MODELLING MIGRATION AND AGGREGATION

APPLICATIONS IN FISHERIES, ENVIRONMENTAL CHANGE, AND EVOLUTION

CHRISTOPHER DAVID WEST

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ABSTRACT

Commercially important fish stocks worldwide are in danger of collapse due to fisheries exploitation compounded by environmental change. Many species exhibit seasonal migratory homing behaviour to and from spawning grounds. In this thesis, models are developed to explore the consequences of migratory behaviour and spatial structure on fisheries management and responses to environmental change.

Initially, a simple population model of a migratory fish population is presented. Migration occurs between an exploited feeding area and a protected spawning area in which no fishing occurs (a marine protected area, or MPA). The model supports the notion that MPAs can be useful management tools, especially in combination with other management techniques. However, the efficacy of MPAs is likely to decrease as the propensity for migration increases. Results which include stochastic recruitment differ from deterministic conclusions, highlighting the importance of considering environmental variability in models of fisheries.

A novel individual based model (IBM) is then developed, characterised by behavioural information retrieved from fish tagged with electronic data storage tags. The IBM enables more realistic simulations of movement to be undertaken, with population-scale breeding aggregations forming via simple rules governing individual behaviour. The model is used to analyse the response of aggregated breeders to range expansion following environmental change. Despite relatively rapid individual movement, breeding aggregation locations change slowly and aggregations are therefore at risk of collapse during rapid environmental change. Importantly, this slow response occurs within an homogeneous environment, highlighting the potential for responses to be limited by behavioural rather than environmental constraints. The model is then extended to explore fisheries exploitation. Fishing may cause aggregation collapse and fragmentation, but MPAs can prevent collapse and enhance yields. It is determined that large-scale measures of population health may not reveal the collapse of individual aggregations, highlighting the need for management at appropriate spatial scales.

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DECLARATION

This thesis is composed of original research conducted by myself, under the supervision of Dr. Calvin Dytham, Dr. Jonathan Pitchford and Dr. David Righton. All information sources have been acknowledged.

No part of this thesis has been submitted for a degree at any other university.

Unless specified below, I performed all literature research, programming, analysis, and writing of the thesis chapters. The following chapters of the thesis have been published in peer-review journals or are in preparation to be submitted. I am the first author on all papers, but have received feedback and corrections from my supervisors who are co-authors.

Chapter 2:

WEST, C.D., DYTHAM, C., RIGHTON, D., and PITCHFORD, J.W. (2009). Preventing overexploitation of migratory fish stocks: the efficacy of marine protected areas in a stochastic environment. *ICES Journal of Marine Science*, 66, 1919-1930.

Note that the model presented in this chapter/manuscript is an extension of the model of Pitchford *et al*. (2007) and segments of the original model code, supplied by the authors, were used and modified for the purposes of this research.

Chapter 4:

WEST, C.D., PITCHFORD, J.W, RIGHTON, D. and DYTHAM, C. (in preparation) Species with breeding aggregation may fail to respond to environmental change.

Chapter 5:

WEST, C.D., PITCHFORD, J.W., DYTHAM, C. and RIGHTON, D. (in preparation) The impact of exploitation on spawning aggregation persistence in migratory populations.

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AN INTRODUCTION

1.1 SYNOPSIS

Worldwide, commercially important fish stocks are in danger of collapse due to fisheries exploitation and the effects of environmental change (Worm *et al*. 2006, Worm *et al*. 2007). At the same time, advancements in technology mean that our knowledge of individual movement and the structure of populations is increasing. For example, the use of electronic tagging allows new insight into the migrations of individuals to and from spawning aggregations (Righton *et al*. 2007, Rutz and Hays 2009), and genetic analysis is being used to differentiate between population sub-stocks (Hutchinson *et al*. 2001). There is a need to understand the ecological and evolutionary consequences of this migratory behaviour and stock structure on fisheries management and the response of populations to environmental change (Turner *et al*. 2002). This is especially important as traditional fisheries management methods are replaced with approaches such as the use of marine protected areas (MPAs), where areas of the sea are protected from fishing pressure.

This research uses two different modelling approaches to examine the consequences of migration and aggregation on the persistence of populations, fisheries yield, and evolution of dispersal distance under exploitation and environmental change. The models are simple and theoretical, being concerned with the general consequences of the modelled behaviour rather than an accurate representation of real-world fisheries. However, modelled movement has been characterised principally from migratory commercial fish species such as the Atlantic cod, *Gadus morhua*. Particular attention is given to the role that marine protected areas may play in the protection of migratory species. Most previous models of MPAs have not accounted for seasonal migration, or do so very simply. This research has therefore attempted to address new questions about migration and aggregation, including increasing the realism with which movement behaviour is modelled.

In this chapter, an overview is given of the historical and current importance of fisheries, and the problems associated with managing fish stocks, including the issues of fisheries-induced evolution and climate change. Details are given of current knowledge of fish migration and stock structure, which has been enhanced by recent advances in technology and which underlies the assumptions made in the models presented in later chapters. Finally, a summary is presented of the life-history and behaviour of the Atlantic cod.

1.2 FISHING

Evidence for the use of bone tools to catch fish dates back to Palaeolithic times, perhaps as long as 80,000 years ago (Yellen *et al*. 1995, Henshilwood *et al*. 2001), and both marine and freshwater fish have been important in the diet of many ancient civilisations (Smith 2002). Jackson *et al*. (2001) recognise three periods of human impact on marine ecosystems; aboriginal, colonial, and global. These periods encompass the development of fishing as a subsistence activity; to the exploitation of foreign seas to support developing economies; to the system which dominates today where intense and widespread exploitation of coastal, shelf and oceanic fisheries is integrated into a global market of resource consumption (Jackson *et al*.

2001). In the 18th century, hook-and-line fishing was replaced with equipment such as the beam trawl, and from the Industrial Revolution in the 19th Century fishing intensified with the introduction of steam- and diesel-powered vessels and the otter trawl (Jackson *et al.* 2001, Jennings *et al*. 2001). The greatest expansion in fisheries exploitation, however, followed World War II, with the adoption of new technology such as sonar and refrigeration, allowing fish to be targeted more efficiently and stored for longer (Jennings *et al.* 2001, Pauly *et al*. 2002). Today, fish is principally caught using just four simple but highly effective fishing methods deployed from fishing vessels; gill-netting, purse-seining, long-lining, and trawling (Misund *et al*. 2002). Gill-nets form invisible net walls which fish swim into, becoming ensnared by their gills. Purse seines capture shoaling fish by surrounding them with a large net. Long-lines utilise rows of baited hooks. Trawls filter water masses faster than the swimming speed of the fish (Figure 1.1, Misund *et al*. 2002).

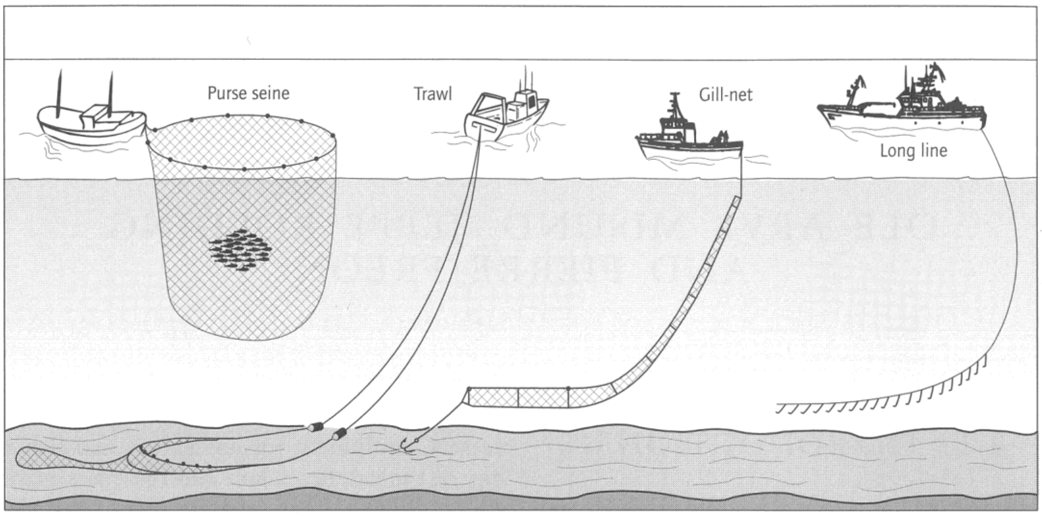

FIGURE 1.1. THE FOUR MAIN CAPTURE FISHING TECHNIQUES. REPRODUCED FROM MISUND *ET AL*. (2002).

In 2006, fish provided more than 2.9 billion people with at least 15% of their average per capita animal protein intake, and global fish consumption was estimated at 16.7 kg per capita (FAO 2009a). A large proportion of this was supplied from marine sources, with 81.9 million tonnes produced by capture fisheries with an estimated first-sale value of US$91.2 billion (FAO 2009a), although estimates which include discards as well as illegal and unreported fishing are around 120 million tonnes (Pauly 2008). Following the period of rapid increase after World War II, total catches from 1995 have remained relatively stable and the maximum wild capture potential of the world's oceans has now probably been reached (Figure 1.2, FAO 2009a), although total fish production has continued to increase due to the growth of aquaculture. China catches the most fish with over 14 million tonnes caught in 2007. Peru is the next largest producer with over 7 million tonnes, and is followed by Indonesia, the USA, and Japan which all produce over 4 million tonnes (FAO 2009b).

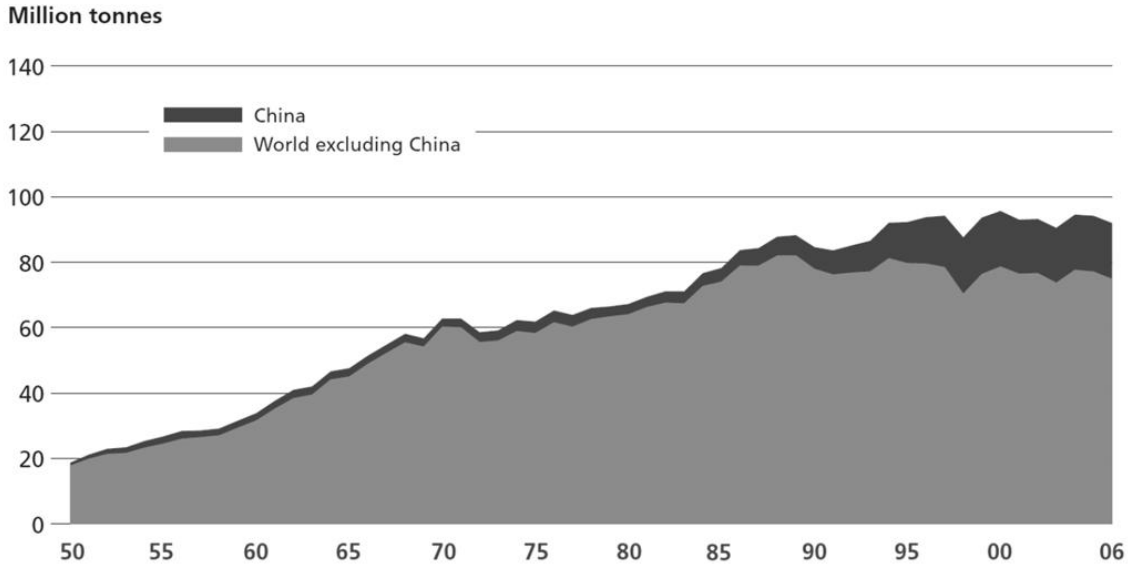

FIGURE 1.2. WORLD CAPTURE FISHERIES PRODUCTION. REPRODUCED FROM FAO (2009A).

1.2.1 FISHERIES IMPACTS

As demand for fish continues to rise, so does the pressure exerted on fisheries (Hilborn *et al*. 2003, Pauly *et al*. 2005). In 2007 it was estimated that 52% of stocks were fully exploited, and a further 28% were either overexploited (19%), depleted (8%), or recovering from depletion (1%) and therefore yield less than their potential due to excess fishing pressure (FAO 2009a). The potential for fishing to dramatically reduce stock abundance was highlighted following the halt in fishing during the First and Second World Wars. When fishermen returned, fish were both larger and more abundant (Smith 1994). Since industrialisation it has been estimated that global populations of large predatory fish have been reduced to 10% of their original stock size (Myers and Worm 2003), and we may soon be left with only low trophic level fish species in the sea (Christensen *et al*. 2003). The concept of 'fishing down marine food webs' (Pauly *et al*. 1998, Pauly *et al*. 2005) describes the trend in global catches from large piscivorous fish towards invertebrates and planktivorous fish at lower trophic levels. Catches may increase at first, but are then likely to stagnate and decline (Pauly *et al*. 1998). As shallow-water stocks decline, fishing has begun to move to deeper waters which have lower productivity (Koslow *et* *al*. 2000, Roberts 2002). Many deepwater species exhibit extreme longevity, slow growth, large size, late age-at-maturity, and low fecundity (Koslow *et al*. 2000, Roberts 2002). Large size and late maturation are key indicators of vulnerability to exploitation (Jennings *et al*. 1998) and are likely to lead to depletion of deep water fisheries at an even faster rate than those in shallower waters (Roberts 2002). It has recently been suggested that all currently fished taxa may have collapsed globally by as early as the middle of the 21st Century (Worm *et al*. 2006, Worm *et al*. 2007).

There have been numerous examples of fisheries collapses throughout history (Hutchings 2000, Jackson *et al*. 2001, Roberts 2007). In 1885, the Canadian Ministry of Agriculture said, “Unless the order of nature is overthrown, for centuries to come our fisheries will continue to be fertile.” (Kurlansky 1997). Yet, in 1992, after being harvested for five hundred years, the Newfoundland stock of Atlantic cod, *Gadus morhua*, collapsed (Hilborn *et al*. 2003), and overfishing rather than environmental change was to blame (Hutchings and Myers 1994, Myers *et al*. 1997). The stock has not recovered (Rose and O’Driscoll 2002, Schrank 2005), and the system has undergone a shift to organisms such as crabs and shrimps which occupy lower trophic levels (deYoung *et al*. 2004, Steele 2004). Evolutionary changes in the life-history of cod (Hutchings 2005, and see Section 1.4 Fisheries-induced evolution) and competition from lower trophic levels (Bundy and Fanning 2005) are likely explanations for the lack of cod recovery. On the other side of the Atlantic, in the North Sea and Baltic Sea, cod are also in danger of collapse (Cook *et al*. 1997, Jonzén *et al*. 2002). In the 1970s, fishing began for the deep-sea orange roughy, *Hoplostethus atlanticus*, and boomed in the 1980s around New Zealand and Australia (Roberts 2002). However, a serial depletion of seamount populations occurred and populations collapsed to less than 20% of their pre-exploitation levels (Clark 1999, Koslow *et al*. 2000). Orange roughy may take up to 30 years to mature and can live for over a hundred years (Horn *et al*. 1998, Roberts 2002). Slow growth rate, high longevity, and low fecundity of orange roughy make recovery from overfishing slow (Clark 1999). The slow recovery observed in these two examples is unlikely to be an anomaly. With the exception of herring, *Clupea harengus*, and related species which mature early, recovery in many overfished species may take considerable time (Hutchings 2000).

The impacts of fishing, however, extend beyond those of the targeted species. A large problem with modern fishing gear is that in its quest to become more efficient it can lack species selectivity, leading to bycatch (Kennelly and Broadhurst 2002). Bycatch is the capture and discard of untargeted individuals and species (including non-fish species such as dolphins and albatross) which are accidentally caught (Alverson *et al*. 1994). Bycatches of target species may be discarded for legal reasons, for example if individuals are under-sized or quota has been exceeded, or if they are of little commercial value to the fishermen (Kaiser and Jennings 2002). Non-target species may also be caught accidentally. For example, in the 1960s the mortality of dolphins attributed to tuna purse-seining was an average of approximately 350,000 individuals per year (Kennelly and Broadhurst 2002). An alternative method of fishing for tuna, long-lining, may result in the bycatch of albatross, with estimates of up to 44,000 individuals killed in the mid-80s by the Japanese tuna fishery (Brothers 1991, Bergin 1997, Tasker *et al*. 2000). Fisheries for shrimp are some of the worst offenders for bycatch, with an estimated 11.2 million tonnes in 1994, and some fisheries discarding more than 10 kg of bycatch for every kilogram of landed shrimp (Alverson *et al.* 1994). Modifications such as increased net mesh size and other changes to gear design, or the use of alternative methods of fishing, can help to reduce bycatch (Broadhurst 2000, Kennelly and Broadhurst 2002) but it is always likely to be an unwanted side-effect of modern fishing.

Fishing may not stop when vessels return to port. When nets are lost as a result of bad weather or when damaged by other gear, they may continue fishing (Kaiser *et al*. 1996). ‘Ghost fishing’, as this is known, has the potential to continue for many months after net loss, and may catch large numbers of individuals (Kaiser *et al*. 1996, Matsuoka *et al*. 2005, Brown and Macfadyen 2007). Fishing, especially the use of trawls, may also cause long-term damage to the sea bed (Kaiser 1998, Collie *et al*. 2000, Kaiser *et al*. 2002), having been compared to forest clear-cutting (Watling and Norse 1998), and may disturb behaviour such as spawning (Morgan *et al*. 1997). Damage to the sea bed and removal of competition and predation as a result of the removal of target species, has the potential to drastically impact ecosystem structure (Jennings and Polunin 1996, Kaiser and Jennings 2002). For example, the green sea urchin, *Strongylocentrotus droebachiensis*, may devastate kelp forests and has become an increasing problem in recent years as predatory fish have been reduced in abundance (Tegner and Dayton 2000). Effects on communities are not, however, limited to aquatic life. Many seabirds feed on discarded fish and the presence of fishing vessels may have a significant effect on the abundance and distribution of many species (Garthe 1997, Tasker *et al.* 2000).

1.3 FISHERIES MANAGEMENT

The negative effects of fishing, both on target and non-target species, highlight the need for effective management. For many years, the goal of fisheries management was to maintain a maximum sustainable yield (MSY) of fish, with little regard for social, economic or environmental impacts (e.g. Jennings *et al*. 2001). More recently, minimum population size thresholds have been used as targets to prevent overfishing (Roberts 2007). Historically, control of fisheries has been carried out using catch controls, effort controls, and/or technical measures (Jennings *et al*. 2001). In Europe, under the management of the Common Fisheries Policy (CFP), a combination of all three measures is used. A total allowable catch (TAC) system sets limits for the total amount of fish which can be landed from particular regions. Technical measures include gear regulations, closed seasons, and minimum allowable sizes for individual species. Additionally, effort is regulated by restrictions on fleet capacity and days spent at sea (Daw and Gray 2005). These measures are implemented following scientific recommendations. Fisheries scientists from the International Council for the Exploration of the Sea (ICES) meet once a year to present their findings which are then discussed by the ICES Advisory Committee on Fishery Management (ACFM) and used to provide scientific advice for the European Commission. The commission then forms a proposal based on this evidence and discussions with other committees including the Scientific, Technical and Economic Committee on Fisheries (STECF) and the European Parliament Fisheries Committee. These proposals are then sent to the Council of Ministers, made up of negotiators from member states, which makes the final decision about how much can be caught by vessels from each country (Figure 1.3, Day and Gray 2005, Roberts 2007). In this process, however, recommendations can be diluted. It is not uncommon for quotas to be set much higher than those recommended from the scientific advice (Karagiannakos 1996, Roberts 2007). Dilution of scientific advice, problems with enforcement, and deficiencies in the science itself, are to blame for what is widely perceived to be the failure of the CFP to conserve species which continue to decline (Daw and Gray 2005). Methods of fisheries management such as the use of TACs and MSY are vulnerable to uncertainties in the environment and accuracy of stock assessments (Daw and Gray 2005, Kell and Fromentin 2006, Pitchford *et al*. 2007) and do not solve, or can even exacerbate, problems such as bycatch and habitat destruction (Roberts *et al*. 2005, and see Section 1.1.1 Fisheries impacts). A possible solution is the incorporation of marine protected areas into the fisheries management toolbox.

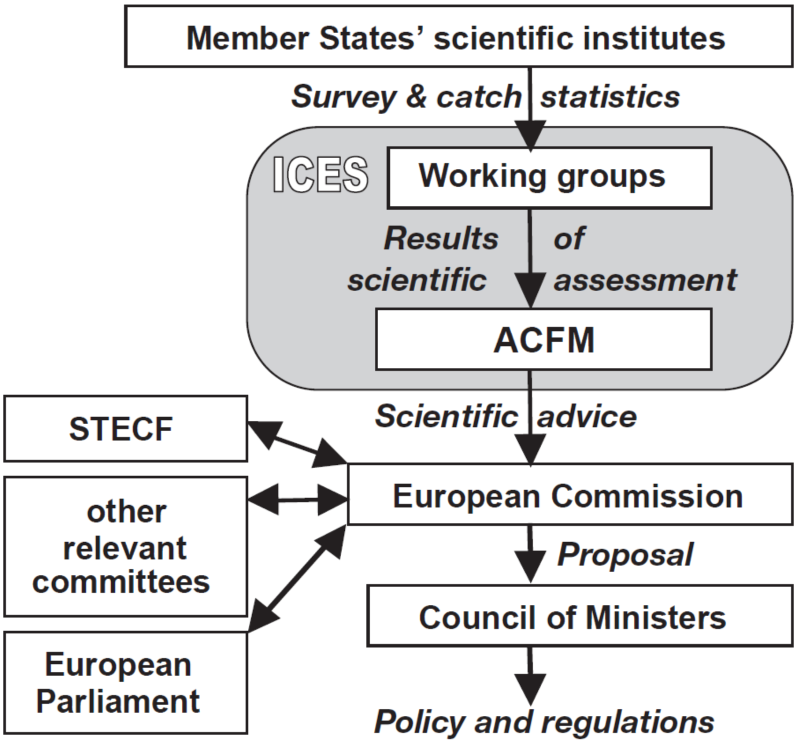

FIGURE 1.3. ROUTE FOR THE IMPLEMENTATION OF SCIENTIFIC RESEARCH INTO FISHERIES POLICY WITHIN THE EUROPEAN COMMUNITY. REPRODUCED FROM DAW AND GRAY (2005).

1.3.1 MARINE PROTECTED AREAS

Areas of the sea where exploitation is prohibited are termed marine protected areas (MPAs). Creating refuges from fishing has a long history, with communities on Pacific Islands closing reef areas for rest periods (Roberts 2007). In Europe, the concept of protecting areas of the sea arose in the 18th and 19th centuries when experiments were made on the effect of closing areas to trawling, not to protect species but to benefit fisheries when they were re-opened (Roberts 2007). However, they fell out of favour and it was only in the second half of the 20th century when their use began anew. Initially, their benefits were discovered by accident. In the 1960s a large wildlife refuge was established around Merritt Island in Florida, as an exclusion zone around the Kennedy Space Center. In the 1970s, scientists in Chile, the Philippines, and New Zealand began to establish areas around their research stations to protect their experiments from fishing. As a result of this protection, populations of fish expanded and catches in adjacent fisheries increased (Roberts *et al*. 2001, Roberts 2007). In the Apo Island reserve in the Philippines, population sizes of fish important to local fisheries tripled in 18 years of protection and catch per unit effort outside the reserve increased by as much as 50%

over pre-reserve levels (Russ *et al*. 2004). The size of individuals can also increase inside reserves. In three reserves in New Zealand, the number of snapper, *Pagrus auratus*, above the legal landing size was 14 times higher than in fished areas, and egg production was 18 times higher (Willis *et al*. 2003). In 1994, in an attempt to promote the recovery of species such as cod, 17,000 km^2 of the Georges Bank in the northwest Atlantic was closed to trawling and other fishing methods capable of catching demersal fish including scallop dredges. Although the target species have responded relatively little to this protection, scallop biomass increased 14-fold between 1994 and 1998, with fishermen concentrating their effort at reserve boundaries where larvae export has resulted in population increases (Murawski *et al*. 2000, Gell and Roberts 2003). These examples demonstrate the potential for the conservation of species within MPAs to benefit surrounding fisheries. This can occur as increased egg production leads to the export of eggs and larvae on ocean currents. Alternatively, as stocks of juveniles and adults increase within reserves, there may also be density-dependent spillover (i.e. dispersal across reserve boundaries into fisheries) of individuals (Roberts *et al*. 2001, Gell and Roberts 2003).

Interest in MPAs as potential management tools has increased recently (Botsford *et al*. 1997, Polunin 2002). In addition to the conservation and fisheries benefits described above, a reason for this may be the increasing recognition that fishing gears are responsible for physical damage to marine habitats (Kaiser 1998, Collie *et al*. 2000, Kaiser *et al*. 2002), and that these impacts may be reversed in protected areas (Roberts and Hawkins 2000). It is expected that indirect ecosystem effects on communities caused by fishing (Kaiser and Jennings 2002) can be reversed by protection in MPAs (Pinnegar *et al*. 2000). MPAs also have the potential to reduce fisheries-induced evolution (see Section 1.4 Fisheries-induced evolution). The perceived failure of traditional fisheries management to prevent fisheries collapse has also led to calls for the introduction of MPAs (Roberts 1997, Beddington *et al*. 2007). Fisheries science is moving from a single-species to an ecosystem-based approach to fisheries management, and MPAs may play an important role in maintaining healthy marine ecosystems and the fisheries they support (Pauly *et al*. 2002, Pikitch *et al*. 2004). In addition to benefits specifically related to fisheries, the increase in abundance and diversity within MPAs may encourage tourism (such as recreational diving) and therefore generate local revenue (Polunin 2002). However, MPAs are few in number and are generally very small in area. Worldwide, the median size of MPAs is about 1600 ha (Polunin 2002). Yet, even small MPAs can significantly enhance fish stocks (Roberts and Hawkins 1997). Until recently in the UK the use of MPAs has been limited. Only

2.2% of UK waters are protected for marine conservation with the only statutory protected areas around Lundy and Skomer islands, although several other voluntary reserves exist (Jones 1999, Anon. 2009). Recent legislation means that more may follow in their new guise as Marine Conservation Zones (Anon. 2009).

1.3.2 MODELS OF MPAS AND MIGRATION

Recent advances in tagging and genetic technologies (see Section 1.3 Recent insights on fish migration and stock structure) have advanced our knowledge of migration and stock structure in commercially important fish species. With this new knowledge comes the responsibility to protect genetically differentiated populations in order to maintain genetic diversity (Ryman *et al*. 1995). By protecting areas of the sea from exploitation, MPAs are likely to be an important tool in achieving this goal (Pérez-Ruzafa *et al*. 2006). Models have shown the potential for fisheries benefits from MPAs (Guénette and Pitcher 1999, Sladek Nowlis and Roberts 1999, Hart 2006), and that MPAs may be effective as a buffer against uncertainty (Lauck *et al*. 1998, Mangel 2000, Pitchford *et al*. 2007). It has been assumed that mobile species will be less well protected, and will require larger MPAs than those with small home-ranges (Kramer and Chapman 1999, Gell and Roberts 2003, Gerber *et al*. 2003). However, traditional models of MPAs are simplistic, failing to account for the complex movement behaviour that occurs in many species (Guénette and Pitcher 1999, Roberts and Hawkins 2000, Gell and Roberts 2003). In fact, even migratory species may spend relatively long periods within restricted areas (Turner *et al*. 2002, Gell and Roberts 2003, Hobson *et al*. 2009) and therefore MPAs may still be a useful protective tool. Some models have attempted to include explicit seasonal migration to analyse the effect of MPA use. For example, Apostolaki *et al*. (2002) present a population model of European hake, *Merluccius merluccius*, in the Mediterranean, migrating seasonally between a spawning and nursery area, and conclude that MPAs can bring spawning stock biomass and yield benefits. Röckmann *et al*. (2007) model migratory cod in the Baltic Sea and determine that MPAs can help prolong the persistence of populations subject to climate change. Guénette *et al*. (2000) analyse the collapse of cod in Newfoundland, and include seasonal migrations. They conclude that a closure of 80% of the fishing grounds would have prevented collapse, but that migration can hinder MPA effectiveness. Stefansson and Rosenberg (2005, 2006) use transfer matrices to model spawning and feeding migrations in a theoretical model and conclude that properly designed MPAs can be effective at protecting migratory species. Andrews *et al*. (2006) also make use of transfer matrices to model the movement of cod in European waters, with individuals migrating instantaneously to their nearest spawning ground at spawning time. Their results suggest that the use of fishery closures may benefit spawning stock biomass. The extent of protection offered by MPAs in these populations models differ, but they all demonstrate that MPAs may be a useful tool for migratory species.

The models described above all simplify the movement behaviour revealed by the use of electronic tags. In comparison to population models, individual based models (IBMs) have the potential to allow the behaviour of individuals to be modelled more realistically, and this may have consequences for the design of MPAs and other fisheries management measures. IBMs keep track of each individual within a population, allowing individuals to be characterised by state variables and behavioural strategies to be implemented in a spatial context. This, in turn, allows properties of the population to be described by the properties of the individuals which it contains (Huse *et al*. 2002, Strand *et al*. 2002). IBMs also have the same basic unit (i.e. individuals) as natural selection, allowing the adaptation of individuals to their environment over evolutionary time to be explored (Huse *et al*. 2002, Strand *et al*. 2002). IBMs have been used to explore the evolution of fish migration in response to spatially heterogeneous and seasonal environments (Fiksen *et al*. 1995, Huse and Giske 1998, Hubbard *et al*. 2004). Codling (2008) models the impact of individual movement, in the form of a correlated random walk, on a simple reserve-fishery system. He concludes that the type of movement modelled can have a dramatic effect on the apparent effectiveness of a reserve, and that using a grouped population average in a system with environmental heterogeneity and high individual variability can lead to misleading results. Therefore, in order to gain insights into highly dynamic and variable systems such as marine environments, an IBM which includes the key dynamical features of the system is likely to be more appropriate than a predictive model based on population averages (Codling 2008).

1.4 RECENT INSIGHTS ON FISH MIGRATION AND STOCK STRUCTURE

Fish are not static. Instead they make movements at different spatial scales throughout their lives, for example to improve food intake, avoid predation, or maximise reproductive potential. Many commercially important marine fish undertake seasonal migrations (Giske *et al*. 1998) and fishermen and scientists have known about these migrations for centuries (Kurlanksy 1997, Metcalfe 2006).

