators were also arriving at Gladden from Ambergris Caye, Southwater Caye and Tobacco Caye (north Belize) and Guatemala.
The mean cost of a snorkel trip with whale sharks in 2002 was US$57.00 (range: US$ 48.6-75.6, n = 9 tour operators) and US$ 127.55 for a two-tank whale shark dive trip (range: US$ 108-150, n = 8). All tour operators have a physical base and the majority of tour operators (n = 15) have a web page to advertise their activities.

Tour operator boat sizes and capacities ranged from 23 ft (7.0 m), with a safe capacity of six snorkelers or boat-based watchers and the captain, to 42 ft (12.7 m) with a maximum capacity of 24 visitors, 2-3 divemasters and the captain. The mean boat size for dive operators was 29 ft (8.8 m) with a maximum safe capacity of about 18 divers. With calm conditions, smaller boats take about 1.5 to 2 hours to reach the reef whereas the larger boats take 1 to 1.5 hours.

Estimating a mean cost of operating a tour boat to the reef was not meaningful in this study as costs varied greatly amongst tour operators. Factors that shape running costs

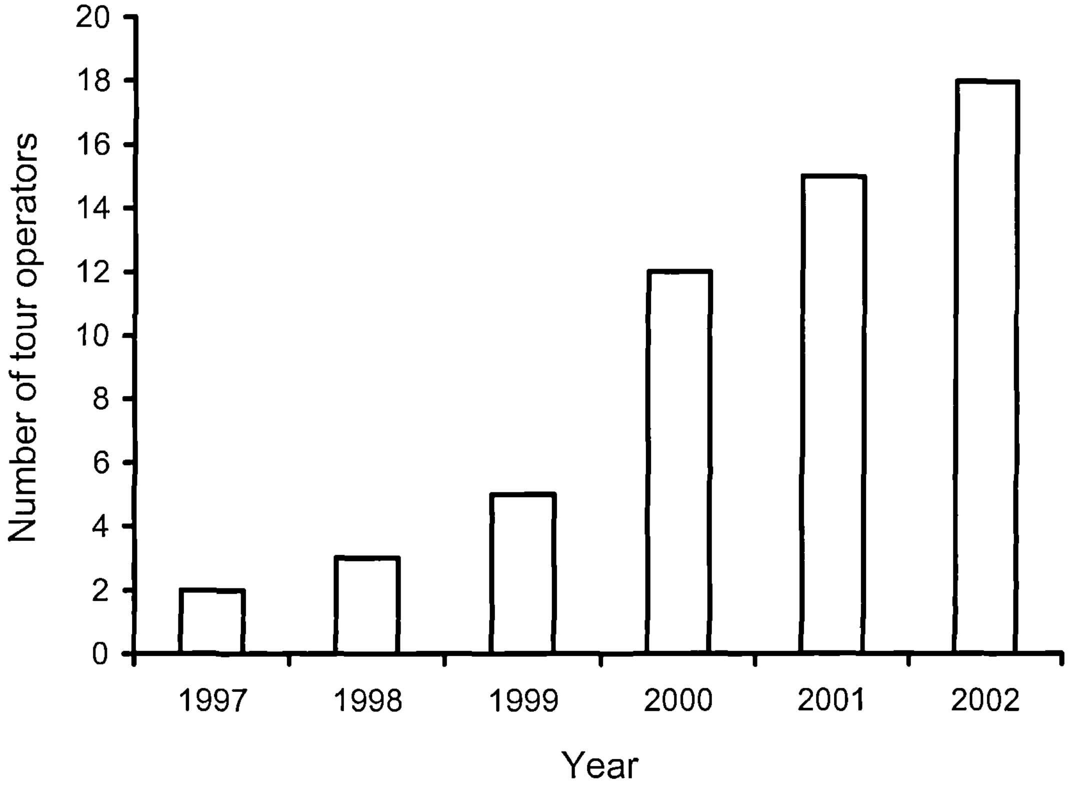


Figure 7.2: Number of tour operators in Belize offering whale shark tours at Gladden Spit from 1997 to 2002.

depend primarily on boat size, engine size and number, number of staff employed, and whether the tour focuses on snorkelling or diving.

7.3.2 Tourist boat and visitor numbers

There were 71 tour boat visits recorded in the Gladden Spit and Silk Cayes Marine Reserve in 2000 during the peak whale shark season. This figure rose to 93 in 2001 and 206 in 2002. The mean number of tourist boats per day recorded in the marine reserve differed significantly between 2000 and 2002 with an increase noted from 3 to 6 boats (Kruskal-Wallis test: df = 2; $\chi^2 = 11.48$; $p < 0.05$) (Figure 7.3). However, the number of visitors per boat differed significantly between 2000 and 2002 with a decrease noted from 11.1 to 8.1 visitors per boat (Kruskal-Wallis test: df = 2; $\chi^2 = 7.42$; $p < 0.05$) (Figure 7.3). The number of tourists also increased significantly during the same period in both observed and estimated numbers (Table 7.1).

Table 7.1: Number of visitors to the Gladden Spit and Silk Cayes Marine Reserve from 2000-2002.

Year	No. of tourists observed	No. of tourists estimated
2000	661	795
2001	709	1059
2002	1139	1668

7.3.3 Tourist surveys

Combined, both surveys generated 331 responses out of a total of 507 visitors who indicated their willingness to participate in the surveys. This represented a response rate of 65.3% and combined surveys captured 17.9% of tourists observed in the reserve in 2001 and 2002. Failure to respond in 2002 was due to a combination of non-working emails and lack of interest in completing the survey despite two email reminders. Also, several visitors (n = 21) refused to give out their emails citing privacy issues. Six of the respondents (2.5%) had snorkelled or dived with the whale sharks in 2001. Please refer to Appendix 7.B and 7.C (2001 and 2002 survey instruments) for details pertaining to variables in the results tables or specific questions in the survey questionnaires.

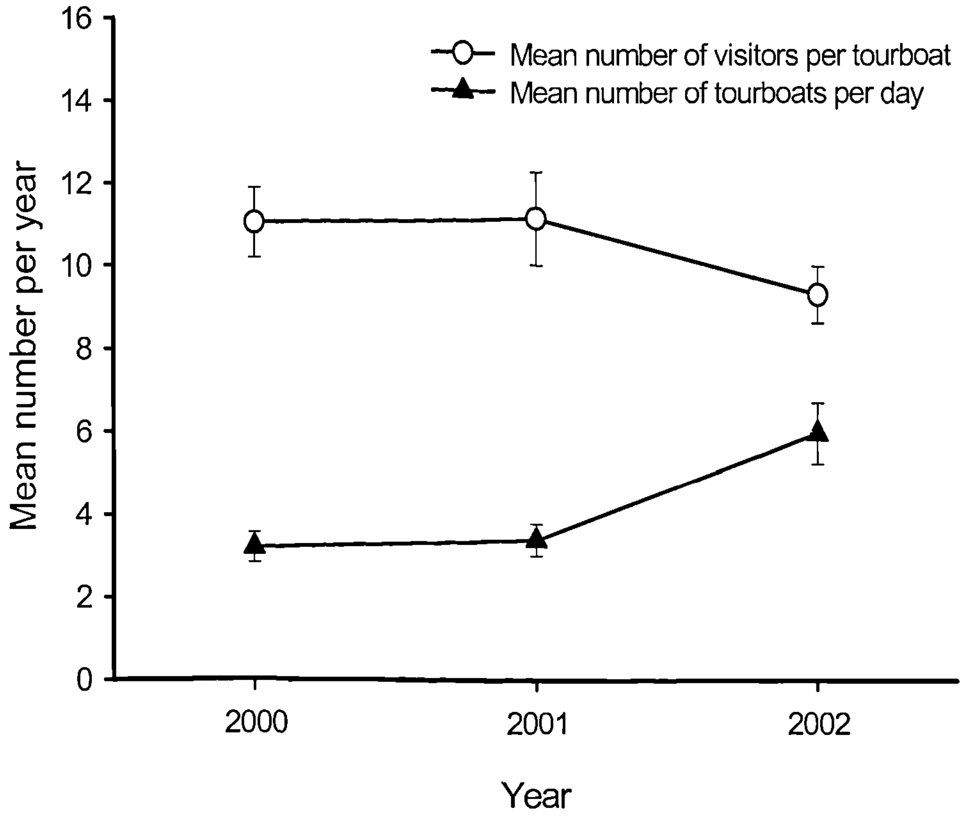


Figure 7.3: The mean number of visitors per tour boat per day and mean number of tour-boats per day observed per year (± SE) in the in the Gladden Spit Marine Reserve during the peak snapper and whale shark periods in 2000 to 2002.

Socio-economic data

Women accounted for 46.0% (n = 133) of the survey responses and men 54.0% (n = 156). The majority of respondents were in the age bracket 30-39 years old (36.0%) followed by people aged 20-29 years (23.5%) and 40-49 years (22.5%). Of 289 respondents who stated their residence, visitors from the USA made up 70.0% followed by the UK and Ireland (10%), Canada (6.2%), with the remaining visitor provenance including Europe, Mexico, Caribbean, Asia-Pacific. Belize-based visitors accounted for only 4.5% of visitors surveyed. Most visitors were highly educated with over half of the respondents (total n = 197) obtaining an undergraduate or an undergraduate and master's degree. Income was spread throughout all brackets with over half (58.5%) making above US$ 60,000 per year (Table 7.2).

Table 7.2: Income of visitors to Gladden Spit and Silk Cayes Marine Reserve (n = 176).

Yearly income (US$)	%	n
<20,000	11.4	20
20,000-40,000	11.9	221
40,001-60,000	18.2	32
60,001-80,000	17.6	31
80,001-100,000	11.9	21
100,001-140,000	14.2	25
140,001-180,000	7.4	13
<180,001	7.4	13

Travel data and trip expenditures

The majority of 288 respondents answering the question (64.2%) indicated that this was their first trip to Belize and the most (57.6%) travelled alone or with one other person. At least 18 respondents lived in Belize and 26 were staying in Belize from 30 days to 5 months. Among the short-term visitors (stays under 30 days), the mean stay in Belize was 8.9 nights ± 4.7 SD. In Placencia and the GSSCMR stakeholder communities, short-term visitors stayed a mean of 4.9 nights ± 3.0 SD (n = 276). Tourists stayed for a range of durations in Belize with a mean stay of 18 days (median 8 days), and a mean of 6 days (median 5 days) spent in Placencia (n = 278). The long period of visitation in Belize is primarily due to the number of respondents who had been in country for up to 210 days and worked with organizations such as Raleigh International or Trekforce. Over 55% of visitors (n = 255) stayed in hotels and 31.1% in resorts. Only 14.0% of visitors were booked on a package tour (n = 193).

Based on questionnaire responses, estimated total trip expenditures for visitors who went to Gladden Spit in 2001 reached US$ 147,500 with a mean of US$ 1,777 ± 707 SD. In 2002, total expenditures reached US$ 374,770 for 169 respondents, with a mean trip cost of US$ 2,218 ± 1,804 SD. Total trip expenditures included airfare, in-country transportation, lodging and meals, tips, purchases and recreational activities including whale shark tours and visiting the Silk Cayes. Disaggregated expenditures made in Placencia or one of the marine reserve stakeholder communities in 2002 accounted for about 37% of total trip costs or US$ 98,234 with mean local expenditures of US$ 812 ± 999 SD or US$ 135 ± 167 SD per day. Pooled trip expenditures for whale shark and Gladden Spit visitors for both 2001 and 2002 reach US$522,270 with a mean of US$ 2,073 ± 1,544 SD.

To estimate total revenue from visitors to the reserve, mean total trip costs for 2001 were multiplied by the observed number of visitors to Gladden Spit (n = 709) to yield a total of US$ 1,259,893. In 2002, total trip expenditures for observed visitors (n = 1059) reached US$ 2,526,302, of which the Gladden Spit stakeholder communities captured US$ 924,868 over a period of 6 weeks during the peak whale shark season of March to June.

If the estimated number of visitors to the marine reserve is used (n = 1059 in 2001 and n = 1668 in 2002) total trip expenditures increase to US$ 1,881,843 and US$ 3,699,624 respectively, with US$ 1,354,416 captured locally in 2002.

Encounters with whale sharks

Out of 322 responding visitors, 41.0% snorkelled while at Gladden Spit and 56.5% were SCUBA diving. Only 2.5% visitors surveyed were either on a boat or recreational fishing tour. At least 206 of 324 respondents (63.6%) encountered whale sharks during their trip to Gladden Spit and the Silk Cayes. Of these, 77% were booked on a whale shark tour at the time. 75.2% of respondents (n = 153) deemed the encounter "Excellent" and another 11.1% considered it "Good". Only 23 of 185 respondents (12.4%) had seen a whale shark before, primarily on previous visits to Gladden Spit.

Whale shark size, closeness, beauty and number were key elements to visitors' experiences with whale sharks. Statements included: "they're so big", "it was so close", "so close to a large and gentle creature", "beautiful creature", "an amazing experience", "gentle, calm, graceful, beautiful", "the number of whale sharks". Many tourists also mentioned how impressed they were with the large aggregations of reef fish and the spawning phenomenon (Appendix 7.E for detailed visitor statements about encounters).

To ascertain if the presence of tags deployed on whale sharks detracted from visitors' experiences of the encounter, respondents were asked if they had seen a tag and whether they minded seeing the tag a little, a lot, or not at all. At least 62 respondents saw a whale shark with a tag and 84.8% did not mind the presence of tags. Even those visitors who did mind the tags "a little" noted that they understood that tags were part of a research project and the results were important to managing and protecting whale sharks. No respondent mentioned that they minded "a lot" seeing a tag on a whale shark.

Most guides briefed their guests on how to behave with whale sharks. Yet, 22.6% of respondents did not receive a whale shark briefing from their tour-guide or divemaster (n = 266). The number of visitors briefed increased slightly from 2001 (74%, n = 81) to 2002 (79%, n = 185). For those who were briefed, 93% of visitors rated the briefing as "OK" to "Excellent" for 2001 and 2002 combined. However, 17 out of 157 respondents (10.8%) touched a whale shark during their encounter, behaviour that is not allowed according to the provisional whale shark tour regulations, and strictly enforced by several tour guides. Disaggregated data shows that in 2001 8% touched a whale shark whereas only 4% touched one in 2002.

Tour experience

Over 70% of tourists (n = 305) indicated that they had not come to Belize exclusively to encounter whale sharks. However, at least 84.7% of visitors booked their tour once in Belize (total n = 169) after finding out about whale shark tours through friends (32.8%), dive shops (20.3%) and the Internet (15.9%).

Most visitors who had encountered whale sharks considered their group to be the "right size" where group size primarily consisted of less than 10 people (Table 7.3). Visitors felt that the perfect whale shark group size should fall between 6 and 8 people ± 2.7 SD. Of 238 respondents, 72.7% were willing to pay more to be in a smaller group. Specifically, 82.6% were willing to pay at least US$ 20.00 more per day. On average, visitors (n = 230) paid US$ 104.20 ± 66.60 SD for their daily whale shark trip. However, they were willing to pay a maximum of US$ 143.00 ± 107.30 SD for their whale shark tour, an increase of US$ 38.77 over the mean amount.

Table 7.3: Size of whale shark tour groups and visitor perception of size at Gladden Spit and Silk Cayes Marine Reserve.

Group		%	n
Group size (n = 264)	1-5 people	35.6	94
	6-10 people	36.0	95
	11-15 people	19.3	51
	16-20 people	4.9	13
	20+ people	4.2	11
Perception of group size (n = 261)	Too many people	23.4	61
	Too few people	1.1	3
	Just the right number	75.5	197

Diver experience and characteristics

Diving with whale sharks at Gladden Spit often entails dives in open water over deep depths and occasionally in rough seas with waves of 1-2 m. These conditions are considered as advanced diving by divemasters and tour operators, so novice divers are encouraged to gain more experience before undertaking whale shark dives. To determine the level of diving experience of visitors at Gladden Spit, divers were asked how long they had been diving, the level of certification and number of dives taken per year. Of the 197 diving respondents, 56% had been diving for over 6 years. However, 64% of respondents (n = 205) log less than 20 dives per year. Most tourists were certified with the Professional Association of Diving Instructors (PADI), with 81% holding Open-Water or Advanced certifications and the remainder having reached Rescue to Instructor levels.

About half of the snorkelers (n = 107) own their gear whereas 89% of divers (n = 138) own their snorkelling gear, and 55% own a Buoyancy Control Device (BCD) and regulator. A greater percentage of snorkelers own underwater camera gear (83%) compared to divers (60%).

Gladden Spit and the Silk Cayes Marine Reserve

Only 44.7% of the 295 respondents knew that Gladden Spit and the Silk Cayes formed part of a marine protected area (MPA), despite the inclusion of this information in many guide briefings. Visitors surveyed were well travelled as 67.7% had previously visited an MPA in states or countries such as Bonaire, California, Hawaii, Mexico, Galapagos, Egypt, Pacific, Australia, etc., and the majority had previously paid to enter an MPA (Table 7.4). Several mentioned having visited Hol Chan and Shark Ray Alley and the Blue Hole or Glovers Reef, indicating knowledge of the Belize network of marine reserves.

Table 7.4: Most paid in the past by visitors to a marine protected area (n = 229).