1.4.1 EXPERIMENTS AND TECHNOLOGY

Early investigations into migrations made use of conventional mark recapture studies where individuals are caught, tagged, and then released. On capture, tags can be returned with the capture position and date to build a picture of the extent of migration (Robichaud and Rose 2004, Righton *et al*. 2007). Such simple studies can be useful in describing gross patterns in the movement of populations but provide little information on the way in which individual fish migrate (Metcalfe *et al*. 2006). Combining mark recapture studies with recent advances in technology have allowed a clearer picture of individual movement behaviour to be developed (Righton *et al*. 2007, Rutz and Hays 2009). The development of electronic radio and acoustic tags allows fish to be tracked through continuous time for relatively short periods (Clark and Green 1990, Arnold *et al*. 1994, Green and Wroblewski 2000, Robichaud and Rose 2002) but can be prohibitively expensive (Metcalfe 2001). The development of electronic data storage tags (DSTs), which record data such as light, temperature and pressure, allows fish behaviour to be monitored over long periods (Metcalfe and Arnold 1997, Righton and Metcalfe 2002). DSTs have been used to reconstruct the movement of species such as cod, *G. morhua* (Righton *et al*. 2001, Righton *et al*. 2007, Righton and Mills 2008, Hobson *et al*. 2009), plaice, *Pleuronectes platessa*, (Metcalfe and Arnold 1997, Hunter et al. 2004a, Hunter *et al*. 2004b), thornback rays, *Raja clavata* (Hunter *et al*. 2006), bluefin tuna, *Thunnus thynnus* (Block *et al*. 2005, Rooker *et al*. 2007), and basking sharks, *Cetorhinus maximus* (Sims *et al*. 2005, Sims *et al*. 2006). The tidal location method of geolocation analysis uses spatial hydrostatic data in the form of tide times and tidal range which is cross-referenced with pressure measurements from DSTs and used to determine the geographic location of individuals when they remain stationary on the sea bed for a full tide cycle or longer (Metcalfe and Arnold 1997, Hunter *et al*. 2003). Ambient daylight levels and temperature data recorded by DSTs may also be compared with data such as day length and sea surface temperature to determine individual location (Metcalfe and Arnold 1997, Hill and Braun 2001, Metcalfe 2001).

The recent development of sensitive genetic markers, particularly microsatellites, and the ability to efficiently extract DNA from preserved material, has allowed more detailed analysis of the population structure of marine fishes (O'Connell and Wright 1997, Hutchinson *et al*. 2001, Hutchinson *et al*. 2003). Microsatellites (rapidly mutating, repeated nuclear DNA regions) are well suited for examining the genetic structure of fish populations because their high mutation rates and selective neutrality results in high levels of allelic divergence and heterozygosity (O'Connell and Wright 1997, Hutchinson *et al*. 2001). Recent genetic analysis of populations of cod (Bentzen *et al*. 1996, Ruzzante *et al*. 1998, Ruzzante *et al*. 2000, Hutchinson *et al*. 2001), plaice (Hoarau *et al*. 2002, Hoarau *et al*. 2004), and other species (O'Connell *et al*. 1998, Shaw *et al*. 1999, Nesbø *et al*. 2000), has revealed finer stock structure than that achieved with coarser genetic techniques (Hutchinson *et al*. 2001).

1.4.2 OUTCOMES OF RESEARCH

Analysis of data from conventional tags led Robichaud and Rose (2004) to divide the movement behaviour of Atlantic cod into four categories. Sedentary individuals exhibit strong site fidelity and are found year-round in a relatively small geographic range. Accurate homers are migratory, perform seasonal movements, and home to a relatively small area to spawn. Inaccurate homers are also migratory, but home to a much broader area. Dispersers move and spawn in a haphazard pattern within large geographical areas. Although Robichaud and Rose (2004) concluded that individuals within populations could exhibit a variety of behavioural types, they noted that the north-east Atlantic has several large cod groups which home with accuracy, whereas fjordal areas tend to be occupied by sedentary populations. Experiments using cod in the northwest Atlantic tagged with acoustic tags have shown that they exhibit a strong homing tendency to their original spawning location after artificial displacement (Green and Wroblewski 2000, Robichaud and Rose 2002) or after long-distance migrations to feeding areas (Robichaud and Rose 2001). In European waters, analysis of conventional and electronic tags has shown clear differences in behaviour between populations in different areas (Righton *et al*. 2001, Righton and Metcalfe 2002, Wright *et al*. 2006, Righton *et al*. 2007). Analysis of DSTs from cod released in the southern North Sea and English Channel has revealed that during migrations to and from spawning grounds fish are highly active, but that after dispersing to summer feeding areas individuals become relatively inactive, ranging over only a relatively small geographic area (Turner *et al*. 2002, Hobson *et al*. 2009). Hotspots of spawning and feeding activity have also been defined (Righton *et al*. 2008). During periods of activity individuals may travel as far as 70 km in a single day (Righton *et al*. 2008, Hobson *et al*. 2009). Figure 1.4 shows an example of a migration route reconstructed from data from a DST for a cod released in the southern North Sea (Righton and Mills 2008). It clearly highlights the potential for individuals to undertake long-distance movement away from spawning locations, followed by homing behaviour back to an area close to the point of release.

Genetic studies are able to differentiate between population sub-stocks. In the northwest Atlantic, microsatellite analysis has revealed significant differences between stocks at a large oceanic basin scale, at a medium continental shelf scale, and at a smaller spawning bank scale (Bentzen *et al*. 1996, Ruzzante *et al*. 1998, Ruzzante *et al*. 2000). In the North Sea, recent analysis suggests the presence of at least four genetically divergent cod populations (Hutchinson *et al*. 2001). Homing behaviour is likely to be a primary explanation for genetic differentiation between stocks (Svedäng *et al*. 2007). It is still not clear what mechanisms cod use in order to return so accurately each year, but suggestions include the use of sources of the sound of other cod grunting, physical markers on the sea bed or currents, geomagnetism, chemical concentrations, and social transmission of route information within groups (Rose 1993, Robichaud and Rose 2002, Svedäng *et al*. 2007).

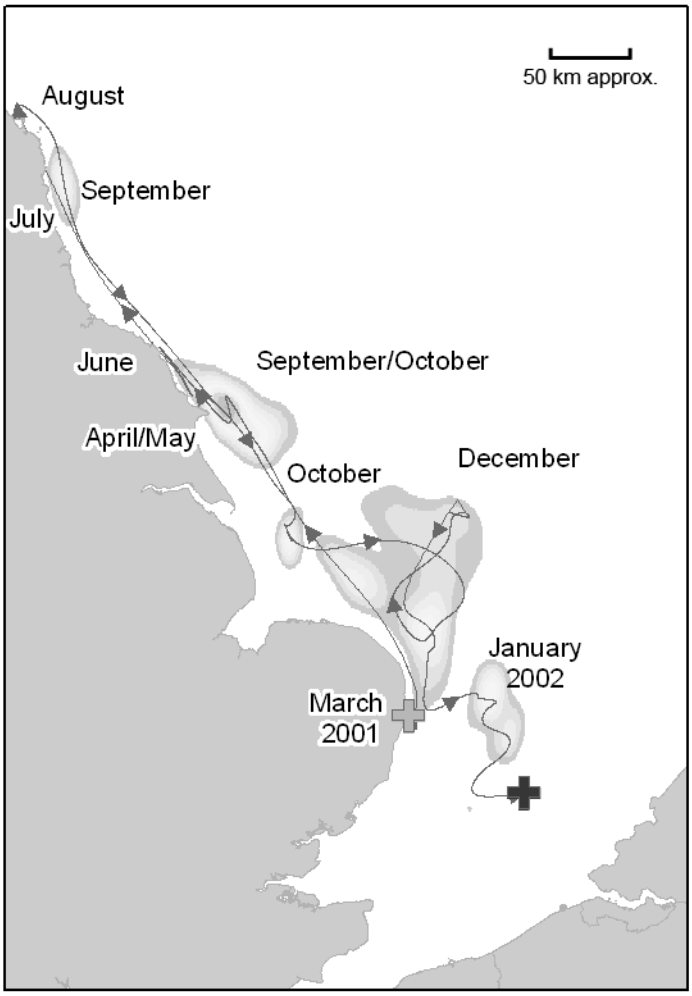

FIGURE 1.4. RECONSTRUCTION OF THE MOVEMENT OF A COD (ID 2255) TAGGED IN 2001 IN THE SOUTHERN NORTH SEA. LIGHT AND DARK GREY CROSSES INDICATE RELEASE AND RECAPTURE POSITIONS RESPECTIVELY. RECONSTRUCTED FROM RIGHTON AND MILLS (2008).

Other species also exhibit interesting patterns of movement behaviour and stock structure. For example tagging studies have shown that plaice in the North Sea segregate into three distinct feeding aggregations during the summer feeding season and show a strong homing behaviour back to spawning sites following extensive migrations (Hunter *et al*. 2004a, Hunter *et al*. 2004b). Similar behaviour is seen in Icelandic plaice. (Solmundsson *et al*. 2005). Genetic studies on plaice have revealed differentiation between North Sea, Baltic, Norwegian and Icelandic stocks (Hoarau *et al*. 2002, Hoarau *et al*. 2004). Thornback rays in the Thames estuary have been shown to migrate into the deeper waters of the North Sea during the winter, before returning to the estuary in the summer to spawn (Hunter *et al*. 2006). Genetic studies on thornback rays show differentiation between stocks, and suggest that populations become mixed during the winter feeding season, and more isolated during summer spawning (Chevolot *et al*. 2006a, Chevolot *et al*. 2006b).

1.5 FISHERIES-INDUCED EVOLUTION

An impact of fishing which has not been discussed so far is that of fisheries-induced evolutionary change. If fishing increases the fitness of certain genotypes within a population then these genotypes would be expected to increase in frequency (Law and Grey 1989, Conover 2000). For example, there has been a lot of interest in the potential for fishing to cause adaptive change in age or size at maturation in exploited species (Law 2007). If larger, older fish are more vulnerable to fishing, as they commonly are with size-selective fishing gears, then late-maturing individuals are likely to be caught before having a chance to reproduce. It is therefore predicted that, given appropriate genetic variation, reproduction will increase at ages younger than those harvested, and decrease at ages older than those harvested (Law 1979, Law and Grey 1989). Non-selective fishing may also induce evolutionary change in age at maturation because it also includes the mortality of older individuals (Conover 2000, Heino and Godø 2002). Although selection for increased size may occur due to the effects of natural mortality (Carlson *et al*. 2007), the strength and temporal persistency of fishing is likely to have an overpowering effect (Edeline *et al*. 2007, Darimont *et al*. 2009). Selection for decreased size at maturation has been inferred for heavily exploited species such as plaice (Grift *et al*. 2003, Grift *et al*. 2007) and cod (Olsen *et al*. 2004, Hutchings *et al*. 2005, Olsen *et al*. 2005). Fisheries-induced selection for smaller size at maturation may lead to reductions in the reproductive potential and fisheries yield from populations (Law and Grey

1989, Heino and Godø 2002) but may also reduce genetic diversity and, if fishing is relaxed, surviving individuals may have reduced fitness with respect to natural selection (Conover 2000).

By protecting a proportion of a population from fishing, MPAs may be useful as a tool to slow or prevent fisheries-induced evolution (Conover and Munch 2002, Allendorf *et al*. 2008). However, the protective benefit of MPAs can depend on location. MPAs located on feeding grounds are predicted to protect against evolution towards small size at maturation, while MPAs located on spawning grounds may have little effect and can even exacerbate the problem (Baskett *et al*. 2005, Dunlop *et al*. 2009, Miethe 2009, Miethe *et al*. 2010a). Additionally, the presence of MPAs has the potential to induce selection in another trait; that of dispersal distance. In comparison to mobile individuals, sedentary individuals located within an area of protection are less likely to cross the reserve boundary into the fishery and are therefore less likely to suffer fishing mortality. MPAs may therefore have the effect of reducing evolved dispersal distance which may decrease connectivity between populations and have consequences for fisheries yield (Baskett *et al*. 2007, Miethe 2009, Miethe *et al*. 2009, Miethe *et al*. 2010a).

1.6 CLIMATE CHANGE

During the 21st century it is predicted that global temperatures will rise between 1.1°C and 6.4°C due to climate change, following rises in global temperatures of approximately 0.74°C in the 20th century (IPCC 2007). However, climatic changes are not just a recent phenomenon, they have been happening throughout the entire history of the earth, with large scale perturbations brought about by natural processes such as Milankovitch cycles (Middleton 2003). At points during the Pleistocene many land masses, including much of the North Sea, were covered with ice sheets, and the last ice-age finished just over 10,000 years ago (Ehlers and Wingfield 1991). Thus, the North Sea as we know it today is relatively young in geological and evolutionary terms. The current North Sea ecosystem is therefore a result of immigration and adaptation over a relatively short period. Over even shorter timescales, fluctuations in the climate have the potential to bring about large changes in marine communities. A classic example of this is the impact of El Niño on Peruvian anchoveta, *Engraulis ringens*, fisheries. During El Niño, which occurs regularly over a period of 3 to 7 years, warmer surface waters result from a weakening in the South Pacific trade winds caused by a rapid change in atmospheric pressure. This sharply reduces the upwelling of nutrients along the coast of South America, and results in a reduction in fish numbers (Middleton 2003). A combination of El Niño and overfishing has been blamed for the collapse of the Peruvian anchoveta fishery in the 1970s (Walsh 1981). El Niño serves as an example of the way in which climatic changes can lead to a complex chain of events which can drastically affect ecosystems and the abundance of exploited populations.

Human-induced climate change, resulting from an increase in greenhouse gases in the atmosphere, also has the potential to bring rapid and unpredictable changes to the marine environment. The predicted rise in global temperature over the next 100 years has been highlighted above, but the effects will be further reaching than a simple warming of the seas. For example, as temperatures rise the ice-caps will melt. The extent of sea ice in the Arctic during the summer has been below long-term averages in recent years, reaching a minimum in 2007 (NSIDC 2007), and glaciers around the world are receding (IPCC 2007). Ice-melt and increased rainfall leading to increased river runoff may reduce the salinity of some seas (Myers *et al*. 1990), whereas reductions in rainfall may decrease run-off in other areas leading to an increase in salinity (Hansson *et al*. 2010). Salinity is an important factor in the distribution of many species (Daan 1990, Castillo *et al*. 1996). For example, the fertilisation and survival of cod eggs and the development of larvae may be dependent on salinity levels (Laurence and Rogers 1976, Yin and Blaxter 1987, Nissling and Westin 1997). As ice over land masses continues to melt, sea levels will continue to rise, changing the current distribution of coastal areas and opening up new marine habitats (IPCC 2007). Melting ice also has the potential to disrupt ocean currents. For example, changes in the Atlantic thermohaline circulation via freshwater influx have occurred throughout history and have the potential to greatly change the climate of the northern hemisphere, with impacts on surface winds, rainfall and temperatures (Manabe and Stouffer 1995, Vellinga and Wood 2002). Changing climatic conditions mean that other currents are likely to also be affected, including those in the North Sea (Pingree 2005). Currents and winds can affect the distribution and settlement location of eggs and larvae (Lough *et al*. 1989, Pepin and Helbig 1997, Rindorf and Lewy 2006). Another impact of climate change is that extreme weather events such as storms are likely to become more common (IPCC 2007). The increased wind speeds and wave action associated with these storm events are likely to affect the distribution and survival of eggs and larvae either mechanically (Bunn *et al*. 2000) or by dissipating planktonic food sources (Peterman and Bradford 1987). A rise in carbon dioxide levels will cause acidification of the seas and has the potential to have direct (e.g. physiological) and indirect (e.g. effects on planktonic food) effects on fish growth and survival (Fabry *et al*. 2008). Human efforts to mitigate the extent of future climate change may also affect marine ecosystems. Offshore windfarms, for example, may act as small reserves or artificial reefs in a similar manner to oil and gas rigs (Soldal *et al*. 2002), but may also cause disturbance during both construction and operation (Hofmann *et al*. 2000, Wahlberg and Westerberg 2005). Tidal barrages have the potential to cause large changes in estuarine ecosystems and may disrupt fish migration (Parker 1993, Dadswell and Rulifson 1994, Wells 1999). Thermal effluent from nuclear power stations may change community structure in neighbouring ecosystems (Barnett 1971).

Some of the events described above, such as changes in temperature or salinity, may occur over decades or centuries, whilst the effects of others, such as storms, may be more short-lived. However, all have the potential to affect the persistence and distribution of species which have evolved and adapted to their current environment over thousands of years. For example, cod occupy temperatures from -1°C to over 20°C, but are usually found in waters of between 0°C and 12°C (Drinkwater 2005). If temperatures in the North Atlantic change then the range of this species may be expected to respond. The ranges of many species have already shifted in response to recent climatic change (Walther *et al*. 2002, Perry *et al*. 2005, Parmesan 2006). In order to respond to change, individuals must be able to disperse to new areas of suitable habitat (Thomas *et al*. 2004). In marine systems, many species are free-swimming and therefore barriers to dispersal may not be as obvious as in terrestrial environments. It might therefore be expected that fish populations should have little problem responding to environmental changes. The North Sea has warmed in recent years, and evidence suggests that species such as cod have already responded with a change to a more northerly distribution (Perry *et al*. 2005). However, in cod, responses to temperature at the individual level may not be apparent and perceived changes in distribution may actually be caused by changes in local abundance (Neat and Righton 2007). In the southern North Sea, where cod are at the southern limit of their range, reductions in recruitment success (O'Brien *et al*. 2000) or growth rates (Blanchard *et al*. 2005) with warmer temperatures could explain stock reductions. Given the recently discovered stock structure of cod (Hutchinson *et al*. 2001), and the fact that strong homing behaviour may limit mixing (Svedäng *et al*. 2007), the potential loss of populations at receding range margins is of great concern.

If climate change causes a contraction of range at southern boundaries (in the northern hemisphere) then a concurrent expansion of the northern boundary might also be expected as previously unexploited habitat becomes more favourable. The potential for MPAs to affect the evolution of dispersal ability has been discussed above but expanding range margins resulting from environmental change also have the potential to induce evolutionary changes. Individuals which arrive first in an unexploited population will be at an advantage, able to exploit the habitat without competition, and therefore evolution towards higher dispersal may be expected (Travis and Dytham 2002, Dytham 2009). However, Allee effects such as an increased difficulty in finding a mate may reduce the reproductive potential of isolated individuals, prevent evolution in dispersal distance, and slow the population's response to change (Keitt *et al*. 2001, Travis and Dytham 2002, Courchamp *et al*. 2008). Despite the potential for Allee effects, there is evidence for the evolution of dispersal ability at expanding range margins in nature (Simmons and Thomas 2004, Parmesan 2006, Phillips *et al.* 2006). The seasonal nature of the distribution of migrating fish species, and the potential for strong homing behaviour, provides an interesting case for the investigation of impacts of environmental change on the distribution and speed of response of populations, and the evolution of dispersal ability.

1.7 ATLANTIC COD

The Atlantic cod, *Gadus morhua*, is a commercially important fish found throughout North Atlantic waters. Its movement behaviour is the chief inspiration for the movement modelled in this thesis and therefore a brief overview of its importance to fisheries, life-history and behaviour is warranted.

1.7.1 HISTORICAL AND PRESENT COD FISHERIES

Cod, with its bright white flesh, high protein and low fat content, is prized above all other fish from the family Gadidae (Kurlanksy 1997, Björnsson *et al*. 2010), which includes species such as haddock, *Melanogrammus aeglefinus*, saithe, *Pollachius virens*, and whiting, *Merlangius merlangus*. Cod fisheries have a long history and have resulted in the exploration of new lands. In the 10th century, the Vikings were able to travel and survive the vast distances between Iceland, Greenland, and Canada because they ate cod which they had learnt to preserve by drying (Kurlansky 1997). Later, by salting the cod before drying, the Basque people of what is now Spain were able to expand cod markets way beyond that of the cod's northern habitat. However, the Basques were not using European waters to source their cod, and it was not until around five hundred years later that it was discovered that they were fishing off the coast of Canada, long before Columbus was credited with his discovery of North America (Kurlansky 1997). By the 19th century, the cod fishery in the northwest Atlantic was booming, with reports of cod more than six feet long and weighing more than 90 kg (Kurlansky 1997). Yet, by the end of the following century the fishery had collapsed (see Section 1.1.1 Fisheries Impacts). In 20th century Europe, the pursuit of cod brought three wars between Iceland and Great Britain in the 50s and 70s as a result of disputes over territories and fishing rights (Kurlansky 1997, Roberts 2007). In the North Sea, there has been a decline in spawning stock biomass since the 1970s which coincides with increasing fishing effort (Cook 1998, ICES 2009), and it is possible that stocks will fail to recover to previous levels even with reductions in fishing pressure (Hislop 1996, O'Brien *et al*. 2000). Cod catches from the North Sea are now composed mostly of young immature fish (Daan *et al*. 1990, O'Brien 2000). Cuts in quota (O'Brien *et al*. 2000, ICES 2009) and a temporary closure of the fishery (Rijnsdorp *et al*. 2001) have been imposed in an attempt to aid recovery but the stock may still be close to collapse (Cook *et al*. 1997). Additional conservation methods and an increased knowledge of cod behaviour are needed to safeguard stocks (Anon. 2001a, Turner *et al*. 2002).

1.7.2 BIOLOGY, LIFE HISTORY AND DIET

Cod are one of more than 25,000 species of fish; aquatic poikilothermic vertebrates with fins and gills (Nelson 1984). Cod are demersal, living predominantly near the sea floor, and are distributed throughout waters of the North Atlantic, including areas such as the North Sea, Baltic Sea and Barents Sea, and occupying a range of water temperatures from -1°C to over 20°C (Drinkwater 2005) and depths of up to 600m (Pawson 1995). The life cycle of cod is divided into several distinct periods (Jobling 2002). The embryonic period, which starts with the fertilisation of the egg, is characterised by endogenous nutrition from a yolk. After hatching, the cod enters the eleutheroembryonic period which continues until most of the yolk has been used and the fish begins to feed on exogenous food. When this transition takes place the larval period begins. Larvae then undergo metamorphosis into juveniles which includes extensive morphological changes and is characterised by full fin differentiation and a replacement of temporary larval organs. The juvenile phase then lasts until the maturation of the gonads and the production of gametes, whereupon the fish becomes an adult (Jobling 2002). The transition from egg to adult stage may take as little as two years, or as long as seven (Oosthuizen and Daan 1974, Brander 2005).

Spawning generally occurs in large aggregations on traditional spawning grounds (Rose 1993) during winter and early spring, although limited spawning may also occur in autumn (Daan *et al*. 1990). Within these aggregations, cod are hypothesised to exhibit a lekking mating structure with males competing to mate with females (Rowe and Hutchings 2003, Windle and Rose 2007). The exact timing of spawning is subject to regional or annual variation (Brander 1994, Fox *et al*. 2000, Wieland *et al*. 2000). Female cod produce around 500 eggs per gram of body weight, meaning that millions can be released by each spawning individual (Kjesbu *et al*. 1996). Larger females produce more eggs of larger size (Pitcher and Hart 1982, Kjesbu 1996). After release into the water column, the vast majority of eggs are destroyed as a result of predation or environmental stresses (Bailey and Houde 1989, Bunn *et al*. 2000). On hatching, larvae feed initially on their yolk sac, before switching to planktonic food such as the juvenile stages of copepods (Last 1978). The growth rate of larvae is influenced by temperature and food availability (Houde 1989, Blaxter 1992, James *et al*. 2003). Larval mortality is high (Bailey and Houde 1989), but if they survive to the juvenile stage they eventually settle to the sea floor where they may find protection in the form of gravel or macroalgae (Gotceitas *et al*. 1995, Gregory and Anderson 1997). Annual recruitment success is largely determined by environmental factors acting upon the egg and larval stages, with subsequent demersal juvenile survival regulated by density-dependent processes (Anderson and Gregory 2000).

Adult growth is determined by food availability and temperature (de Cárdenas 1996, Clark *et al*. 2003, Yoneda and Wright 2005a) and is indeterminate but slows with age (Pitcher and Hart 1982). Adult cod may feed on a variety of fish species including sand eels, haddock and herring, as well as molluscs, crustacea, and polychaetes (Daan 1973, Link and Garrison 2002) and diet may vary seasonally and with predator size (Høines and Bergstad 1999). Cod are also cannibalistic, especially when abundance of recruits is high and the distribution of young cod overlaps with that of older individuals (Daan 1973, Anderson and Gregory 2000, Uzars and Plikshs 2000). Feeding may be suppressed for a considerable proportion of the year during the spawning season which is followed by an abrupt increase in feeding, especially in females, during late- or post-spawning (Fordham and Trippel 1999). In order to reach spawning condition, cod therefore rely on reserves of energy acquired during the non-spawning period (Fordham and Trippel 1999). Failure to build up adequate reserves may result in individuals skipping spawning (Rideout *et al*. 2000, Jørgensen *et al*. 2006).

1.8 THESIS AIMS AND OUTLINE

Recent technological developments have given us clearer insight than ever before into the population structure and movement behaviour of commercially important fish stocks which have potential consequences for the way in which species are managed. The overall aim of this thesis is to incorporate this new understanding into spatially explicit models of migration and aggregation to explore questions on the response of populations to fisheries management and environmental change in terms of the persistence of populations and, where applicable, the effects on fisheries yield. Chapter 2 presents a simple population model of a population exhibiting seasonal migration between a feeding and spawning area. The aim of this chapter is to explore whether an MPA located on a spawning area is able to protect migratory species from overfishing within an uncertain environment. Chapter 3 presents a novel IBM which incorporates fish movement characterised by the behaviour observed from DST studies. The aim of this model is to recreate migration with more realism than can be achieved with population models and to allow the formation and movement of spawning aggregations as a dynamic consequence of individual behaviour rather than as an imposed trait. This design allows the ecological and evolutionary response of fish at the individual and population levels to be explored in light of environmental change (Chapter 4) and fisheries management, including the use of MPAs (Chapter 5). These chapters address previously underexplored questions in animal movement behaviour, responses to environmental change, and general consequences for the management of exploited seasonally migrating species. Chapter 6 summarises the research findings and discusses enhancements to the IBM which would allow the extension of the modelling framework to species-specific scenarios.

2

2

PREVENTING OVEREXPLOITATION OF MIGRATORY FISH STOCKS: THE EFFICACY OF MARINE PROTECTED AREAS IN A STOCHASTIC ENVIRONMENT

2.1 ABSTRACT

Marine protected areas (MPAs) have been widely proposed for protecting overexploited fish populations. It has been suggested that fisheries may be enhanced by spillover of individuals from MPAs into fishing grounds. However, traditional spillover studies fail to account for the seasonal migrations of many populations. Most fisheries models also fail to include the stochasticity inherent in marine environments explicitly. Here MPA efficacy is assessed using a simple population model simulating the migration of fish populations between a spawning ground MPA and a fishery. Including realistic environmental stochasticity in the model allows the population to deviate from, and shift between, positive stable equilibria, something that is

impossible in a deterministic analysis. This deviation may result in population collapse in cases where deterministic analysis predicts population persistence. It is shown that, although effective at low migration levels, the ability of MPAs to protect stocks from collapse generally decreases as migration increases. However, an MPA provides greater protection and greater expected fisheries yield than a system without an MPA, irrespective of migration level. Combining MPAs with a harvest control rule may further increase protection and yield. It is therefore argued that MPAs can play a role in the protection of migratory species.

2.2 INTRODUCTION

Marine protected areas (MPAs) have been advocated as a way to slow or reverse the decline in fish stocks and biodiversity in our oceans attributed to overfishing (Worm *et al*. 2006, Worm *et al*. 2007). In addition to the protection of target species, MPAs can protect the seabed and associated benthos from the damaging effects of trawling (Kaiser *et al*. 2002). They can also eliminate the fishing mortality of non-target species locally, something which is difficult to achieve with traditional management measures (Sobel and Dahlgren 2004). However, it must be emphasised that MPA implementation should not stem from what has been termed “faith-based fisheries” (Hilborn 2006). Rather, it should be based on solid scientific knowledge and an understanding of the consequences and benefits in specific management areas.

In addition to the obvious survival benefits to fish located within MPAs, there is also the potential for the spillover of fish into neighbouring fisheries. This occurs when there is a net emigration of adult and juvenile fish across the boundary of an MPA, and/or by the export of pelagic eggs and larvae (Gell and Roberts 2003). There are examples where spillover has enhanced catches in adjacent fisheries (Roberts *et al*. 2001, Gell and Roberts 2003). However, if the rate of spillover is too high, then the protective benefit of the MPA can be weakened because a greater proportion of the fish stock will be exposed to fishing (Kramer and Chapman 1999). Empirical studies have shown that fish with small home ranges are more readily protected by MPAs than more mobile species (Kramer and Chapman 1999, Gell and Roberts 2003), and it is typically assumed that very large MPAs will be necessary to protect highly mobile species (Gerber *et al*. 2003).

In many temperate regions, commercial fish stocks are in decline, and many are below safe biological limits (ICES 2005). Considerable interest has been shown in using MPAs as a management tool to help stocks recover (Anon. 2000, Anon. 2001b, Kaiser *et al*. 2002), but their protective benefit may be affected by the seasonal migratory behaviour exhibited by many species (Horwood *et al*. 1998). For example, it has been demonstrated that species such as Atlantic cod, *Gadus morhua*, plaice, *Pleuronectes platessa*, thornback ray, *Raja clavata*, and Atlantic bluefin tuna, *Thunnus thynnus*, perform extensive seasonal migrations to and from spawning areas (Hunter *et al*. 2004a, Hunter *et al*. 2006, Metcalfe 2006, Righton *et al*. 2007, Rooker *et al*. 2007). Traditional spillover models are therefore insufficient as a tool to assess the potential of MPAs to protect such migratory stocks, because they consider only non-directional dispersive movement across MPA boundaries into fisheries. A more suitable model is that of Apostolaki *et al*. (2002), who present a deterministic model based on a migratory species, European hake, *Merluccius merluccius*, in the Mediterranean, and show benefits to fisheries yield and spawning-stock biomass following MPA establishment for a range of fish mobility values. Röckmann *et al*. (2007) go further by including environmental variability in their model of migratory Baltic cod, *G. morhua*, and show that MPAs can prolong population persistence when faced with climate change.

One of the difficulties in assessing the potential benefits of MPAs is that many populations are highly dynamic and annual recruitment can be extremely stochastic (Myers 2001, Needle 2002). Despite this inherent uncertainty, most population models do not take stochasticity into account (Gerber *et al*. 2003). A recent analysis by Pitchford *et al*. (2007) models the effect of uncertainty in both recruitment and fishing pressure on the efficacy of different fisheries management measures for a fish population exhibiting simple diffusive movement. They conclude that, in a stochastic world, MPAs are more effective than traditional methods of management: MPAs act as buffers against uncertainty and help to prevent population collapse and decrease variability in the catch. Similar conclusions have been reached by Lauck *et al*. (1998) and Mangel (2000), and the economic benefit of the stabilizing properties of MPAs has also been demonstrated (Armsworth and Roughgarden 2003).

The central aim of this paper is to investigate whether an MPA can protect overexploited migratory fish stocks. More precisely, the efficacy of a spawning area MPA is assessed for fish stocks exhibiting different propensities for migration. A simple population model is presented with directed seasonal migration between spawning and feeding areas. It is assumed that an MPA has been proposed or implemented within the study area, adjacent to an overexploited stock, and that fish migrate to and from that MPA yearly. The model assesses whether the protective effect of the MPA after immigration will be sufficient to prevent population collapse, or whether migratory fish stocks are inadequately protected from the fishery, as predicted in non-migratory spillover studies. Importantly, to account for the uncertainty inherent in fisheries, the effect of environmental stochasticity on MPA efficacy is also evaluated. Additionally, a harvest control rule (HCR) is introduced to mirror the management regimes currently in effect in many fisheries (ICES 2007a).

2.3 METHOD

2.3.1 MODEL OVERVIEW

A simple, discrete-time, single-species population model is presented that simulates a population of fish exhibiting migratory behaviour. Two areas are defined, one acting as a spawning and nursery ground, the other as a feeding ground. Each year is divided into two time-steps (termed half time-steps), with fish migrating to the spawning area to spawn at the start of the year, and returning to the feeding ground after six months. The half time-step format is used for ease of understanding as it allows clear distinction between the two seasonal migration events in the model. At each half time-step there is natural mortality, and a predefined total allowable catch (TAC) is removed, unless there are insufficient fish present in an area, in which case all remaining fish are taken. Recruitment is confined to the spawning area, with recruits added to the population within the spawning area at the end of the year. A model overview is given in Figure 2.1.

Chapter 7 includes appendices relevant to this chapter. Section 7.1 details the equilibria present in the deterministic version of this model. Section 7.2 compares the stochastic recruitment used in this chapter with fisheries data. Section 7.3 presents the results of alternative parameterisations of the model.

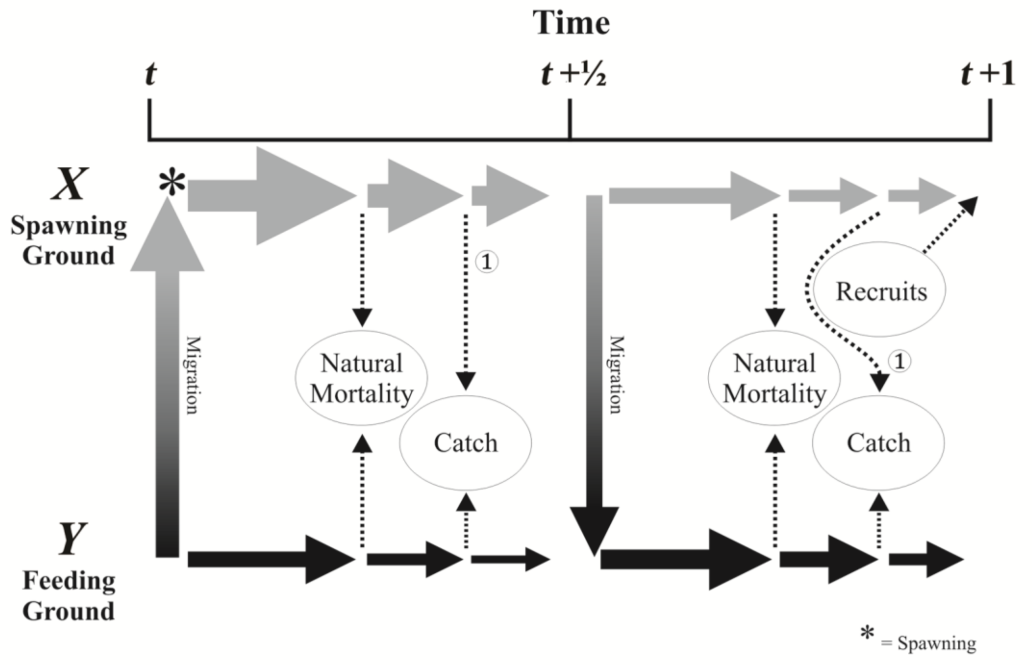

FIGURE 2.1. A DIAGRAMMATIC REPRESENTATION OF THE PROCESSES UNDERLYING THE SIMPLE MIGRATION MODEL. THE DIRECTION OF ARROWS SHOWS THE DIRECTION OF MOVEMENT EITHER THROUGH SPACE TO (OR FROM) THE SPAWNING GROUND FROM (OR TO) THE FEEDING GROUND (VERTICAL ARROWS), OR THROUGH TIME FROM ONE HALF TIME-STEP TO ANOTHER (HORIZONTAL ARROWS). THE CHANGES IN ARROW WIDTH INDICATE CHANGES IN POPULATION SIZE. THE * IN THE DIAGRAM INDICATES THE POSITION IN TIME AND SPACE OF SPAWNING, I.E. AT THE START OF THE YEAR, t, WITHIN THE SPAWNING GROUND. RECRUITS ARE ADDED TO THE SPAWNING GROUND POPULATION AT THE END OF THE YEAR. ARROWS MARKED "1" INDICATE THAT CATCH IS TAKEN FROM THE SPAWNING GROUND IN THE ABSENCE OF AN MPA. WHERE THERE IS AN MPA IN PLACE CATCH IS NOT TAKEN FROM THE SPAWNING GROUND.

2.3.2 DETERMINISTIC MODEL

No marine protected area

In the absence of an MPA, fishing is assumed to take place with equal intensity within both spawning (*X*) and feeding (*Y*) areas, i.e. the catchability of fish within each area is the same. The model is represented in Equations 2.1 to 2.6 below, in half time-step format:

$$N_{X,t+½} = (1-\mu)(N_{X,t} + \gamma N_{Y,t}) - C_{X,t} \qquad (2.1)$$

$$N_{Y,t+½} = (1-\mu)(N_{Y,t} - \gamma N_{Y,t}) - C_{Y,t} \qquad (2.2)$$

$$N_{X,t+1} = (1-\mu)(N_{X,t+½} - \gamma N_{X,t+½}) - C_{X,t+½} + R(N_{X,t}, N_{Y,t}) \qquad (2.3)$$

$$N_{Y,t+1} = (1-\mu)(N_{Y,t+½} + \gamma N_{X,t+½}) - C_{Y,t+½}\ , \qquad (2.4)$$

where $N_{X,t}$ and $N_{Y,t}$ are the number of adult fish on the spawning and feeding grounds, respectively, at the start of year t, and $N_{X,t+½}$ and $N_{Y,t+½}$ are the number of adult fish half way through year t. Fish move via directed migration from one area to the other at the beginning of each half time-step, with direction dependent on the time of year and with a specified proportion γ of fish migrating. Equations 2.1 and 2.2 include migration from population Y to X, and Equations 2.3 and 2.4 include migration from X to Y. Fish die from natural mortality μ, and the quota c is caught from each area (after mortality and emigration or immigration at each half-time step), given enough survivors, or else all survivors are caught. Thus, for Equation 2.1 this gives

$$C_{X,t} = \min[c, (1-\ \mu)(N_{X,t} + \gamma N_{Y,t})]\ . \qquad (2.5)$$

Finally, one-year-old recruits are added to the X population at the end of the year according to a logistic recruitment function based on the total number of adults within X when spawning follows migration onto the spawning ground at the start of the year (see Figure 2.1):

$$R(N_{X,t}, N_{Y,t}) = r(N_{X,t} + \gamma N_{Y,t})(1 - (N_{X,t} + \gamma N_{Y,t})/K)\ , \qquad (2.6)$$

with maximum per capita growth rate, r, and carrying capacity of the spawning ground, K. Note that, in addition to the fish within X at the start of the year, the number of adults on the spawning ground at spawning time includes all fish that have previously migrated from Y. To avoid the possibility of negative recruitment, if the population size within the spawning ground is above the carrying capacity, then the number of recruits is set to zero.

Recruitment is assumed to take place solely within the spawning area. It is also assumed that all recruits remain within the spawning area, i.e. that the spawning area also acts as a nursery. Simulations reveal that relaxing this assumption so that recruits are spread evenly across the whole system does not alter the qualitative results of the model.

To investigate the impact of migration on population persistence, γ is fixed at a value between 0 (no migration) and 1 (all fish migrate), throughout each model simulation. The parameters used in the model and the values they take are summarized in Table 2.1, and justification of parameter choice is given below.

Parameter	**Value**	**Description**
μ	0.1	Natural mortality
γ	0.0 – 1.0	Proportion migrating
r	1.0	Maximum per capita growth rate
K	200	Carrying capacity
c	2.5 – 12.5	Target catch
CV_R	0.6	Coefficient of variation

TABLE 2.1. PARAMETERS USED IN MODEL SIMULATIONS.

Addition of an MPA

An MPA is established by allowing zero catch within the spawning ground. The quota that would have previously been taken from the spawning ground is reassigned to the feeding ground. Assuming that both areas have the same quota before implementation of the MPA, this means that the quota on the feeding ground is doubled. Therefore, in Equations 2.1 to 2.4, the catch in area X becomes $C_{X,t} = 0$ and $C_{X,t+½} = 0$, and the catch in area Y is replaced by $D_{Y,t}$ and $D_{Y,t+½}$:

$$N_{X,t+½} = (1-\mu)(N_{X,t} + \gamma N_{Y,t}) \tag{2.7}$$

$$N_{Y,t+½} = (1-\mu)(N_{Y,t} - \gamma N_{Y,t}) - D_{Y,t} \tag{2.8}$$

$$N_{X,t+1} = (1-\mu)(N_{X,t+½} - \gamma N_{X,t+½}) + R(N_{X,t}, N_{Y,t}) \tag{2.9}$$

$$N_{Y,t+1} = (1-\mu)(N_{Y,t+½} + \gamma N_{X,t+½}) - D_{Y,t+½} \tag{2.10}$$

$$D_{Y,t} = \min[2c, (1-\mu)(N_{Y,t} - \gamma N_{Y,t})] \tag{2.11}$$

$$D_{Y,t+½} = \min[2c, (1-\mu)(N_{Y,t+½} + \gamma N_{X,t+½})]\,. \tag{2.12}$$

2.3.3 STOCHASTIC MODEL

To assess the effect of stochasticity, variability in recruitment is introduced. A recruitment value, R_{st}, is drawn from a normal distribution with mean R (Equation 2.6) and coefficient of variation CV_R. Values of R_{st} are drawn independently each year, i.e. there is no correlation between years. The default value of CV_R is 0.6, which results in a realistic level of variability when compared with the recruitment success of real-world fish stocks (see Figure 7.1). If negative values of R_{st} are drawn from the normal distribution, then R_{st} is set to zero. Sampling from alternative distributions (such as Weibull or truncated normal distributions) does not alter the qualitative results of the model (see Section 7.3). Other forms of stochasticity (e.g. uncertain catch), where the degree of variability is lower than in recruitment, have a minimal impact on the qualitative results of the model, so are not included (see Pitchford *et al*. 2007).

2.3.4 HARVEST CONTROL RULE

An HCR, which is a commonly used method of fisheries management (ICES 2007a), can be applied in addition to the MPA. The HCR can be thought of as a modification of the quota system described above that allows the fishing quota to be adjusted annually to allow for changes in population size. A method similar to Pitchford *et al*. (2007) is followed, namely that at the end of each year, the total population size (T_t) is calculated, and if this is below some critical value, the target catch for the following year is reduced. The HCR is implemented as follows:

$$\text{If } T_t \geq K/2 \text{ then } c_{(t+1)} = c;$$

$$\text{if } T_t < K/2 \text{ then } c_{(t+1)} = c(T_t/(K/2)),$$

i.e. if the total population size in year t, T_t, is higher than half the carrying capacity, $K/2$, then the catch in the following year, $c_{(t+1)}$, is set to the target catch; if T_t is less than $K/2$ then $c_{(t+1)}$ is reduced by a factor of $T_t/(K/2)$. A further constraint is applied such that when the target catch is reduced, the maximum year-on-year change is restricted to be no greater than 15%. This is a reasonable restriction. For example, the mean annual change where reductions occurred in absolute fishing quota for plaice in the North Sea (ICES Subarea IV) between 1987 and 2007 was 10.1% (calculated from raw data in ICES 2007b).

2.3.5 DYNAMIC QUOTA

A consequence of the ability of a fish to migrate is that the quota system outlined above may not realistically model the fishers' response to the stock location. In the first half time-step, a proportion of fish move into the MPA, meaning that the quota, $2c$, may not be caught if γ is high. In the second half time-step, the fish move back to the fishery, but the quota in the second half time-step is still restricted to $2c$. In that case the total catch would be lower than the total yearly quota, $4c$. Therefore, as an alternative to the static quota system, a dynamic quota system is introduced, allowing any remaining quota from the first half time-step to be added to that of the second half time-step.

2.3.6 PARAMETER CHOICE

The parameter values used in the model are listed in Table 2.1. The value for natural mortality, $\mu = 0.1$, was chosen because it approximates to the annual natural mortality rate of 0.2 commonly used in fisheries models (ICES 2007c). The r and K values chosen in the logistic recruitment function were fixed at the same value as used in Pitchford *et al*. (2007), although changing them does not alter the qualitative behaviour of the model. In the model with the MPA, a c value of 12.5 was chosen because, in the model without the MPA, the population was overfished across the whole range of γ, and the model investigates how effective MPAs are at preventing overexploitation in overfished populations. Validation of the model using different assumptions and parameter choices is shown in Section 7.3.

All model simulations were conducted in the open-source language R 2.4.0 (R Development Core Team 2006).

2.4 RESULTS

2.4.1 MODEL WITHOUT AN MPA

Deterministic investigation

Model equilibria were determined from analytical model analysis (see Section 7.1). Setting $c = 7.5$ (with c representing an overall annual quota of 30 divided between spawning and feeding areas and between the two half time-steps) and the remaining parameters as in Table 2.1 results in values for γ that determine four alternative fishing scenarios at equilibrium:

(i) For very low values of γ ($\gamma < 0.08$ for the default parameter values), there are sufficient fish in both half time-steps within the spawning ground to support the full quota c. However, on the feeding grounds the population size is insufficient to support the full quota, so all remaining fish are taken.

(ii) At low ($0.08 \leq \gamma < 0.24$) and high γ ($0.86 \leq \gamma < 0.92$), there are again sufficient fish in both half time-steps on the spawning grounds to support the full quota c. On the feeding grounds there are insufficient fish in the first half time-step, but following migration onto the feeding grounds, there are sufficient fish to support the full quota c.

(iii) At intermediate γ ($0.24 \leq \gamma < 0.86$), there are sufficient fish in both areas in all half time-steps to support the full quota c.

(iv) At very high γ ($\gamma \geq 0.92$), there are sufficient fish on the spawning grounds but not the feeding grounds in the first half time-step. There are sufficient fish on the feeding grounds but not the spawning grounds in the second half time-step.

When the model is run deterministically, the population will reach one of these stable equilibrium points. Depending on the value of γ, it may take up to 23 years for the population size to fall within 1% of the equilibrium population size. The exact position of these equilibrium points varies with the parameter choice, but there is always a unique stable equilibrium for $r = 1$ (with much larger r, e.g. $r > 2.35$ with the default model parameters, stable limit cycles or chaos can be obtained; Kot 2001). There exists a stable equilibrium point at zero population size only for very high values of c (results are not shown, but equilibrium points exist at zero when $c > 17$), for all values of γ.

Stochastic investigation

Introducing stochasticity in recruitment allows the system to deviate from the behaviour described above, with the potential for population collapse. Figure 2.2 shows the probability of collapse within 100 years, with a range of c values, for the full range of γ, from 0 to 1 interpolated from calculations carried out for increments of 0.01. This allows comparison of the probability of collapse under different fishing regimes. It is clear from Figure 2.2 that increasing fishing pressure increases the probability of collapse across the full range of γ. It is apparent that different propensities for migration lead to a different risk of collapse. At intermediate values of γ, the probability of collapse is very high. However, at low and high values of γ, the probability of collapse is lower. From the deterministic analysis, it is clear that at low values of γ, migration into the feeding area is very low, meaning that the full quota c is not taken in the feeding ground. The population size within the spawning ground is large because there is little movement out of it, but the number of fish caught is limited by the quota. In effect then, because fishing pressure does not respond to the location of the fish stock and the full quota cannot be taken from the feeding ground, the stock is better protected than it would be if there was greater migration. Therefore, the probability of collapse is lower at low γ. At high values of γ, a large proportion of the population moves from one area to another. This means that few fish remain in the area from which the fish have migrated, so the full quota c cannot be caught. Catch in the area into which the fish have migrated is limited by the quota. Again, because the fishing pressure does not respond to the location of the fish, the stock is better protected than it might be if a lesser proportion moved. See Section 2.5 Discussion for further analysis of this result.

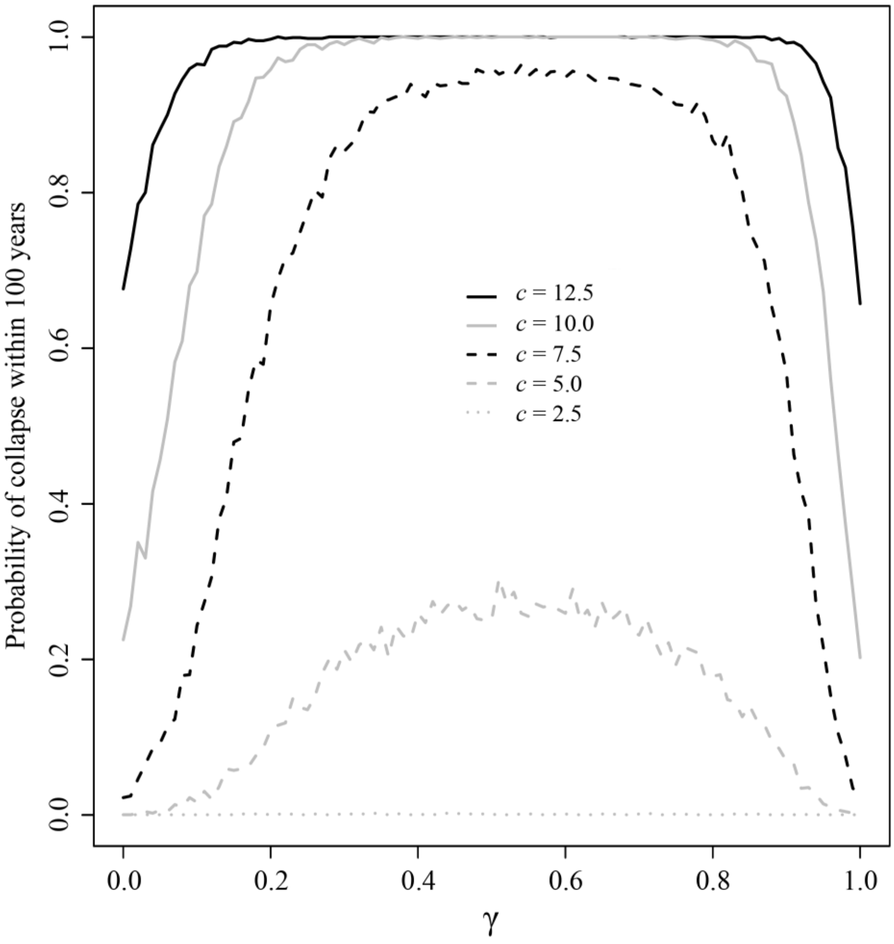

FIGURE 2.2. PROPORTION OF EXPLOITED POPULATIONS COLLAPSING WITHIN 100 YEARS WITH DIFFERENT FISHING PRESSURES AND NO MPA PRESENT, FROM 1000 SIMULATIONS OF THE STOCHASTIC MODEL.

2.4.2 MODEL WITH AN MPA

Deterministic investigation

For the MPA model, a value of *c* = 12.5 (i.e. a total annual quota of 50) is used and the remaining parameters are as in Table 2.1. Examining the deterministic model, it is theoretically possible for three fishing scenarios to exist at equilibrium, with the existence and exact position of these stable equilibrium points dependent on the parameters used:

(i) The population size on the feeding grounds is sufficient in each of the two half time-steps to allow the full quota $2c$ to be taken.

(ii) The population size on the feeding grounds is only sufficient in the second half time-step (after migration of fish onto the feeding ground from the MPA), i.e. all fish are removed from the feeding grounds in the first half time-step.

(iii) The population size is not sufficient to support the quota in either half time-step, i.e. all fish are removed from the feeding grounds in each half time-step. Replenishment of the feeding grounds must come via recruitment within the MPA.

When the model is run deterministically, the population will reach one of these (analytically determined) stable equilibrium scenarios. A description of the deterministic model equilibria is given in the Section 7.1. A phase portrait showing the position of the equilibrium point when $\gamma = 0.2$ is shown in Figure 2.3. The unique stable equilibrium point occurs in the Scenario 3 region of the phase diagram, meaning that the population size within the feeding grounds is not sufficient to support the complete quota in either half time-step. In this case, because the proportion of the population moving into the fishery by migration from the MPA is low, the number of fish present in the fishery is not large enough to support the full quota (i.e. $N_Y = 0$ at the end of each half time-step).

A phase portrait showing the existence of equilibria when γ is 0.8 is shown in Figure 2.4. In that case, there are two stable equilibrium points, the higher one corresponding to Scenario 2 and the lower one to Scenario 3. Between these two stable equilibrium points lies an unstable equilibrium point. The stable equilibrium point reached in a deterministic environment will depend on the initial population size of the population, i.e. the population is unable to switch between stable states. This is illustrated in Figure 2.5 (grey lines). When the initial population size at the start of the model simulation is high (Figure 2.5a), the population reaches the higher of the two equilibria asymptotically (marked by the upper dashed line) and is unable to reach the lower equilibrium point. When the population size at the start of the simulation is low (Figure 2.5b), the population reaches the lower of the two equilibria. Except the lower equilibrium point when $\gamma = 1$, none of these equilibrium points are at zero (i.e. there is always a proportion of the population retained within the MPA), so the population will never collapse.

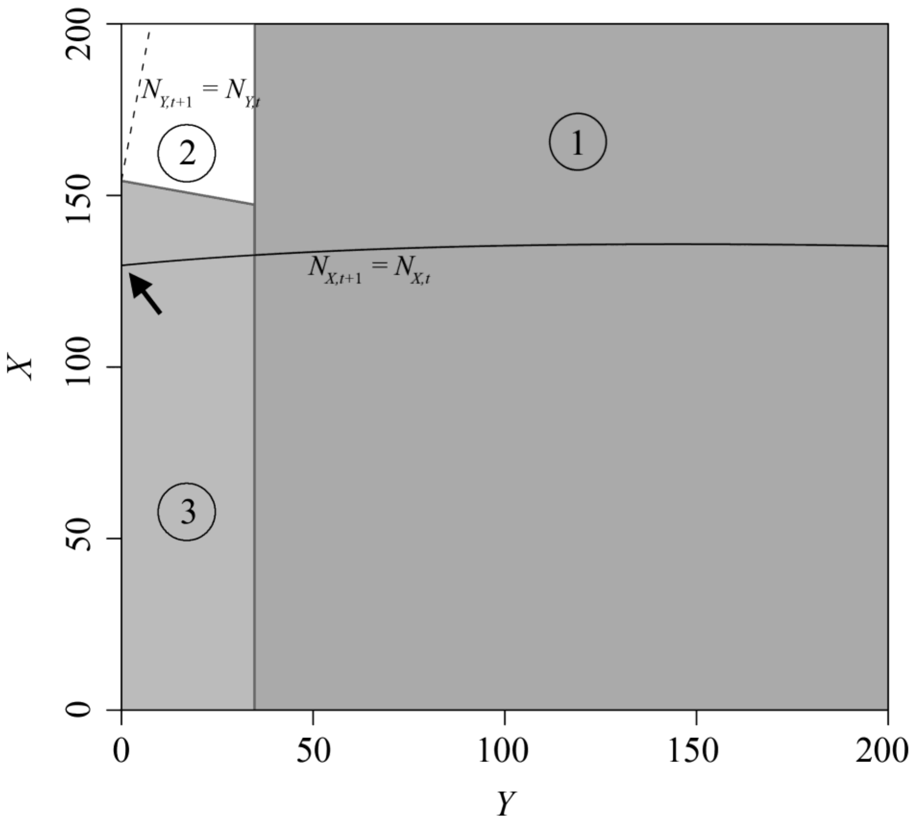

FIGURE 2.3. PHASE DIAGRAM SHOWING THE POSITION OF THE EQUILIBRIUM POINT IN THE MPA MODEL WHEN $\gamma = 0.2$. THE NUMBERED REGIONS CORRESPOND TO THE THREE POSSIBLE SCENARIOS DESCRIBED IN THE TEXT. SOLID LINES REPRESENT X NULLCLINES, I.E. WHERE $N_{X,t+1} = N_{X,t}$ (SEE EQUATION 7.4), AND DOTTED LINES REPRESENT Y NULLCLINES (SEE EQUATIONS 7.5 TO 7.7). NOTE THAT THE Y NULLCLINE IN REGION 3 IS THE SAME AS THE VERTICAL AXIS IN THE DIAGRAM, SO CANNOT BE SEEN. IN THIS CASE, EQUILIBRIUM IS WHERE THE TWO NULLCLINES INTERSECT IN REGION/SCENARIO 3 ($N_{Y,t} = 0$) WHICH IS MARKED BY THE BLACK ARROW.

Stochastic investigation

Introducing stochasticity allows the population size to deviate from the stable equilibria. However, rather than deviating from a single equilibrium point as in the model without an MPA, at high values of γ there are two stable equilibria and the population is able to switch between them. Figure 2.5 (black lines) shows example simulations when $\gamma = 0.8$ and that the population size is able to alternate between values close to the upper and lower equilibrium points before eventually crashing. Note that the presence of two equilibrium points may facilitate collapse: if only the upper equilibrium point was present, collapse would be less likely (but not impossible). Stochastic fluctuations can allow the system to enter the basin of attraction of the lower stable equilibrium, from which transition to population collapse is more likely.

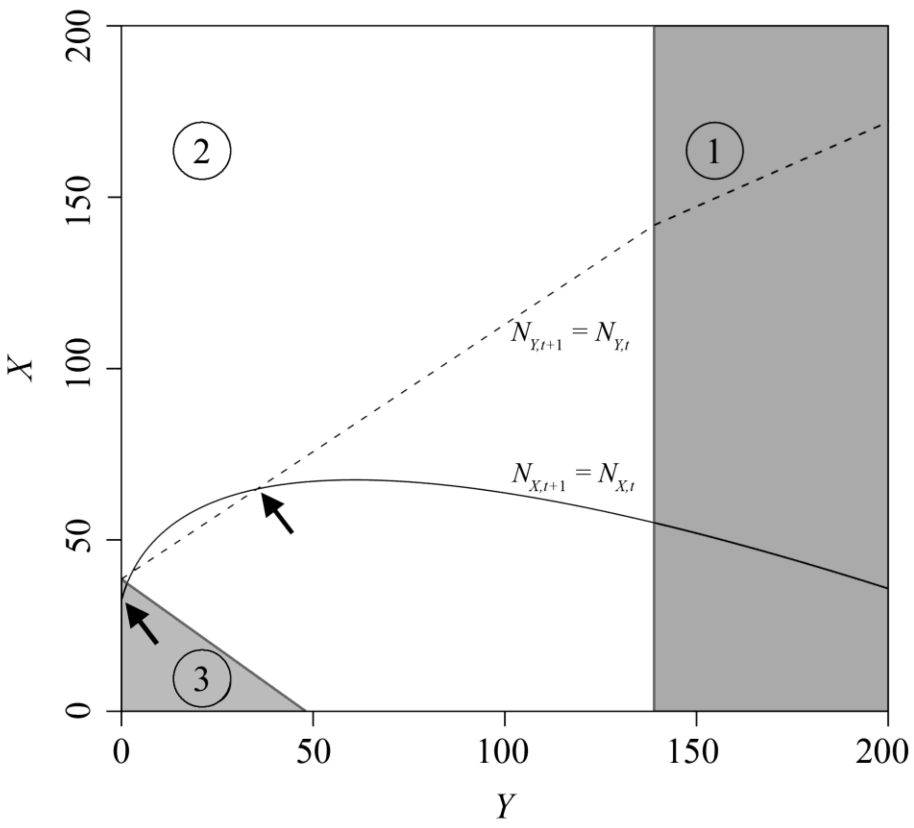

FIGURE 2.4. PHASE DIAGRAM SHOWING THE POSITION OF THE EQUILIBRIUM POINTS IN THE MPA MODEL WHEN $\gamma = 0.8$. THE NUMBERED REGIONS CORRESPOND TO THE THREE POSSIBLE SCENARIOS DESCRIBED IN THE TEXT. SOLID LINES REPRESENT X NULLCLINES (SEE EQUATION 7.4), AND DOTTED LINES REPRESENT Y NULLCLINES (SEE EQUATIONS 7.5 TO 7.7). NOTE THAT THE Y NULLCLINE IN REGION 3 IS THE SAME AS THE VERTICAL AXIS IN THE DIAGRAM, SO CANNOT BE SEEN. IN THIS CASE, THERE ARE TWO STABLE EQUILIBRIA, THE HIGHER WHERE THE TWO NULLCLINES CROSS AT HIGHER POPULATION SIZE IN REGION/SCENARIO 2, AND THE LOWER WHERE THE TWO NULLCLINES CROSS IN REGION/SCENARIO 3 ($N_{Y,t} = 0$). THE POSITIONS OF THE STABLE EQUILIBRIUM POINTS ARE MARKED WITH BLACK ARROWS. THERE IS ALSO AN UNSTABLE EQUILIBRIUM POINT WHERE THE NULLCLINES CROSS AT LOWER POPULATION SIZE IN REGION/SCENARIO 2.