Amount (US$)	%	n
0	21.8	50
1-5	27.9	64
6-10	26.2	60
11-15	7.9	18
16+	16.2	37

Of the 92 visitors surveyed in 2001, 91 (97.8%) were willing to pay a daily fee for the management of the GSSCMR and its whale sharks in addition to tour costs (Table 7.5). The mean fee visitors were willing to pay was US$ 8.70 based on the number of averaged responses for all bid amounts. In 2002 the number of visitors willing to pay a daily fee dropped to 55% (n = 85 respondents) primarily due to the higher bid amounts and closed-ended nature of the survey. No dramatic decrease in WTP occurred at the higher bid amounts of US$ 20 and US$ 30 as would be expected. For those who refused to pay a fee, at least 61% felt that the fee was too expensive and 6% did not believe in paying to visit a protected area. However, the mean daily fee visitors were willing to pay in 2001 increased by US$ 0.92 in 2002 to US$ 9.62. Overall, the presence of whale sharks at Gladden Spit in 2002 was considered "Important" (30.7%) to "Very important" (47.8%) in determining the daily entrance fee to the reserve that visitors were willing to pay.

Table 7.5: Visitor willingness to pay (WTP) to visit the Gladden Spit and Silk Cayes Marine Reserve in 2001 (n = 91) and 2002 (n = 85). NA = not applicable.

Year	Survey number	Amount (US$)	No. of respondents	No. willing to pay	Amount generated per WTP and mean WTP fee (US$) for all respondents willing to pay
2001	NA	0	1	1	0
	NA	1-5	25	25	75
	NA	6-10	37	37	296
	NA	11-15	9	9	117
	NA	16+	19	19	304
			Total: 91	Total: 91	Total: US$ 792 Mean: US$ 8.70
2002	1	8	18	11	88
	2	14	27	15	210
	3	20	20	11	220
	4	30	20	10	300
			Total: 85	Total: 47	Total: US$ 818 Mean: US$ 9.62

Regarding the payment of marine reserve management fees, visitors indicated that they were more inclined to pay only for marine reserves visited yet they were mostly interested in having that fee collected upon entry to Belize (Table 7.6).

Table 7.6: Visitor perceptions regarding the payment of a management fee to visit marine reserves in Belize. 1 = Strongly disagree, 5 = Strongly agree.

Statement	n	1(%)	2 (%)	3 (%)	4 (%)	5 (%)	Mean score (out of 5)
Pay fee only for marine reserves visited	193	5.2	7.8	23.8	36.8	26.4	3.72
Fee collected locally	190	16.8	29.5	29.5	18.9	5.3	2.66
Regional fee charged	194	16.0	29.4	28.4	16.5	9.8	2.70

Statement	n	1(%)	2 (%)	3 (%)	4 (%)	5 (%)	Mean score (out of 5)
Fee collected upon entry into Belize	196	6.1	9.7	17.9	44.9	21.4	3.55
Pay fee at the start of the Belize trip	195	23.1	39.5	19.5	10.8	7.2	2.35

Four logistic regressions were run to determine which variables (Table 7.7) were significant in a visitor's willingness to pay a daily fee to visit the marine reserve. Only 74 respondents included all ten regression variables in model 1, and 85 respondents included regression variables in models 2-4. The regressions revealed two influencing variables significant at the $p < 0.15$ levels with all other variables remaining unresponsive to a visitor's willingness to pay. Significant variable were: 1) the presence of whale sharks at Gladden Spit (models 2 and 4), and 2) Visitor satisfaction with the trip to the Gladden Spit and Silk Cayes Marine Reserve (model 3).

Management of the GSSCMR and whale shark tourism

In 2001, visitors provided many recommendations for better management of Gladden Spit whale shark tours and of the Silk Cayes (see Appendix 7.D for detailed recommendations). Recommendations that appeared repeatedly included limiting the number of boats and visitors and protecting the whale sharks from too many people. Visitors also felt that patrols and enforcement of regulations were needed at Gladden Spit. Many tourists requested more education on whale sharks and Gladden Spit from their guides, particularly on the boat ride from Placencia. Several visitors were unhappy with the level of litter on the Cayes. They further noted that Gladden Spit should not be used as a check-out dive site for novice divers and that dive shops should work together more instead of competing for access to whale sharks.

In 2002 visitors were asked to rate several statements based on reserve and whale shark tourism management issues in the GSSCMR (Table 7.8), many of which were raised by visitors in 2001 (Appendix 7.D). Their feedback was tabled at two meetings with local tour-guides during the formulation of final whale shark tourism guidelines. Visitors agreed or strongly agreed with all statements indicating the perceived need in 2001 for greater management and enforcement at Gladden Spit.

Table 7.7: Results from four *logistic* regressions of *influences* on the *probability* that *a* visitor to the Gladden Spit and Silk Cayes Marine Reserve (GSSCMR) would be willing to pay a daily fee to visit the marine protected area.

	Model 1	Model 2	Model 3	Model 4
	(n = 74)	(n = 85)	(n = 85)	(n = 85)
Variable (coding)	B (*p*)	B (*p*)	B (*p*)	B (*p*)
Encountered a whale shark	-0.425			
(1 = yes, 0 = no)	(0.412)			
Group number	0.009			
(median of categories)	(0.384)			
Satisfied with trip to the GSSCMR	-0.004		-0.001	0
(1 = very satisfied and satisfied; 0 = average satisfaction to very disappointed)	(0.582)		(0.102)*	(0.711)
Satisfied with trip to Belize	0			
(1 = very satisfied and satisfied; 0 = average satisfaction to very disappointed)	(0.871)			
Age	0.009			
(median of categories)	(0.688)			
Income	0			
(median of categories)	(0.543)			
WTP bid amount	-0.012	-0.14		
(recorded bid amounts: US$ 8, 14, 20, 30)	(0.705)	(0.624)		
Importance of whale sharks in paying a daily fee	-0.009	-0.002		-0.002
(1 = very important & important; 0 = average to not important at all)	(0.887)	(0.036)**		(0.120)*

	Model 1	Model 2	Model 3	Model 4
	(n = 74)	(n = 85)	(n = 85)	(n = 85)
Variable (coding)	B (*p*)	B (*p*)	B (*p*)	B (*p*)
Male	0.543			
(1 = male, 0 = female)	(0.330)			
Diver	-0.734			
(1 = diver, 0 = snorkeler)	(0.396)			
Constant	-0.395	0.257	0.057	0.014

Overall model 1 classification accuracy, 55.4%, -2 *Log likelihood* = 92.173, *Chi-square* = 10.197, df = 10, $p < 0.15$.

* *p* significant to the 0.15 level; ** *p* significant to the 0.05 level

Table 7.8: Visitor perceptions regarding management of whale shark tours at the GSSCMR in terms of percentage of responses to each statement. 1 = Strongly agree, 5 = Strongly disagree. (n = 207).

Statement	1	2	3	4	5	Mean score (out of 5)
Implement a daily fee to manage the GSSCMR	32.4	34.3	25.1	6.8	1.4	2.09
Limit the number of boats allowed in the GSSCMR	50.7	34.8	9.7	4.3	0.5	1.69
Set a maximum number of divers and snorkelers per boat	44.4	40.6	12.6	1.9	0.5	1.73
Require guides to brief visitors on whale sharks and the GSSCMR	63.3	30.0	5.8	0.5	0.5	1.45
Set a daily limit on number of people allowed to visit the Silk Cayes	40.1	35.3	18.4	4.8	1.4	1.92
Enforce a no-touch policy with whale sharks	63.3	22.7	12.1	2.4	0.5	1.57

Visitor perceptions and trip satisfaction

Most respondents were well travelled and had snorkelled or dived in other sites and countries (n = 94 snorkelling; n = 156 diving) including many with a global reputation for excellent snorkelling and diving such as the Red Sea, Palau, Tahiti, Galapagos, etc. Snorkelers considered Gladden Spit an “Average” to “Above average” destination and divers rated Gladden Spit as “Average” compared to other sites visited worldwide (Table 7.9).

Table 7.9: Visitor rating of Gladden Spit compared to other snorkelling or diving sites. 1 = Superior to other sites, 3 = Average, 5 = Very inferior to other sites.

	n	1(%)	2 (%)	3 (%)	4 (%)	5 (%)	Mean score (out of 5)
Snorkelers	100	15.0	51.0	26.0	7.0	1.0	2.29
Divers	126	11.9	46.8	26.2	12.7	2.4	2.47

Visitors rated the degree of importance marine fauna and environmental factors had for them during their visit to the marine reserve. The presence of whale sharks was more important to divers than snorkelers, as were large schools of fish (e.g., snappers and jacks). Dolphins proved more important to snorkelers than divers, possibly reflecting the accessibility each group had to the different fauna due to the stratification of these fauna in the water column. Turtles, also considered a charismatic fauna, rated well compared to large individual fish (e.g., groupers, barracuda), and lobster and conch as very important to the quality of their dive or snorkel. Coral cover and good visibility were considered more important than warm water in the environmental factors rated (Table 7.10).

Table 7.10: Snorkeler and diver rating of importance of fauna and physical characteristics at Gladden Spit. 1 = Very important, 3 = Average, 5 = Not important at all, 6 = NA.

Fauna	n	1(%)	2 (%)	3 (%)	4 (%)	5 (%)	6 (%)	Mean score (out of 5)
Snorkelers								
Whale sharks	125	46	40	16	5	9	9	2.06
Other sharks and rays	125	30	51	23	13	2	5	2.23
Dolphins	125	45	42	21	6	3	8	1.97
Large schools of reef fish (>300 fish)	126	47	46	22	5	1	5	1.90
Large individual fish	125	36	59	22	3	2	3	1.98
Other reef fish	126	44	53	22	4	1	2	1.91
Lobster, conch, octopus	125	27	44	29	15	7	3	2.43
Turtles	99	33	39	18	0	3	6	1.94
Coral cover	129	66	49	12	1	1	0	1.62
Warm water	128	49	45	27	5	2	0	1.95
Visibility (>60ft/20 m)	125	71	44	7	1	1	1	1.52
Divers								
Whale sharks	199	155	20	12	2	4	6	1.34
Other sharks and rays	194	60	28	39	3	6	8	2.02
Dolphins	194	71	59	40	9	4	11	1.99

Fauna	n	1(%)	2 (%)	3 (%)	4 (%)	5 (%)	6 (%)	Mean score (out of 5)
Large schools of reef fish (>300 fish)	196	80	68	34	7	2	5	1.86
Large individual fish	193	52	64	46	17	5	9	2.23
Other reef fish	193	45	55	54	23	7	9	2.41
Lobster, conch, octopus	194	35	53	54	23	17	12	2.64
Turtles	130	47	38	23	6	3	13	1.97
Coral cover	199	104	55	21	8	8	3	1.78
Warm water	198	54	72	58	9	2	3	2.14
Visibility (>60ft/20 m)	199	107	69	21	1	1	0	1.59
Combined								
Whale sharks	324	201	60	28	7	13	15	1.61
Other sharks and rays	319	90	129	62	16	9	13	2.10
Dolphins	319	116	101	61	15	7	19	1.99
Large schools of reef fish (>300 fish)	322	127	114	56	12	3	10	1.88
Large individual fish	318	88	123	68	20	7	12	2.13
Other reef fish	319	89	108	76	27	8	11	2.21
Lobster, conch, octopus	319	62	97	83	38	24	15	2.56
Turtles	229	80	77	41	6	6	19	1.96
Coral cover	328	170	104	33	9	9	3	1.72
Warm water	326	103	117	85	14	4	3	2.07
Visibility (>60ft/20 m)	324	178	113	28	2	2	1	1.57

NB. NA responses were not included in the analysis of scores and total responses were adjusted to reflect this.

Visitors partaking in whale shark tours were overall "Satisfied" to "Very satisfied" with their trip to Gladden Spit and to Belize (Table 7.11) and stated that they would definitely return to Belize and probably dive or snorkel with whale sharks again and/or recommend the experience to a friend (Table 7.12).

Table 7.11: Visitor satisfaction with trip to Gladden Spit and the Silk Cayes and to Belize in General, in terms of percentage of responses. 1 = Very satisfied, 5 = Very disappointed, 6 = NA. (n = 292).

Statement	1	2	3	4	5	6	Mean score (out of 5)
Trip to Gladden Spit and Silk Cayes	54.1	24.7	9.6	6.2	5.1	0.3	1.67
Trip to Belize	72.2	19.2	4.8	1.7	0	2.1	1.34

Table 7.12: Visitor desire to return to Belize, to swim with whale sharks and to recommend whale shark experience in Belize to a friend, in terms of percentage of responses. 1 = Definitely, 4 = Definitely not, 5 = NA.

Statement	n	1	2	3	4	5	Mean score (out of 4)
Would you return to Belize?	299	62.5	29.4	4.7	1.0	2.3	1.15
Return to dive or snorkel with whale sharks?	296	54.4	34.1	8.1	1.7	1.7	1.56
Recommend the whale shark experience in Belize to friends?	292	57.5	25.0	7.5	4.1	5.8	1.56

7.3.4 Whale shark sightings

Mean whale shark sightings per day remained relatively steady throughout 1998-2001 ranging from 3-5 sightings per day, dropping to 2 sightings in 2002. A Kruskal-Wallis test revealed a significant difference in whale shark sightings within the peak whale shark season between years (df = 4; $X^2 = 14.4$; $p < 0.05$) (Figure 7.4). This result was primarily due to the dramatic drop in mean sightings in 2002 when the whale sharks were not seen predictably at the Gladden Spit spawning aggregation site for a period of 6 days from 24-29 May 2002.

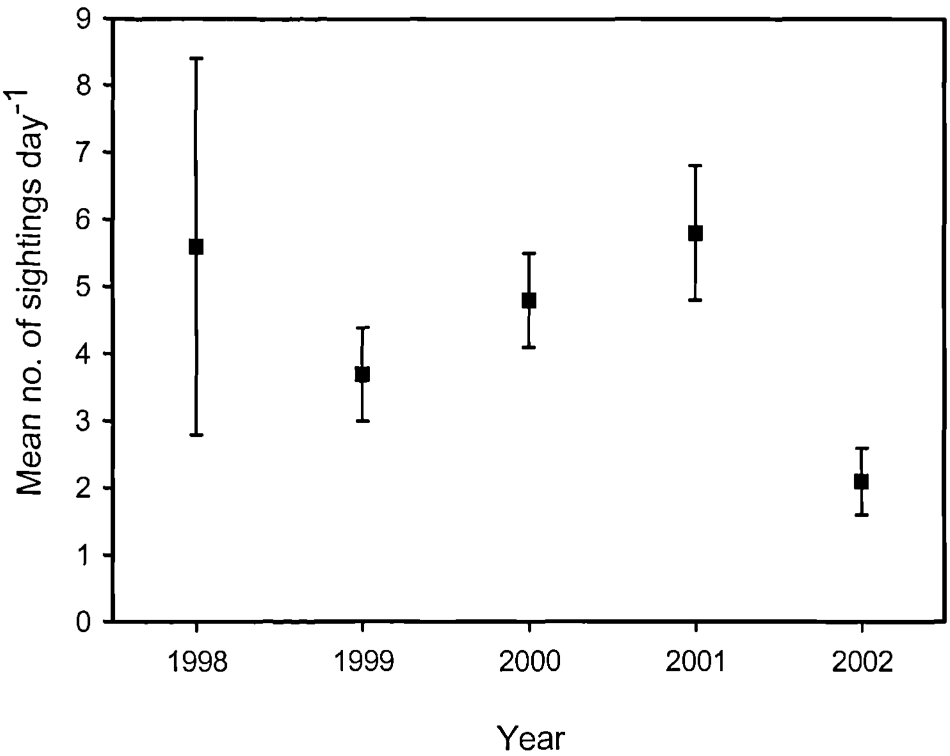


Figure 7.4: The mean number of whale shark sightings per day during the peak whale shark season from March to July between 1998 to 2002 (± SE).

The chance of seeing a whale shark in-season between 1999 and 2001 remained steadily close to 80% (Figure 7.5). Years 1998 and 2002 proved the worst for sightings with only a 67% and 52% chance of seeing a whale shark on a given search day during the peak season. Although sighting days were few in 1998, this was also the year during which the greatest number of sharks (n = 25) were sighted on the surface at one time (Heyman *et al.*, 2001).

7.4 Discussion

7.4.1 Tourism in Belize, Placencia and Gladden Spit

Since its inception, marine tourism in Belize has focused primarily on established coastal and island tourist destinations in the north such as Ambergris Caye and Caye Caulker. However, tourists are increasingly seeking adventure in remote areas, and searching further south for less developed tourist sites.

Placencia has become the recently discovered "unspoiled" tourism site for visitors escaping the north's established tourism infrastructure. This small village located at the end of an ecologically fragile peninsula in Southern Belize was once a fishing village primarily dependent on the lobster fishery. However, Placencia is rapidly becoming popular and developing to provide the infrastructure and resources required to meet the recent influx in visitors. As the local population rises beyond the 501 people recorded in 2000 (CSO, 2000), the tone of the village has shifted from tranquil to bustling.