Figure 2.6 shows the probability of population collapse within 100 years for the full range of values of γ from zero to one, in increments of 0.01. The dashed black line in Figure 2.6 corresponds to the results with an MPA in place. Note that there is a slight downturn in the probability of collapse with extensive migration (see Section 2.5 Discussion for an explanation). However, with the default parameters, the downturn in the probability of collapse is small and the relative probability of collapse remains high with high values of γ. Reducing mortality (μ, c) and increasing recruitment (r, K) parameters can lead to a bigger downturn in the probability of collapse, but this also reduces the overall probability of collapse across all values of γ. Allowing recruits to be distributed between both MPA and fishery shifts the curve to the left (i.e. decreases the level of MPA protection), but the qualitative shape of the curve remains the same.

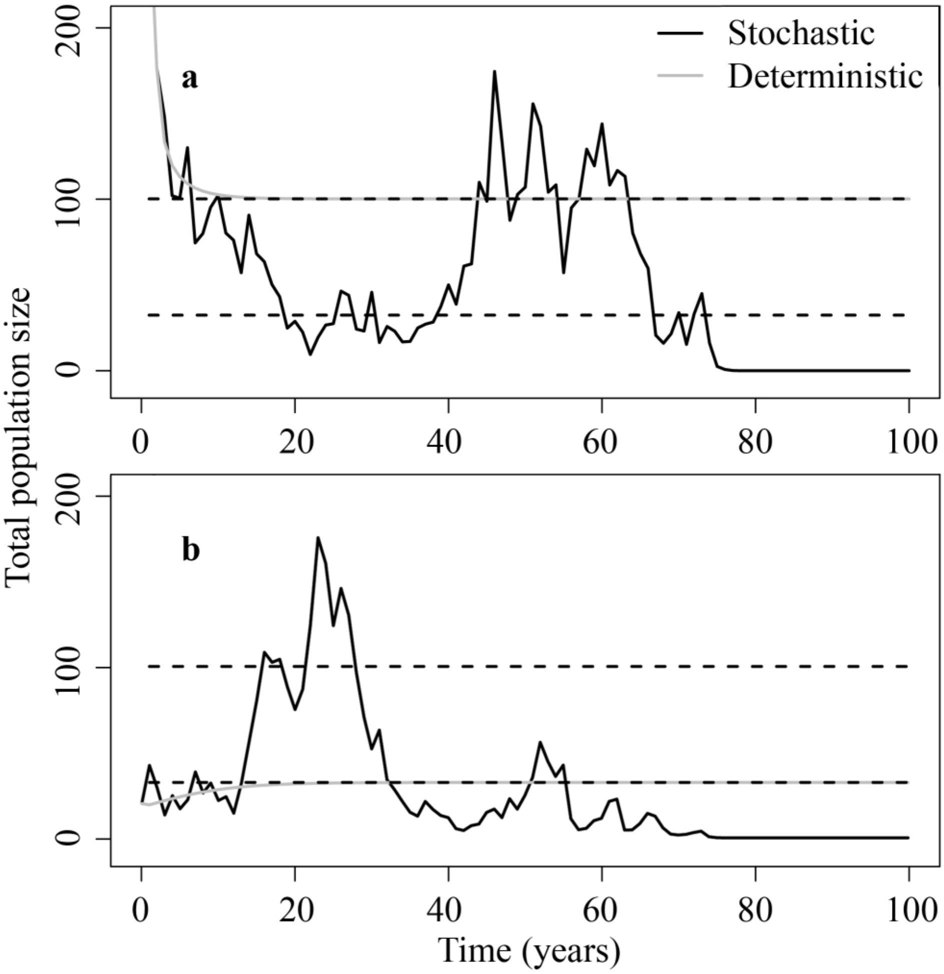

FIGURE 2.5. POPULATION SIZE OVER 100 YEARS FROM ONE REALISATION OF THE DETERMINISTIC AND STOCHASTIC SIMULATIONS WITH AN MPA, WHERE $\gamma = 0.8$. THE UPPER DASHED LINE SHOWS THE POSITION OF THE SCENARIO 2 EQUILIBRIUM POINT, AND THE LOWER DASHED LINE SHOWS THE POSITION OF THE SCENARIO 3 EQUILIBRIUM POINT. INITIAL POPULATION SIZE a) ABOVE THE UPPER EQUILIBRIUM POINT AND b) BELOW THE LOWER EQUILIBRIUM POINT.

It is possible to compare the yields (i.e. the realised catch) of the stochastic simulations from the model with the MPA with those of the model without the MPA. Figure 2.7 shows expected yields in year 50 taken from 1000 simulations across the range of values of γ from 0 to 1, with c

set at 12.5 (i.e. annual quota = 50). The solid black line shows the results without an MPA, the dashed black line that following MPA establishment. Except extreme low and high values of γ, the expected yield is higher when an MPA has been introduced into the model. Within the MPA system, expected yields initially increase with increased mobility, but then decrease as the propensity for migration increases further. Figure 2.8 shows the distribution of yields at year 50 from 1000 simulations when $\gamma = 0.5$. Figure 2.8a corresponds to the system without an MPA, and clearly demonstrates that usually little or no yield is taken in year 50. Figure 2.8c corresponds to the system with an MPA, and shows much higher yields generally.

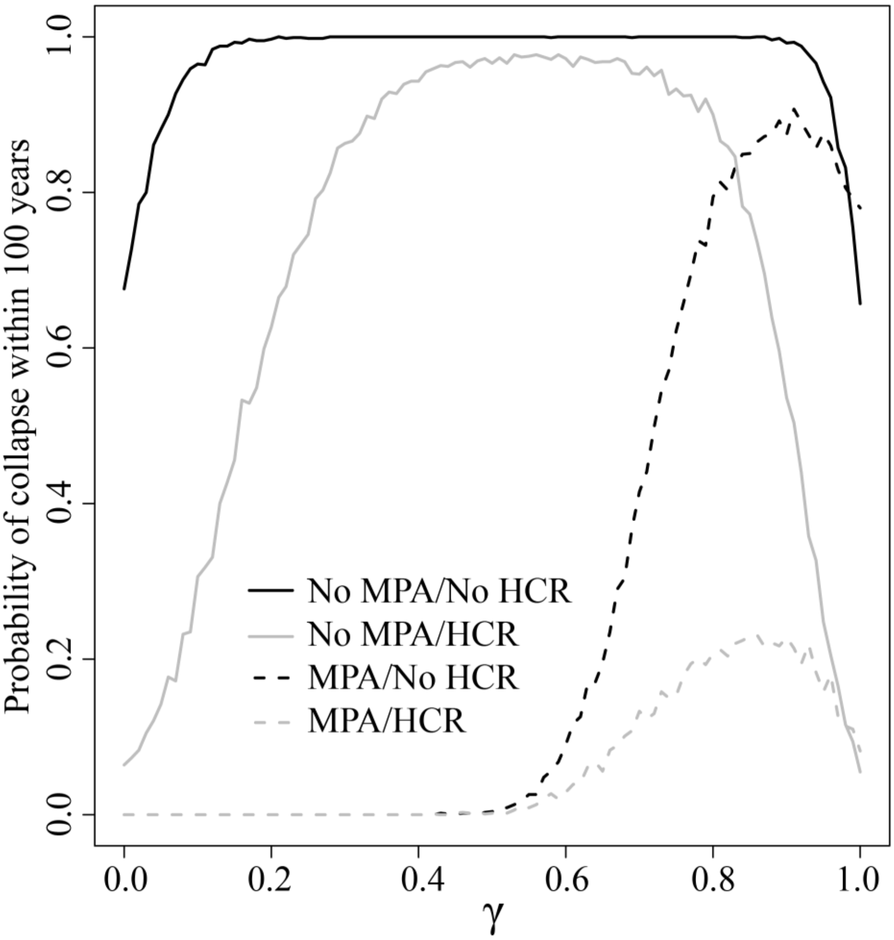

FIGURE 2.6. PROPORTION OF EXPLOITED POPULATIONS COLLAPSING WITHIN 100 YEARS WITH $c = 12.5$, FROM 1000 SIMULATIONS OF THE STOCHASTIC MODEL.

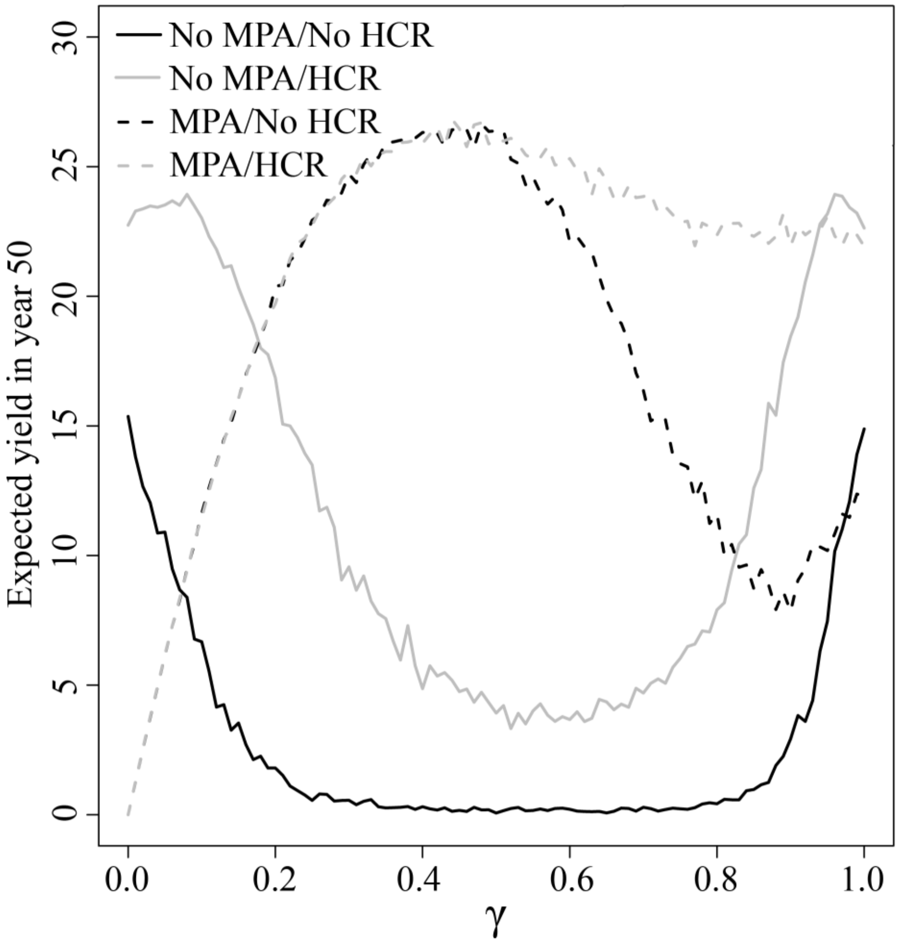

FIGURE 2.7. THE EXPECTED YIELD IN YEAR 50, WITH c = 12.5, FROM 1000 SIMULATIONS OF THE STOCHASTIC MODEL.

2.4.3 FURTHER ANALYSIS

Having already argued that the results from the deterministic analysis are likely to be misleading, the following analysis describes the stochastic output of the MPA model only. The aim here is to explore alternative fisheries management measures to assess their effect on population persistence and fisheries yield.

Inclusion of a HCR

Figure 2.6 (dashed grey line) shows the probability of population collapse within 100 years when the HCR is implemented in addition to the MPA system. It is clear that with the HCR, the probability of collapse is reduced from the situation with a simple fixed quota system, although it remains higher for larger values of γ. The shape of the curve does not change.

Using an HCR in addition to an MPA is more effective at reducing collapse than using an HCR alone (Figure 2.6, solid grey line). Figure 2.7 shows the effect of HCR introduction on yield with (dashed grey line) and without an MPA (solid grey line). Yield is increased across the whole range of values of γ for the non-MPA system when an HCR is introduced. When an HCR is introduced in addition to an MPA, the yield remains similar for lower values of γ, but at higher values the yield increases. Excluding extremely high and low values of γ, an HCR in addition to an MPA returns a higher yield than an HCR alone. Figure 2.8b shows the distribution of yields in year 50 resulting from 1000 simulations with $\gamma = 0.5$, when an HCR is implemented alone. It is clear that, like the system without an HCR or MPA (Figure 2.8a), yield is very low. Figure 2.8d shows the distribution of yield in year 50 for a system with an HCR and MPA, showing increased yields compared with an HCR alone, but, with this value of γ, yields do not markedly increase over the situation with an MPA alone (Figure 2.8c).

Including dynamic quota

Figure 2.9 (dashed line) shows the probability of population collapse within 100 years when the remaining quota from the first half time-step is allowed to be added to the quota of the second half time-step. In cases where γ is high, this allows the total annual catch to more closely approach the total annual quota when compared with the static quota system. This results in greater fishing pressure and increases the probability of population collapse. Using an HCR in addition to this new fishing system reduces the probability of collapse slightly (Figure 2.9, dotted line), but the benefits are not as pronounced as when an HCR is included with a static quota system (Figure 2.6, dashed grey line). Note that there is no longer a downturn in the probability of collapse with extensive migration (see Section 2.5 Discussion for an explanation). Figure 2.10 shows the effect of the dynamic quota system on yield with (dotted line) and without an HCR (dashed line). Expected yield increases slightly in comparison with the static quota system (solid line) for low to intermediate values of γ (i.e. $\sim 0.25 < \gamma < \sim 0.5$) where the probability of collapse is low. However, at higher values of γ, the expected yield decreases when compared with the static quota as the probability that the population will have collapsed is increased. When an HCR is introduced, the expected yield increases slightly for high values of γ (i.e. $\gamma > \sim 0.65$), but is otherwise similar to the no-HCR case.

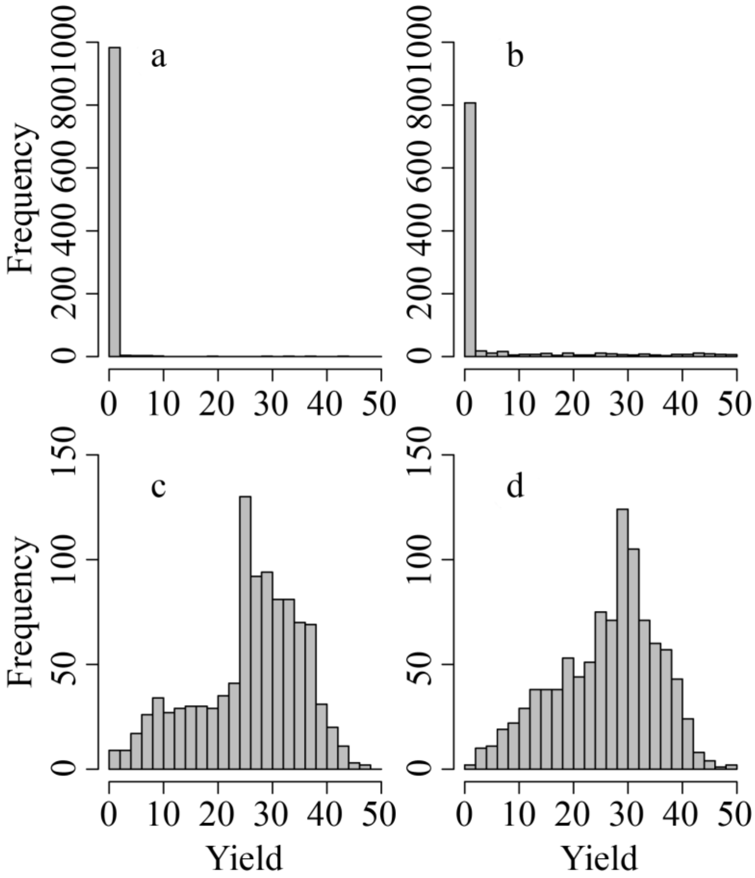

FIGURE 2.8. THE DISTRIBUTION OF YIELD OBTAINED IN YEAR 50, WITH $\gamma = 0.5$, FROM 1000 SIMULATIONS OF THE STOCHASTIC MODEL. a) NO MPA AND NO HCR; b) HCR WITH NO MPA; c) MPA WITH NO HCR; AND d) MPA AND HCR.

2.5 DISCUSSION

The results show that, in a stochastic environment, the efficacy of an MPA decreases as the propensity for migration increases within a fish population. Pitchford *et al*. (2007) suggest that MPAs can act as a buffer against uncertainty to prevent collapse. Although this certainly holds in this model for fish populations that rarely migrate, the population is very likely to collapse when most fish in the population exhibit migratory behaviour. The high probability of collapse also leads to a marked reduction in expected yield with highly migratory populations in comparison with less migratory populations.

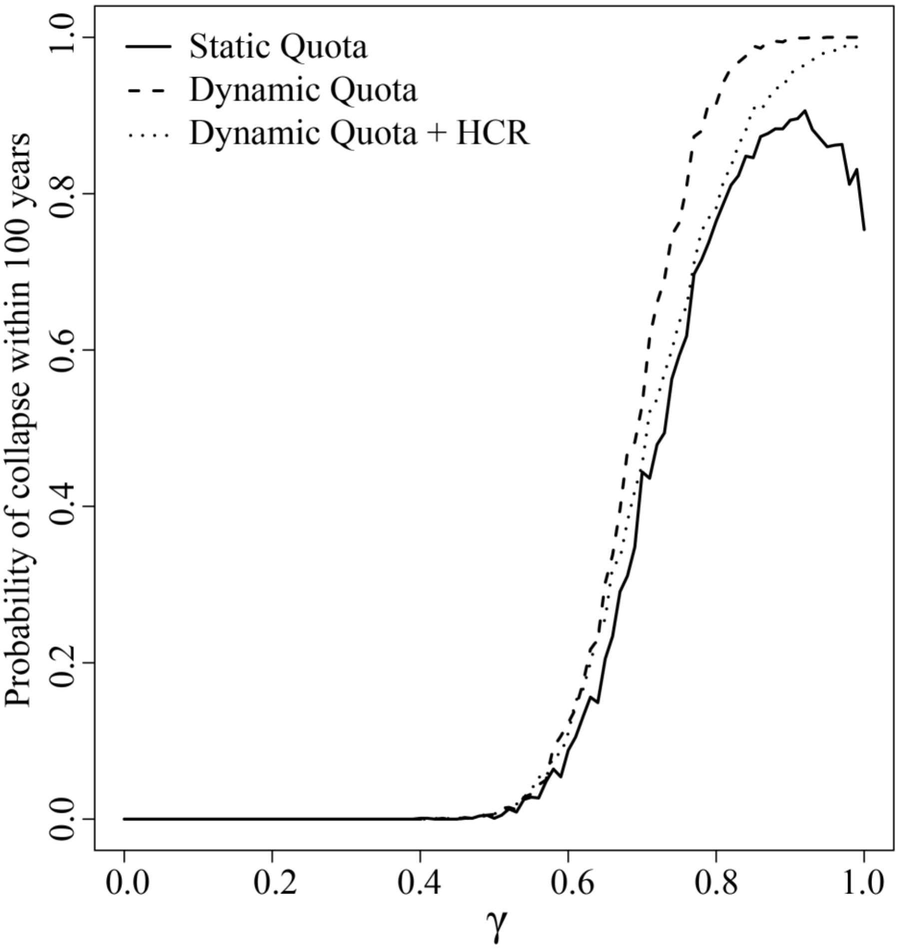

FIGURE 2.9. PROPORTION OF EXPLOITED POPULATIONS COLLAPSING WITHIN 100 YEARS, WITH STATIC AND DYNAMIC QUOTA SYSTEMS, FROM 1000 SIMULATIONS OF THE STOCHASTIC MODEL.

However, compared with the model without the MPA, the MPA generally does a better job of protecting fish stocks. It should be noted that, because of the simplicity of the model, the fishing strategies exhibited in the model without the MPA may not be very realistic for high and low values of γ. At low γ, the feeding ground population is not replenished at a sufficient rate and, with sufficient fishing pressure, the population quickly becomes locally extinct. The remaining population becomes restricted to the spawning ground, with replenishment of the stock through spawning. Fishing pressure is not adjusted to account for this, so there is essentially only half the fishing pressure in this situation, meaning that the probability of collapse is lower. Similarly, at high values of γ, the stock is highly mobile, which means that the stock in one of the two areas will always be very small. Again, this effectively halves the fishing pressure. If fishing pressure was re-distributed (as would be expected in the real world, and as implemented in the dynamic quota system with MPAs in place), it would be expected that the rates of collapse would rise, so the dome-shaped curve seen in Figure 2.2 is probably exaggerated and conservative for low and high γ. Comparing the curves with and without the MPA, it is clear that the probability of collapse is generally lower with an MPA in place. Therefore, for all levels of migration, the presence of an MPA is likely to be an improvement on the simple quota system.

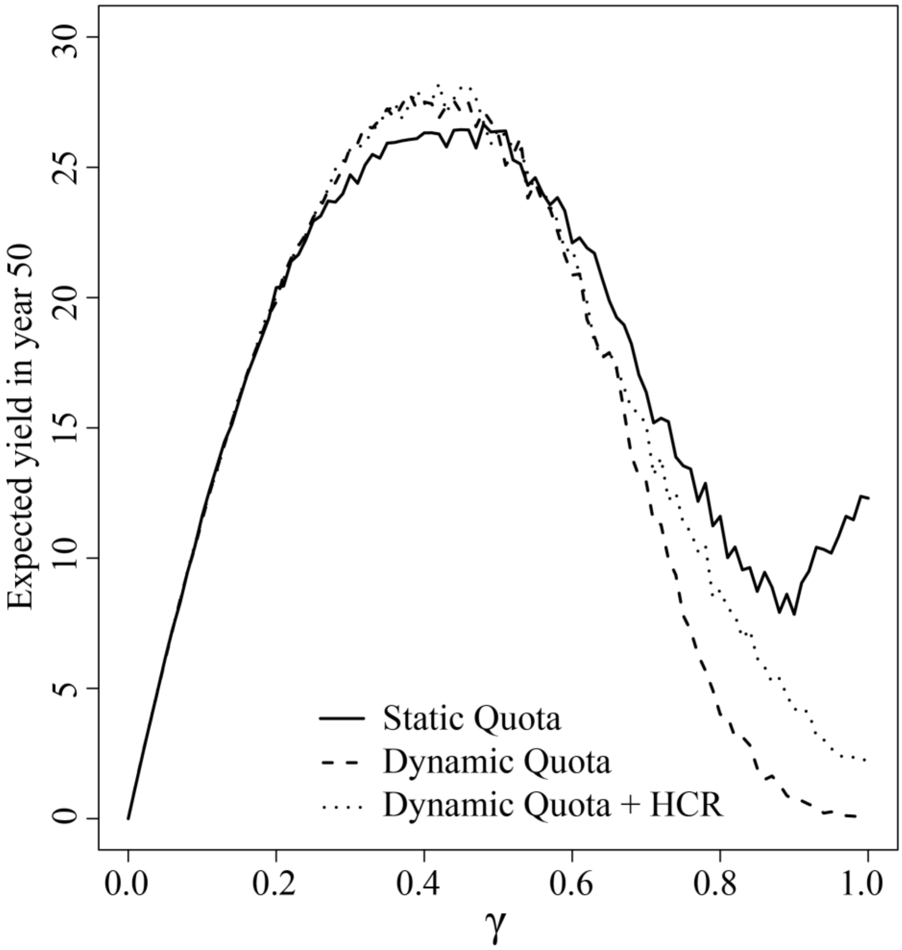

FIGURE 2.10. EXPECTED YIELD IN YEAR 50, WITH STATIC AND DYNAMIC QUOTA SYSTEMS, FROM 1000 SIMULATIONS OF THE STOCHASTIC MODEL.

Spillover has been suggested as a mechanism whereby fish from inside an MPA may move across an MPA boundary, thereby increasing the fish available to the fishery (Kramer and Chapman 1999, Lundberg and Jonzén 1999, Roberts *et al*. 2001, Gell and Roberts 2003). Spillover is usually considered to take place through non-directional movement across the MPA boundary. Apostolaki *et al*. (2002) developed a deterministic model that incorporates more realism through directed seasonal migrations, and concluded that MPA implementation could increase yields across all fish mobility values. The current model allows directed movement into the MPA during the spawning season, followed by directed movement out of the MPA during the feeding season. Highly migratory fish are therefore protected during spawning because most of the population will reside in the MPA, but may be heavily exploited during the feeding season when most are available to the fishery. The results agree with those of Apostolaki *et al*. (2002) in that yields are expected to increase with the implementation of an MPA over a system with no MPA. The results also suggest that population persistence is improved with MPAs in place when compared with a simple quota system. Similarly, Röckmann *et al.* (2007) conclude that the use of MPAs may improve the persistence of Baltic cod in the face of environmental change. However, incorporating environmental stochasticity in this model allows variability around equilibria that commonly results in population collapse for more mobile populations (Figure 2.6). Therefore, the results are perhaps less encouraging in terms of the ability of an MPA to protect more mobile species.

Although the model was not parameterized for any particular species, the underlying messages in the model can be applied generally. The model behaves in a qualitatively predictable fashion when alternative parameterisations are used (see Section 7.3), and the conclusions are therefore expected to be robust to alternative life history parameterisation. One aspect not investigated here is the effect of age structure on MPA efficacy. To maintain simplicity and focus on the specific effects of migration on MPA success, the model assumes that all fish contribute equally to recruitment and catch. Without age structure, a fish only needs to be protected within the MPA for one year in order to reproduce. It is therefore possible that the addition of age structure may reduce the yield and protective benefits of MPAs when compared with traditional effort-based management (Hastings and Botsford 1999, Hart 2006). For example, with age structure in place, similar yield may be obtained by age-selective fishing as with an MPA (Beverton and Holt 1957). Age- or size-selective fishing may also lead to an evolutionary change in size at maturation that has the potential to alter the expected benefits of MPAs (Law 2007). For example, yield may be reduced when compared with simulations without evolution (Miethe *et al*. 2009). Development of an age-structured model would provide insight into these issues and would also allow different ages to exhibit different propensities for migration. The extent to which a particular species will be protected by an MPA will depend on its life history, but the model results indicate that more mobile species will generally be less well protected. Strong selection against movement would therefore be anticipated because sedentary individuals have better long-term fitness

(Travis and Dytham 1999). However, long-term changes in habitats (e.g. increased natural predation within an MPA) may favour migration away from those areas (Dytham and Simpson 2007). Such detailed evolutionary considerations are beyond the scope of this model.

At very high values of *γ*, with an MPA in place and a static quota system, there is a downturn in the probability of population collapse (Figure 2.6). This can be explained by the fact that there is a limited quota allowed in the fishery in each half time-step. With extensive migration, almost all fish will be present in the MPA during spawning, leading to very little catch. During feeding, almost all the stock is on the feeding grounds but, given sufficient population size, fishing is limited by the assigned quota. Lowering *γ* slightly would increase the number of fish on the feeding ground during spawning, so increasing the overall annual catch and lowering the protective effect of the MPA. Despite this slight increase in MPA efficacy with very high values of *γ*, MPAs remain relatively ineffective at protecting the most migratory populations in comparison to sedentary ones. When a more realistic dynamic quota system is introduced, the remaining quota from the first half time-step is redistributed to the quota in the second half time-step. In that case, higher values of *γ* do not cause a reduction in catch as the reduced population size within the fishery in the first half time-step is compensated by the increased population size in the second half time-step. Therefore, the downturn in the probability of collapse is not seen with a dynamic quota system.

The bi-stability exhibited in the MPA model for higher values of *γ* is an interesting example of the presence of alternative stable states (or regimes; May 1977, Scheffer *et al*. 2001) where there may be two or more alternative equilibria present in the population dynamics. In the deterministic model, highly migratory fish populations can stabilize at either a large or a small population size, depending on the size of the initial population (Figure 2.5). This leads to the existence of different equilibrium fishing scenarios. When stochasticity is introduced, the population can switch between stable states. Such switches in population size or community structure, termed regime shifts, have been demonstrated before in fisheries (Holling 1973, Jackson *et al*. 2001, Collie *et al*. 2004, Steele 2004, Oguz and Gilbert 2007). The consequence of the ability to shift between stable states is that a highly productive population may quickly and unexpectedly shift to a low population size if, for example, there is a particularly poor spawning season. This would then increase the probability of subsequent population collapse. Measures that reduce the likelihood of switching between stable states, e.g. reducing the intensity of catch, may be possible. The HCR introduced in this model could be seen as an example of such a measure. However, bi-stability is not necessary to allow population collapse.

In the model without the MPA there was no bi-stability, but population collapse was still possible.

The model with the static quota system demonstrates the simplest possible incorporation of migration and fishing strategy. Alternative management strategies have the potential to alter the conclusions. Inclusion of an HCR alone decreases the probability of collapse and increases yield over the simple non-MPA model, but is generally less effective than implementing an MPA without an HCR except at very high rates of migration (Figure 2.6). A combination of an MPA and an HCR has increased benefits both in preventing population collapse (Figure 2.6) and increasing expected yields (Figures 2.7, Figure 2.8) when compared with either an MPA or an HCR alone. Despite this, the HCR implemented in the model was not sufficient to protect more mobile stocks comprehensively, even when modelled in addition to an MPA. Constraints were deliberately included in the HCR to reflect the inadequacies of stock assessments and the problem of political interference in many fisheries (Daw and Gray 2005). These weaknesses mean that an HCR is insufficient to prevent population collapse. For example, by setting a maximum year-on-year change in target catch, rates of population change may exceed changes in catch. Therefore, decreases in population size may not be matched by decreases in quota, and the stock may still be overfished to collapse. Additional biases involved when implementing HCRs may further reduce their effectiveness (Pitchford *et al*. 2007). When the dynamic quota system, which is more realistic than a static quota system, is introduced, the increase in fishing pressure leads to an increase in the probability of collapse for larger values of γ (Figure 2.9). At lower values of γ, the presence of an MPA still allows population persistence. Implementation of an HCR in addition to the dynamic quota system reduces the probability of collapse (Figure 2.9) and increases the expected yield (Figure 2.10), but to nowhere near the same extent as when an HCR is implemented in addition to a static quota system. With a dynamic quota system, the constraints in the HCR are such that they are unable to limit the greater fishing pressure effectively. A perfectly implemented HCR where stock assessment information is not biased and there are no constraints on annual quota change would solve this problem, but may be impractical. As a consequence, it may be unwise to rely solely on HCRs to prevent overexploitation of fish stocks. Implementing multiple management measures is therefore preferable to using management measures in isolation.