Once a favoured haunt of backpacking tourists enjoying cheap "no frills" accommodation, the number of hotels with 11 or more rooms has increased in the village by 12.9% between 2000 and 2001 and is set to increase again, as greater number of visitors seek hotels with more amenities or opt to stay in higher-end resorts. From 1991 to 2001, the number of facilities offering accommodation in Placencia rose from 18 to 57 (with 396 rooms) (BTB, 2001). In 2002 the Placencia Tourism Board listed only 36 hotels in Placencia, Seine Bight and Maya Beach as operational following landfall of the Category 4 Hurricane Iris that badly damaged much of Placencia and its infrastructure in October of 2001 (Ellie Dial, Placencia Tourism Association, pers. comm.). These provided a total of 338 rooms, or space for about 676 people at any one time – and was not considered sufficient for demand that year. However, several new resorts and hotels opened in 2003 promising increased visitor capacity. In addition, recent paving of Placencia's main road

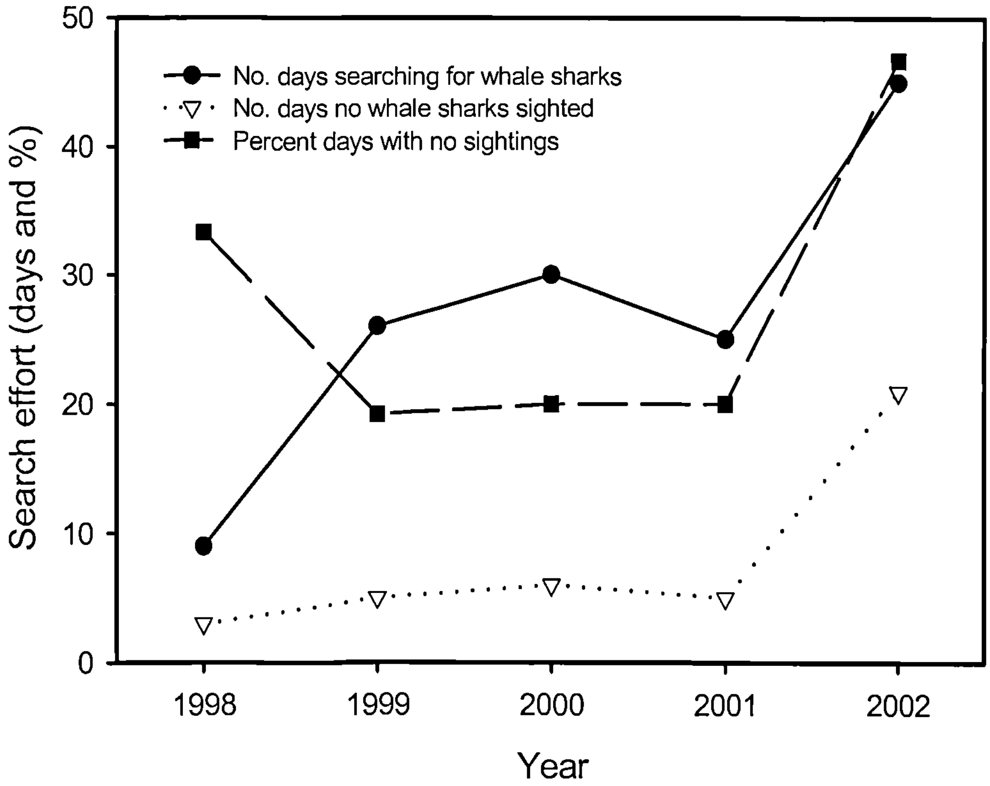


Figure 7.5: The total number of search days for whale sharks in peak snapper spawning season (1998-2002) versus the number of days and percentage of days with no sightings.

from the village to the airstrip five miles away has steeply increased vehicular traffic, contributing to the change of tone and pace of the village. The near completion of the southern highway joining the northern and southern regions of Belize has greatly facilitated transport from the north to Independence, Placencia's largest neighbouring town, and further stimulated the development process. Although the physical environment and current infrastructure in the village appear to constrain large-scale expansion of the peninsula, similar limitations have been overcome in other environmentally fragile areas including Cancún, Mexico which currently caters to over 4 million visitors a year and generates over US$ 2 billion a year –one third of Mexico's tourism revenue (Cothran & Cothran, 1998).

It is likely that Placencia will continue to see a rapid rise in tourism and concomitant development. This conforms with a global pattern of serial alteration of once-pristine areas, whereby tourism often destroys its resource base (Hawkins & Roberts, 1994; Cothran & Cothran, 1998; van Treeck & Schuhmacher, 1999; Duffy, 2000; Gossling, 2002; Gossling *et al.*, 2002). Additionally, the seasonal nature of tourism in Belize and Placencia can only increase the pressure on the village and Gladden Spit during specific and often vulnerable times of the year such as the snapper spawning and whale shark aggregation season. Peak tourist visitation months are recorded in January through May based on monthly visitation rates and room occupancy and revenue (BTB, 2001). This period coincides with the dry season and encompasses the Easter holiday and the peak snapper spawning season at Gladden Spit. Tourism tapers off with the start of the rainy season in June, as Placencia's focus shifts to the lucrative lobster fishery following the opening of the lobster season on 15 June.

Surveyed visitors spent most of their Belize trip time in Placencia and their daily per capita expenditure in Placencia was high at US$ 135.00 per day compared to Belize's mean of US$ 94.00 (BTB, 2001) possibly explained by the participation in expensive marine activities such as whale shark tours. Visitors indicated a high degree of satisfaction with Belize and Gladden Spit as a destination with the majority wishing to return, identical to that recorded by national tourist survey statistics (BTB, 2001).

In this context, whale shark tourism conducted out of Placencia and four nearby communities has risen sharply with a 900% increase in the number of tour operators offering whale shark encounters between 1997 and 2002. Rapid increases in visitor and tour operator numbers were also noted in other sites hosting predictable aggregations of whale sharks including Ningaloo Reef in Western Australia (Davis, 1998b), Yucatan Peninsula

(M.C. Garcia, pers. comm. 2003) and Baja California, Mexico (J. Ketchum, pers. comm. 2002). Surprisingly, Hurricane Iris did not reduce the number of tourists visiting in the 2002 whale shark season. Reasons for the rapid increase in visitation between 2001 and 2002 in particular may be due to increased international access to Belize and a greater knowledge of the Gladden Spit phenomenon following the televised broadcast of National Geographic's documentary on Gladden Spit's whale sharks and fish spawning aggregations[2].

The rapid rise in the number of visitors and tour boats recorded at Gladden Spit from 2000 onwards has caused concern for tourguides, fishermen, conservationists, and researchers. Although the GSSCMR was declared in May 2000 and an emergency statutory instrument outlining whale shark tourism regulations effected, these measures did little to check growth and congestion at the spawning aggregation and whale shark site (Figure 1.4). This was primarily due to a lack of oversight and education on interim regulations while the Government determined the management fate of the new marine reserve. The situation was resolved in April 2002, when the Government declared FON co-managers of the GSSCMR with the Department of Fisheries. Co-management agreements are being used increasingly in MPAs in Belize and other countries worldwide to decentralize management and increase participation of local stakeholders in decision-making involving their resources (White *et al.*, 1994; King & Faasili, 1999; Sandersen & Koester, 2000).

7.4.2 Funding marine reserve management costs through user-fees

Marine protected areas require a constant source of funding to operate. Most MPAs survive through a combination of public and private funding, debt swaps and endowments, although the vicariousness of outside funders can make this source of income highly uncertain. To foster greater autonomy and sustainability over the long-term, many MPAs are seeking to cover their costs through tourist user-fees, particularly if these are located in developing countries (Lindberg *et al.*, 1996; Walpole *et al.*, 2001; Green & Donnelly, 2003). However, tourism can be an unstable source of revenue particularly if based on foreign arrivals (Dixon *et al.*, 1993). Regardless, many MPAs do not charge for visitation or greatly undercharge (Laarman & Gregersen, 1996; Green & Donnelly, 2003), barely covering the costs of fee collection let alone other MPA management costs. In fact, only a

[2] "Feast of the Giant Sharks" a National Geographic Explorer documentary aired in the US and internationally in August 2001.

fraction of the 484 MPAs in the wider Caribbean (Green & Donnelly, 2003) can boast of being fully or near self-sustaining through user-fees; two examples include the Bonaire Marine Park (Dixon *et al.*, 1993) and St. Lucia Marine Protected Area (Barker, 2003).

Belize's Fisheries Department has been seeking a means of charging and efficiently collecting visitation fees for five of the 12 marine reserves it manages, thus offsetting many of the operational costs and capital expenditures not covered by government funding. It co-manages the remaining seven marine protected areas with non-governmental organisations and defers fundraising responsibility to them under the terms of the co-management agreement. Currently, only three of the 12 marine reserves in Belize charge visitors a daily fee and only one of these, Hol Chan/Shark Ray Alley (managed by the Department of Fisheries) sells a wildlife experience of swimming with sting rays and nurse sharks. Hol Chan charges US$ 2.50 per day, Half Moon Caye and Laughing Bird Caye charging US$ 5.00 per day. None of these MPAs is currently fully self-sustaining, making up shortfalls primarily through private donations. However, instead of charging a site-specific daily fee that requires greater infrastructure and resources to capture revenue, the Department of Fisheries is evaluating the application of regional fee that would cover multiple-day visitation to marine reserves located in any one of three national areas divided into north, central and south zones. The effectiveness of a centralized collection point for fees has been debated, as this may delay revenue return to co-managing organisations and undermine management of marine reserves in their care. Surveyed visitors at Gladden Spit indicated that they did not agree or disagree with paying a regional fee to visit MPAs but were most inclined to pay only for the marine reserves visited.

As co-manager of the GSSCMR, FON gained the mandate to enforce regulations and raise funds from national and international sources to manage the marine reserve. The majority of capital purchases required to operate 46 km offshore at Gladden Spit (boat, ranger station, island base etc.) were covered through national and foreign grants and donations. However, FON was seeking sustainable income to cover operational costs of running the reserve, leading to several local consultations on the levying of a daily tourist visitation fee to the GSSCMR. In 2001 FON wanted to charge US$ 25.00 visitor^{-1} day^{-1} a move that was strongly opposed by local tour-operators. Only one other site in the Caribbean, the Exuma Land and Sea Park in the Bahamas, charges a fee of US$25.00 per day. By comparison, Cocos Island (Costa Rica) charges US$ 105.00 per trip and the Galapagos Islands (Ecuador) charge US$ 100.00 per visitor per trip. These trips often last at least seven days and the fee therefore represents a daily charge of US$ 15.00 and US$ 14.28 respectively.

Several WTP surveys have also shown that the majority of visitors are willing to pay a fee to visit and conserve a protected area (Dixon *et al.*, 1993; Dixon & Hof, 1997; Lindberg & Halpenny, 2001; Walpole *et al.*, 2001), with many willing to pay up to US$ 20-30 per trip (Roberts & Hawkins, 2000). As a result of local opposition and the inability to guarantee whale shark presence or sightings – locally-perceived as the main reason for levying such a high fee, FON revised the proposed daily fee to US$ 15.00 visitor^{-1} day^{-1} (FON, 2003). This still represented more than the amount levied by Western Australia's Department of Conservation and Land Management (CALM) (Aus$ 15.00 = US$ 10.00) at Ningaloo Reef for whale shark tours (Davis, 1998a). However, CALM is a subsidised government entity whereas FON receives no subsidies and must raise all of its funds.

Over 70% of tourist surveyed spent 2 days or less at the GSSCMR, which represents a total fee of US$ 30.00 or 1.4% of their total trip expenditure, similar to the 1% determined by Roberts and Hawkins (2000) for divers visiting MPAs. As such, most surveyed visitors to Gladden were willing to pay a daily fee to visit the marine reserve. There was no change in price response to increased WTP fees suggested, even though over half of visitors did not know that Gladden Spit was a marine reserve. Survey respondents in 2002 were willing to pay a mean fee of US$ 9.62. Surprisingly, visitor's willingness to pay was unresponsive to an encounter with a whale shark. However, WTP was responsive to the presence of whale sharks at Gladden and to visitor satisfaction with the trip to the GSSCMR. This suggests that visitors are willing to pay for the existence of whale sharks at Gladden Spit. Although visitors to Ningaloo Reef currently pay a daily fee of ~US$ 10.00[3] to encounter whale sharks, when asked if they were willing to contribute more towards management costs, visitors were found to be willing to pay a mean of ~US$ 18.59 or 64% of FON's revised fee of US$ 15, to visit the GSSCMR and its whale sharks (Davis, 1998a). Davis (1998a) also found that ethnicity was the single most important factor in visitor's willingness to pay with Japanese consumers willing to pay less than other ethnic groups.

The US$ 9.62 WTP to visit Gladden Spit represents 64% of FON's revised fee of US$ 15.00 to visit the GSSCMR and its whale sharks. This 2002 fee further represents less than a dollar in difference to the 2001 mean WTP amount suggesting little change in visitor

[3] Assuming an exchange rate of Aus$ 1.50 = US$ 1.00

WTP between the two years. However, both fee amounts are low considering the unique nature of Gladden's fauna and their interactions. Nonetheless, FON may encounter resistance or refusal from visitors to pay the US$ 15.00 fee to visit the marine reserve. Additionally, based on the estimated number of visitors during the 2002 whale shark season, either fee would only generate US$ 16,046 and US$ 25,020 respectively, or 9.2% and 14% of the reserve's estimated yearly operating expenses. Annual operating costs for running the GSSCMR were conservatively estimated at US$ 175,000[4]. By comparison, Bonaire's near-shore MPA had an estimated running costs of 150,000 year^{-1} in 1993 (Dixon *et al.*, 1993) indicating that the GSSMCR estimates are low based on distance from shore and general costs in 2002. It is important to note that the majority of surveys were conducted *ex-post* to the trip to Gladden Spit and a whale shark encounter, and therefore the WTP may have been even lower than a WTP elicited during an *ex-ante* survey as it incorporated several visitors who may have been disappointed in not encountering a whale shark.

One of FON's primary goals is to manage tourism and reduce boat congestion at Gladden during the whale shark season. Western (1986) found with predator viewing in East African game parks that visitor predilection for a single species also increases the congestion around areas where it can predictably be viewed and therefore lowers the carrying capacity for the species and the target site. This can consequently raise rates charges as the experience becomes more exclusive (Western, 1986). Boat congestion experienced at Gladden Spit in 2002 led to FON's development of boat and time slots to encounter whale sharks and counter traffic at the site.

Following numerous consultations with local tour-operators on how to manage tourism at the site, FON suggested allocating time and boat slots during the peak season for three full moon periods from March through June. Each moon is estimated at 14 days, or a total of 42 peak whale shark days each season. Six boats with a maximum of 12 guests each would be permitted into the whale shark zone (Figure 1.1) during each 2-hour time slot. By comparison, CALM does not enforce time slots and allows each tour vessel at Ningaloo Reef 90-minutes of contact time with whale sharks, after which they must move on and let

---

[4] This estimate included salaries, office costs, and field costs and reserve patrolling. It assumed that all infrastructure and capital costs had been paid for, and it did not include maintenance of equipment, collection of marine reserve fees, costs of meetings and / or workshops, publications and research.

another tour-operator take over. There has been a debate about how many time slots would be permitted per day and how many are feasible based on travel time to Gladden Spit's whale shark zone from any coastal point. Realistically, four slots or eight hours in the zone (09:30-17:30 h) is possible. Tourguides are reluctant to leave Placencia or the stakeholder communities earlier than 08:00 h as they also feel that there is less of a chance to see whale sharks that early. Although whale sharks can be seen in the marine reserve at all times of the day, visitation results from Chapter 3 indicate that sharks spend more time at the aggregation zone as the afternoon progresses, with peak time spent close to 17:00 h when the snappers spawn. There is therefore increased emphasis to book later rather than earlier time slots.

If all boats and time slots were filled to capacity, then levying a US$ 15.00 fee day^{-1} $visitor^{-1}$ would yield a total of US$ 181,400 per whale shark season, enough to cover the estimated basic costs of running the marine reserve. However, several boats currently used in whale shark tours cannot safely carry more than 6 guests and it is unlikely that all slots on all peak days will be filled due to cancellations, adverse weather conditions, etc. At 50% boat and time slot capacity, income would be reduced to US$ 90,720. It is worth noting that this represents revenue only from the whale shark season, no data on visitation rates are available for other times of the year. The lack of predictable whale shark sightings during the rest of the year (supported by findings in Chapter 3) has raised the as yet unresolved issue of whether a US$ 15.00 should be charged outside of the whale shark season to visit the GSSMCR.

Tour guides have been under increasing pressure from guests to guarantee whale shark sightings. As a result, guides will often flaunt interim regulations and stay out at the site past the recommended hours with larger than recommended groups sizes to increase the probability that a greater number of guests see a shark and therefore secure tips. Similarly, rangers taking tourists to see mountain gorillas (*Gorilla gorilla beringei*) in the Virunga Conservation Area (Rwanda, Uganda and the Democratic Republic of Congo) have infringed regulations by extending viewing time, decreasing the minimum permissible distance between visitors and gorillas and increasing group size (Butynski & Kalina, 1998). Guides have been sceptical about the suggested US$ 15.00 daily marine reserve fee because they are not able to guarantee shark sightings and they feel that they would lose business through decreased visitation. Additionally, raising marine reserve fees did not appear to decrease visitation in protected areas such Bonaire Marine Park and therefore did not necessarily decrease congestion (Dixon *et al.*, 1993; Lindberg & Halpenny, 2001). Additionally, several WTP studies indicate that visitors are enthusiastically willing to pay for protected areas without decreasing visitation (Dixon, 1993; Dixon *et al.*, 1993; Walpole *et al.*, 2001).

Although the daily fee to visit the marine reserve would cover entrance to the reserve and possible encounters with whale sharks, it was difficult to separate the importance of the marine reserve from the whale sharks in visitor's willingness to pay. Visitors indicated in both surveys that the payment of a daily fee to Gladden was contingent on the presence of whale sharks, further supported by the results of the logistic regressions. They mentioned that the high fee was not warranted if they couldn't be guaranteed seeing a whale shark, particularly as the diving was considered only average in the absence of the sharks. However, this was contradicted by the results of the logistic regression where the sighting of a whale shark was not a significant variable in a visitor's willingness to pay. Wells (1997) noted that visitors expressed a greater WTP to conserve the destination as opposed to visiting it. Although this study's survey noted that the fee would be levied to visit the marine reserve, it was stated that it would be used to manage and conserve the site and its fauna and as such explains the high percentage of visitors willing to pay a high fee.

Changes in predictability of wildlife tourism-focused species can lead to changes in fee structures and marketing of tours to account for changes in effort to view the wildlife. When grey whales (*Eschrichtius robustus*) predictably aggregating near Tofino on Vancouver Island, British Columbia shifted to other feeding sites further away, whale watching tours had to accommodate higher fuel prices and longer travel times that could impact visitor recreational satisfaction (Duffus, 1996). Less time spent seeing a target species or even not seeing them at all will not always impact a visitor's satisfaction with their trip experience as Orams (2000) discovered with whale watching tours in Kaikoura, New Zealand and Kenchington (1990) found with recreational fishing. Both discovered that visitor motivations in tourism are complex with satisfaction derived from several aspects of the tour, also mirrored in visitors to Gladden Spit who rated their overall satisfaction on the trip and presence of whale sharks as the most important variables in their WTP of a daily fee to the marine reserve.

Belize has near-daily direct access to four major US-based destinations. Visitors can reach Placencia from Miami or Houston in less than three hours of international and internal flights, far cheaper and faster than the travel time required to reach other whale shark aggregation sites such as Western Australia, the Philippines, South Africa or the Seychelles from either Japan, the US or Europe. Additionally, it is expected that pressure on the marine reserve and its whale sharks and spawning aggregations will continue to grow as American and European tourists seek safer alternatives to popular destinations in Africa and Asia that have recently suffered declines in visitation due to terrorism. Therefore, demand for whale shark tours at Gladden Spit is unlikely to decline in the near future providing sightings remain predictable. Consequently, strong management measures to monitor shark numbers and fish behaviour and regulate traffic at the site will be key to sustainability of the whale shark and spawning snappers phenomenon. During the 2002 season, the decline in predictable shark sightings already indicates that expansion of this tourism, even to the levels suggested by FON, may not be compatible with its sustainability. As such, the whale sharks runs the risk of being "loved to death" as has been recorded for other target species of the tourism industry (Mellor, 1990; Shackley, 1990; Laycock, 1991).

7.4.3 Visitor-whale shark interactions

Visitors who encountered a whale shark at Gladden were overwhelmingly affected by the experience and primarily impressed with how close they got to the sharks (see comments in Appendix 7.E). Davis *et al.* (1997) also found that closeness to whale sharks was an important factor in the visitor's encounter experience at Ningaloo Reef, Western Australia. However, the quality of the experience did not alter if the tourist was further away from the shark. This supports the current interim GSSCMR regulation (Appendix 7.A) that requires people to remain a minimum of 3 m away from all parts of the shark. Similar to Belize, 7.3% of survey respondents in Australia professed to touching a shark despite a pre-encounter briefing that explicitly warned against touching and the threat of a Aus$ 10,000 fine (Davis, 1998b). Although a fine of US$ 5,000 for touching a shark was recently included in the provisional regulations for whale shark tourism in the GSSCMR (FON, 2003), the fine has not yet been implemented. Furthermore, it is difficult to determine how such a fine would be levied with the current lack of oversight and reluctance from tour-operators to enforce regulations. Touching is occasionally difficult to avoid as curious sharks swim into and bump visitors, an occurrence sometimes made more likely by crowding.

Gladden Spit's visitors' repeated attempts to touch sharks despite education and warnings by guides, suggests that smaller group sizes and snorkelling should be favoured for the long-term sustainability of the marine reserve's whale shark tourism. Despite a decline in whale shark group size in Australia over two consecutive years, touching sharks still took place (Davis, 1998b). Only snorkelling is permitted during organised whale shark tours in Ningaloo Reef and in the Philippines. Local government and conservation groups in Mexico's Yucatan Peninsula are also strongly recommending snorkelling as the only permissible means of interacting with whale sharks (MC. Garcia and J. Gonzalez, pers comm. 2003). Tour-operators working whale shark aggregation sites such as the Seychelles and Mozambique are attempting to self regulate and seeking to adopt the no-touch rule to reduce impacts on whale sharks and promote sustainability of interactions (Graham, unpublished data).

Contact time between whale sharks and visitors was not assessed in this study. However, during the research whale sharks have either passed by or spent over 25 minutes circling researchers and even non-aggressively burying their snout into divers. Interactions between whale sharks and visitors are wholly voluntary as sharks approach and leave visitors at will. However, divers have a greater ability to chase sharks and aggregating reef fish than do snorkelers. Several guides also attract the sharks at the aggregation site using large concentrations of scuba bubbles that appear to simulate fish spawning activity. In the afternoon, sharks have recently and rapidly learnt to swim vigorously towards the surface from over 70 m deep to investigate and eat the exhaled bubbles. The impact on the sharks through increased energy expenditure in return for empty calories is unknown, as is whether this behaviour is rapidly deconditioned through lack of food reward, potentially leading to less "predictable" behaviour and a future avoidance of divers.

Making the whale shark experience "special" and reducing crowding was a recurring theme with visitors who are keen to maintain small boat numbers and group sizes. Although most visitors felt that their dive or snorkel group was just the right size, 80% urged keeping group sizes smaller than ten people. Over 80% visitors to Gladden Spit were also willing to pay at least US$ 20 more to be in a smaller group to ensure a more exclusive experience. Davis (1998b) found that 71% of his survey respondents suggested groups sizes of six or less during encounters with whale sharks at Ningaloo Reef. In addition to increasing a visitor's recreational and experiential satisfaction, smaller group sizes are more manageable for guides, important factors in mitigating impacts on wildlife and increasing safety in occasionally rough seas. However, the newly proposed regulations at Gladden Spit (Appendix 7.A) state that only 12 visitors with two guides or 14 people in total can be in the water with a whale shark at any one time. Tour operators may wish to self-regulate and charge more to maintain groups of less than eight that will promote greater sustainability of tours and lead to higher levels of visitor experiential satisfaction (and potentially larger tips).

Visitors to the marine reserve were willing to pay a mean maximum of US$ 143.00 ± 107.30 SD for their whale shark tour, US$ 38.77 over the mean amount of US$ 104.23, snorkelling and diving combined, for a day's excursion to encounter whale sharks. Davis (1998a) found that visitors to Ningaloo Reef, Western Australia, who were asked what maximal cost they would be willing to pay to swim with whale sharks, responded with a mean of ~US$ 166.46 per day for their whale shark tour, also inferior to the median cost of ~US$ 183.00 for a day with whale sharks at Ningaloo Reef (1996 rates) (Davis, 1998a). Although these amounts are similar to those elicited in Belize, by comparison, current Ningaloo Reef regulations only allow tourists to snorkel with whale sharks, and sightings are less predictable as aggregations of sharks are dispersed over a greater area. Additionally, Ningaloo Reef is also destination that requires comparatively longer travel times and higher costs to reach from other countries of tourist provenance. Surprisingly, the WTP does not appear to reflect the rarity of the phenomenon and the relative ease of access to Belize and lower travel costs and the enthusiastic responses gathered from visitors following an encounter both in Belize, a situation also identified by Davis (1998a) at Ningaloo Reef (Appendix 7.E). Such results and feedback suggests that the WTP amounts undervalue the resource as they represent lower amounts than most tour-operators charge for a day's diving with whale sharks.

Management of whale shark encounters

Whale sharks are present at Gladden Spit throughout the day although visitation at the fish aggregation site is significantly higher later in the afternoon than earlier in the day as the fish prepare to spawn (see Chapter 3). Tour-operator knowledge of increased predictability of sightings in the late afternoon has led to boat congestion at the spawning aggregation site that measure less than 500 m in diameter around the point named G2 (Figure 7.1). Additionally, tour-boats often overlap with fishers leading to conflict over site use. Divers have been observed to swim into fishing lines and surface under or next to fishing boats leading to accusations by fishers that divers are scaring away the fish and constraining their fishing.

Despite early consensus from tour-operators to finish whale shark tours at 17:00 to avoid impacting spawning fish, a last minute concession by the marine reserve managers in 2003 allowed whale shark operators an additional half hour and the ability to stay in the area as long as they like. Several tour-operators have guaranteed whale shark sightings to visitors further increasing the pressure to stay out late despite the 1.5-hour boat-trip back to the mainland in the hopes of seeing a shark. The time extension enables tourists to be in the water at the same time as the spawning fish. Divers can modify fish spawning behaviour and subsequently whale shark predictability as witnessed at Gladden Spit in May 2002 (Graham, unpublished data). Limiting interactions with fish during this time period would be a wise precaution to take to ensure the sustainability of spawning and whale shark visitation. The extension further conflicts with research efforts at the site, limiting efforts such as whale shark counts, tagging, photo identification and assessment of fish spawning behaviour, studies that help to determine if levels of use are sustainable. Oliver (1995) notes that these are issues that may push the "Limits of acceptable change". In Australia, only 15 tour-operators are licensed to conduct whale shark tours and once a boat is with a whale shark, others have to wait 90 minutes for their turn or find another shark (Davis, 1998a).

Although whale sharks do not appear to be affected by divers and snorkelers so long as they are not chased, touched or ridden, groups of divers appear to impact spawning aggregations of snappers, cuberas in particular. Whale sharks are definitely affected by boats with 17 individuals seen with nicks, gashes, scrapes, cuts or lost fins, most or all of which appear to have been due to collisions with boats or propellers, similar to that recorded by Norman (pers. comm. 2000) with whale sharks encountered in Ningaloo Reef (see Chapter 2).

Education and outreach for visitors and guides

Education on the biology, behaviour and vulnerability of whale sharks and spawning fish was a key component in providing valuable biological data tour guides and tourists. Education appeared to promote greater self-regulation among tourguides and visitors. Surveys registered a decrease in the number of respondents who had touched a whale shark between 2001 and 2002. Orams and Hill (1998) recorded a similar result visitors participating in the Tangalooma dolphin encounters, where the levels of inappropriate behaviour such as touching the dolphins declined significantly following the implementation of an education program. Survey comments (Appendix 7.D and 7.E) and direct feedback indicated that visitors appreciated knowledgeable briefings and often requested more education and materials, particularly on the way to the site as travel time varied between one and two hours.

Few whale shark marker-tagging studies have been undertaken worldwide and none other than the Belize based study requested feedback from visitors regarding tag perception. Balancing the needs of tourism and visitor desire for a "true wilderness" experience with necessary research that underpins the tourism can be difficult. It is therefore reassuring for researchers to know that the majority of tourists surveyed were not affected by seeing tags on the whale sharks. Many tourists who had seen tagged sharks were enthusiastic about reporting numbers or tag types, although they were not always able to correctly identify tag numbers or types. This highlights the researcher's dilemma: whether or not to use visitor derived data. During the course of this study, no visitor resightings data was used, as its accuracy could not be vouched for.

7.4.4 Competition and tradeoffs between tourism and fishing

At Gladden Spit, whale shark tourism takes place at the same time as the seasonal fishery on snapper spawning aggregations as spawn provides the food that draws the whale sharks to Gladden Spit every year (Heyman *et al.*, 2001). The sharing of a same resource and space has led to conflict between fishers and tour-operators. Originally it was thought that Belizean fishers competed directly with the sharks for the same resource, e.g., mutton snapper (*Lutjanus analis*) eggs. However, recent findings (Chapter 3 and 6) indicate that whale sharks appear to only feed on the spawn of cubera and dog snappers (*L. cyanopterus* and *L. jocu*) caught illegally at night. Therefore eliminating illegal fishing will also eliminate the two-pronged pressure on spawning fish populations, increase the likelihood of continued predictable whale shark visitations and potentially promote greater compliance of local fishers with new marine reserve fishing regulations. Although direct competition between whale sharks and local fishers does not appear to exist, fishing spawning aggregations is nonetheless unsustainable and often leads to the decline and extirpation of the population fished (Sadovy, 1992; Sadovy, 1996). Such a decline is already in evidence with the mutton snapper fishery at Gladden Spit (see Chapter 6).

Sala *et al.* (2001) suggested that the loss of revenue from fishing spawning aggregations, particularly of groupers, could be offset by diving on them. However, this is not recommended as there are strong indications that fish modify their courtship and pre-spawning behaviour when approached by divers (Graham, unpublished data). In the case of Gladden Spit, a compromise is required since the whale sharks occupy the same space as the spawning aggregations of reef fish. Maintaining a distance of no less than 15 m away from aggregating fish or groupers is suggested to minimize impacts on fish courtship behaviour. For many local fishers, tourism during the snapper and whale shark season is providing both direct and indirect economic alternatives to fishing the vulnerable spawning aggregations. Tourism to the marine reserve generated US$ 1.35 million per season in the stakeholder communities, clearly outperforming revenues from fishing the snapper spawning aggregations during the same period. Income generated from the mutton snapper spawning aggregation fishery was estimated at US$ 35,497 for the 2002 season (see Chapter 6). However, not all traditional fishers from the stakeholder communities accept the shift into a new tourism-based occupation.

Lindberg *et al.* (1996) found that ecotourism has generated significant local economic benefits in four protected areas of Belize, similar to what is noted in the marine reserve's stakeholder communities, and Placencia in particular. However, an increasingly larger portion of the benefits is perceived locally to be accruing to foreigners or Belizeans residing outside of the marine reserve stakeholder communities. As such, there is a strong protectionist tendency to ensure that jobs related to the rapidly growing tourism in Placencia and the marine reserve (restaurants, boat captaining, guiding, recreational fishing, divemastering, etc.) are allocated to local stakeholders. This would ensure that those who depend on their local resources are the first to benefit from them.

7.5 Conclusions

Tourism at the Gladden Spit and Silk Cayes Marine Reserve is an important source of revenue for stakeholder communities. Although tourism is an imperfect social and cultural alternative for several of the traditional fishers fishing the snapper spawning aggregation, it is a lucrative economic alternative that generates 39 times more revenue during the same time period.

At current and expected use levels, visitor numbers and boat traffic in the reserve are impacting the whale sharks and fish aggregations. Pressure from the tourism industry to maximize time and use of the marine reserve and its fauna needs to be balanced with the need to protect the resources and sustain the aggregations, to avoid "killing the golden goose" or "loving the resource to death".

The whale shark zone will not benefit from being an open access site and limits on the number of tour operators operating with a whale shark license are required. Strong management directives that benefit the long-term health of the reserve and its resources in combination with economic instruments such as daily fees and self-regulation among tour-operators will be necessary to promote sustainable use of the marine reserve and mitigate impacts on its resources.

Additional education such as whale shark tourism and conservation courses will help to foster tour operator compliance with provisional regulations and continue to inform and educate tour-guides about whale sharks and associated research. Continued research to monitor both whale shark sightings per unit effort, number and site fidelity of sharks at the aggregation site and the behaviour of fish spawning aggregations in relation to divers will be key to determining levels of impact on these resources.

7.6 References

Alava M. N. R., Dolumbalo E. R. Z., Yaptinchay A. A. & Trono R. B. 2002. Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In: *Elasmobranch Biodiversity Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997.* (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 132-147. Sabah, Malaysia. IUCN, Gland, Switzerland.

Anderson R. C. 2002. Elasmobranchs as a recreational resource. In: *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997.* (Fowler S. L., Reed T. M. & Dipper F. A. eds.), pp 46-50. Gland, Switzerland and Cambridge, UK. IUCN SSC Shark Specialist Group.

Anderson R. C. & Ahmed H. 1993. Shark fisheries of the Maldives. Ministry of Fisheries and Agriculture. Maldives and the Food and Agriculture Organisation, Rome. 73 pp.

Arnold P. W. & Birtles R. A. 1993. Towards sustainable management of the developing dwarf minke whale tourism industry in Northern Queensland. CRC Reef Research Technical Report. Townsville, Australia. 30 pp.

Barker N. 2003. PhD. Environment Department, York.

Barnes J., Burgess J. & Pearce D. 1992. Wildlife tourism. In: *Economics for the Wilds: Wildlife, Wildlands, Diversity and Development.* (Swanson T. M. & Barbier E. B. eds.) London. Earthscan.

Baum J. K., Myers R. A., Kehler D. G., Worm B., Harley S. J. & Doherty P. A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science.* **299** (5605): 389-392.

BTB. 2001. Visitor expenditure and motivation survey. Belize Tourism Board. Belmopan, Belize. 19 pp.

Butynski T. M. & Kalina J. 1998. Gorilla tourism: a critical look. In: *Conservation of Biological Resources.* (Milner-Gulland E. J. & Mace R. eds.), pp 294-313. Oxford. Blackwell Science Ltd.

Clark E. & Nelson D. R. 1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environmental Biology of Fishes.* **50** (1): 63-73.

Colman J. G. 1997. A review of the biology and ecology of the whale shark. *Journal of Fish Biology.* **51** (6): 1219-1234.

COP12. 2002. Proposal for inclusion of whale sharks on Appendix II - Proponents India and Philippines. CITES. 24 pp.

Cothran D. A. & Cothran C. C. 1998. Promise or political risk for Mexican tourism. *Annals of Tourism Research.* **25** (2): 477-497.

CSO. 2000. Belize Population Census 2000. Central Statistical Office. Belmopan, Belize.

CSO. 2001. Belize statistics 2001. Central Statistical Office. Belmopan, Belize.

Davies M. 1990. Wildlife as a tourism attraction. *Environments.* **20** (3): 74-77.

Davis D. 1998a. Tourist levies and willingness to pay for a whale shark experience. *Tourism Economics.* **5** (2): 161-174.

Davis D. 1998b. Whale shark tourism in Ningaloo Marine Park, Australia. *Anthrozoos.* **11** (1): 5-11.