It is worth considering what role, if any, MPAs may play in protecting highly migratory fish stocks, given that they are not totally effective at protecting stock collapse in this simple model. First, it should again be stressed that, in this model of an overfished fishery, having an

MPA in place is more effective than having no MPA. Therefore, MPAs offer better protection than the worst case scenario of no fisheries management. Figure 2.6 represents a sliding scale of γ from low to high and, as already discussed, considered coarsely implies that as γ increases, the probability of collapse increases. To protect a stock with a high propensity for migration, a way of reducing γ is therefore needed. The simplest way of doing this, at least theoretically, is to increase the size of the MPA. The model structure with a spawning and feeding ground makes no explicit assumptions about the physical size of these two areas. The MPA protects a spawning aggregation that theoretically may cover a wide geographic range. However, it has been assumed that the spawning and feeding areas contribute equally to the fishing quota. Therefore, when an MPA is established, the quota within the feeding area is doubled. If the spawning and feeding areas are of different size, their contribution to the quota is unlikely to be equal. Moreover, if the spawning area is small, catchability may increase when fish aggregate to spawn.

These complex interactions between catchability, geographic area, and population density have not been considered in this model and warrant further attention within spatially explicit models. However, it would be expected that increased MPA size would decrease the number of fish migrating into a fishery. Larger MPAs would therefore effectively shift the curve in Figure 2.6 to the right, allowing the more migratory populations to be protected. The result when overfishing leads to a decrease in population size can also be considered. In the model, the value of *γ* remains constant throughout and is independent of the size of the population. As population size decreases, however, density-dependent factors such as competition for food are likely to decrease in relative importance, and the stimulus for migration away from spawning areas may decrease. This will effectively reduce the value of *γ* exhibited by a stock, and MPAs may become more effective as stock size decreases. In such a case, an MPA can be thought of as a final barrier against collapse when population sizes become depleted. The length of time populations spend in each area is also likely to have implications for the effectiveness of an MPA. For example, coordinating MPA location with the migration patterns of fish will permit protection for more of the year. It is also worth considering whether the extreme values of *γ* modelled here are likely to be reflected in the real world. It is unlikely that all fish in a population will undergo migration. For example, immature fish in a population do not spawn and are less likely to migrate (Righton *et al*. 2007). There is also evidence to suggest that mature fish skip spawning in certain years and do not migrate (Jørgensen *et al*. 2006). It is also likely that a proportion of the fish will remain on the spawning grounds to feed. The extreme values of γ may therefore not arise, perhaps strengthening the protective power of the MPA. In addition to reducing fishing pressure, MPAs may have other benefits, such as protecting habitat (Kaiser *et al*. 2002), or preventing the disruption of spawning aggregations by trawling (Morgan *et al*. 1997). For the reasons given above, the potential of MPAs should not be overlooked in the management of migratory species.

Importantly, the movement modelled here oversimplifies the migratory behaviour exhibited by many commercially important species of fish. For example, Robichaud and Rose (2004) showed from mark-recapture data that Atlantic cod behaviour can vary between residence, homing (with varying accuracy), and random dispersal. Traditional mark-recapture experiments have recently been augmented by the use of data-storage tags (DSTs), which allow greater insight to be gained into the movements of fish species over time (Metcalfe and Arnold 1997). For example, analysis of both conventional and DST data has demonstrated that cod in the North Sea may undergo extensive seasonal movements to and from a spawning area, similar to the movements modelled in this case, whereas the population within the English Channel exhibits more limited dispersal (Metcalfe 2006, Righton *et al*. 2007). Ontogenetic differences are also apparent because juvenile fish tend to be more restricted in their dispersal than adults (Righton *et al*. 2007), and there is a greater tendency for cod to move greater distances as they grow (Robichaud and Rose 2004). Similar results have been reported for other species such as plaice, thornback ray, and Atlantic bluefin tuna (Hunter *et al*. 2004a, Hunter *et al*. 2006, Metcalfe 2006, Rooker *et al*. 2007). These complex differences in behaviour, both between and within populations of a single species, are not captured in this simple population model, but they may have important implications for the type of management measures that should be introduced. Temporary fishery closures in the North Sea, for example for Atlantic cod in 2001 (Anon. 2001b), have been relatively ineffective in promoting stock recovery (Horwood *et al*. 2006), and more complex models may give insight into how such spatial management measures should be developed to enhance protection.

The conclusions drawn from the simple population model are all taken from the stochastic simulations. If only the deterministic output had been considered, the conclusions would have been different and misleading; the population would always be sustainable with any level of migration unless extremely high values of c are used (See Section 2.4.1; for $c > 17$, the deterministic model and stochastic models agree; both predict population collapse). Alternative stable states are present in the more extensive migration scenarios in the MPA system, but without any variability in the population dynamics, the population comes to rest on only one of the possible equilibrium points. Stochasticity allows variation around equilibria and, where they exist, a switch between alternative stable states. The central message of Pitchford *et al.* (2007) is that deterministic models for non-migratory stocks with positive stable equilibria can be vulnerable to collapse via amplified stochastic effects. Likewise, in the case of migratory stocks, this potential management problem cannot be addressed without explicit consideration of stochasticity and uncertainty. The addition of stochasticity into the model is a simple way of investigating how the presence, position, and basins of attraction of equilibria may affect the potential for population collapse. Without stochastic investigation, this is impossible to quantify, and results about the potential for collapse are difficult to infer. Pitchford *et al*. (2007) concluded that in a deterministic environment, there was no benefit in incorporating an MPA in preference to other more traditional marine management measures. However, in a stochastic environment, an MPA acted as a buffer against uncertainty, and allowed the population to persist where others would collapse. The conclusions here about the benefit of MPAs for migratory species are somewhat different, but the underlying message from these two studies is identical; namely, that the effects of stochasticity are extremely important in many marine environments, and are highly influential in the assessment of the efficacy of fisheries management measures. Therefore, where environments are highly stochastic, such as with fisheries, it is imperative that uncertainty is incorporated into models. Doing so will generate results that reflect the real world more accurately, and should discount fears that the adoption of new management measures is faith-based (Hilborn 2006).

3

3

AN INDIVIDUAL BASED MODEL OF FISH MIGRATION AND AGGREGATION

3.1 INTRODUCTION

Individual based models (IBMs) are flexible tools that, in contrast to population models which can only allow divisions of populations into groups, allow populations to be simulated from their individual members. An IBM approach has several advantages over population modelling including the ability to include individual variability, greater spatial detail, and easy comparison with observational data from individuals (Huse *et al*. 2002, Strand *et al*. 2002). Another advantage of IBMs is that their basic unit, the individual, is the same as that in evolution, allowing studies of the evolution of behaviour (Huse *et al*. 2002, Strand *et al*. 2002). IBMs allow the entire life history of organisms to be simulated, including behaviour such as spatial movement, foraging, growth, and reproduction (Huse et al. 2002, Strand *et al*. 2002). As such, they are especially suitable for modelling the behaviour of migratory fish where records of individual behaviour have been collected by the use of electronic data storage tags (Metcalfe and Arnold 1997, Righton and Metcalfe 2002, Righton *et al*. 2007).

Here, an IBM is described which is designed to allow a population-level structure of spatially-defined spawning aggregations to develop over evolutionary time using simple individual behavioural rules. The model incorporates individual movement characterised by data collected from commercially important marine fish which undertake seasonal migrations and form spawning aggregations. A combination of homing behaviour and positive density-dependence at breeding time leads to the emergence of spatially-structured breeding aggregations within an otherwise homogeneous environment. This chapter serves only to outline the details of the model. The IBM described in this chapter is then applied to answer specific questions related to the ecological and evolutionary response of migratory aggregative breeders to environmental change (Chapter 4) and fisheries exploitation (Chapter 5). Refer to these chapters for full details of the application of the IBM to these scenarios. Potential model enhancements are described in Chapter 6.

IBMs are often more complex than population models which can make their communication difficult. Whereas population models can usually be described mathematically, IBMs are often described verbally due to their complexity (Grimm *et al*. 2006). Recently, a protocol has been developed for the description of IBMs in an attempt to make them easier to understand and duplicate (Grimm *et al*. 2006, Grimm *et al*. in press). The model description presented here follows this ODD (Overview, Design concepts, Details) protocol. In this description some aspects of the model are applicable only to Chapter 4 or Chapter 5, and this is highlighted in the text. The default parameters used in the model are presented in Table 3.1 and a sensitivity analysis with alternative parameters is presented in Section 7.4.

3.2 OVERVIEW

3.2.1 PURPOSE

The purpose of the model is to investigate:

- how population-scale breeding aggregations emerge with simple individual-level behaviour;
- how populations respond to the creation of new exploitable environments with different rates of environmental change;
- how fisheries yield, population size, spawning aggregation structure, and evolution of dispersal are affected by different levels of fishing effort, including protection by marine protected areas.

3.2.2 Entities, state variables and scales

The model comprises a (female-only) population of individuals held in a 'holding vector'. Individuals are characterised by a set of state variables held in individual-level vectors:

- current location in the form of *x*- and *y*-coordinates;
- breeding location in the form of *x*- and *y*-coordinates (differentiated from the 'current location' coordinates in this description by the subscript *br*), i.e. the location to which individuals will attempt to migrate to breed;
- mean individual step-length *d,* i.e. the mean step-length moved by an individual each time-step;
- new recruit/adult, i.e. whether the individual is a new recruit or has already had the opportunity to breed.

Individuals are contained within a homogeneous environment of 100 pixels high by a user-determined width of *w* pixels. Although the model is characterised by the movements of commercial fish which can cover tens of kilometres per day, the model could equally represent smaller or larger scales depending on the model purpose. Here, it is the general response of modelled aggregations to exploitation or environmental change which is of interest. An accurate representation of the scales over which these may occur can be reserved for more detailed explorations of real-world scenarios, which would also involve significant increases in model complexity.

Individuals undergo processes such as movement and mortality (density-independent, density-dependent, movement-related, and fishing-related) within a daily time-step. There are 365 modelled days in each year.

3.2.3 PROCESS OVERVIEW AND SCHEDULING

The model proceeds in discrete daily time-steps, t. Within each time-step individuals undergo '*Movement*' and '*Natural mortality*' (see Section 3.4.3 Submodels). The type of movement and mortality is dependent on the time of year. If fishing pressure is taking place (Chapter 5) then individuals also undergo *'Fishing mortality'* immediately following *'Natural mortality*' in each time-step. On the final day of the year all individuals undergo '*Breeding'*. '*Recruitment*' of the previous year's individuals then occurs. '*Movement*', '*Natural Mortality*', '*Fishing Mortality*' and '*Breeding*' proceed through individuals sequentially from the start of the holding vector. However, the location of individuals within the holding vector is not constant because as individuals die in each time-step they are replaced by the individual at the end of the holding vector and the population becomes mixed. It is therefore impossible to predict beforehand how each process will proceed through individuals in the model. '*Recruitment*' adds new individuals to the end of the holding vector in the order in which they were born by '*Breeding*', i.e. the order in which they are added is dependent on the position of their parent within the holding vector at breeding time. In Chapter 4, in each simulation 2000 years are modelled to allow the emergence of a stable breeding aggregation structure. In Chapter 5, a simulation of 2000 years without fishing (allowing the emergence of a stable breeding aggregation structure) is used as the starting point for fisheries models. Fisheries models are then modelled over 200 years.

3.3 DESIGN CONCEPTS

Emergence

Breeding aggregations emerge from the imprinting of individual breeding locations (x_{br} and y_{br}) and evolution of mean individual step-length, d. Over time, aggregations develop which increase the reproductive fitness of an individual and reduce the effect of density-dependent mortality, M_D, by distributing the population to minimise competition between individuals. In addition to altering population size, the introduction of new exploitable habitat (Chapter 4) or fishing pressure (Chapter 5) has the potential to alter this spatial population structure.

Adaptation

Individuals are not able to directly adapt to their environment, their behaviour is inherited from their parent. Rather, adaptation of individuals occurs over evolutionary time as non-competitive behaviour is selected against.

Interaction

Individuals undergo density-dependent competition during dispersal with individuals within the same pixel. The number of individuals within a pixel determines the strength of density-dependent mortality, M_D. They also interact at breeding time with individuals within a fixed radius, r, to determine breeding success.

Stochasticity

Individuals follow random walks with turning angles drawn randomly from uniform (when not undergoing breeding migrations) and normal distributions (when undergoing breeding migrations) and step-lengths drawn from negative exponential distributions. This allows each individual to follow a different path within the environment. Imprinting of individual breeding coordinates (x_{br} and y_{br}) and inheritance of mean step-length, d, occur by drawing values from normal distributions with mean equal to the value of the parental breeding location and parental step-length parameter respectively, with standard deviations (σ_b and σ_m). The initial location of new recruits is determined by drawing x- and y-coordinates randomly from a normal distribution around the site of breeding with standard deviation, σ_r. Individual mortality per time-step (caused by both fishing, if applicable, and natural mortality), M, is determined by probabilities which can change according to an individual's location and movement, and the time of year.

Collectives

Groups of individuals gathered together at breeding time are termed 'breeding aggregations'. These collectives are emergent results of individual behaviour.

Observation

Visual output in the form of diagrammatic representations of individual locations at breeding time can be obtained to locate and count breeding aggregations. Data on population size, fisheries catch (if applicable) and mean step-lengths can also be output for analysis.

3.4 DETAILS

3.4.1 INITIALISATION

In the static models (see Chapter 4), fifty thousand individuals (new recruits) are initially created and distributed randomly across the grid of 100 by w pixels. Each individual is randomly assigned breeding coordinates (x_{br} and y_{br}). All individuals initially share the same mean step-length, d, but this value evolves through time with individuals inheriting their parent's value with error.

In the expansion models (exploring the response of populations to new exploitable environments – see Chapter 4) the state variable of individuals at the end of a static model simulation are input, i.e. these models proceed from the conclusion of a static model. The expansion model involves initialisation using a static model with $w = 50$ and then increases w at different rates to 100 to explore expansion of populations into a previously unexploited environment. In the instantaneous expansion model w is set to 100 instantly at the start of the simulation. In the fast expansion model w is increased by one pixel column every year, in the medium-rate expansion model w is increased by one pixel column every five years, and in the slow expansion model w is increased by one pixel column every 10 years.

The static model is also used to initialise the fisheries models with $w = 100$. The fisheries models (exploring the response of populations to fishing effort – see Chapter 5) proceed from the conclusion of the static model. In the fisheries models, the location of breeding grounds is determined by the location of individuals at breeding time in the last year of the static model, defined as two or more adjoining pixels (including diagonals) which contain three or more fish at spawning time. This spawning aggregation location can be updated periodically throughout the model if required.

3.4.2 INPUT

This model does not use input data to represent time-varying processes i.e. the model dynamics are not driven by a time-series of external environmental variables.

3.4.3 SUBMODELS

Default model parameters and variables are shown in Table 3.1. Examples of values for recruitment success and the distribution of step-lengths that result from these sub-models are shown in Section 7.5.

Parameter	Value	Description
w	50-100	Width of modelled environment (w = 100 in Chapter 5)
x	0-w	Current coordinate
y	0-100	Current coordinate
x_{br}	0-w*	Breeding coordinate
y_{br}	0-100*	Breeding coordinate
d	2.0*	Mean step-length (initial value in the static model shown)
t	1-365	Time (days)
r	1.0	Breeding radius
σ_r	5.0	Recruitment location standard deviation
σ_b	0.5	Breeding location standard deviation
σ_m	0.2	Mean step-length standard deviation
n	0.125	Navigation error
λ	0.6	Survivorship rate from natural mortality
μ	0.0024	Density-dependent mortality parameter
γ	0.0004	Movement mortality parameter
F	0.1-0.9	Fishing pressure (Chapter 5 only)
a	0.2	Ricker parameter
b	8.0	Ricker parameter
		* = evolvable value

TABLE 3.1. THE PARAMETERS AND VARIABLES USED IN THE IBM, WITH A DESCRIPTION AND THEIR DEFAULT VALUES.

Movement

In each time-step individual step-lengths are drawn randomly from a negative exponential function with mean *d*, unless:

- the individual is within one pixel of its breeding location at breeding time (t>265; allowing migration to occur over a time-frame which corresponds to the length of the spawning season of cod and plaice (Daan 1990, Hunter *et al*. 2004b)) in which case the mean step-length is 0.2 (if d>0.2), i.e. once an individual has reached its breeding location it reduces its movement so that it stays in the vicinity (if d<0.2 it does not make sense to *increase* the step-length of an individual, so the mean step-length of *d* is used). At spawning time it is therefore assumed that only localised movement occurs, which is reflected in species such as cod, *Gadus morhua*, where females may visit territories established by males, perhaps in a lekking system (Windle and Rose 2007).
- the individual is within five pixels of its breeding location at breeding time (t>265) in which case the mean step-length is 1.0 (if d>1.0), i.e. as an individual approaches its breeding location it reduces its step-length to help avoid ‘overshooting’ the breeding location (if d<1.0 it does not make sense to *increase* the step-length of an individual, so the mean step-length of *d* is used).
- it is post-breeding dispersal time (t≤265) and t>100 in which case the mean step-length is 0.2 (if d>0.2), i.e. once an individual has moved for 100 days it reduces its step-length to settle in an area (if d<0.2 it does not make sense to *increase* the step-length of an individual, so the mean step-length of *d* is used). Data storage tags from cod reveal that, after dispersal to feeding areas, individuals become relatively inactive and range over only a relatively small geographic area (Turner *et al*. 2002, Hobson *et al*. 2009).

The maximum step-length drawn from the negative exponential distribution is set to *w* to prevent unrealistically high (but rare) step-lengths being drawn.

Post-breeding (t≤265), an individual’s bearing is drawn randomly from a uniform distribution with range 0 to 2π, i.e. individuals move randomly in any uncorrelated direction. Although for some groups of species such as plaice, *Pleuronectes platessa*, and cod there is evidence for directed movement towards specific feeding areas, these migrations are often associated with currents or landscape features (Hunter *et al*. 2004a, Righton *et al*. 2007). Since these environmental factors are not modelled, and populations are known to disperse and mix during feeding time (Metcalfe 2006, Wright *et al*. 2006, Righton *et al*. 2007), uncorrelated dispersal following spawning in this case is not an unreasonable assumption. If it is breeding time (t>265), then the bearing between the individual's current position and the position of its desired breeding location (x_{br}, y_{br}) is taken and used as the mean of a normal distribution with standard deviation equal to the 'navigation error', n. A bearing is then drawn at random from this distribution. Movement during breeding time therefore takes the form of a biased random walk towards the intended breeding location. This concurs with the homing behaviour towards historical spawning locations observed in migratory fish species (Hunter *et al*. 2004b, Robichaud and Rose 2004, Solmundsson *et al*. 2005, Righton *et al.* 2007, Rooker *et al*. 2008). In cod in the North Sea, the spawning season runs from winter to early spring over a period of about three months (Daan 1990), and similar periods are documented for plaice (Hunter *et al*. 2004b). To correspond approximately with this time-frame, spawning migrations begin 100 days before the end of the year. The value of n is fixed across all individuals at all times i.e. all individuals are assumed be equally imprecise in their navigation ability.

If an individual's bearing and step-length takes it out of the modelled area of 100 by w pixels then the individual is reflected by the boundary (i.e. the total step-length is upheld).

Figure 3.1 shows an example of the distribution of individuals immediately prior to the breeding migration (t = 265) and on the day of breeding (t = 365) which results from individual movement behaviour.

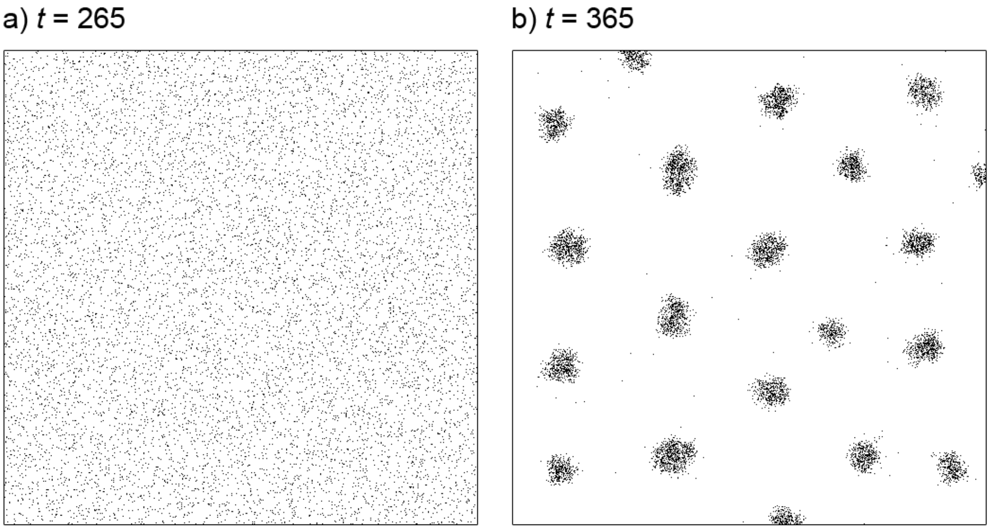

FIGURE 3.1. AN EXAMPLE OF THE OUTPUT FROM THE MODEL SHOWING THE LOCATION OF INDIVIDUALS (BLACK DOTS) IMMEDIATELY BEFORE THEIR BREEDING MIGRATION (t = 265) AND AT BREEDING TIME (t = 365).

Natural Mortality

The yearly density-independent survival rate for individuals is λ. To transform this into daily mortality the following equation is used:

$$M_I = 1 - \lambda^{1/365} . \qquad (3.1)$$

Mortality associated with movement is added to this background rate. Its strength is calculated by taking the step-length made by an individual in that time-step and multiplying it by the movement mortality rate, γ, i.e.:

$$M_M = \gamma(\text{step-length}) . \qquad (3.2)$$

In practice, increased movement would be associated with increased energetic costs, which would otherwise be used for maintenance, growth and reproduction (Videler 1993). As such, it is not unreasonable to include a cost to movement. Due to the simplicity of this model, this is modelled as an increase in the probability of mortality but this could also be seen as a proxy for a loss in reproductive potential. For example, there may be a trade-off between swimming activity and the production of gonads (Videler 1993) which may lead to an individual skipping spawning (Rideout *et al*. 2000, Jørgensen *et al*. 2006). Both mortality and failure to reproduce will have the same ultimate effect; a failure to contribute to the next generation.

During the competitive dispersal phase (t≤265 for new recruits; 25<t≤265 for all other individuals) density-dependent mortality acts in addition to the background mortality rate and movement mortality. Its strength is dependent on the number of individuals within a pixel. To calculate the strength of density-dependent mortality acting upon an individual the following equation is used:

$$M_D = \mu(N-1)^2 \tag{3.3}$$

where N is the number of individuals within a pixel and μ is a parameter used to determine the strength of density dependence. N-1 is used so that if only one individual is present within a pixel no density-dependent mortality is applied. A maximum value of M_D of 0.04 is allowed to prevent mass mortality in a single time-step. This limit will cut in if there are 6 or more individuals in a pixel using the default value of μ. During breeding time M_D = 0, i.e. no density-dependent mortality is applied because individuals are assumed to be competing for mates, not food. For example, cod populations are known to suppress feeding for a considerable proportion of the year during the spawning season (Fordham and Trippel 1999). Note that new recruits undergo density-dependent mortality from t = 1 as they are assumed not to have bred and to be undergoing competitive behaviour. All other individuals are assumed to have attempted to breed and therefore are undergoing a post-breeding dispersal for 25 days before starting to compete. This allows aggregations to disperse before density-dependent mortality occurs to prevent unrealistically high levels of mortality following breeding. Although, in order to maintain model simplicity, density-dependent competition is modelled as a mortality term, this can additionally be seen to indirectly incorporate a cost to reproductive success (in a similar way to the cost of movement described above). Although individuals are unable to sense and respond to their environment in this model (sub-optimal behaviour leads to a response over evolutionary time), in reality individuals may move to alternative locations if under competitive stress. However, according to ideal free distribution theory, these are likely to be areas of lower quality (e.g. less food, sub-optimal temperature, more predation; Blanchard *et al*. 2005) which may increase the mortality effect. Modelling competitive mortality in the manner described in this model is therefore a reasonable assumption.

In each time-step, the Poisson process rates for each form of natural mortality for each individual are summed to give a resultant mortality rate of:

$$M = M_I + M_M + M_D\,. \tag{3.4}$$

A random number for each individual is then generated between 0 and 1. If this random number is less than M then the individual dies and is removed from the population.

Fishing Mortality (applicable in Chapter 5)

Fishing mortality follows natural mortality. If fishing is taking place within a pixel then the mortality associated with fishing is given by:

$$f = 1 - (1 - F)^{1/365} \tag{3.5}$$

where F is the strength of fishing effort i.e. large F equals high mortality from fishing. If uniform fishing is taking place then this equation is applied to all pixels. If breeding areas are protected then fishing does not take place in any pixels specified as breeding grounds (using the method in Section 3.4.1 Initialisation). If feeding areas are protected then fishing only takes place in pixels defined as breeding grounds. In models where 50% of the area is protected from uniform fishing effort, then fishing takes place on half of all pixels as a continuous unit.

In each time-step a random number for each individual is then generated between 0 and 1. If this random number is less than f then the individual dies and is removed from the population. This individual then counts towards the number of fish caught through fishing.

Breeding

On the final day of the year (t = 365) breeding occurs. The number of new recruits produced per individual is determined using a Ricker-type equation:

$$R = N_r e^{a(1-(N_r/b))} \tag{3.6}$$

where N_r is the number of individuals within a radius of r pixels from the target individual, and a and b are parameters which determine the shape of the Ricker function. This equation describes the number of offspring which survive for one year before being recruited to the population as adults with the potential to breed at the following spawning event (see below) and therefore encompasses survival of eggs, larvae, and juveniles.

The use of a Ricker function means that recruitment success will initially increase with breeder density, but will decrease if density becomes too high. The necessity of individuals to be within a given radius to spawn, and the initial increase in spawning success with density, implies a depensation, or Allee, effect when there is low local abundance. Depensation occurs in many species, including fish, and may occur for a variety of reasons including difficulty in finding a mate, environmental conditioning, and predator saturation (Liermann and Hilborn 2001). For example in cod and other species, a ‘cultivation’ effect may occur if adults prey on potential predators or competitors of their offspring (Walters and Kitchell 2001). Low densities may also disrupt the ability of individuals to find a mate, especially where there is mate competition or lekking behaviour (Rowe and Hutchings 2003). Depensation may be partially responsible for the failure of the Newfoundland cod stock to recover since collapse (Rose 2004).

At high densities, reproductive success also decreases in this model. Mechanisms which support this assumption include cannibalism by adult cod which is known to occur when the abundance of recruits is high and the ranges of young and adults overlap (Daan 1973, Anderson and Gregory 2000, Uzars and Plikshs 2000). High concentrations of recruits may also result in increased predation via the aggregation of predators (Bailey and Houde 1989), or lower growth rates and starvation (Anderson 1988).

R is the number of new recruits produced per adult. To prevent part-recruits the value of R generated in the equation above is rounded down to the nearest integer. New recruits are assigned a breeding location drawn from a random distribution using the location in which they were born as the mean, and with standard deviation σ_b, i.e. it is assumed that the location in which new recruits will attempt to breed is imprinted at their place of birth, plus error. A new recruit’s mean step-length, d, is inherited from its parent with error by drawing from a normal distribution with mean equal to its parent’s d and standard deviation σ_m.

Recruitment

Recruits are added to the population one year after the breeding event in which they were born, i.e. there is a lag of one year between breeding and recruitment into the population. In the absence of modelled environmental factors such as currents which may affect the distribution of recruits (Lough *et al.* 1989, Pepin and Helbig 1997, Rindorf and Lewy 2006), it is assumed that the x- and y-coordinates to which they are added are drawn randomly from normal distributions with means corresponding to their imprinted breeding location (x_{br} and y_{br}) and standard deviation σ_r.

4

4

SPECIES WITH BREEDING AGGREGATIONS MAY FAIL TO RESPOND TO ENVIRONMENTAL CHANGE

4.1 ABSTRACT

Dispersal limitation, especially in the presence of physical barriers to movement, will reduce the capacity of species to respond to environmental change. However, behavioural barriers to movement may play an equally important role in a species' response. Many species form breeding aggregations, nesting colonies or leks, and these may form such a behavioural barrier. Here the role of aggregative breeding as a behavioural barrier to dispersal and range expansion is explored using an individual based evolutionary model of a theoretical species within a homogeneous environment. Individuals exhibit patterns of diffusive movements followed by directed movement back to breeding areas. Through a combination of homing

behaviour and positive and negative density-dependence acting at different times, it is demonstrated that although individual movement is rapid, population-level movement is not. Breeding aggregations struggle to respond to an expanding habitat boundary. Evolution of increased mobility in lineages at the expanding habitat boundary gives a competitive advantage to individuals in breeding aggregations at this margin. These enlarged aggregations may then outcompete aggregations located further from the margin, especially when the rate of environmental change is rapid. These predictions show that, even in the absence of a physical barrier, a behavioural barrier means that species with aggregative breeding may be particularly vulnerable to the effects of environmental change.