Davis D., Banks S., Birtles A., Valentine P. & Cuthill M. 1997. Whale sharks in Ningaloo Marine Park: managing tourism in an Australian marine protected area. *Tourism Management.* **18** (5): 259-271.

Dixon J. A. 1993. Economic benefits of marine protected areas. *Oceanus.* **36** (3): 35-40.

Dixon J. A. & Hof T. v. t. 1997. Conservation pays big dividends in Caribbean. *Forum for Applied Research and Public Policy.* **Spring**: 43-48.

Dixon J. A., Scura L. F. & Vanthof T. 1993. Meeting ecological and economic goals: marine parks in the Caribbean. *Ambio.* **22** (2-3): 117-125.

Dixon J. A. & Sherman P. B. 1990. *Economics of Protected Areas - A New Look at benefits and Costs.* Island Press, Washington DC. 234 pp.

Dowdell N. R., Andrade R. E., Torres N. C., González A. Z., Haikin A. V. & Reyes C. G. 2003. Conservación y aprovechamiento sustentable del tiburón ballena (*Rhincodon typus*), a través del ecoturismo en Bahía de los Ángeles, Baja California. Universidad Autonoma de Baja California. La Paz, Baja California. 61 pp.

Duffus D. A. 1996. The recreational use of grey whales in southern Clayoquot Sound, Canada. *Applied Geography.* **16** (3): 179-190.

Duffy R. 2000. Shadow players: ecotourism development, corruption and state politics in Belize. *Third World Quarterly.* **21** (3): 549-565.

FFWCC. 2000. Shark and reef fish feeding by divers, issues and options. Workshop report. Division of Marine Fisheries, Florida Fish and Wildlife Conservation Commission. Florida. 6 pp.

FON. 2003. Gladden Spit and Silk Cayes Marine Reserve Management Plan. Friends of Nature. Placencia, Belize. 72 pp.

Gossling S. 2002. Global environmental consequences of tourism. *Global Environmental Change.* **12** (4): 283-302.

Gossling S., Hansson C. B., Horstmeier O. & Saggel S. 2002. Ecological footprint analysis as a tool to assess tourism sustainability. *Ecological Economics.* **43** (2-3): 199-211.

Green E. & Donnelly R. 2003. Recreational scuba diving in Caribbean marine protected areas: do the users pay? *Ambio.* **32** (2): 140-144.

Hawkins J. P. & Roberts C. M. 1994. The growth of coastal tourism in the Red-Sea: present and future effects on coral-reefs. *Ambio.* **23** (8): 503-508.

Heyman W. D., Graham R. T., Kjerfve B. & Johannes R. E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology-Progress Series.* **215**: 275-282.

Isaacs J. C. 2000. The limited potential of ecotourism to contribute to wildlife conservation. *Wildlife Society Bulletin.* **28** (1): 61-69.

Kenchington R. A. 1990. *Managing marine environments.* Taylor and Francis, New York. 175 pp.

King M. & Faasili U. 1999. Community-based management of subsistence fisheries in Samoa. *Fisheries Management and Ecology.* **6** (2): 133-144.

Laarman J. G. & Gregersen H. M. 1996. Pricing policy in nature-based tourism. *Tourism Management.* **17**: 247-254.

Laycock G. 1991. Good times are killing the Keys. *Audubon.* **93** (5): 38-41.

Lindberg K., Enriquez J. & Sproule K. 1996. Ecotourism questioned: case studies from Belize. *Annals of Tourism Research.* **23** (3): 543-562.

Lindberg K. & Halpenny E. 2001. Protected area visitors fee: country review. Cooperative Research Centre for Sustainable Tourism. Gold Coast, Queensland, Australia. 30 pp.

McClanahan T. R. & Mangi S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications.* **10** (6): 1792-1805.

Mellor B. 1990. Loving the reef to death? *Time.* **45**: 48-55.

Miller M. L. 1993. The rise of coastal and marine tourism. *Ocean and Coastal Management.* **20**: 181-199.

Myers R. A. & Worm B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature.* **423**: 280-281.

Nowlis J. S. & Roberts C. M. 1999. Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin.* **97** (3): 604-616.

Oliver J. 1995. Is the "Limits of Acceptable Change" concept useful for environmental managers? A case study from the Great Barrier Reef Marine Park. In: *Conservation Through Sustainable Use of Wildlife.* (Grigg G. C., Hale P. T. & Lunney D. eds.), pp 131-139. Centre for Conservation Biology, The University of Queensland.

Olson T. L., Gilbert B. K. & Squibb R. C. 1997. The effects of increasing human activity on brown bear use of an Alaskan River. *Biological Conservation.* **82** (1): 95-99.

Orams M. B. 1997. Historical accounts of human-dolphin interaction and recent developments in wild dolphin based tourism in Australasia. *Tourism Management.* **18** (5): 317-326.

Orams M. B. 2000. Tourists getting close to whales, is it what whale-watching is all about? *Tourism Management.* **21** (6): 561-569.

Orams M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management.* **23** (3): 281-293.

Orams M. B. & Hill G. J. E. 1998. Controlling the ecotourist in a wild dolphin feeding program: is education the answer? *The Journal of Environmental Education.* **29** (3): 33-38.

Perrine D. 1989. Reef fish feeding; amusement or nuisance? *Sea Frontiers.* **35** (5): 272-279.

Reynolds P. C. & Braithwaite D. 2001. Towards a conceptual framework for wildlife tourism. *Tourism Management.* **22** (1): 31-42.

Richardson J. A. 1998. Wildlife utilization and biodiversity conservation in Namibia: conflicting or complementary objectives? *Biodiversity and Conservation.* **7** (4): 549-559.

Roberts C. M. 1995. Rapid buildup of fish biomass in a Caribbean marine reserve. *Conservation Biology.* **9** (4): 815-826.

Roberts C. M., Bohnsack J. A., Gell F., Hawkins J. P. & Goodridge R. 2001. Effects of marine reserves on adjacent fisheries. *Science.* **294** (5548): 1920-1923.

Roberts C. M. & Hawkins J. P. 2000. Fully protected marine reserves: a guide. World Wildlife Fund. Washington DC. 131 pp.

Roberts C. M. & Polunin N. V. C. 1994. Hol-Chan: demonstrating that marine reserves can be remarkably effective. *Coral Reefs.* **13** (2): 90-90.

Rudd M. A. & Tupper M. H. 2002. The impact of Nassau grouper size and abundance on scuba diver site selection and MPA economics. *Coastal Management.* **30** (2): 133-151.

Sadovy Y. 1992. The case of the disappearing grouper: *Epinephelus striatus*, the Nassau grouper, in the Caribbean and Western Atlantic *45th annual meeting of the Gulf and Caribbean Fisheries institute, Merida, Mexico*, Merida, Mexico, pp 1-18.

Sadovy Y. 1996. Reproduction of reef fishery species. In: *Reef Fisheries.* (Polunin N. V. C. & Roberts C. M. eds.), pp 15-59. Chapman and Hall.

Sala E., Ballesteros E. & Starr R. M. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: Fishery management and conservation needs. *Fisheries*. **26** (10): 23-30.

Sandersen H. T. & Koester S. 2000. Co-management of tropical coastal zones: The case of the Soufriere marine management area, St. Lucia, WI. *Coastal Management*. **28** (1): 87-97.

Shackley M. 1990. Manatees and tourism in Southern Florida: Opportunities or threat? In: *Proceedings of the 1990 Congress on Costal and Marine Tourism*, pp 311-316.

Taylor J. G. 1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*. **47** (4): 637-642.

van Treeck P. & Schuhmacher H. 1999. Mass diving tourism: a new dimension calls for new management approaches. *Marine Pollution Bulletin*. **37** (8-12): 499-504.

Vivanco L. A. 2001. Spectacular quetzals, ecotourism, and environmental futures in Monte Verde, Costa Rica. *Ethnology*. **40** (2): 79-92.

Vogt H. 1996. The economic benefits of tourism in the marine reserve of Apo Island, Philippines. *Proceedings of the 8th Internatinoal Coral Reef Symposium*. **2**: 2101-2104.

Waheed A. 1998. Economic value of marine ecotourism to the Maldives. BSc. Institute of Marine Studies, Plymouth. 68 pp.

Walpole M. J. 2001. Feeding dragons in Komodo National Park: a tourism tool with conservation complications. *Animal Conservation*. **4**: 67-73.

Walpole M. J., Goodwin H. J. & Ward K. G. R. 2001. Pricing policy for tourism in protected areas: Lessons from Komodo National Park, Indonesia. *Conservation Biology*. **15** (1): 218-227.

Wells M. P. 1997. Economic perspectives on nature tourism, conservation and development. *World Bank Environmental Economics Series*. **55**: 56.

Western D. 1986. Tourist capactiy in East African parks. *UNEP Industry and Environment*. **9**: 14-16.

White A. T., Hale L. Z., Renard Y. & Cortesi L. (eds.). 1994. Collaborative and Community-Based Management of Coral Reefs. Kumarian Press, West Hartford. 130 pp.

Wilson S. G., Taylor J. G. & Pearce A. F. 2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/Southern Oscillation. *Environmental Biology of Fishes*. **61** (1): 1-11.

Appendix 7.A

Whale shark tourism regulations for the Gladden Spit and Silk Cayes Marine Reserve (from the reserve management plan)

The purpose of these regulations is to properly control visitation to the whale shark zone, particularly during the peak fish spawning and whale shark aggregating season. Friends of Nature hopes to ensure that this magnificent spectacle of nature will persist for generations to come. Tour guides wishing to conduct whale shark interaction tours within the Whale Shark Zone must obtain a special whale shark license and carry their IDs. All whale shark tours must operate from boats that are also specially licensed with the Reserve.

The following regulations apply throughout the year:

1. Dive and snorkel guides are required to provide briefing on regulations to tourists before entering the area.
2. No touching, chasing, or molesting whale sharks will be permitted.
3. Divers and snorkelers should remain at least 10 feet / 3 m away in any direction from any whale shark.
4. Maximum depth for divers of any certification is 80 feet / 24 m (to avoid disturbing fish aggregations and for safety considerations)
5. All boats will fly the "divers down" flag when they have divers in the water.
6. For snorkel tours, a maximum ratio of 8 snorkelers to each licensed snorkel guide is permitted.
7. For SCUBA tours, a maximum ratio of 8 divers to each licensed dive master is permitted.
8. Dive and snorkel boats must approach all whale sharks at idle speed (not exceeding 2 knots) and maintain idle speed in the vicinity of whale sharks.
9. Boats should remain at least 50 feet /15m from any whale shark.
10. Dive and snorkel boats should maintain a distance of at least 200 feet / 60 m between each other.
11. All divers and snorkelers should be out of the water by 5:30 PM.

The following regulations also apply from March 1 – July 31:

12. Dive and snorkel tours shall be limited to two hours
13. Two-hour visits will be allocated on a first-come, first-served basis by the ranger on duty (inside the reef at the Gladden Entrance).
14. A maximum of six dive and snorkel boats will be permitted into the Whale Shark Zone at one time.
15. A maximum of two boats per day per tour operator.
16. All boats shall check-in with FoN Rangers stationed inside the reef before proceeding to the Whale Shark Zone.
17. Each boat will carry a maximum of 12 clients – divers and/or snorkelers, and/or watchers.
18. All tourists – divers, watchers, and snorkelers – must pay a fee: a mandated fee of $15US or 15 BZ for Belizeans.

Visitors may choose to pay the higher recommended fees of $25US or $25BZ for Belizeans, in order to further assist conservation efforts.

19. **The Fisheries Department reserves the right to close the Whale Shark/Spawning Zone because of weather or for any other reason it deems necessary.**

Licensing:

1. Any person who wishes to conduct whale shark tours must be resident in one of the five communities served by Friends of Nature (Hopkins, Seine Bight, Independence, Placencia, Monkey River), must have a valid tour guide license, dive master certification (for SCUBA), skin diver certification (for snorkelers) a certificate of graduation from a whale shark course. The whale shark license has an initial fee of $50 BZ and an annual renewal fee of $25 BZ payable to Friends of Nature.
2. Any boat used for whale shark tours must be at least 23 feet and no longer than 48 feet.
3. Any boat used for whale shark tours must carry oxygen, safety sausages, radio, and lights.
4. The annual fee for the whale shark boat license is $100, payable to the Friends of Nature.

Sanctions:

1. Any person who contravenes any of the provisions of these regulations is guilty of an offense and liable on summary conviction to a fine not exceeding two thousand Belize dollars or to imprisonment for a period not exceeding six months, or to both such fine and period of imprisonment and/or revocation of whale shark license.
2. Notwithstanding the above, anyone touching a whale shark is also liable for a $10,000BZ fine.
3. Notwithstanding the above, any person who damages corals shall pay a fine not exceeding $10,000BZ, or some higher penalty based on the assessed damage not exceeding $1,000,000BZ.

Appendix 7.B Tourist Survey – Gladden Spit & Silk Cayes 2001 (pilot)

Date: __________Interviewer: ______________Visitor name: __________________________Site: ____________

The following questions will help us to know more about visitors to Belize who use the Gladden/Silk Cayes proposed marine reserve							
1	***What country do you live in?*** *Ask for the state if USA/Canada*						
2	**Is this your 1st visit to Belize?**	Yes	No	**If yes, no. of previous visits:**			
3	**No. of people in your party:**	Gender of surveyee:	Female Male	**Profession:**			
4	**What is your age group?**	Under 20	20-29	30-39	40-49	50-64	65+
5	**Nights spent in Belize:** **Nights spent in Placencia:**	**Where are you staying in Placencia:**		**Where else are you visiting in Belize?**			
6	**What is the total cost of your trip to Belize airfare included (US$)?**	<1000	1001-1500	1501-2000	2001-3000	3001+	
7	**Are you visiting Belize to dive or snorkel?**	Snorkel	Dive	Other (please specify):			
8	**Are you in Belize specifically to encounter whale sharks?**	Yes	No				

9	IF 8 is a "NO" then go to 10, IF "YES" then ask: **Will you book or have you booked a whale shark tour while you are here?**	Yes	No	**If yes, how many days spent on whale shark tours?**	**How much did you pay (US$) per whale shark day trip/tour?**	
10	**How many dives or snorkel days do you have planned during this trip?**	(Specify no of dives or days snorkeling)				
11	***IF no. 7 is a YES THEN ASK 12-14:* How many years have you been diving?**	Less than 1	1-5	6-10	11-15	16+
12	**Level of certification?** Certifying org:	Open water	Advanced	Rescue	Divemaster	Instructor+
13	**How many dives do you do a year?**	0-10	11-20	21-30	31-50	51+
14	**Where else have you dived or snorkeled in the world?**					
15	**Have you visited the Silk Cayes?**	Yes	No	***ASK 16 and 17 only if on a trip that takes them out to silk cayes and or a whale shark tour***		

16	**Please rate the importance of the following marine life to your diving experience at Gladden/Silk Cayes**	Very important 5	important 4	average 3	Not so important 2	Not important at all 1
	Whale sharks					
	Other sharks & rays					
	Dolphins					
	Large schools of reef fish (Jack, snappers)					
	Large reef fish (barracuda, grouper)					
	Other reef fish (triggerfish, spadefish, butterflyfish)					
	Lobsters, conch					
	Other (please specify):					
17	**How important are the following physical attributes to your diving/snorkeling experience?**	Very important 5	important 4	average 3	Not so important 2	Not important at all 1
	Coral cover					
	Warm water					
	Good visibility (65+ feet/20m)					

Ask the following only if surveyee is on a whale shark tour

18	**Have you encountered whale sharks in Belize yet?**	Yes	No			
18a	**Did any of the sharks have tags**	Yes	No	ID tags?	Pingers?	Sat-tags?
18b	**What numbers did you see on the tags?**					
18c	**Did seeing the tags on the whale sharks detract from your experience?**	Not at all	A little	A lot		
19	**How do you rate your encounter with whale sharks in Belize?**	Excellent	Good	Satisfactory	Poor	Very poor
19a	**How large was your dive/snorkel group?**					
19b	**On the dive/snorkel, did you feel that there were:**	Too few people	Too many	Just right		
19c	**What would be the perfect sixe of a whale shark dive/snorkel group? (estimate)**					
19d	**Would you be willing to pay more to dive in a smaller group making the experience more exclusive?**			Yes	No	
19e	**If yes, how much more (US$)?**	$10	$20	$30	$40	$50

20	**What made the encounter excellent/good/satisfactory/poor/v. poor:**					
21	**Had you dived with whale sharks before?**	Yes	No	**Where?**		
22	**What is the most you would be prepared to pay for your daily Belize whale shark trip?**					
23	**How did you find out about the whale shark tours in Belize?**	Friend	Internet	Newspaper or magazine article	Travel organization	Other:
24	**Which tour guide or resort are you diving/snorkeling with?**					
25	**Did your tour guide say how you should behave in the presence of whale sharks?**	Yes	No			
26	**How do you rate the whale shark briefing?**	Excellent	Good	Satisfactory	Poor	Very poor
27	**Did you or anyone else in your group touch a whale shark?**	Yes	No			
Ask the following to all surveyees:						
28	**Have you ever visited, snorkeled or dived in a Marine Protected Area?**	Yes	No	**Where:**		

29	**What is the most you have paid to visit an MPA (US$)**	0	1-5	6-10	11-15	16+
30	**Did you know that Gladden Spit/Silk Cayes was declared a marine reserve in 2000?**	Yes	No			
31	**What daily entrance fee would you be willing to pay to protect Gladden Spit, the Silk Cayes and its fish? (US$)**	0	1-5	6-10	11-15	16+
32	**How important is the presence of whale sharks at Gladden Spit in determining the daily entrance fee?**	Very important 5	important 4	average 3	Not so important 2	Not important at all 1
33	**Overall how satisfied are/were you with your trip to Gladden/Silk Cayes?**	Very important 5	important 4	average 3	Not so important 2	Not important at all 1
34	**How satisfied were you with your trip to Belize?**	Very important 5	important 4	average 3	Not so important 2	Not important at all 1
35	**Would you return to Belize?**	Definitely	Probably	Probably not	Definitely not	
36	**Would you like to return to Belize to dive with whale sharks?**	Definitely	Probably	Probably not	Definitely not	

37	**Will you recommend the whale shark experience in Belize to friends?**	Definitely	Probably	Probably not	Definitely not	
38	**What suggestions would you like to make for the better management of whale sharks, whale shark tours, and Gladden/Silk Cayes Marine Reserve management (use back for more space)?**					

39	**Any further comments or suggestions you would like to make (use back for more space)? Anything you'd like to be quoted on?**	

Appendix 7.C 2002 tourism survey instrument

Welcome to the Belize whale shark tourism survey

Thank you for taking part in our survey of Belize whale shark and Gladden Spit tour visitors. Your information and feedback are vital to understanding who is taking part in these tours. The information you provide is valuable in helping Belize manage its growing whale shark tourism and the Gladden Spit Marine Reserve. Survey results will be disseminated to whale shark tour guides, to marine conservation non-governmental organisations and the Belize Government.

Whale sharks are considered vulnerable by the World Conservation Union and are threatened by fishing in several regions of the world. In Belize, whale sharks also represent for many local fishermen a sustainable economic alternative to fishing the snapper spawning aggregation.

The information you provide will remain strictly confidential and you will NOT be identified with your answers. The survey should take about 20 minutes or less to complete. Once you have answered a question you will not be able to change your answer, so please answer all questions carefully. If you do not feel that a question pertains to your tour experience, please move to the next question. If you leave off the survey, you can come back to it and it will pick up where you left off.
Your time and effort are very much appreciated.

Belize-UK Darwin Initiative Whale Shark Research and Conservation Project Team
Belize and the University of York, UK

Encountering whale sharks

1. Did you encounter at least one whale shark during your trip to Gladden Spit and the Silk Cayes?

Yes No

Your whale shark encounter

Please take a moment to answer a few questions regarding your experience of diving with whale sharks in Belize.

2. Were you on a "whale shark tour" when you encountered the whale shark(s)?

Yes No

3. If you had one or several encounters with whale sharks, how would you rate them?

Excellent Good OK Disappointing Very disappointing N/A

4. What made your encounter excellent/good/Ok/disappointing/V. disappointing?

5. Had you encountered whale sharks before?

Yes No

6. Did any of the sharks you saw in Belize have tags, if so what type?

Numbered tag Acoustic (grey cylinder) tag Satellite tag No tags seen

7. Please note down the tag numbers you recorded during your whale shark encounter e.g. B-052:

8. Did seeing tags on whale shark detract from your experience?

Not at all A little A lot

9. Did you photograph a whale shark during your tour?

Yes No

10. Did you or anyone in your group touch a whale shark?

Yes No

Snorkeling or Diving?

11. Were you primarily snorkeling or diving on your trip to Gladden Spit and/or whale shark tour?

Snorkeling Diving Other

Snorkelers

If you were mainly snorkeling during your recent trip to Belize, please fill answer the following questions. Thank you.

12. How many days of snorkeling did you do during your recent trip to Belize?

1 2 3 4 5 6+

13. How many days snorkeling to you do a year?

0-10 11-20 21-30 31-50 51+

14. Where else have you snorkeled in the world?

Galapagos

West Pacific

West Coast of USA

Gulf of Mexico

Hawaii

East Africa
Australia
Mediterranean
East Coast of USA
East Pacific
Caribbean
Red Sea
Indian Ocean
Please specify sites visited

15. Do you own or rent your gear?

	Own	Rent
Snorkeling gear		
Camera gear		

16. Please rate the importance of the following marine life to your snorkeling experience:

	Very important	Important	Average	Not so important	Not important at all	N/A
Whale sharks						
Other sharks and rays						
Dolphins						
Large schools of reef fish (over 300 fish)						
Large individual reef fish (barracuda, grouper)						
Other reef fish (triggerfish, spadefish, butterfly)						
Lobster, conch, octopus						
Turtles						

17. How important are the following physical attributes to your snorkeling experience?

	Very important	Important	Average	Not so important	Not important at all	N/A
Coral cover (over 50% cover)						
Warm water						
Good visibility (over 20m or 60ft)						

18. Compared to other sites you have snorkeled, how would you rate Gladden Spit?

Superior to other sites	Above average	Average	Inferior to other sites	Very inferior

Divers

If you were mainly diving during your recent trip to Belize, please answer the following questions. Thank you.

19. How many dives did you make during your recent trip to Belize?

1-2	3-5	6-10	11-15	16-25	25+

20. How many years have you been diving?

Less than 1	1-5	6-10	11-15	16+

21. What is your level of dive certification?

Open Water   Advanced   Rescue   Divemaster   Instructor

22. Who is your primary dive certifying organization?

PADI   NAUI   SSI   YMCA   CMAS   BSAC   Other

23. On average, how many dives do you do a year?

Less than 10   11-20   21-30   31-50   51+

24. Where else have you dived in the world?

Mediterranean

Indian Ocean

West Coast of USA

West Pacific

Red Sea

Galapagos

East Africa

Australia

East Coast of USA

Gulf of Mexico

East Pacific

Hawaii

Caribbean

Please specify sites visited

25. Do you own or rent your dive gear (assume that the dive shop provides weights and tanks)?

	Own	Rent
Mask,fins, snorkel		
BCD		
Regulator		
Wetsuit		
Camera equipment		

26. Please rate the importance of the following marine life to your diving experience at Gladden Spit:

	Very important	Important	Average	Not so important	Not important at all	N/A
Whale sharks						
Other sharks and rays						
Dolphins						
Large schools of reef fish (over 300 fish)						
Large individual reef fish (barracuda, grouper)						
Other reef fish (triggerfish, spadefish, butterfly)						
Lobster, conch, octopus						
Turtles						

27. How important are the following physical attributes to your snorkeling experience?

	Very important	Important	Average	Not so important	Not important at all	N/A
Coral cover (over 50% cover)						

Warm water
Good visibility (over 20m or 60ft)

28. Compared to other sites that you have dived in the world, how do you rate Gladden Spit as a dive site?

Superior to other sites	Above average	Average	Inferior to other sites	Very inferior

Your Gladden Spit and/or whale shark tour

Please tell us a little about the Gladden Spit and/or whale shark tour- you took on your recent trip to Belize. Your information will help us to understand who is visiting Gladden Spit and help tourguides to better cater to their whale shark visitors.

29. Did you visit Belize specifically to encounter whale sharks?

Yes No

30. Which Gladden Spit and/or whale shark tour operator did you use?

31. Did you? (Please answer even if you only undertook a Gladden Spit/Silk Cayes tour)

☐ Book a whale shark tour through a tour operator from home

☐ Book a whale shark tour through a dive shop from home

☐ Book a whale shark tour through a tour operator in Belize

☐ Book a whale shark tour through a dive shop in Belize

☐ Walk in and sign up on the day of the tour

32. How much did you pay in US$ for your Gladden Spit/silk Cayes or whale shark tour per day?

33. How many days did you go out on Gladden Spit/silk Cayes or whale shark tours?

1 2 3 4 5 6 7 8+

34. How did you find out about Gladden Spit and or whale sharks and whale shark tours in Belize?

☐ Friend

☐ Dive shop

☐ Article

☐ Internet

- Sign
- Travel Organisation
- Other (please specify)

35. How many people excluding the divemaster were in your last dive or snorkel group? If you were on a boat-based tour only with no water activity, then please note the number of people in the boat excluding the captain.

1-5 6-10 11-15 16-20 20+

36. As regards the group size, did you feel that there were:

Too many people Too few people Just the right number

37. In your estimation what would be the perfect size of a whale shark dive, snorkel or boat-based group?

38. Would you be willing to pay more to dive, snorkel or have a boat-based encounter in a smaller group, making the experience more exclusive?

Yes No

39. IF yes, how much more per dive (US$) would you be willing to pay to make the experience more exclusive?

10 20 30 40 50 more

40. Considering that the Belize whale shark aggregation is one of the densest and most predictable in the world, what is the most you would be prepared to pay in US$ for a day-long whale shark trip in Belize?

41. Did your whale shark guide brief you on how you should behave in the presence of whale sharks?

Yes No

42. How do you rate the whale shark briefing?

Excellent Good OK Unsatisfactory Very unsatisfactory

Gladden Spit Marine Reserve

Your feedback on the Gladden Spit Marine Reserve is invaluable in helping to better manage the area and its visiting whale sharks.

43. Did you visit the Silk Cayes during your recent trip to Belize and Gladden Spit?

Yes No

44. Before your trip, did you know that Gladden Spit and the Silk Cayes form part of a marine reserve?

Yes No

45. Please indicate whether you support or oppose each of the following for Gladden Spit-silk Cayes and/or whale shark tours in the Gladden Spit Marine Reserve. Although none of these ideas are currently regulated we are interested in your feedback to better understand the site's visitor clientele.

Strongly support Support Neutral Oppose Strongly oppose

Implement a daily marine protected area fee for Gladden Spit and Silk Cayes

Set a limit on the number of dive and snorkel boats allowed to operate in the Gladden Spit area

Set maximum number of divers or snorkelers per boat

Require guides to provide a detailed briefing on whale sharks and Gladden Spit

Set a daily limit to the number of people allowed to visit the Silk Cayes

Enforce a 'no-touch' policy with whale sharks

46. Had you ever visited snorkeled or dived in a Marine Protected Area before Gladden Spit?

Yes No

47. If yes, which marine protected areas have you visited?

48. What is the most you have paid to visit a Marine Protected Area (in US$)?

0 1-5 6-10 11-15 16+

49. To finance the management of marine reserves in Belize including Gladden Spit and the Silk Cayes Marine Reserve, several tourist fee structures are being considered in Belize. Please indicate whether you agree or disagree with the following statements about marine reserve tourist user fees.

I would prefer to:

Strongly disagree-1 Disagree - 2 Neutral - 3 Agree - 4 Strongly agree - 5

Pay a fee only for the marine reserves I visit

Have the fee collected locally during the visit to the marine reserve

Pay a regional fee that covers visits to marine reserves grouped together in North, Central, South sections

Have the fee collected upon entry to Belize

Pay one fee at the start of my trip in Belize that covers visits to all marine reserves in country

50. Some divers and snorkelers feel that Gladden Spit and the Silk Cayes and its whale sharks and fish require additional management and protection by national and local organisations. These efforts will cost money and must be financed in some way (e.g., licence fees, higher diving-related expenses, taxes, etc.).

If additional management and protection meant that each visitor to the marine reserve would pay US$8 more per day, would you dive or snorkel with whale sharks and fish aggregations at Gladden Spit?

Yes No

51. If you answered "No" the question above, is this because you:

Believe this daily fee to visit and protect Gladden Spit is too expensive

Believe this daily fee to visit and protect Gladden is too cheap

Don't believe in paying a daily fee to visit a protected area

Other (please specify)

52. How important is the presence of whale sharks at Gladden spit in determining this daily entrance fee?

Very important	Important	Average	Not so important	Not important at all

53. How satisfied were you with:

	Very satisfied	Satisfied	OK	Disappointed	Very disappointed	N/A
Your trip to Gladden Spit and the Silk Cayes?						
Your trip to Belize?						

54. Would you:

	Definitely	Probably	Probably not	Definitely not	N/A
Return to Belize?					
Like to return to dive or snorkel in Belize with whale sharks?					
Recommend the whale shark experience in Belize to friends?					

55. What suggestions would you like to make for the better management of whale sharks, whale shark tours and the management of Gladden Spit and the Silk Cayes?

Getting to know more about you as a whale shark tour visitor

The following questions will help us to know more about whale shark visitors which will help Belize to better manage whale shark tourism and cater to visitors. The information you provide will remain strictly confidential and you will NOT be identified with your answers.

56. Are you?

Male Female

57. What is your age group?

Under 20	20-29	30-39	40-49	50-64	65+

58. What level of education have you completed?

Grade school	High School	University undergraduate	Masters	Doctorate	Business or technical trade school

59. What is your approximate annual household income before taxes (US$)?

UNDER $20,000

$20,000 to $39,999

$40,000 to $59,999

$60,000 to $79,999

$80,000 to $99,999

$100,000 to $139,000

$140,000 to $179,999

$180,000 AND ABOVE

60. What country do you live in? If in USA or Canada, please also indicate the state.

61. Was this your first visit to Belize?
Yes No

62. If this was not your first trip to Belize, how many previous trips had you made?

63. How many people accompanied you on your trip (excluding yourself)?
0 1 2 3 4 5-8 9-12 13+

64. What is your profession or professional field? (please pull down the menu)
Self-employed
Construction
Medical Doctor
Nurse
Researcher
Administrator
Manager
Director
Salesperson
Homemaker
Artist
Writer
Teacher
Volunteer
Student
Other, please specify.

65. How many nights did you spend in Belize on your most recent trip?

66. How many nights did you spend in Placencia?

67. Where did you stay in Placencia? (please pull down menu)
Hotel
Resort
Rental Apartment
Boat
Friends
Other

68. Where else did you visit or stay in Belize?

69. Was your trip a package (airfare, transfers, meals, lodging, diving all included)?
Yes No

70. On your recent trip to Belize, how much did you spend in total (US$) on the following items (we would like to know how much you spent personally, or your share - if '0', please enter '0' in the blank.) Estimate to the nearest $10.

If you were on a package trip please go straight to question 72 after filling in 0 in the spaces below. If you live in Belize please go on to questions 71.

Airfare to Belize

Transportation in-country
Lodging (hotel, resort, rental, etc)
Restaurant meals
Groceries, drinks, etc
Leisure (diving, caving, kayaking, etc)
Rental of equipment (diving, snorkeling etc)
Tips
Purchases

71. How much did you spend in US$ in Placencia or nearby communities (Seine bight, Mango Creek, Hopkins, Monkey River)?
Please estimate to the nearest $10.

Transportation (boat, taxi, etc)
Lodging (hotel,resort, rental etc)
Restaurant meals
Groceries, drinks, etc
Leisure (diving, kayaking, boat trips etc)
Rental of equipment (dive, snorkel gear etc)
Tips
Purchases

72. What was the total amount in US$ that you spent on your recent trip to Belize? If you live in Belize, please put down the total amount for this in-country trip to encounter whale sharks.

73. Was the survey completed by the person to whom it was addressed?
Yes No

74. Is there anything else you would like to share with us?

75. Would you like to receive the survey results when the study is completed?
Yes No

Thank you

Thank you very much for taking the time to complete this survey. Your feedback is invaluable in helping us understand who participates in whale shark tourism.

This information will be summarised and given to the whale shark tour operators, the managers of Gladden Spit Marine Reserve and the Belize Government for the management of Gladden Spit's natural resources.

Appendix 7.D

Visitor recommendations for the management of the GSSCMR made in 2001 and 2002

Survey 2001 - What suggestions would you like to make for the better management of whale sharks, whale shark tours and the management of Gladden Spit and the Silk Cayes?