4.2 INTRODUCTION

The ranges of many species have shifted in response to recent climatic change (Walther *et al*. 2002, Perry *et al*. 2005, Parmesan 2006). In terrestrial systems, barriers to a species' ability to respond to change can be obvious and accounting for dispersal ability may be key in determining whether species are able to move between areas of suitable habitat (Thomas *et al*. 2004). Similarly, if suitable habitat is reduced and fragmented, the ability of species to respond to climate change is diminished (Travis 2003). In comparison to terrestrial systems, it is generally assumed that marine species will adapt more quickly to environmental change because there are fewer restrictions to movement e.g. a lack of physical barriers. Taking dispersal limitation and habitat availability into account is important when considering how to achieve conservation or management goals and underpinning this is the need to understand a species' ability to respond to changing environments. For example, if a species is already vulnerable to extinction or extirpation, the location and size of existing protected areas may have to be adjusted to account for the additional effects of climate change (Hannah *et al*. 2007, Hole *et al*. 2009), including the establishment of conservation corridors to provide migration pathways (Killeen and Solórzano 2008). However, the ability of many species to respond to environmental change will depend on movement at a population scale in addition to individual mobility. Many fish, mammal, bird, arthropod, and amphibian species experience positive density-dependence at breeding time, returning to historical locations to group together in aggregations or lekking structures (Högland and Alatalo 1995). The ability of such species to respond to environmental change may strongly depend on the rate at which these aggregations are able to move, even if individual movement is relatively unrestricted. It is demonstrated here that the consequences of animal behaviour in the formation of an aggregative breeding structure may act as an important additional barrier to redistribution following environmental change.

An individual based model (IBM) is introduced to explore the effects of aggregative breeding on the ability of individuals and populations to move in response to environmental change. The model is deliberately simple, allowing breeding aggregations to be established within an homogeneous environment over evolutionary time from simple behavioural rules at the individual level. Although characterised by data collected from marine fish, which undertake spawning migrations and form spawning aggregations (Hunter *et al*. 2004a, Hunter *et al.* 2004b, Wright *et al*. 2006, Righton *et al*. 2007, Svedäng *et al.* 2007), the simplicity of the model means that the results may be applied to many species that undergo aggregative breeding or lekking behaviour. In the IBM, via homing behaviour and positive density-dependence at breeding time, spatially-structured breeding aggregations emerge within an otherwise homogeneous environment. It is demonstrated that population-scale movement occurs on a much longer time-scale than individual movement. This slow rate of population movement has consequences for a species' ability to expand into new habitat. It is demonstrated that, in cases of rapid environmental change, population movement is unable to keep up with the moving habitat boundary, and may result in sub-population collapse via competition. Importantly, this behavioural limitation to a populations' response to environmental change occurs in the absence of habitat constraints and may therefore reduce population persistence even where suitable habitat is plentiful and contiguous.

4.3 METHOD

The IBM represents a theoretical migratory aggregative breeder. A schematic representation of the model is shown in Figure 4.1a. In brief, individuals in the model undergo dispersive movement followed by directed movements back to breeding locations. In each modelled year of 365 days (t), individuals within the model initially undergo random walks (in continuous space but discrete time) away from a breeding location (t = 1-265). The movements away from the breeding site have three phases. First, there is post-breeding diffusive movement (t = 1-25). In this phase, in addition to density-independent mortality, individuals experience mortality associated with a cost to movement (e.g. increased energetic expenditure, enhanced predation risk) controlled by the fixed movement mortality parameter γ. Adult individuals are then assumed to undergo further dispersive behaviour and, in addition to density-independent mortality and movement mortality, are assumed to be competing for unmodelled resources (with competition determined by population density within a pixel-sized grid-square) and therefore subject to density-dependent mortality (*t* = 26-100). New recruits bypass the post-breeding dispersal period and undergo competitive behaviour from the start of the year and thus undergo density-dependent mortality from *t* = 1. Following the period of random dispersal, daily movements are reduced and each individual undergoes a period of 'settlement' within a restricted area (*t* = 101-265). Individuals then switch to 'breeding behaviour' and undergo biased random walks towards an imprinted breeding location (*t* = 266-365). During this period, density-independent and movement mortality occur but density-dependent mortality does not, as individuals are no longer assumed to be competing for resources (e.g. cod populations are known to suppress feeding during the spawning season (Fordham and Trippel 1999)). At the end of the year, individuals attempt to breed, with individual success determined by a 'Ricker-type' equation based on the number of neighbours within a radius of one pixel of the breeding individuals. Low density individuals have low breeding success. As local population density increases, breeding success increases (via increased encounter rate) before decreasing after local population density reaches a threshold (e.g. via cannibalism (Daan 1973, Anderson and Gregory 2000, Uzars and Plikshs 2000), predation (Bailey and Houde 1989), or starvation (Anderson 1988)). New recruits are added to the population after a lag of one year, distributed around their site of birth. The distance that an individual travels in each time-step is randomly drawn from a negative exponential distribution with mean determined by the heritable mean step-length, *d*. Each individual's value of *d* is inherited from its parent with a chance of error and is therefore evolvable within the model (Dytham and Travis 2006). An individual's desired breeding location is imprinted at birth as the location in which it was born, plus error. An example of an individual's movement track over three years is shown through space (Figure 4.1b) and time (Figure 4.1a). The IBM is inspired by behaviour exhibited by commercial marine fish. Real data from an Atlantic cod, *Gadus morhua,* tagged with a data storage tag is shown in Figure 4.1c for comparison with the simulated example.

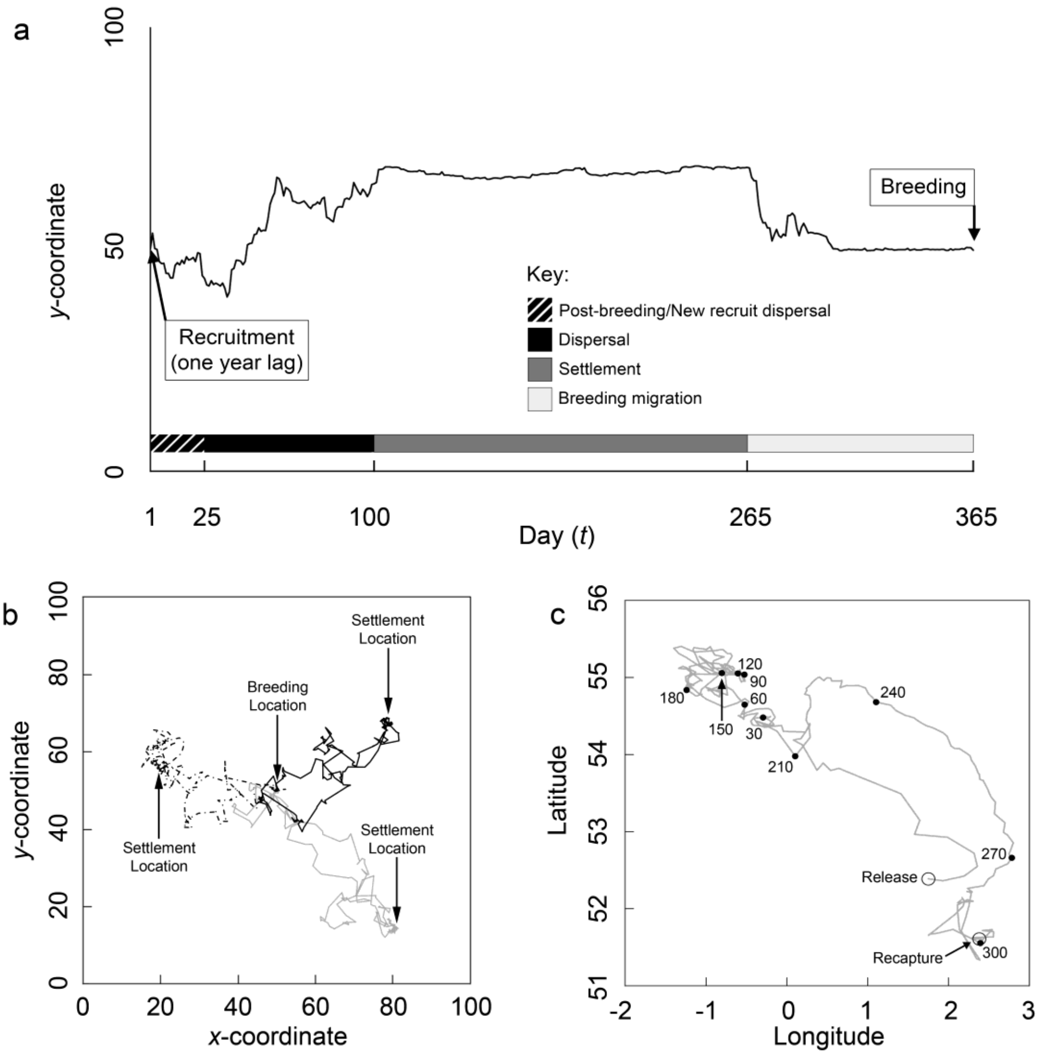

FIGURE 4.1. THE TIMING OF MODELLED BEHAVIOURS, RESULTING MOVEMENT, AND COMPARISON WITH REAL DATA. a) AN OUTLINE OF THE BEHAVIOURS EXHIBITED BY INDIVIDUALS IN THE MODEL AND THE TIME OF YEAR AT WHICH THESE OCCUR. THE BLACK LINE SHOWS THE RESPONSE OF AN INDIVIDUAL'S *Y*-COORDINATE TO THESE CHANGES IN BEHAVIOUR. b) AN EXAMPLE MOVEMENT TRACK FOLLOWING AN INDIVIDUAL FOR THREE YEARS WHOSE BREEDING LOCATION IS LOCATED IN THE MIDDLE OF THE ENVIRONMENT. EACH YEAR IS REPRESENTED BY A DIFFERENT LINE. THE BLACK LINE CORRESPONDS TO THE EXAMPLE IN FIGURE 4.1a. ARROWS INDICATE APPROXIMATE BREEDING AND SETTLEMENT LOCATIONS. c) AN EXAMPLE OF A TRACK CONSTRUCTED FROM DATA RECORDED BY A DATA STORAGE TAG ATTACHED TO A THREE YEAR-OLD COD RELEASED IN THE NORTH SEA (TAG ID 2255, MODIFIED FROM RIGHTON AND MILLS 2008). RELEASE AND RECAPTURE POSITIONS ARE MARKED BY OPEN CIRCLES. POSITIONS EVERY 30 DAYS ARE MARKED BY BLACK DOTS.

Two models are presented. The 'static' model is initialised using individuals with randomly assigned breeding locations and simulations show the emergence of breeding aggregations over time. A modified version of the static model is then used as a starting point for the 'expansion' model which simulates population expansion into a previously unexploited environment following environmental change. Both the static and expansion models are run for 2000 modelled years. The static model is first run in an area of 100 by 100 pixels. A static model with an area of 50 by 100 pixels is then used to initialise the expansion model. In the expansion model, the width of the area is expanded at varying rates, with the final area being 100 by 100 pixels.

A detailed explanation of the model, following the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm *et al*. 2006, Grimm *et al*. in press), is presented in Chapter 3.

4.4 RESULTS

4.4.1 EMERGENCE OF BREEDING AGGREGATIONS (STATIC MODEL)

Initially, individual breeding locations are distributed at random but aggregations quickly emerge within the system. Figure 4.2 illustrates a single realisation of the model and shows the development of breeding aggregations at four different stages at breeding time (i.e. at the end of the modelled year, t = 365). Several realisations were simulated with analogous results. Breeding aggregations are defined as two or more adjoining pixels (including diagonals) which contain three or more individuals at breeding time. Following initialisation of the model many breeding aggregations quickly emerge. As the model develops this is followed by a loss of aggregations via competition. This loss is relatively quick at first but slows as aggregations become more established and able to compete more effectively with other established aggregations. Over time, through the loss of breeding aggregations and a slow creeping of aggregations across the landscape, breeding aggregations become distributed evenly over the environment (Figure 4.2d) approaching the optimum packing solution of one aggregation surrounded by six equidistant neighbours. At the end of the simulation the total population size is 8817 with a mean of 416.7 (s.d. = 121.6) individuals per breeding aggregation. Over the modelled time period, the mean step-length, d, evolves and stabilises. The mean value of d (from five model simulations) after 2000 years is 1.52 (s.d. = 0.05).

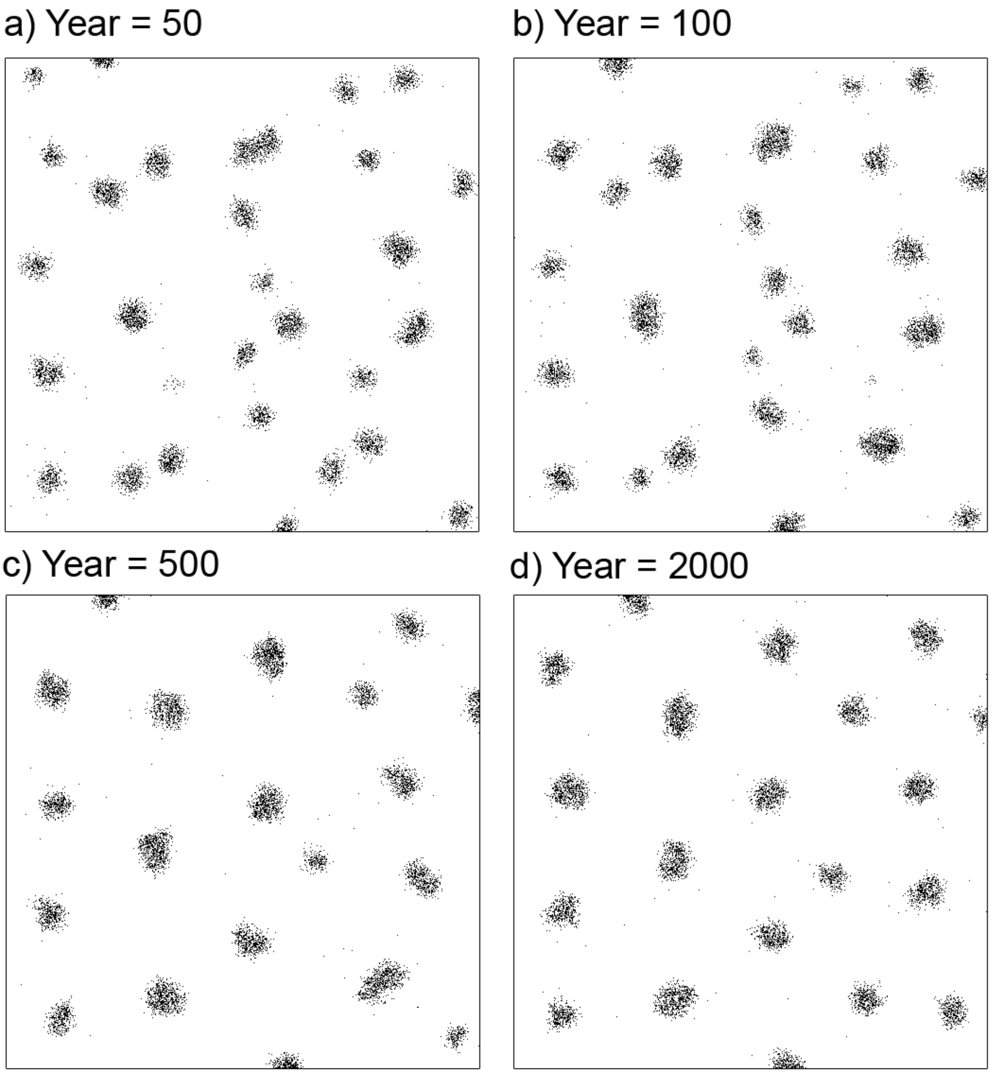

FIGURE 4.2. AN EXAMPLE OF THE OUTPUT FROM THE STATIC MODEL SHOWING THE LOCATION OF INDIVIDUALS AT BREEDING TIME (BLACK DOTS). a) AFTER 50 YEARS THERE ARE 29 BREEDING AGGREGATIONS, b) THREE ARE LOST BETWEEN 50 AND 100 YEARS TO TAKE THE TOTAL TO 26, c) SIX ARE LOST BETWEEN YEARS 100 AND 500, AND d) NONE ARE LOST BETWEEN 500 AND 2000 TO TAKE THE FINAL TOTAL TO 20. A BREEDING AGGREGATION IS DEFINED AS GROUPS OF TWO OR MORE ADJOINING PIXELS (INCLUDING DIAGONALS) WHICH CONTAIN THREE OR MORE INDIVIDUALS AT BREEDING TIME.

4.4.2 RESPONSE TO ENVIRONMENTAL CHANGE (EXPANSION MODEL)

With the static model run within a reduced area of 50 by 100 pixels, the mean step-length, *d*, evolves and stabilises. The mean value of *d* (from five model simulations) after 2000 years is 1.56 (s.d. = 0.04). Figure 4.3a (inset) shows an example of the final output from this model which results in 10 breeding aggregations. The total population size is 4513 with a mean of

427.3 (s.d. = 108.1) individuals per breeding aggregation. Additional realisations of the model are analogous. The static model was used to initialise the expansion model where the habitable environment was increased over time to double the exploitable area. This model was run with a number of different environmental change scenarios: instantaneous doubling in size at the start of the simulation; addition of one extra habitable pixel column per modelled year; addition of one extra habitable pixel column every five years; addition of one extra habitable pixel column every 10 years. These different scenarios represent different rates of environmental change; instantaneous, fast, medium and slow rates respectively. Figure 4.3 shows an example output from the instantaneous model, while Figure 4.4 shows an example output from the slow model in years 50, 100, 500 and 2000. Additional simulations are analogous to the results shown. Table 4.1 shows the mean number of breeding aggregations remaining in each of the models in these years from five repeat simulations. Figure 4.5 shows the mean value (averaged over all individuals) of the evolvable individual step-length parameter *d* for all models. It is clear from Figure 4.3 that an instantaneous doubling of the modelled landscape allows aggregations closer to the moving boundary to expand their population size rapidly. This causes a decrease in the success of aggregations closer to the left hand side which are outcompeted and collapse (Figures 4.3a and 4.3b). The remaining aggregations then slowly move throughout the landscape and towards the end of the modelled period fission of some aggregations occurs to slightly increase the final number of aggregations (Figures 4.3c and 4.3d). As the speed of environmental change decreases, the advantage that the aggregations on the right have is weakened and the breeding aggregations on the left are more likely to persist (Figure 4.4 and Table 4.1). In the instantaneous model, the mean value of the step-length parameter, *d*, (Figure 4.5) evolves upwards quickly, before decreasing as aggregations spread across the area. In the models with slower environmental change, the rate at which *d* increases is lower and the maximum value achieved is also lower (Figure 4.5).

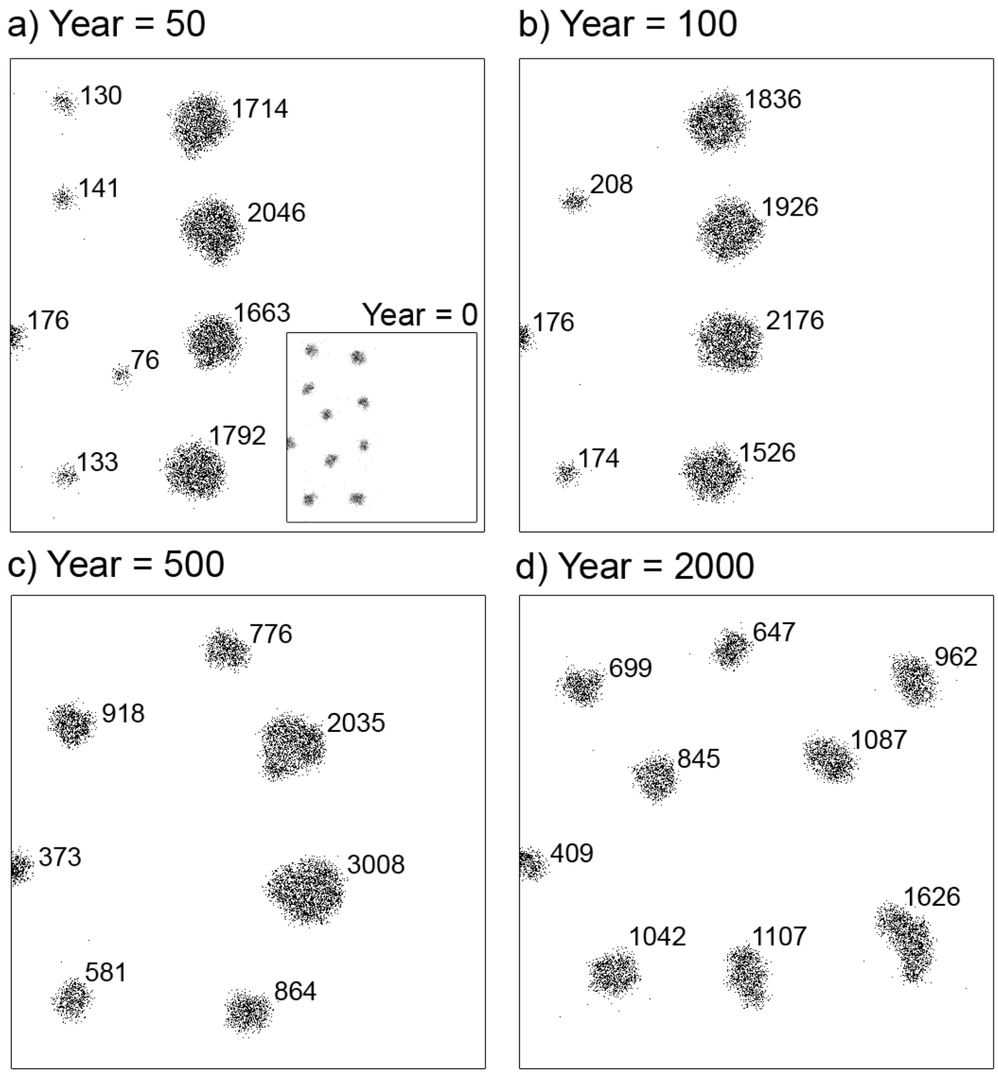

FIGURE 4.3. OUTPUT FROM THE EXPANSION MODEL SHOWING THE LOCATION OF INDIVIDUALS AT BREEDING TIME (BLACK DOTS) AFTER AN INSTANTANEOUS DOUBLING IN THE EXPLOITABLE ENVIRONMENT (INSTANTANEOUS ENVIRONMENTAL CHANGE). THE NUMBER OF INDIVIDUALS IN EACH BREEDING AGGREGATION IS SHOWN. a) ONE AGGREGATION HAS BEEN LOST FROM THE INITIAL DISTRIBUTION, TAKING THE TOTAL TO NINE. AGGREGATIONS ON THE RIGHT HAND SIDE HAVE EXPANDED IN SIZE. b) AND c) TWO FURTHER AGGREGATIONS ARE LOST, TAKING THE TOTAL TO SEVEN. d) FISSION OF TWO OF THE AGGREGATIONS OCCURS AS AGGREGATIONS SPREAD, TAKING THE FINAL TOTAL TO NINE. INSET IN FIGURE 4.3a: THE STARTING CONFIGURATION OF INDIVIDUALS USED IN EXPANSION MODEL SIMULATIONS. IN YEAR 50 THE MEAN NUMBER OF INDIVIDUALS PER AGGREGATION (S.D. IN BRACKETS) IS 874.6 (±837.2), WITH A TOTAL POPULATION SIZE OF 8120. IN YEAR 2000 THE MEAN NUMBER OF INDIVIDUALS PER AGGREGATION IS 936.0 (±327.6), WITH A TOTAL POPULATION SIZE OF 8708.

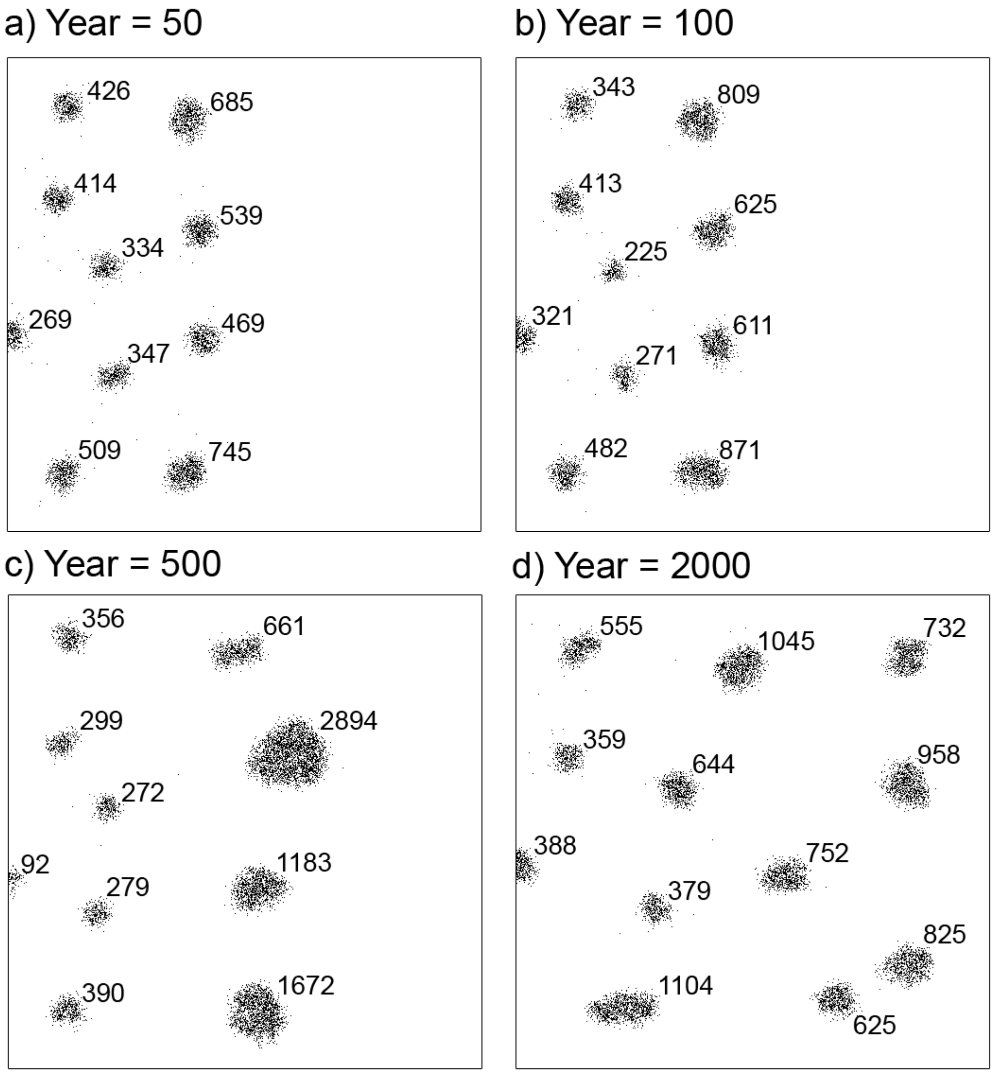

FIGURE 4.4. OUTPUT FROM THE EXPANSION MODEL SHOWING THE LOCATION OF INDIVIDUALS AT BREEDING TIME (BLACK DOTS) WITH ONE EXTRA EXPLOITABLE PIXEL COLUMN ADDED EVERY 10 YEARS (SLOW ENVIRONMENTAL CHANGE). a) AND b) NO AGGREGATIONS HAVE BEEN LOST FROM THE INITIAL DISTRIBUTION. AGGREGATIONS ON THE RIGHT HAND SIDE HAVE EXPANDED IN SIZE LESS IN COMPARISON TO FIGURE 4.3. c) AGGREGATIONS ON THE RIGHT HAVE EXPANDED IN SIZE, BUT NO AGGREGATIONS HAVE BEEN LOST. d) FISSION OF TWO OF THE AGGREGATIONS OCCURS AS AGGREGATIONS SPREAD, TAKING THE FINAL TOTAL TO TWELVE. THE NUMBER OF INDIVIDUALS IN EACH BREEDING AGGREGATION IS SHOWN. IN YEAR 50 THE MEAN NUMBER OF INDIVIDUALS PER AGGREGATION (S.D. IN BRACKETS) IS 473.7 (±143.9), WITH A TOTAL POPULATION SIZE OF 4980. IN YEAR 2000 THE MEAN NUMBER OF INDIVIDUALS PER AGGREGATION IS 697.2 (±244.0), WITH A TOTAL POPULATION SIZE OF 8725.

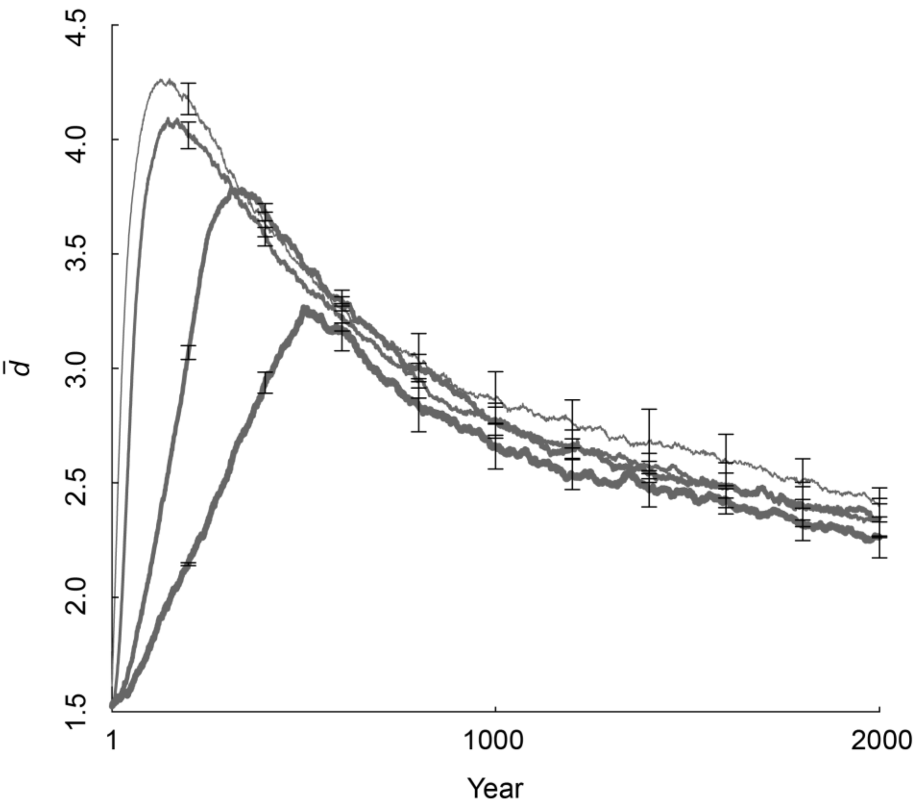

FIGURE 4.5. THE EVOLUTION OF INDIVIDUAL MEAN STEP-LENGTH, *d* (WITH STANDARD DEVIATIONS), AVERAGED ACROSS ALL INDIVIDUALS IN THE POPULATION (FROM FIVE SIMULATIONS). INSTANTANEOUS, FAST, MEDIUM AND SLOW RATES OF ENVIRONMENTAL CHANGE ARE SHOWN BY LINES OF INCREASING THICKNESS.