1. More education components with tours. Better publicity that Gladden/ Silk is an MPA
2. Conservation. Control of fishing area
3. Laws. No so many tourists. Fishing (decrease)
4. Lack of info makes it difficult to comment
5. None
6. The least amount of harassment for sharks
7. Inconsistent knowledge about whale sharks (from Hotels, guides, etc.)
8. Tour somewhat hectic in going out due to weather complications. If entry fee is collected should be used HERE for preservation and research. Tourism should be limited so as not to interfere with normal whale shark behavior.
9. Doesn't know enough about area to make suggestions
10. Keep pollution down. Perhaps visitation #'s. no fees for Belizeans
11. Restrict # of daily divers/ snorkelers. Restrict fishing. Control distance divers should be from shark. Restrict boat size
12. Education. More information on WS from tour guides
13. Don't let it get too crowded and be a tourist trap. Leave it how it is and have people be respectful of marine life
14. Install moorings to minimize anchor damage
15. Guarantee for max four size. More info-leaflets on WS and general area. Donation to marine reserve and mechanism for using it.
16. No
17. Coordinate with dive shop to ensure # of snorkelers & divers are predetermined
18. Need to know it's a protected area to promote its conservation. High price to limit people for park.
19. Garbage is distressing on the beaches and in the water.
20. There were many people camping there, and there was some garbage on the beaches. Also, there did no appear to be any sanitation stations for those campers. Are the campers charged a fee at all or educated on how to dispose of garbage?
21. Control on volume of people if needed. Limit amount of fishing in the area
22. Education. Continued look at who should be managing this resource
23. Do not know a lot about whale sharks- provide further info about the area
24. Restrict # of boats in area. Only allow boats in certain areas. Full-time ranger
25. More info needed and answer more background. Prohibit commercial fishing when it is damaging. Keep pollution to the minimum
26. Keep clean (ocean) and oil free
27. Likes the fact that the area is relatively undeveloped/ undisturbed
28. Make more information available about WS life history and conservation
29. Not allow beginning snorkelers/ divers to come to Gladden. Limit on numbers tourists in MR. Classes on whale shark for tourists more info. on whale shark.
30. Very satisfied with experience

31. More information available to people, especially divers
32. Reducing the number of boats. Briefing about the whale sharks learn more about them(show an introductory video)
33. Mejor manejo de lanchas con cuerda y linea y escalera (better handling of boats with ropes, lines and a ladder).
34. It would be very good to instruct better the people on the boats to handle the group safer and easier like throwing a rope to help the divers to hold it before they return to the boat. It is clear that to see the whale sharks is a matter of good luck but a better training to the company to make it easier and safer is welcome.
35. Need more trained guides. Control on snapper fishing (especially night fishing). Enforcing park laws/ rules
36. One time fee vs. daily fee. Strong legislation of PA with community support with money invested for enforcement capable of dealing with net pressure. Universal regulations for tour operators including research. Limit # of boats tour, research. Regulations be conservative and precautionary.
37. Divers to dive masters. Info available on migration, biology of the sharks to tour guides
38. Park fees should be charged but tourists should be informed as to where funds are going. Educate guest on area/ WS etc. Laminated brochures would be great to circulate on board.
39. Interpretive sign on Silk Caye about being a marine reserve. Pass out brochures at dive shops about habitat, life cycle. Have dive master brief about the tags so people won't be surprised/ feel bad about seeing something on the shark
40. Regulate # of tours/ tourists
41. Divers should be briefed and educated on the whale sharks, area, etc.
42. Control the amount of fishing and tourist boat that go out to Gladden Spit
43. Bring a lot of tourists here. More education about regulations
44. Control the number of dive boats that enter
45. Have guest properly briefed on importance of preserving, respecting, and protecting the reef
46. Crowd control
47. Control #s of people at Cayes.
48. Do not let snorkel boats follow the dive boats
49. Good briefings, diver etiquette, limit # of dives/day
50. Don't over book # of boats to the MPA
51. Keep protecting the whale sharks
52. Not really
53. No
54. More info on whale shark esp. on the whale shark
55. Not sure- whole experience very positive; feels that there is some level of monitoring
56. Lack of information to answer question
57. No garbage
58. No
59. Better planned trips for snorkelers. Protect the whale shark from too many tourists
60. Silk Caye camping be limited to certain # of campers at any time
61. Like more information on WS. Carrying capacity!
62. Well managed.
63. Only dive shops who show responsibility should be able to go there
64. Tour operators should be certified as WS divemasters and operators. Control # of boats and tourists. Need enforcement

65. Make sure tour guides acknowledge enough information about whale shark and whale shark tours
66. Instead of having the attitude of whose better at finding whale sharks dive shops-operators/ guides should together a bit more pool their ideas and thoughts together so more people will have the opportunity to see these wonderful/ rarely seen creatures. It seems to me that there is jealousy about who know the most about whale sharks. This is a beautiful, beautiful country and I would be sad and depressed to know that it was being destroyed like our beautiful rainforest in Canada (British Columbia). Hope to enjoy your beautiful country again.
67. Instructions key to create more of a team effort with the divers so divers are less competitive in trying to see the whale sharks (aggressive divers scared them away)
68. Wardens to patrol area. Clean up litter. Restrict # of visitors. Shelter for tables. BBQ grill
69. Want area board anchored inside
70. Come to Silk Caye to rest more leisurely. More benches
71. Limit the number of divers per day. Set guidelines for diver behavior while with whale sharks.
72. Mooring, bathroom
73. Not the place for first time divers use checkout dives. Limit # of dives on the area. Limit # of boats/ divers. No anchoring, suggest mooring
74. Limit # of boats & people per boat. Restrict speed limits of boat in the area
75. Educating the people

Survey 2002 - What suggestions would you like to make for the better management of whale sharks, whale shark tours and the management of Gladden Spit and the Silk Cayes?

1. Enforcement of conservation policies within the reserve to eliminate illegal fishing etc. Connect the reserve to the well being of local communities so that they see a direct link between the conservation of the Marine Resource at Gladden and their own well being.
2. Space dive groups apart too many times we ran into other operators and the scene underwater was confusing. Who belonged to who...who was at what depth
3. I found the Diving Guide from Roberts Grove to be very misinformed about environmental issues and protection. He was enthusiastic about the marine reserve but failed to connect the pending land development on the peninsula with issue of long-term sustainability of the marine environment. He did not understand that protection is not the same as sustainable management. If this is a prevailing attitude then the entire marine environment is threatened. Better regulations relating to land development, sewage, garbage, boats, etc. is critical to life in the marine reserve and the entire peninsula eco system.
4. The number of dive boats/ divers on Gladden Spit should be strictly limited. I fear strongly that the line between observation and interference will be crossed all too easily with too many boats/ divers. Also for selfish research and sustainable eco tourism reasons if there are too many boats / divers then there must be a strong possibility that the whale sharks will become wise to the divers and sightings will become less common
5. Continue to develop the international recognition of these sites and their global ecological significance
6. Based on my experience right now the briefings prior to diving/snorkeling with whale sharks are very poor. One woman on our boat had no idea of the dive plan or

activities prior to boarding (and departing). There were little or no announcements about the expected conditions (which were rough) or the length of boat ride (which was long -- over one hour each way). And I felt that there wasn't much attention to the safety of the clients during our dives. Several were very poorly led and the divemaster seemed to have little idea of what he was doing and seemed only to want to be done with the dive. If anything, I think the local operators need more training than the clients.

7. Introduce standards for boat size and type. In bad weather beginners or snorkelers should not be taken out.
8. People who can't manage to follow the instructions given by boat captain and dive master should not be allowed to dive. It ruins the experience for all on the boat.
9. Strong oversight of dive operations going to Gladden Spit...briefing could have been better. Perhaps you could give out a sheet to read prior to the dive not only on how to behave but about the whale shark itself. Stop the guarantee...this only encourages false expectations. Warn divers prior to signing up that there are other dangers inherent in this type of dive...shark encounters for example are more likely...
10. 1) The fishermen need to be persuaded/taught/regulated to lay off the spawning aggregations until the fish have spawned. There were several fishing boats working the snapper aggregation at the May full moon; and I heard of (I did not see this firsthand) a lot of snappers being cleaned with ripe unreleased egg sacs. Quite apart from the issue whether whale sharks will return to Gladden Spit if the snapper populations are significantly diminished the long run sustainability of the fishermen's livelihood will be better served if they allow their target populations to reproduce. 2) As for your exampled fee amount of $14 US per day -- that is much too high to be economically viable for several reasons. If such a fee were levied, all diving other than whale shark diving would tend to shift to sites outside the marine reserve. Other than to see the spawning aggregations and whale sharks, there is absolutely no reason for recreational divers to dive at Gladden Spit. And Silk Caye sites, such as North Wall and White Hole (assuming they are within the reserve, I'm not sure) are nice but no better than numerous barrier reef and faroe reef sites in southern Belize. So it is probable that recreational diving other than whale shark diving would for the most part be diverted to sites where the fee was not applicable. As for whale shark dives, $14 is too high in view of the fact that whale shark encounters are decidedly not a sure thing. Local dive operators have been getting a large premium for the whale shark trips. Brian Young/Seahorse Dive Shop was charging US$150+tax; Vance Cabral/ Advanced Diving was charging US$130+tax; this for two-tank dive trips that probably cost them no more to conduct than the two-tank barrier reef trips they do for US$75+tax. As word gets around through dive clubs and internet dive-related message boards that whale sharks were not seen at the May snapper spawn, demand for and thus the premium paid for the whale shark trips will decline. An attempt to levy a significant additional fee on an already overpriced service will likely exacerbate a decline in demand for that service. Finally $14 will meet resistance from divers if not from dive operators simply because it is egregiously high relative to marine park fees levied elsewhere. The highest fee I remember paying is US$5 per day at Hol Chan (and will not pay again given that diving within the park is inferior to that available at Ambergris Caye sites outside the park). Cozumel Marine Park now assesses a fee of US$2 per day. The fee at Bonaire Marine Park is only US$10 per year. Most marine parks do not levy a fee (or perhaps assess the dive operators who include the fee in their price).
11. Our dive was strictly a blue water dive. If whale sharks are not seen the dive is not much fun. While we we're in our formation a boat came over us and dropped off snorkelers. I thought if that is very attractive to the whale shark. I would recommend

that traffic in the area be regulated as how to release divers and snorkelers. Reduce traffic in the area. Reduce the number of people at one time in the area. Reduce the speed/noise in the area. Boats should come quietly in the area drop people off and move off to the sides.

12. Overall the experience was great. I brought 12 other people to visit Belize. I have been before. This time it was to visit the whale sharks...no one seemed to be disappointed not to see them...but it would've been nice. That's just nature!!!! I would hope the tagging would help determine where the sharks are and maybe help the divers have more of an idea (and the dive masters) where the sharks are. It kind of felt like we were looking for the fishermen and relying on what they said. They seemed to give conflicting info. Which makes me wonder do they really want the divers invading there fishing holes???? Why do they want to tell the divers the sharks are under them???? The locating aspect seems like the most prominent point of improvement. I love Belize and will return within a year....and the research group was informative friendly and attractive....I'm envious of the job.
13. Don't over regulate.
14. The whale shark trips need to be done by permit with a naturalist (?) present on each boat.
15. The resorts are charging an arm and a leg already to visit Belize and the reef is one of the least healthy I have ever seen. I would suggest a fee to protect the reef and whale sharks, but it needs to be: you see the sharks, and then you pay. We paid $75 extra each just to go out to see whale sharks and never saw one. At the current price of a trip to dive there and see whale sharks I would rather take my wife to Galapagos and see a lot of other special critters too. I would suggest getting the dive operators together and working out a better way to make the overall trip to Belize cheaper so that you can attract divers and then implementing a plan where the divers pay additional charges of around $10 per person if they do see whale sharks and maybe a $5 per day of diving fee for going to Gladden Spit and the Silk Cays. This way you would invite tourism to help the economy and get funding proportional to the number of divers you have visiting. Also boat size should be limited so that Dive Masters can keep a better eye on divers and prevent the mauling of the reef.
16. The pica pica at Gladden is a problem for many divers and should be discussed before divers go there. It is NOT caused by jellyfish but by a cyanobacterium *Trichodesmium erythrium*, which does not respond to most cnidarian medications. Divers should put on additional oily lotion before diving in cyanobacteria and should lather with soap after exiting the water. We are working on a project to identify the toxin and develop a better treatment. More as it is available.
17. None
18. I felt we were ripped off and taken advantage of. I will definitely return to Belize but not to Placencia
19. Tour operators are not honest about the likelihood of seeing a whale shark if you are snorkeling. There were no fish on the first trip and on the second the single fish was too deep to spot. I felt manipulated by both tour operators. They greatly exaggerated our chances of seeing one particularly the first operator.
20. If fees are to be charged.... MAKE SURE THE PROCEDES GO TO ENFORCEMENT OF COMMERCIAL FISHING AND MANAGEMENT FEES....NOT SOME GOVERNMENT COFFER... I know how fees can get lost in the cutting of the pie.

Appendix 7.E

Visitor comments on their encounter with a whale shark at Gladden Spit made in 2001 and 2002

Survey question: What made your encounter with a whale shark excellent/good/etc.?

1. I only had a brief look at a single whale shark but it was great to be out there amongst them.
2. These sharks are the biggest fish in the world so that in it's self-made it very exciting to see them and be right next to them (I didn't actually get in the water because I was so afraid of the massive fish). Also the whale shark is such a rare fish to see so it was probably a once in a lifetime opportunity!
3. They came right up to us as if to give us a close up encounter!
4. The dive guide did a wonderful job with keeping our group together and informing us on the possible movements the sharks might make.
5. We saw the whale shark/sharks at least 6 times and got amazing photos of them. They came right up to the boat and appeared very curious.
6. The guides were very professional and stayed with us at all times, so I felt very informed and safe. We were so close that I could of touch them. Also the beauty of the snapper fish.
7. Able to snorkel and dive with them quite close up, which is a remarkable experience.
8. Being able to see the whale shark in its natural habitat. Being able to snorkel with them hopefully this does not disturb them.
9. The beauty of the nature snappers, the 5 whale sharks at the same time the last day when we went with a different dive master. Excellent as the activity with the tunas: 3 different species, sharks, silky ones, snappers, all in the surface, wonderful although the diving organization was not too professional.
10. It was the most exciting experience I've ever had & I've been a commercial diver for 21 years all over the world & lived in Belize for 23 years.
11. The gentleness and beauty of the animals. I saw 9 the first day and 15 the next. And the spawning dog snapper were amazing as well.
12. Just seeing one
13. Beautiful creatures.
14. We only saw one whale shark (or at least we think it was the same whale shark over and over again) but he/she spent a lot of time near our fishing boat. In other words we didn't just catch a glimpse of the whale shark but we got to hang out with it.
15. The excitement of being so close to such a large gentle creature
16. I was at the surface w/ ear trouble and personally missed the whale sharks
17. The beauty and appearance of these creatures.
18. The whale sharks themselves was like watching the cross-town bus glide by 80 ft under. Extraordinary experience. Lifetime memory. I've gone a few trips and didn't see them but didn't care. I knew nothing was guaranteed and would go again risk seasickness and bumpy seas to see another.
19. Learning about the relationship between fish spawning and whale shark behaviors. In my opinion the fish spawning was even more impressive than the sharks but many would likely disagree with me on that.

20. The fact that there were only three of us in the boat including our guide. My husband jumped in and swam with the whale shark the whole experience was fun.
21. Simply a spectacular experience to see these magnificent creatures in the wild. We were on a snorkeling fishing trip when we came upon two whale sharks. One tagged, one not. We jumped in the water and snorkeled with them in amazing visibility and close to the W. Sharks
22. What an excellent experience! I felt both fear and excitement as I hopped in the water. Intellectually I understood that whale sharks are primarily plankton feeders but emotionally when it looks like a shark, swims like a shark and is the size of a small bus, it was more than thrilling.
23. Frequency, closeness, variety
24. It took three days to find them...when they arrived the wait made it better. That they stayed around us for so long made it very interesting. My worry is that the area will become over- dived...on one day there were about 5 groups of divers...too many to my mind and I fear this will cross the line between observing and interacting/ interfering the latter of which I hope you can guard against
25. The sea was quite rough and as there was no ladder to get back on the boat I was apprehensive to not be able to get back onto the boat so I didn't go into the water and only saw the whale shark through the water with its fin sticking out.
26. Out guide's interpersonal skills and his knowledge of the environment were major factors in the excellence of my experience.
27. Amazing creatures and a privilege to see them (finally after > 1000 dives!) in person!
28. I have never experienced anything so amazing - I couldn't believe how close the sharks came to us.
29. I was diving and we were well below the area where the whale shark was swimming. I would have preferred to be more or less on the same level so that the views could have revealed more detail. As it was the shark was only a dark shadow against the lighter surface.
30. The number of whale sharks seen in the water and witnessing the actual spawning of snappers
31. They were beneath me in murky water so I could not see them very well. My cohorts who were deeper had a great time.
32. We were able to drift in very near to the whale shark (in a boat) and got a good look. We ended up seeing the shark (or possibly more than one) for about two hours.
33. They were difficult to see because they swam around me at all angles.
34. First encounter with such a large animal. There were at least 2 possibly 3 seen during one dive.
35. We encountered whale sharks on both dives: two on the first dive and at least four on the second dive. Each dive resulted in at least one 'close pass' by a shark.
36. Just a truly amazing sight - there is nothing better then seeing any living creature in it's natural environment
37. Their beauty and size were stunning. To be surrounded by several whale sharks while in the midst of a spawning aggregation was amazing. I only wish I could have taken better pictures.
38. Having spent 16 years as a Federal Fisheries Biologist at Scripps Institute of Oceanography, I have an appreciation for pelagic species and have done little work on inshore fisheries such as the snapper. To have been in the middle of the snapper spawn with 5 whale sharks feeding on this soup became as close to a religious experience as one could ever imagine. I am impressed that some of your protectionism is focused at the snapper for their congregation at Gladden is more remarkable than the whale shark present to capitalize on this activity. A concerted

effort MUST be made to limit the hand line fishery for these fish or you can kiss the snapper and the whale sharks.... GOOD BYE

39. Being in small groups instead of cattle herding. Taking part in research instead on only diving for fun. Being with people who respected the sharks and not wanting to touch or ride them.
40. Impression of big creatures moving close to me. Disappointing was the fact that there was so many people under the surface.
41. I came to Belize specifically to see the whale sharks. I had come a few years earlier and gone without a sighting. I went out for a week and saw the whale sharks on my last two dives. They were so gentle, calm, graceful, beautiful. The visibility was good on the first dive. The shark came straight from the deep and circled us three times. The second shark was much bigger but the viewing was clouded but limited visibility.
42. At first I didn't believe really to see one. And then when the whale shark appears - it was great. Although the whale sharks are so huge, they are so peaceful, silent and seem so vulnerable. The next good thing was nobody from our group got nervous or want try to touch the whale shark.
43. I swam with the whale shark we encountered! What a great experience!
44. V. weak swimmer who having jumped in backwards into 6000m of open water saw only the fin of the whale shark and then concentrated on not drowning and getting back to the boat with only snorkeling gear. Maybe one day I'll swim and float better and be able to go under and experience a meeting with the royalty of the seas!
45. The incredible number of animals
46. We saw 6 in a single dive!!!!!!!! This was after 5 disappointing days of seeing none.
47. Several whale sharks in the water (3 or 4). Dive was conducted with individuals who were doing whale shark research, and provided excellent pre and post dive info.
48. Took a while to find one but the wait was worth it!
49. Proximity, number, size, visibility
50. We merely saw a shadow of one from our boat.
51. I hope you're not looking for the short answer! I had a great experience. After three days of no show at the critical full moon we had encounters on four consecutive dives. While the whale sharks were smaller than I anticipated (I have since learned that immature males are typical to the area) I was awed by the experience. By far the most fantastic encounter was with a single whale shark that we saw on the surface before entering the water with SCUBA gear. The dive master and I were the first in the water to swim with the shark. I am an avid free diver and this was my dream come true. The shark seemed to have absolutely no fear of humans and on the contrary seemed unconcerned that there were twenty or so people many with cameras in the water following him. Thanks to my free dive skills and really long fins, I was a much faster than the group and was able to swim side by side with the whale shark. While I knew that divers are supposed to keep a distance and not approach the whale sharks the dive master had sort of been leading him and the whale shark seemed unconcerned. I was within arms reach but did not touch him, as I was told not to. The shark made no moves to distance himself and in fact I had to move out of his way. The shark seemed to at least accept if not somehow enjoy having me swim along side. So when the shark started to head for depth I went down with him. This was the best experience. As I went deeper I got in front of and below him. Rather than fleeing from me it really seemed that the shark was curious about me and followed. He could have easily outswam me and gone anywhere he wanted as we were probably at thirty feet or more and well below all the other snorkelers who remained on the surface. Maybe I'm crazy, but it seemed

like he turned with me as I turned back toward the group. He actually returned to the surface with me. He stayed there much to the delight of the others. The boat captain eventually called us back in. If not I'm sure he would have stayed with us much longer. The only negative part of the experience had nothing to do with the sharks but the behavior of the divers. It was a circus. It is really easy to get caught up in the experience and some of the divers do really stupid things. The rules regarding interaction with the whale sharks were somewhat unclear and I know in talking with dive operators in Placencia that they are only now being developed. It is certainly of the utmost experience to protect these amazing creatures. Yet I'm less immediately concerned with the shark interactions as I am that there may be a dive accident. Everyone gets caught up in the experience and for some basic rules of diving go out the window. The experienced divers seem to be the worst. It seems that the role of the great white hunter replaces common sense.