	Rate of environmental change			
Year	Instantaneous	Fast	Medium	Slow
50	8.2 ± 0.4	10.0 ± 0.0	10.0 ± 0.0	10.0 ± 0.0
100	7.8 ± 0.4	8.0 ± 0.0	10.0 ± 0.0	10.0 ± 0.0
500	7.6 ± 0.5	8.0 ± 0.0	8.0 ± 0.0	10.0 ± 0.0
2000	8.8 ± 0.4	9.2 ± 0.4	9.0 ± 0.6	11.0 ± 0.6

TABLE 4.1. THE MEAN NUMBER OF BREEDING AGGREGATIONS OVER TIME (WITH STANDARD DEVIATIONS) FROM FIVE SIMULATIONS OF THE EXPANSION MODEL FOR EACH DIFFERENT RATE OF ENVIRONMENTAL CHANGE.

4.5 DISCUSSION

Over the modelled time period, density-dependent effects on mortality and breeding success lead to the formation of breeding aggregations as a consequence of simple individual behavioural phenotypes. Individuals are at an advantage if they group together at breeding time, but at a disadvantage if they cluster when competing. This leads to the emergence of groups of individuals at breeding time separated by areas of inhibition. Subsequent movement of breeding aggregations occurs at a much lower rate than that of individual movement due to the imprinting of the historical breeding locations in new recruits and competition between individuals. This slow rate of group movement may severely reduce the ability of aggregative breeders to respond to environmental change.

4.5.1 EMERGENCE OF BREEDING AGGREGATIONS

In the static model, breeding aggregations quickly establish from a random distribution of individuals. There is then a reduction in the number of aggregations until a stable aggregation structure is achieved (Figure 4.2). This loss of aggregations takes place because competition following dispersal means that smaller aggregations are overwhelmed by those containing more individuals because a greater proportion of fish die. Furthermore, individuals in large aggregations breed more successfully (at least initially), and more recruits will therefore return to these locations to breed. These larger aggregations quickly swamp smaller aggregations until the number of aggregations stabilises. The remaining breeding aggregations are those with more individuals, which are therefore more competitive. Loss of aggregations is then unlikely, and the predominant population-level effect is that aggregations become more regularly spaced in the environment. This occurs because individuals within evenly spaced aggregations suffer the lowest density-dependent mortality during and following dispersal. Subsequent movement of aggregations is slow, occurring over hundreds of modelled years. This is due to three factors; a) the imprinting of breeding locations dictating that individuals return to breed close to their birth sites, b) positive density-dependence in breeding (an Allee effect) means that individuals which home to areas outside aggregations suffer reduced breeding success, c) competition between individuals from neighbouring breeding aggregations during and following dispersal resists movement towards other aggregations.

4.5.2 RESPONSE TO ENVIRONMENTAL CHANGE

The expansion model explores the consequences of environmental change on the distribution and persistence of breeding aggregations by opening up new habitat at different rates. As expected, as new habitat is introduced, individuals spread over the available space and the distribution of breeding aggregations also responds. However, there are consequences of this response which are not obvious prior to simulation. Firstly, it might be expected that the number of aggregations at the end of the simulation in the expansion model would be similar to the number at the conclusion of the static model. The static model in Figure 4.2 results in 21 breeding aggregations after 2000 years of simulation. However, in the expansion model the result is fewer aggregations (Table 4.1). In the expansion model, at model initialisation there are 10 breeding aggregations (Figure 4.3, inset). Despite a doubling in habitable area over time it is very difficult for new breeding aggregations to appear for the same reasons that movement of existing breeding aggregations is slow. Splitting of breeding aggregations will only occur if individuals at the edges of the aggregation are more successful than those in the middle, e.g. if the negative impact of Allee effects at the aggregation edge is outweighed by the benefit of being in a less densely populated area with lower competition. This does occur to a few aggregations later in the simulations but is an infrequent process and so the final number of aggregations never approaches the number in the static model. Further confounding the splitting of aggregations is the fact that, following habitat expansion, the population mean of the mean individual step-length, *d*, quickly evolves to a greater value (Figure 4.5). Increasing diffusion rate, via an increase in mean step-length, intensifies competition between individuals from neighbouring breeding aggregations causing the distance between aggregations to increase over time. As the distance between aggregations increases, the total number of aggregations which can be stably supported in the environment decreases. Therefore, rather than splitting, it is more common for existing aggregations to move slowly through the area and become larger. As aggregations begin to spread into new habitat the mean step-length, *d*, evolves back towards a lower value (Figure 4.5). However, even when the number of breeding aggregations increases slightly with the slow rate of environmental change (Table 4.1), the mean value of *d* does not approach its initial value because the area available to individuals has increased. This reduces competition between individuals from neighbouring aggregations and facilitates a higher rate of dispersal away from an individual's breeding location.

4.5.3 EFFECTS OF EVOLUTION OF DISPERSAL

A second consequence of introducing new habitat is the effect on aggregations behind the moving boundary, i.e. aggregations not close to the expanding margin. As mentioned above, there is rapid evolution of the mean step-length, *d*, at the expanding margin. This occurs because as new habitat is made available individuals that move to these areas experience less competition. These individuals are less likely to die through competition, and can therefore pass their larger *d* onto more offspring. Rapid evolution of dispersal ability at the expanding margin during range expansion is well documented in the literature in both theoretical (Travis and Dytham 2002, Dytham 2009) and empirical (Simmons and Thomas 2004, Parmesan 2006, Phillips *et al.* 2006) studies. Mean step-length, *d*, evolves at a rate proportional to environmental change in these simulations (Figure 4.5). Aggregations nearest the expansion margin benefit most as they are only in competition with individuals from aggregations further from the margin. Favourable increases in *d* for individuals at the expanding margin cause increased competition (and therefore mortality) on individuals from aggregations behind the expansion margin. Thus, with instantaneous environmental change some of the breeding aggregations further from the new habitat are at a severe competitive disadvantage and can disappear (Figure 4.3a). Here, a fast evolutionary response to environmental change (Figure 4.5) by individuals and an associated rapid increase in the population size at the expanding margin (Figure 4.3) cause the collapse of aggregations further from the margins. It is predicted that reducing the rate at which individual step-length, *d*, evolves would reduce the probability of population collapse. A simple way to achieve this is to reduce the rate of environmental change (Table 4.1, Figure 4.4). As the rate of environmental change is reduced both the rate of evolution of *d* and the maximum value of *d* are reduced (Figure 4.5). Aggregations near the expanding margin still have an advantage as they exploit the newly available habitat and increase in population size (Figure 4.4), but the rate of increase is reduced. Aggregations away from the margin can therefore compete more effectively and are less likely to collapse (Table 4.1). Thus, while the total environmental change is the same, it is the rate of change that determines the persistence of breeding aggregations. Although these results are qualitatively robust, the response of aggregations to environmental change with different parameterisations of the model will vary, i.e. the rate at which breeding aggregations are able to move will depend on factors such as error in the imprinting of breeding location and the ability of individuals to home accurately. It should be noted that the evolutionary mechanism of inheritance in the model is a simplification of reality; phenotypes are inherited directly from a single female parent, with error drawn from a normal distribution. Increasing realism by allowing inheritance of alleles from both male and female parents, plus the possibility for novel alleles to arise via genetic mutation, would form an interesting model extension. Despite the simplification, the model clearly demonstrates the potential for selective forces to determine the fitness of individual phenotypes, which may have a large impact on the resulting population structure.

4.5.4 FURTHER ENVIRONMENTAL FACTORS

The collapse of aggregations in the expansion model occurs without four considerations which have the potential to exacerbate the problem; a decline in the habitat quality at the trailing boundary, habitat heterogeneity, biotic interactions, and population exploitation. As habitat at the expanding boundary becomes more suitable for occupation, in many cases it might be expected that the trailing range margin will become less suitable (Parmesan 2006). In the model this would reduce suitable habitat in areas where breeding aggregations are historically established, thereby increasing the probability of local population collapse. Secondly, in the model the habitat is treated as homogeneous, i.e. everywhere is equally available for movement and suitable for breeding. Heterogeneity is the norm in the natural world and it is likely that in nature historical breeding aggregations develop in areas which are particularly suitable (e.g. on high ground, or constrained to a particular sediment type (Högland and Alatalo 1995, Wieland *et al*. 2009)). Barriers to movement at the individual-level may also exist, especially for terrestrial species. If populations are finely structured or fragmented, an increased likelihood of localised extinctions with environmental change in heterogeneous systems may be expected. Thirdly, although the modelled species is treated in isolation, biotic interactions between different species may affect rates of expansion and interact with environmental change (Brooker *et al.* 2007). Finally, populations of individuals which are exploited, and therefore more dependent upon yearly recruits to maintain population size, may be more vulnerable to collapse (West *et al*. 2009). If these constraints (or in the case of exploitation, risks) are added to the model, then the rate of breeding aggregation movement is likely to be even more restricted and the probability of aggregation collapse will be increased. Conversely, a mechanism which has not been considered here which may help populations respond to the effects of environmental change is that of individual straying from one breeding aggregation to other, non-natal breeding aggregations (Robichaud and Rose 2001, Heath *et al*. 2008).

The fact that some sub-populations appear more vulnerable to environmental change than others has consequences for the exploitation of habitats and populations, and for our conservation efforts. For example, there is a long history of protected area use in terrestrial habitats, and more recent use in marine environments as protection against overfishing (Gell and Roberts 2003). Models have shown that reserves may be effective for species undergoing migratory behaviour (Apostolaki *et al*. 2002, Martin *et al.* 2007, West *et al*. 2009). However, the location of these protected areas may be critical for the persistence of sub-populations, and consideration also needs to be given to how environmental change might affect the resilience and persistence of important aggregations. In the expansion model the aggregations located behind the moving boundary are most vulnerable and concentrating protection on these individuals may help prevent population collapse. In marine habitats, for example, fishermen may actively target aggregations to maximise catch per unit of fishing effort (Rose and Kulka 1999, Righton *et al*. 2009). Protecting vulnerable areas from exploitation may help to ensure that breeding success is not compromised and increase population resilience and viability. The effects of population exploitation and conservation warrant additional attention from further model development, and are likely to be species and system-specific.

4.5.5 APPLICATIONS

Individuals within the model are able to move freely and quickly within their environment, and therefore a rapid population response to environmental change may have been expected. Recent developments in animal tracking allow the behaviour of individuals in the real world to be observed in detail over extended time-scales (Rutz and Hays 2009). This has provided considerable insights, especially for marine species that had previously been difficult to observe. For example, tagging studies on Atlantic cod confirm that individuals undergo large-scale migrations between spawning and feeding aggregations (Figure 4.1c, Wright *et al*. 2006, Righton *et al*. 2007). In the North Sea, individuals travel as far as 70 km in a single day (Righton *et al*. 2008, Hobson *et al.* 2009) and tolerate a wide range of environments (Neat and Righton 2007). Similar findings have been reported for European plaice, *Pleuronectes platessa* (Hunter *et al*. 2004a, Hunter *et al*. 2004b). At an individual level, therefore, it might be expected that species exhibiting long-range migrations should have little trouble locating suitable habitat. However, tagging and genetic studies of cod also reveal annual movements to specific spawning aggregations (Svedäng *et al*. 2007), resulting in populations that are much more finely structured than previously thought (Hutchinson *et al*. 2001, Knutsen *et al*. 2003, Nielsen *et al*. 2009). Within these consistent spawning locations, cod are hypothesised to exhibit a lekking mating system in which males engage in competitive displays before mating (Rowe and Hutchings 2003, Windle and Rose 2007). Aggregation and lekking at traditional sites are also exhibited in other fish species, as well as mammals, birds, arthropods, reptiles and amphibians (Högland and Alatalo 1995, Wikelski *et al*. 1996). Aggregation solely for breeding purposes is only one mechanism which could result in the regular return of individuals to fixed locations. The return by birds to nests (which may represent significant time and energy investment), or the return by social insects to colonies are just two examples of non-breeding specific behaviour which may occur over different temporal and spatial scales but may also impact the ability of individuals to respond to environmental change.

Studies have indicated that the ranges of many species have shifted in response to recent climatic change (Walther *et al*. 2002, Perry *et al*. 2005, Parmesan 2006). However, in some cases, perceived range shifts may be attributed instead to changes in the abundance of sub-populations (Neat and Righton 2007). The simulations presented here demonstrate this effect, with a rapid shift in population abundance towards the expanding range margin immediately following environmental change. At the population level this may mistakenly be detected as a range shift (the actual populations will have moved very little in the short-term), highlighting the importance of managing populations at the local rather than global level.

In this study, three interacting factors cause the formation of breeding aggregations and influence their subsequent movement; individual homing, an Allee effect at breeding time, and competition. Allee effects have been shown to reduce the rate at which populations are able to spread during range expansion or invasions (Keitt *et al*. 2001, Travis and Dytham 2002, Courchamp *et al*. 2008). However, in this model, by the inclusion of two additional factors within a migratory framework, the spatial population dynamics are markedly different. Here, the extent to which individuals are distributed throughout the environment depends on the time of year. Individual movement is rapid and, via diffusive movements following breeding, individuals are easily able to colonise the entire modelled area following habitat expansion. Conversely, the movement of aggregations is slow, and therefore individuals will be highly restricted in range during breeding time. Movement of breeding grounds will be crucial when considering the adaptation of a species to new habitat as it will determine the ability of a species to persist. However, the distribution of individuals during the post-breeding phase may also be important. For example, a species expanding into a previously unoccupied habitat may compete with existing species even though their ranges do not overlap at breeding time. It is therefore important when monitoring range expansion to consider the spatial distribution of individuals throughout the year in addition to the distribution of breeding sites.

4.5.6 CONCLUDING REMARKS

The results indicate that behaviour can be as much of a barrier to population dispersal as environmental factors. Competition and the slow rate of population-level response following environmental change may lead to a collapse in breeding aggregations, and therefore a loss of biodiversity, despite the availability of suitable contiguous habitat for range expansion. It would be unwise to assume that species undertaking aggregative breeding will respond quickly to environmental change, even when individuals are mobile and there are no environmental barriers to movement.

5

5

THE IMPACT OF EXPLOITATION ON SPAWNING AGGREGATION PERSISTENCE IN MIGRATORY POPULATIONS

5.1 ABSTRACT

Overfishing continues to cause reductions in fish stocks and the localised loss of marine biodiversity. Although commercial fish species are unlikely to become extinct, the loss of intraspecific diversity is of concern. This has been highlighted in the last decade by the results of recent fish-tagging and genetic analyses that suggest that stocks are more finely structured than previously thought. These studies also reveal that sub-populations of commercial fish stocks undertake seasonal migrations between spawning and feeding grounds, with implications for fisheries management, including the use of marine protected areas. Here, an individual based model is used to investigate the ecological and evolutionary impacts of different fishing scenarios on spatially-structured aggregations of fish (sub-populations) that exhibit seasonal migrations to and from discrete spawning locations. High levels of fishing effort are shown to have the potential to cause the extirpation of the entire population, but fragmentation and collapse of spawning aggregations may occur with much lower fishing effort. The addition of marine protected areas may increase population size, enhance the persistence of spawning aggregations, and increase fisheries yield. Long- and short-term evolution in individual dispersal can occur in contrasting directions depending on the spatial location of fishing effort. Importantly, overall population size does not always correlate with the persistence of spawning aggregations. This questions the use of large-scale measures of population health when managing populations with fine-scale stock structure.

5.2 INTRODUCTION

Overexploitation by commercial fisheries continues to cause a reduction in fish stocks and catches (Hilborn *et al.* 2003, Pauly *et al.* 2005), with some analysts suggesting a global collapse in currently-fished taxa by the middle of the 21st century (Worm *et al*. 2006, Worm *et al*. 2007). Whilst the collapse of entire fished populations is, of course, of great concern, under the Rio Convention on Biological Diversity there is also a responsibility to protect intraspecific diversity (i.e. sub-populations) (Ryman *et al.* 1995). Loss of diversity both between and within species may reduce the recovery potential of marine ecosystems, both from fisheries exploitation and within an environment subject to environmental change (Ryman *et al.* 1995, Hilborn *et al.* 2003, Worm *et al.* 2006). Recent genetic and tagging studies show that populations of commercially important species such as Atlantic cod, *Gadus morhua* (Ruzzante *et al.* 2000, Hutchinson *et al.* 2001, Knutsen *et al*. 2003, Metcalfe 2006, Nielsen *et al.* 2009), European plaice, *Pleuronectes platessa* (Hunter *et al*. 2004a, Solmundsson *et al.* 2005, Metcalfe 2006), and thornback ray, *Raja clavata* (Chevolot *et al.* 2006a, Hunter *et al.* 2006, Metcalfe 2006) are more finely structured than previously thought. In the North Sea, current management areas are relatively large and may therefore be unable to protect these population sub-stocks (Hutchinson *et al.* 2001).

An explanation for the formation of these discrete population sub-stocks is the homing behaviour exhibited by commercial migratory marine fish (Svedäng *et al.* 2007). Mark-recapture and data storage tag (DST) studies have revealed complex movement behaviours (Righton *et al.* 2001, Righton *et al.* 2007, Righton and Mills 2008). For example, North Sea studies demonstrate that, as for North-West Atlantic stocks (Green and Wroblewski 2000, Robichaud and Rose 2002), cod show predictable patterns of dispersal to feeding areas followed by returns to spawning grounds (Metcalfe 2006, Wright *et al*. 2006, Righton *et al*. 2007). This strong homing tendency ensures that most fish return to their spawning areas even following artificial displacement (Robichaud and Rose 2002). Icelandic and North Sea plaice also show fidelity to spawning and feeding areas (Hunter *et al*. 2004b, Solmundsson *et al.* 2005, Metcalfe 2006), while thornback rays in the Thames estuary disperse into the North Sea to feed before returning to the estuary to spawn (Hunter *et al.* 2006). Blue-fin tuna, *Thunnus thynnus*, undertake trans-Atlantic migrations, but adults will return to natal spawning areas (Rooker *et al*. 2007, Rooker *et al*. 2008). Such site fidelity will reduce gene flow and lead to the formation of sub-stocks.

In addition to the mismatch between the spatial scale of stock structure and fisheries management areas, the movement behaviour exhibited by these migratory species may have implications for the success of fisheries management measures, including the use of marine protected areas (MPAs). Because of their large ranges, seasonally migratory species may be particularly vulnerable to fishing, experiencing different levels of exploitation at different times of year. Empirical studies suggest that fish with small home-ranges will be more adequately protected by MPAs than highly mobile species (Kramer and Chapman 1999, Gell and Roberts 2003). However, traditional spillover models are insufficient as tools to assess the benefits of MPAs for stocks which migrate seasonally as they consider only non-directional movement across MPA boundaries. A better model (Apostolaki *et al*. 2002) predicts that MPAs may increase yield and spawning stock biomass in the Mediterranean hake, *Merluccius merluccius*, and another model (West *et al*. 2009) considers a migratory stock moving between a spawning and feeding area and concludes that MPAs may be beneficial for stocks exhibiting moderate levels of migration, but do not totally protect fisheries from collapse. However, both these and other models (e.g. Stefansson and Rosenberg 2005, Stefansson and Rosenberg 2006, Röckmann *et al*. 2007) rely on extremely simplified caricatures of migratory behaviour, and do not consider the impacts of fishing on population sub-stocks.

In addition to effects on population size, catch, and sub-stock structure, fishing has the potential to cause evolutionary change. The potential for fisheries-induced evolution in size and age at maturation, which may reduce productivity and sustainability of stocks, is well documented (Law and Grey 1989, Law 2000, Heino and Godø 2002, Olsen *et al*. 2004). MPAs have been shown to reduce such evolutionary effects on maturation size (Baskett *et al*. 2005, Dunlop *et al.* 2009, Miethe *et al.* 2010a). In addition to selection on life-history traits, fishing may impact on behaviour such as dispersal distance. There is the potential for MPAs to select for lower movement by increasing the fitness of less mobile individuals within the MPA with a resulting reduction in spillover (Travis and Dytham 1998, Baskett *et al*. 2007, Miethe *et al*. 2009, Miethe *et al.* 2010b).

In contrast to population models, individual based models (IBMs) allow the movement and behaviour of unique individuals to be modelled through time to reflect the variation in behaviours captured by DSTs. Here, a novel IBM is used to model the exploitation of a theoretical migratory fish species consisting of a number of isolated spawning aggregations (i.e. population sub-stocks). Rather than imposing spawning areas onto the modelled population, spawning aggregations are the result of the behaviour of individuals, allowing investigation of the response of spawning aggregations to fishing pressure. The modelled movement behaviour is inspired by data collected from marine fish which undertake spawning migrations to and from spawning aggregations (Hunter *et al*. 2004a, Hunter *et al.* 2004b, Hunter *et al*. 2006, Wright *et al*. 2006, Righton *et al*. 2007, Svedäng *et al*. 2007). The effects of varying levels of exploitation on population size, fisheries yield, and persistence of spawning aggregations are evaluated. A comparison between uniform exploitation and exploitation targeted on feeding and spawning areas is made, and the effect of introducing MPAs protecting half of the modelled area is investigated. The evolution of individual dispersal distance within the sub-populations following the introduction of MPAs is also explored. It is shown that uniform fishing can lead to population collapse under high levels of exploitation. Protecting spawning aggregations can prevent this population collapse, enhance aggregation persistence, and increase catch. Targeting spawning aggregations may lead to aggregation fragmentation and loss but this effect can be reduced if the location of fishing effort is updated every 10 modelled years or less. Introduction of an MPA over 50% of the modelled area can enhance population sizes and prevent aggregation collapse. Updating the location of the MPA may also enhance yields, with maximum yield obtained by updating every 2 modelled years. It is discovered that long-term and short-term evolution in dispersal distances may occur in different directions depending on the fishing scenario. Crucially, it is found that large-scale measures of population health are not necessarily sufficient to protect against spawning aggregation collapse, bringing into question the suitability of large management areas for the protection of isolated sub-stocks.

5.3 METHOD

The IBM represents a theoretical migratory aggregative spawner. It is based on the model introduced in Chapters 3 and 4 and represented schematically in Figure 4.1a. In brief, in a model which does not include fishing pressure, individuals in the model undergo dispersive movement followed by directed movements back to spawning locations. In each modelled year of 365 days (*t*), individuals within the model initially undergo random walks (in continuous space but discrete time) from their spawning location (*t* = 1-265). The movements from the spawning site have three phases. First, there is post-spawning diffusive movement (*t* = 1-25). In this phase, in addition to density-independent mortality, individuals experience mortality associated with a cost to movement (e.g. increased energetic expenditure, enhanced predation risk) controlled by the fixed movement mortality parameter γ. Adult individuals are then assumed to undergo further dispersive behaviour and, in addition to density-independent mortality and movement mortality, are assumed to be competing for unmodelled resources (with competition determined by population density within a pixel-sized grid-square) and therefore subject to density-dependent mortality (*t* = 26-100). New recruits bypass the post-spawning dispersal period and undergo competitive behaviour from the start of the year and thus undergo density-dependent mortality from *t* = 1. Following the period of random dispersal, daily movements are reduced and each individual undergoes a period of 'settlement' within a restricted area (t = 101-265). Individuals then switch to 'spawning behaviour' and undergo biased random walks towards an imprinted spawning location (*t* = 266-365). During this period, density-independent and movement mortality occur but density-dependent mortality does not, as individuals are no longer assumed to be competing for resources (e.g. cod populations are known to suppress feeding during the spawning season (Fordham and Trippel 1999)). At the end of the year, individuals attempt to spawn, with individual success determined by a 'Ricker-type' equation based on the number of neighbours within a radius of one pixel of the spawning individuals. Low density individuals have low spawning success. As local population density increases, spawning success increases (via increased encounter rate) before decreasing after local population density reaches a threshold (e.g. via cannibalism (Daan 1973, Anderson and Gregory 2000, Uzars and Plikshs 2000), predation (Bailey and Houde 1989), or starvation (Anderson 1988)). New recruits are added to the population after a lag of one year, distributed around their site of birth. The distance that an individual travels in each time-step is randomly drawn from a negative exponential distribution with mean determined by the heritable mean step-length, *d*. Each individual's value of *d* is inherited from its parent with a chance of error and is therefore evolvable within the model (Dytham and Travis 2006). An individual's desired spawning location is imprinted at birth as the location in which it was born, plus error. An example of an individual's movement track over three years is shown through space (Figure 4.1b) and time (Figure 4.1a). The IBM is inspired by behaviour exhibited by commercial marine fish. Real data from an Atlantic cod tagged with a data storage tag is shown in Figure 4.1c for comparison with the simulated example.

In order to explore the impact of different forms of fishing pressure on a population consisting of a number of spawning aggregations, the model above was first run for 2000 simulated years in an area of 100 by 100 pixels. This resulted in the distribution of 20 spawning aggregations shown in Figure 4.2, where spawning aggregations are defined as two or more adjoining pixels (including diagonals) containing three or more individuals. This model was then used to initialise the fisheries models which run for a period of 200 years. Each individual experiences mortality from fishing depending on the fishing pressure within each pixel, with fishing mortality occurring in each time-step immediately following the mechanism of natural mortality described above. The level of fishing mortality applied to each pixel depends on the fishing pressure (fishing pressure increases from $F = 0.1$ to 0.9) and whether the pixel is protected by an MPA. The effects of several different fishing scenarios are explored:

(i) Uniform fishing (i.e. fishing with equal pressure on each pixel);
(ii) Protecting spawning grounds (i.e. no fishing pressure allocated to spawning aggregations);
(iii) Protecting feeding grounds (i.e. fishing pressure allocated to spawning aggregations only), including periodically updating the location of protected areas every 50, 10 and 2 years as movement in aggregations occurs;
(iv) Uniform fishing with 50% of the total area protected (i.e. no fishing pressure allocated to 50% of the area as a continuous unit), including alternating the position of the MPA every 50, 10 and 2 years.

A detailed explanation of the model, following the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm *et al*. 2006, Grimm *et al*. in press), is presented in Chapter 3.

5.4 RESULTS

5.4.1 UNIFORM FISHING

With uniform fishing, mean population size decreases with increasing fishing pressure (Figure 5.1, black line). The number of initial spawning aggregations which remain after 200 years (Figure 5.1, grey line) decreases with increasing fishing pressure. This loss is small initially, but above *F* = 0.5 the loss of aggregations accelerates, with total collapse of spawning aggregations (and hence the entire population) at *F* = 0.9. Catch initially increases with maximum yield obtained with *F* = 0.7 (Figure 5.1, dotted line). With *F* = 0.8 and *F* = 0.9 overall catch is reduced. Catch per unit effort (CPUE; not shown) declines steadily (approximately linearly) when increasing *F* up to 0.7 but then rapidly declines. This CPUE result is analogous to (but not as easy to interpret as) the total yield result and therefore CPUE is not considered further.

5.4.2 PROTECTING SPAWNING AGGREGATIONS

In the second scenario, spawning aggregations are completely protected from fishing. This results in 7.64% of the total area being protected from fishing. Fishing pressure is uniformly distributed across the unprotected pixels. As with uniform fishing over the entire area, mean population size reduces with fishing effort but relative population size is always larger (Figure 5.2, black line). Likewise, the number of initial spawning aggregations (Figure 5.2, grey line) also decreases with fishing pressure but is again higher at equivalent fishing pressures. Unlike uniform fishing, when spawning aggregations are protected the population does not collapse, i.e. some spawning aggregations remain even when *F* = 0.9. Catch is now maximised at a higher fishing pressure of *F* = 0.8 (Figure 5.2, dotted line). Below *F* = 0.7 catch is reduced compared to uniform fishing, but at *F* = 0.7 and above the catch is higher than uniform equivalents. The catch obtained with *F* = 0.8 is over 16% higher than that obtained with the strategy of *F* = 0.7 which maximises catch with uniform fishing. At *F* = 0.8 the population size and number of spawning aggregations remaining is also higher than with uniform fishing with *F* = 0.7.

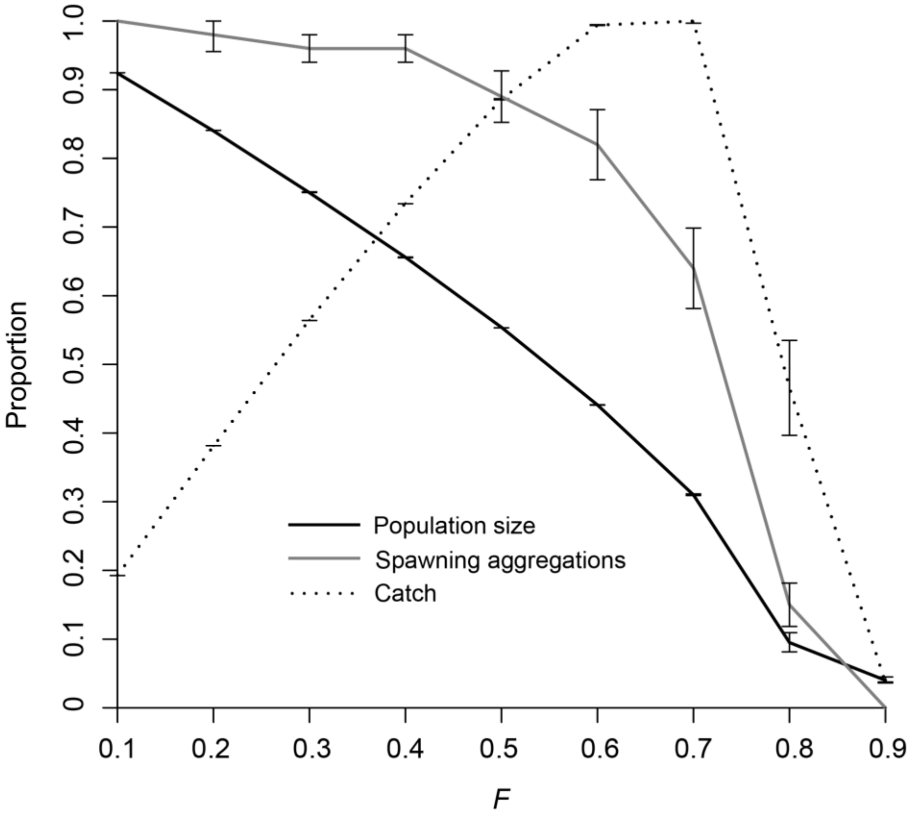

FIGURE 5.1. MEAN POPULATION SIZE, TOTAL CATCH AND PERSISTENCE OF SPAWNING AGGREGATIONS FOLLOWING UNIFORM FISHING PRESSURE. BLACK LINE = MEAN POPULATION SIZE OVER 200 YEARS AS A PROPORTION OF THE INITIAL UNFISHED POPULATION SIZE. GREY LINE = PROPORTION OF INITIAL SPAWNING AGGREGATIONS REMAINING AFTER 200 YEARS. DOTTED LINE = CATCH OVER 200 YEARS AS A PROPORTION OF THE MAXIMUM CATCH OBTAINED AT *F* = 0.7. DATA SHOWN ARE AVERAGES ACROSS FIVE REPEAT SIMULATIONS. STANDARD DEVIATIONS ARE SHOWN AS ERROR BARS BUT ARE SMALL AND DO NOT AFFECT MODEL OUTCOMES. THEY ARE THEREFORE OMITTED FROM OTHER FIGURES.