52. I was snorkeling while a large group below me was diving so it was very confusing with all the bubbles they were blowing up and I didn't expect to see any whale sharks. Then out of nowhere a 15-20 foot whale shark came gliding out of the deep blue and swam towards us gulping the bubbles. It was an awesome sight we got a spectacular frontal view of the shark feeding and then it veered off to the right within 5 feet of us - I got swooshed by its tail. Just breathtaking!
53. I wish I had seen more...
54. The sharks are just gorgeous! What graceful creatures. There was no touching or harassing the sharks, no trash dumped -- which makes me happy because it means I know the sharks are likely go to be in Belize for a long time.
55. We had 5 at the same time and they were very interactive
56. Just to see a whale shark was an awe inspiring experience
57. One whale shark showed remarkable curiosity about the divers initiating close contact even taking the time to nibble at the ends of my fins while I watched motionless at about 40 feet.
58. It was my first experience with a whale shark. The sharks are magnificent peaceful creatures.
59. Closeness. But it did take all afternoon to find one - our guide was very patient.
60. The divers on the boat were able to view the whale shark in about 120 ft (30km). We were snorkeling and the visibility was clouded near 100 ft.
61. The level of activity going on (when the sharks were there) was just overwhelming. Just watching the ball of snappers spawning was an amazing event in itself but then suddenly the sharks would appear and glide past you very closely. The arrival of the dolphins to cause havoc amongst the sharks was just the icing on the cake for the whole experience.
62. One was sun bathing and we could snorkel around I dived with our guide and his bubble/spawn routine really works the sharks came right for us.
63. Excellent guides, beautiful weather, fascinating scientific data gathering going on at the same time.
64. Too deep to observe
65. It was cool to see such a big fish.
66. TOO MANY BOATS, INADEQUATE SAFETY MEASURES FOR THE DIVERS AND SNORKELLERS LACK OF COORDINATION BETWEEN VARIOUS OPERATORS LEADING TO HAZARDOUS CONDITIONS. LACK OF INFORMATION IN ADVANCE ABOUT ROUGH CONDITIONS LIKELY TO BE ENCOUNTERED OUTSIDE THE REEF
67. The number of whale sharks present at the site during the spawning by the snappers. In addition we snorkeled with a whale shark feeding on small sardines which had

been balled up by skipjack, blackfin and little tuna as well as a dozen or more silky sharks in a spot about three miles east of Gladden Spit.

68. We did six dives in all to see the whale sharks and only saw them on the last day of diving (4/29). However on our second dive of that day we saw somewhere between 8 and 10 whale sharks all within the last 20 minutes of the dive. They were all around us. It was just incredible to see these huge creatures in their natural environment!
69. The size of the whale shark was incredible. A person hears how big they are but it isn't until one sees one that one actually realizes how big they are. Actually being on a tour and seeing the whale shark made my trip to Belize.
70. They didn't try to eat me.
71. Not exactly knowing what to expect. The guide was very knowledgeable.
72. On one dive we saw 8-10 sharks some at very close range.
73. The whale shark was approximately 60 ft. to 100 ft. away from us and seemingly unaware of us so I feel as though we did not disturb the animal. This animal is huge! Our siting was of one that was greater than 30 ft. in length (compared to our dive boat) and it had a lot of spots. The whale shark swam along below us and reminded me of a submarine motoring along its course.
74. The shark was everything I had anticipated
75. The whale shark was very far away. When we were here last year we saw up to 17 whale sharks and they were very close. We saw the Cubera Snapper spawning on two occasions so we know the time was ripe - we don't know what caused the whale sharks not to gather during this May's full moon cycle.
76. Very knowledgeable guide and respectful of the animals.
77. Just to see it so close was excellent even though it was a short time
78. Only saw a few
79. That we had 26 sightings in three dives. The six dives preceding the whale shark sightings got tedious. But with natural cycles it is understandable that things don't always work to a schedule. I'm just very grateful that we saw them because I flew to Belize just for this experience. I truly saw nothing else except the underwater experience of Gladden Spit and Placentia.
80. I saw four whale sharks and came face to face with one of them.
81. Closeness to the whale shark
82. Seeing sharks!!!
83. Did not see whale sharks
84. Because I like them and I think that is great to see them free.
85. Our guide was an amazing guide/ teacher
86. Weather, guide, country
87. Seeing the shark so close
88. Young children that were overexcited & too aggressive scared the whale sharks and made them dive down
89. Good guides, very small group there were only 4 of us snorkeling, nice people on tour
90. Only saw them from boat
91. I was surprised at the size of them. This is my first time diving with them.
92. Came very close, have looked for years so happy to see one
93. Number of whale sharks were amazing & seeing fish spawning was great too
94. Saw one from distance
95. Number & closeness of the sharks. Visibility & closeness was better in Thailand but surface contact was better
96. Whale shark brilliant to see. The size of them.
97. Great day, 7 whale sharks, excellent guide

98. Trying to see "Mr.Big" for 10 years. Very close
99. The whale sharks and the large spawning aggregation made up for the sub-par divemaster
100. Actually seeing them
101. Swimming with the sharks
102. Unique opportunity to be with largest fish in ocean, majestic gentleness. Anyone who saw them & wouldn't be warned could be dead
103. Saw more than seven of them
104. Just seeing one being able to video it and share it with friends
105. Excellent
106. First time seeing a whale shark
107. See fish spawning, # of sharks
108. Just seeing the whale shark
109. The shark was so close, so beautiful & you could see it so well
110. Seeing the shark. Several of them up close
111. Spag, seeing that many healthy reef fish, closeness of reef fish, numbers
112. Seeing the whale sharks
113. The large school of snappers and the whale sharks
114. Magnificent creatures! Nobody chased after it
115. Seeing interaction of fish & whale shark
116. Seeing whale sharks, wonderful waters, just being here
117. They came so close
118. Just seeing the whale shark, getting so close
119. The atmosphere and because they came so close
120. They came very close
121. Actual sighting, professional dive master, interest of group
122. First time experience
123. They came
124. They are something special & came close interaction
125. Good visibility, closeness to the whale shark, the slowness with which the experience lasted
126. Being very close to the sharks
127. The number we saw, ability to see them all around us
128. They came very close
129. Excellent
130. Great dive guides, driver
131. The blue to be so close 5ft away
132. The whale sharks, snapper spawning
133. Being too close to the whale shark
134. Biggest fish, they are gentle
135. Just great

Summary

1. **Whale sharks encountered at Gladden Spit do not form a functional population and are predominately transient juvenile males.** The original hypothesis that the population was small but functional is rejected. Reasons for the ontogenetic and sexual segregation of whale sharks at Gladden Spit occur elsewhere worldwide and may be based on differences in prey and habitat preferences, swimming ability and / or feeding efficiency. The sex-ratio of whale sharks and location and distribution of the sexes and mature individuals in the region is unknown.

   Implications: Location of mature individuals of both sexes needs to be identified and characterised to reveal and protect other important sites in the life cycle of whale sharks in the region.

2. **Whale sharks encountered in Belize are highly mobile.** The full extent of whale shark movement away from Gladden Spit is not known, but during the course of this study sharks visited all atolls and performed several movements across political boundaries throughout the Mesoamerican Barrier Reef. Movements charted in this study could be linked to the staggered appearance of relatively large abundances of whale sharks in the large marine ecosystem of the Caribbean Basin. This suggests that whale sharks are moving from one site of high productivity to another, e.g., Gladden Spit to the Yucatan, either circulating around the Caribbean Basin or by fringing the Mesoamerican Barrier Reef. The sharks do not appear to move in groups, and dispersed in different directions following the end of snapper spawning at Gladden Spit. Strong and rapid directed movements towards Gladden Spit in relation to prey availability suggest the existence of a memory map and well developed orientation skills.

   Implications: The fact that whale sharks are moving throughout a large region will require the development of regional protection for this species and the harmonisation of regulations controlling whale shark tourism. Movement with respect to shipping lanes and associated impacts should be investigated.

3. **Non-invasive photo identification of individual whale sharks negates the need for conventional tags.** A paucity of resightings information and apparent low tag retention or legibility limits the effectiveness of conventional tagging programs with whale sharks. Resightings can easily be assessed through photo identification based on spot patterns and scars – preferably using digital photography. Acoustic and satellite telemetry are preferable instruments to conventional tags in the study of large-scale movements and site fidelity.

   Implications: Phasing out conventional tagging of whale sharks and focusing on the use of photo identification can help to minimize invasive interactions with whale sharks and potential impacts of tagging on the sharks and increase visitor recreational satisfaction.

4. **Whale sharks show strong intra- and inter-annual site fidelity to Gladden Spit and can time their movements according the availability of spatio-temporally patchy food sources.** Whale sharks are highly vulnerable due to their spatio-temporal predictability, relative density, and surface-feeding behaviour. Sharks spent up to 10 hours within a 24 h period in a 1 km diameter site at Gladden Spit during the peak snapper spawning period. All fish spawning aggregation activity and whale shark feeding on spawn appears to have taken place within the confines of the marine reserve. Sharks do not show strong site fidelity to any of seven other spawning aggregation sites studied along the Belize Barrier Reef and atolls.

   Implications: Although the marine reserve encompasses the spawning aggregation and shark-feeding site, the eastern boundary should be extended outwards to encompass depth that whale sharks require during their oscillatory diving and create a larger buffer to counter illegal exploitation of fish. Enforcement of regulations for boat, diver and snorkeler distances from sharks and fish spawning aggregations is a necessary precautionary measure to mitigate human impacts and help sustain predictable whale shark visitation.

5. **Cubera and dog snapper spawn are an important component of juvenile whale shark diet during the limited peak snapper spawning-season at Gladden Spit.** It is not known why spawn is primarily important to juvenile males, although, changes in fish spawning behaviour in May 2002 led to a rapid decrease in predictable whale

shark sightings. However, stable isotope analysis suggests that zooplankton, located at a lower trophic level than fish spawn, is the most important component to these whale sharks' overall diet. Local perception at the start of the study suggested that whale sharks fed on mutton snapper spawn and possibly even grouper spawn, and therefore competed with fishers for the same resources. This does not appear to hold true. Observational and acoustic data suggest that they do not aggregate to feed at any other time of the day when mutton snappers or groupers are thought to spawn. Whale sharks were recorded only feeding on cubera and dog spawn, species that continue to be fished illegally at night.

Implications: Halting illegal night fishing is necessary to decrease pressure on the cubera and dog snappers as these species provide the basis for predictable whale shark visitation at Gladden Spit. Enforcing a night fishing ban will further protect the species spawning stock biomass and promote goodwill with local fishers and other marine reserve stakeholders.

6. **Whale sharks are physiologically very robust**, resisting temperatures under 4.5^{0}C, and depths of over 1000 m, abilities that enable them to utilise many parts of the water column in search of food or to orientate themselves. These results help to reject the study's null hypothesis that whale sharks are solely epipelagic. Diving behaviour is highly oscillatory with the majority of deep dives occurring during the day, often at dawn. Whale sharks reduce dive depth at night, possibly to follow the vertical migrations of zooplankton, a key prey. Whale sharks appear to possess a strong circadian and circalunar rhythmic component linked to diving. The activities linked to diving rhythmicity and the geographic locations of the sharks during these dives could not be elucidated during this study.

   Implications: The ability to withstand a range of environmental parameters may confer greater resilience and adaptability to this species as it orients in a patchy environment. These characteristics coupled with the ability to prey on a variety of prey located throughout the water column may further provide whale sharks with a buffer against environmental variability.

7. **The mutton snapper fishery at Gladden Spit is in decline.** The original hypothesis suggested that the small-scale hook and line artisanal fishery did not

impact the mutton snapper spawning aggregation. Catch per unit effort in the mutton snapper fishery declined significantly by 58.5% and led to a 4.2% reduction in fish size in three years (2000-2002). The fishery's worth was estimated at US$35,497 in 2002. This study's results coupled with historical accounts from Gladden Spit fishers of previous high CPUE and sizeable landings suggest that current CPUE, landings and reduction in fish size form part of a downward trend for the mutton snapper fishery. Rapid proactive management with enforcement of fishing regulations in the Gladden Spit and Silk Cayes Marine Reserve could stabilize and reverse the decline in the fishery. Revenues from the fishery are inferior to other locally available economic alternatives such as tourism.

Implications: At the current level of pressure, the fishery will continue to decline until fully exploited. Based on other cases of spawning aggregation extirpations in Belize and worldwide, once extirpated the aggregation may not rebuild. The precautionary principle should be applied whereby fishing on the aggregation during the peak reproductive season is halted. Conservation could be effected through a range of financial instruments including a fisheries easement that is partially subsidised by tourism. Continued development of economic incentives and alternative livelihoods for local fishers are required to ease the transition away from fishing, reduce pressure on spawning stock biomass, and offset the fishers' costs of protecting the spawning aggregations.

8. **Whale shark tourism at Gladden Spit is a lucrative industry with locally distributed benefits.** Worth US$ 1.35 million locally, benefits from whale shark tourism are broadly distributed either directly or indirectly throughout five stakeholder communities. Economically, whale shark tourism is a viable alternative to fishing the mutton snapper spawning aggregation, with the tourism worth 39 times more than fishery. Tourism is an imperfect social or cultural alternative for the older generation of fishers, but has gained acceptance with the younger generation.

   Implications: Whale shark tourism is providing large revenues for stakeholder communities but could destroy its resource base if it remains open-access. This will require strong management directives to establish and maintain tightly regulated closed-access tourism. It will also require the development of other economic alternatives for displaced fishers and other stakeholders unable to engage in whale shark tours.

9. **Visitors to the Gladden Spit and the Silk Cayes Marine Reserve are willing to pay a mean daily visitation fee of US$ 9.62 to underwrite management and conservation of the reserve and its fauna.** A survey established that the existence of whale sharks and satisfaction with the trip to the marine reserve were important in the willingness to pay a daily fee. The fee could cover basic marine reserve management costs estimated at US$ 175,000 yearly if tourism is promoted to the boat and visitor capacities suggested by the managers Friend of Nature (FON).
Implications: Management and conservation of whale sharks at Gladden Spit should focus on the management and protection of snapper spawning aggregations – the basis of whale shark predictability. Visitation at capacities suggested by FON may alter fish spawning behaviour and whale shark predictability, as witnessed in May 2002, when visitor and boat numbers at the spawning aggregation site were at their highest levels recorded. An increase in daily visitation fees may be necessary to reduce suggested visitation targets and sustain the tourism's resource base. Continued research is required to monitor the impacts of tourism levels in the marine reserve and adjust permissible capacities accordingly.

10. **Conservation of whale sharks requires a mixed strategy of protected areas and fishing bans.** This study demonstrated that marine reserves can be designed to adequately protect a migratory species such as whale sharks when sited in areas where they are vulnerable, e.g., the dense and predictable aggregations of surface-feeding sharks at Gladden. Highly productive yet spatio-temporally variable areas such as ocean-fronts are also important feeding grounds for many species of migratory marine animals including whale sharks, and should also be identified and targeted for protection. Whale sharks appear to move along corridors between productive areas on Mesoamerican Barrier Reef, e.g., Gladden Spit to the tip of the Yucatan Peninsula. These pathways also need to be investigated as protection targets, particularly in relation to shipping channel and cargo traffic.
Implications: Flexibility in approaches to conserve migratory marine species such as the whale shark is required. Coastal and open-ocean marine reserves that are

effectively policed are key building blocks in a conservation strategy for mobile species. Yet, however well designed and sited, the costs of open-ocean protected areas may be too onerous in relation to the perceived gains of conserving several migratory species. Protecting migratory marine species during all or most parts of their life-cycle will require developing property rights over open-ocean spaces, strengthening international conventions such as CITES to prohibit fisheries of migratory marine species outside a country's territorial waters and creation of national and regional exploitation bans. Further research is required to identify key sites of importance to the survival of whale sharks and other highly mobile marine species that utilise the same resources.