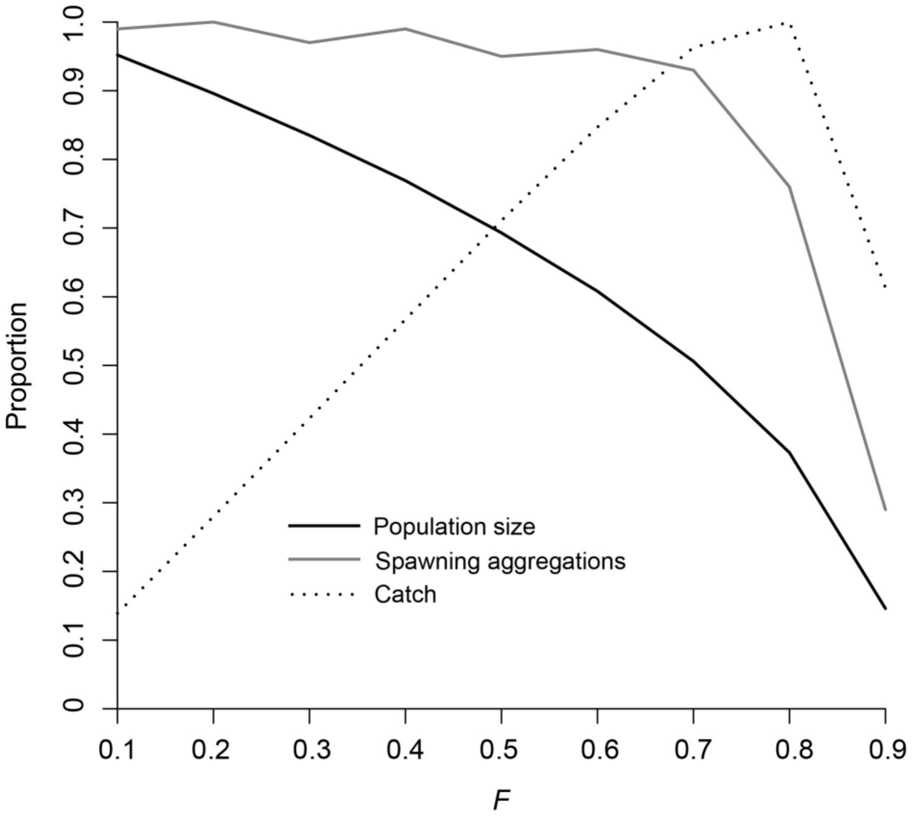

Figure 5.2. Mean population size, total catch and persistence of spawning aggregations following protection of spawning aggregations. Black line = mean population size over 200 years as a proportion of the initial unfished population size. Grey line = proportion of initial spawning aggregations remaining after 200 years. Dotted line = catch over 200 years as a proportion of the maximum catch obtained at *F* = 0.8. Data shown are averages across five repeat simulations.

5.4.3 Protecting feeding areas

In the third scenario, spawning aggregations are fished (with uniform fishing effort taking place on pixels defined as spawning aggregations) and all other areas are protected from fishing. As with uniform fishing and fishing on feeding areas, mean population size reduces with fishing effort (Figure 5.3, black dashed line). Likewise, the number of initial spawning aggregations also decreases with fishing pressure (Figure 5.3, black solid line). Catch is maximised at *F* = 0.9 (Figure 5.3, black dotted line). Figure 5.4 shows an example of the response of spawning aggregations to targeted fishing pressure and clearly shows that fragmentation occurs within 50 years but that aggregations have not moved greatly after 10 years. This is in contrast to uniform fishing or fishing targeted at feeding grounds where aggregations may collapse but do not fragment (not shown).

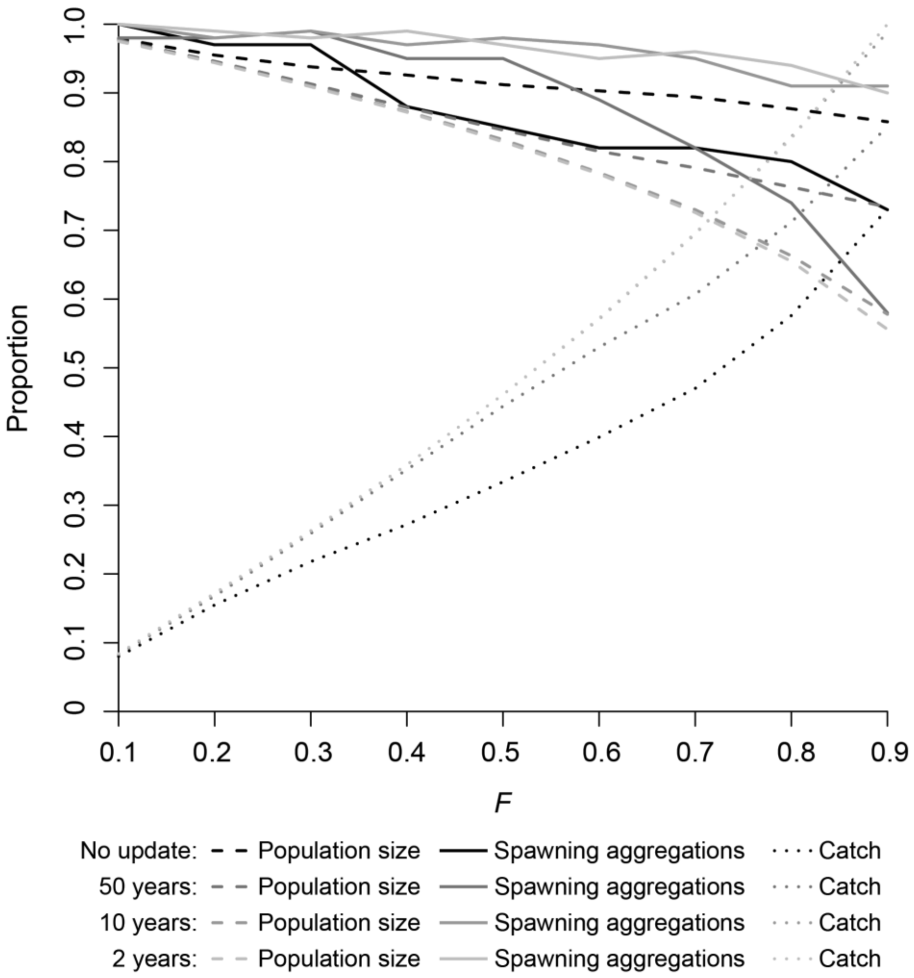

FIGURE 5.3. MEAN POPULATION SIZE, TOTAL CATCH AND PERSISTENCE OF SPAWNING AGGREGATIONS FOLLOWING PROTECTION OF FEEDING AREAS, WITH UPDATES IN SPAWNING AGGREGATION LOCATION. SOLID LINES = PROPORTION OF INITIAL SPAWNING AGGREGATIONS REMAINING AFTER 200 YEARS. DASHED LINES = MEAN POPULATION SIZE OVER 200 YEARS AS A PROPORTION OF THE INITIAL UNFISHED POPULATION SIZE. DOTTED LINES = CATCH OVER 200 YEARS AS A PROPORTION OF THE MAXIMUM CATCH OBTAINED AT *F* = 0.9 WHEN UPDATING EVERY 2 YEARS. LINES FROM BLACK TO LIGHT GREY INDICATE FREQUENCY OF SPAWNING AGGREGATION UPDATES (SEE LEGEND). DATA SHOWN ARE AVERAGES ACROSS FIVE REPEAT SIMULATIONS.

The location of pixels defined as spawning aggregations can be updated periodically to account for movement following fishing pressure. Here, the population is re-sampled after 50, 10 or 2 years and fishing continues only in those pixels now defined as aggregations. Figure 5.3 shows the response in population size, aggregation persistence, and catch following reassignment of spawning aggregations. Updating the location of spawning aggregations leads to a reduction in population size with magnitude depending on the frequency of updates, although results for updates every 10 and 2 years are very similar (Figure 5.3, dashed lines). Updating the location every 50 years increases the persistence of spawning aggregations for fishing pressure up to *F* = 0.7, but above this less spawning grounds persist. Results for updates every 10 and 2 years are similar to each other, but both increase the persistence of spawning aggregations across all fishing pressures (Figure 5.3, solid lines). Catch increases with update frequency although results for updates every 10 and 2 years are almost identical (Figure 5.3, dotted lines).

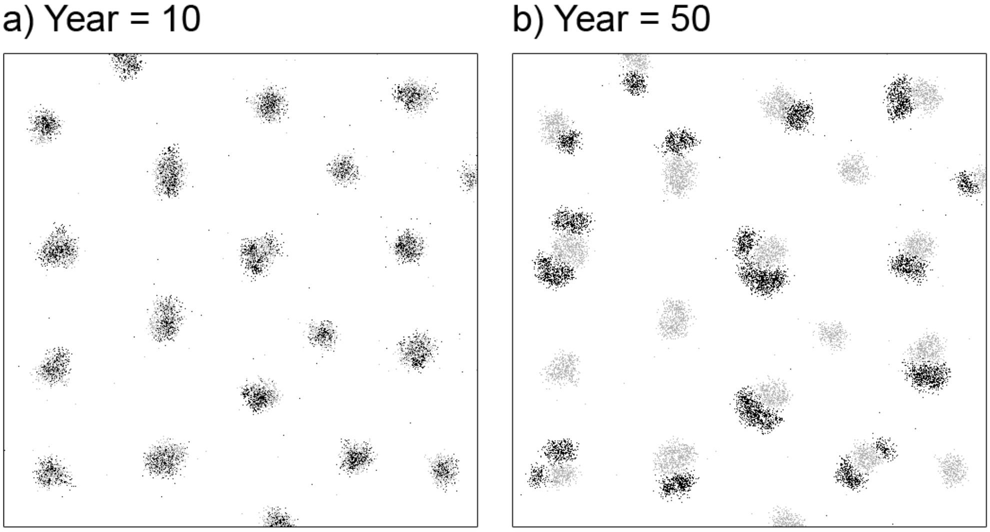

FIGURE 5.4. AN EXAMPLE OF THE DISTRIBUTION OF INDIVIDUALS (BLACK DOTS) AT SPAWNING TIME AFTER a) 10 YEARS AND b) 50 YEARS FOLLOWING PROTECTION OF FEEDING AREAS (I.E. TARGETING SPAWNING AGGREGATIONS). GREY DOTS SHOW THE INITIAL DISTRIBUTION OF INDIVIDUALS PRIOR TO FISHING AND CORRESPOND TO THE LOCATION OF FISHING EFFORT.

5.4.4 UNIFORM FISHING WITH MPA COVERING 50% OF MODELLED AREA

In the final fishing scenario, an MPA protects one half of the modelled area (as a continuous unit) with fishing taking place uniformly over the remaining area. With a static MPA, mean population size decreases with fishing effort (Figure 5.5, black dashed line), but is always higher than with the equivalent fishing pressure with uniform fishing without an MPA. The number of spawning aggregations also decreases with increasing fishing pressure, but again is always higher than with the equivalent uniform fishing pressure without an MPA, and there is never a complete collapse in spawning aggregations (Figure 5.5, black solid line). As with uniform fishing over the entire area, catch is maximised with *F* = 0.7 (Figure 5.5, black dotted line). With fishing pressure up to *F* = 0.7, catch using a static MPA is 50% of the equivalent without an MPA. Above *F* = 0.7, however, this percentage increases. At *F* = 0.8, catch is 74% of the equivalent without an MPA, and at *F* = 0.9, catch is 578% of the non-MPA equivalent.

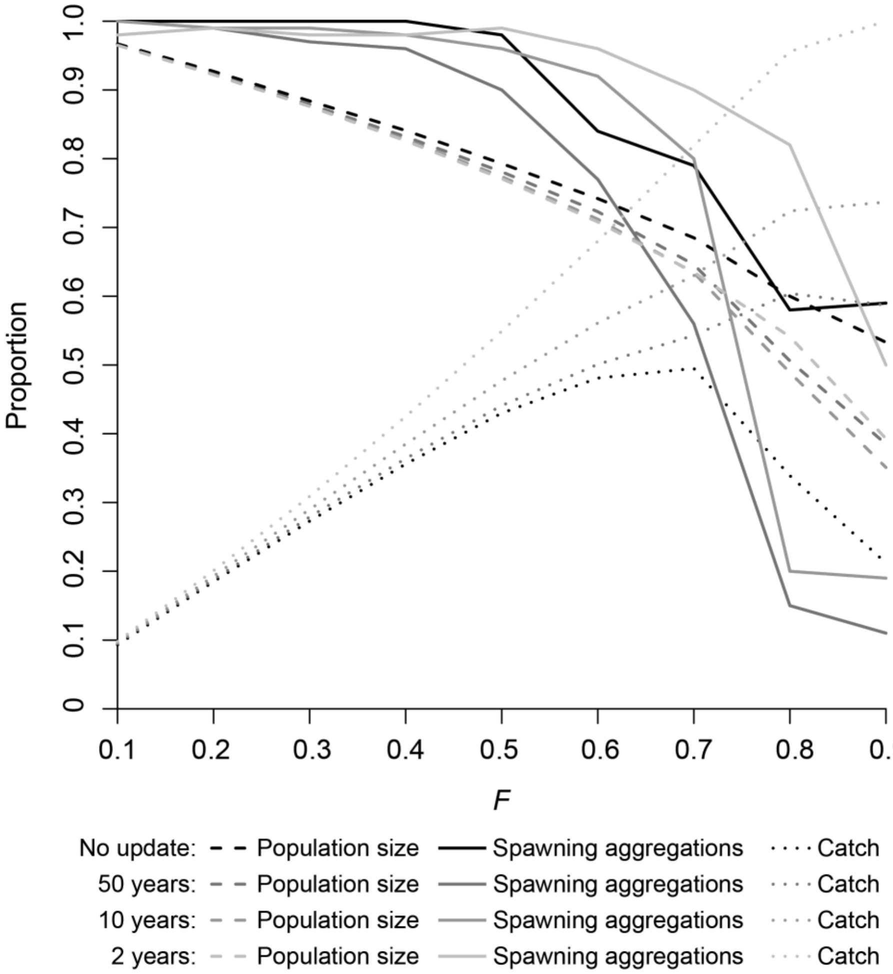

FIGURE 5.5. MEAN POPULATION SIZE, TOTAL CATCH AND PERSISTENCE OF SPAWNING AGGREGATIONS FOLLOWING PROTECTION OF 50% OF THE MODELLED AREA, WITH UPDATES IN MPA LOCATION. SOLID LINES = PROPORTION OF INITIAL SPAWNING AGGREGATIONS REMAINING AFTER 200 YEARS. DASHED LINES = MEAN POPULATION SIZE OVER 200 YEARS AS A PROPORTION OF THE INITIAL UNFISHED POPULATION SIZE. DOTTED LINES = CATCH OVER 200 YEARS AS A PROPORTION OF THE MAXIMUM CATCH OBTAINED AT *F* = 0.9 WHEN UPDATING EVERY 2 YEARS. LINES FROM BLACK TO LIGHT GREY INDICATE FREQUENCY OF MPA LOCATION UPDATES (SEE LEGEND). DATA SHOWN ARE AVERAGES ACROSS FIVE REPEAT SIMULATIONS.

The location of the MPA can be changed periodically so that it protects the other half of the modelled area, i.e. the area which was once fished can be protected and vice versa. Figure 5.5 shows the population size, aggregation persistence, and catch following relocation of the MPA every 50, 10 and 2 years. Updating the location of the MPA leads to a reduction in population size compared to a static MPA, but all update frequencies result in a similar magnitude of reduction (Figure 5.5, dashed lines). Updating the location of the MPA every 50 years decreases the persistence of spawning aggregations for all fishing pressures. At $F = 0.9$, 89% of aggregations are lost compared to 41% with a static MPA. Updating the location every 10 years compares favourably with the static MPA for fishing pressure up to $F = 0.7$, but above this the persistence of spawning aggregations is decreased markedly (81% lost at $F = 0.9$). Updating the location every 2 years leads to equivalent or greater persistence compared with the static MPA for fishing pressure up to $F = 0.8$, but at $F = 0.9$ the persistence of spawning location is decreased slightly (50% lost) (Figure 5.5, solid lines). Catch increases with the frequency of relocation of the MPA. With the location changed every 50 years, maximum catch is obtained at $F = 0.8$ and is 22% higher than the maximum catch with a static MPA at $F = 0.7$. If the MPA location changes every 10 and 2 years, maximum catch is obtained at $F = 0.9$ and is 49% higher and 102% higher respectively than the maximum catch with a static MPA at $F = 0.7$. The maximum catch obtained by updating the MPA every 2 years at $F = 0.9$ is roughly equivalent (2% higher) to the maximum catch obtained with uniform fishing without an MPA at $F = 0.7$, and is 87% of the catch obtained by protecting spawning aggregations only at $F = 0.8$.

5.4.5 EVOLUTION OF DISPERSAL

Figures 5.6 and 5.7 show the effect of fishing pressure on long- and short-term evolution of mean dispersal distance (i.e. the population mean of individual mean step-length, d) with different fishing strategies. In general, fishing pressure leads to a population-level increase in mean dispersal distance in the long-term, although this is not the case when $F = 0.9$ for uniform fishing with an MPA (see Section 5.5 Discussion). In the short-term, mean dispersal distance for uniform fishing and protected feeding grounds do not evolve greatly from the base-line value (although there is a very small apparent increase with protected feeding grounds). There is an obvious decrease in mean dispersal distance with protection of spawning aggregations and uniform fishing with an MPA.

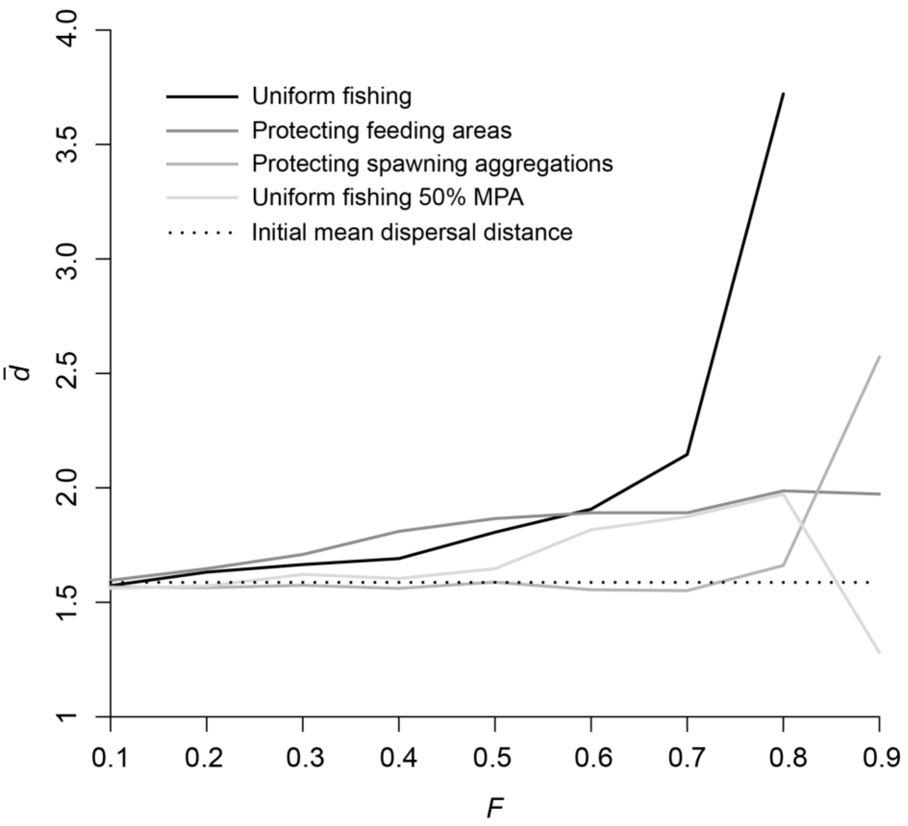

FIGURE 5.6. THE POPULATION MEAN OF INDIVIDUAL MEAN STEP-LENGTH, *d*, UNDER DIFFERENT FISHING STRATEGIES AFTER 200 YEARS (LONG-TERM EVOLUTION). THE DOTTED BLACK LINE SHOWS THE MEAN DISPERSAL DISTANCE BEFORE FISHING. BLACK LINE = UNIFORM FISHING; DARK GREY LINE = PROTECTION OF FEEDING GROUND; MID GREY LINE = PROTECTION OF SPAWNING GROUND; LIGHT GREY LINE = UNIFORM FISHING WITH 50% STATIC MPA. DATA SHOWN ARE AVERAGES ACROSS FIVE REPEAT SIMULATIONS. FOR UNIFORM FISHING, DATA AT *F*=0.9 IS MISSING BECAUSE THE POPULATION HAS COLLAPSED.

5.5 DISCUSSION

For migratory aggregative spawners, the IBM shows that fishing pressure, in addition to reducing overall population size, has the potential to reduce the persistence of discrete spawning aggregations. Through advances in tagging and genetic studies (Hutchinson *et al*. 2001, Knutsen *et al*. 2003, Metcalfe 2006) it is becoming increasingly recognised that such spawning aggregations form isolated sub-populations and as such should be maintained in order to maximise intraspecific diversity (Ryman *et al*. 1995). The results of this study reveal that the response of aggregations to different forms of fisheries management is complex, but that management on a large-scale may be insufficient to protect against a decline in diversity, especially when fishing pressure is high. However, spatially and temporally structured management using MPAs may help to reduce declines in aggregation persistence.

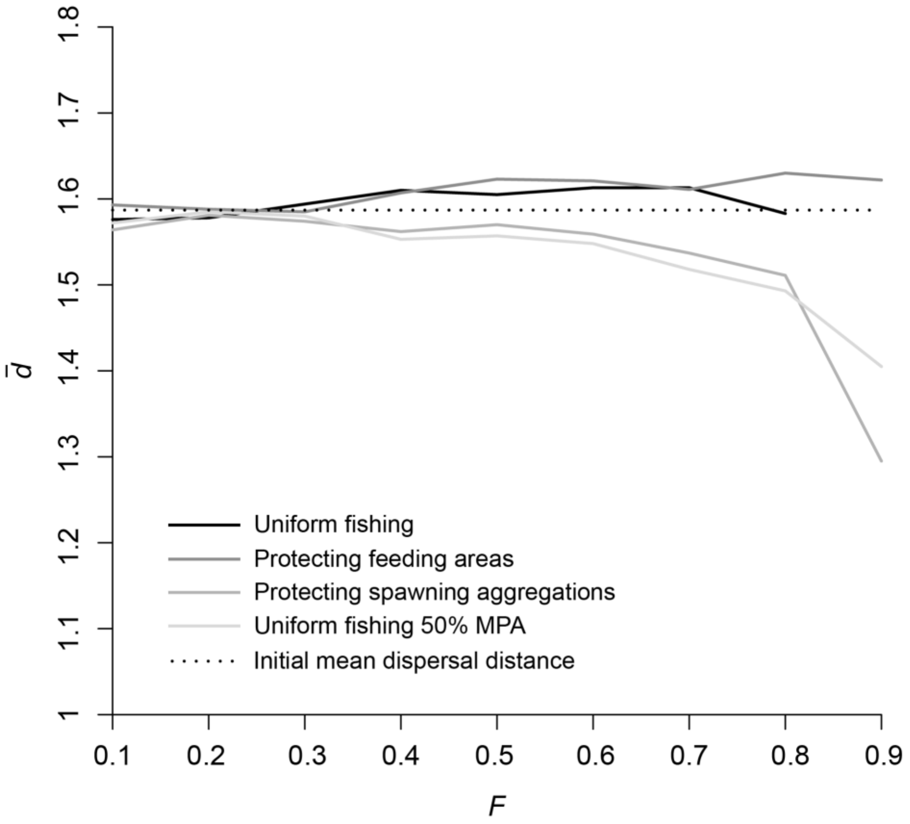

FIGURE 5.7. THE POPULATION MEAN OF INDIVIDUAL MEAN STEP-LENGTH, *d*, UNDER DIFFERENT FISHING STRATEGIES AFTER 10 YEARS (SHORT-TERM EVOLUTION). THE DOTTED BLACK LINE SHOWS THE MEAN DISPERSAL DISTANCE BEFORE FISHING. BLACK LINE = UNIFORM FISHING; DARK GREY LINE = PROTECTION OF FEEDING GROUND; MID GREY LINE = PROTECTION OF SPAWNING GROUND; LIGHT GREY LINE = UNIFORM FISHING WITH 50% STATIC MPA. DATA SHOWN ARE AVERAGES ACROSS FIVE REPEAT SIMULATIONS. FOR UNIFORM FISHING, DATA AT *F*=0.9 IS MISSING BECAUSE THE POPULATION HAS COLLAPSED.

Recent developments in animal tracking allow detailed observation of the behaviour of individuals in the real world over extended time-scales (Rutz and Hays 2009). This has provided considerable insights, especially for individuals that had previously been difficult to observe, such as marine species. For example, DST studies on Atlantic cod confirm that individuals undergo large-scale migrations between spawning and feeding aggregations (Figure 4.1c, Wright *et al*. 2006, Righton *et al*. 2007). In the North Sea, individuals may travel as far as 70 km in a single day (Righton *et al*. 2008, Hobson *et al*. 2009) and tolerate a wide range of environments (Neat and Righton 2007). Similar findings have been reported for European plaice (Hunter *et al*. 2004a, Hunter *et al*. 2004b), thornback ray (Hunter *et al*. 2006), and bluefin tuna (Rooker *et al*. 2007, Rooker *et al*. 2008). These tagging studies, in combination with studies on the genetics of individuals from different areas, also reveal annual movements to specific spawning aggregations (Svedäng *et al*. 2007), resulting in populations that are much more finely structured than recognised previously (Hutchinson *et al*. 2001, Knutsen *et al*. 2003, Nielsen *et al*. 2009). The IBM captures both the complexity of movement at the individual-level and the spatial structure of spawning aggregations in a way which cannot be achieved with population models. In doing so, it allows new insight into how spawning aggregations may respond to different fishing strategies and methods of protection.

5.5.1 UNIFORM FISHING AND PROTECTION OF SPAWNING AGGREGATIONS

In the exploration of uniform fishing (Figure 5.1), fishing takes place with equal effort throughout the modelled area regardless of the stock-structure within that area. With the highest level of fishing effort ($F = 0.9$) the total population completely collapses, but significant collapse of individual spawning aggregations occurs long before total population collapse, and at much lower fishing pressure. Unsurprisingly, mean population size declines as fishing pressure increases. Catch is maximised at $F = 0.7$ with a loss of 36% of spawning aggregations. Beyond this, the population can be thought of as 'overfished' as further reductions in population size cause catch to decline. Protection of spawning aggregations (Figure 5.2) increases both relative population size and resilience to fishing pressure (the population becomes overfished above $F = 0.8$ rather than $F = 0.7$), despite only covering 7.64% of the total area. Catch is reduced at lower fishing effort, but can be enhanced at higher fishing effort because the added protection of the MPA ensures a large amount of spillover into the fishery. Catch is maximised at $F = 0.8$ and is higher than the maximum catch achieved without an MPA. Despite this higher fishing pressure and higher catch, a much lower percentage of spawning aggregations are lost; only 20% collapse with protected spawning aggregations in comparison with 85% under uniform fishing with $F = 0.8$.

5.5.2 PROTECTION OF FEEDING AGGREGATIONS

Protecting feeding aggregations results in fishing pressure on only a small proportion of the modelled area. Despite this, the effect on spawning aggregations is quite dramatic at high fishing pressure (Figure 5.3), with fragmentation and loss occurring over time as the spawning location of individuals responds to fishing effort. Here, individuals are at an advantage if they spawn outside the fished area because they are less likely to be caught when they arrive at their spawning location. Positive density dependence in the model during spawning ensures, however, that fish cannot immediately move outside a spawning aggregation to spawn successfully. This, in combination with the strong homing behaviour, means that the response by the spawning aggregation will occur relatively slowly, i.e. it is a number of years before the aggregation is wholly outside the fished area (Figure 5.4). If the spawning locations of individuals from different 'sides' of the spawning aggregation move in different directions then fragmentation may occur. Because the movement of aggregations following fishing is slow, higher fishing effort may lead to aggregation collapse as individuals are unable to avoid fishing mortality. Further collapse of aggregations may also occur via competition between newly fragmented or relocated aggregations, i.e. if aggregations are forced closer together competition between aggregations may increase leading to collapse (see Chapter 4). Comparison of relative amounts of catch and population size with uniform fishing and protected spawning grounds is largely irrelevant due to the small area which is actually fished, but, as before, population size decreases and catch increases with fishing effort (Figure 5.3), with catch maximised at $F = 0.9$ in this case. However, at $F = 0.9$, although mean population size is slightly higher than with uniform fishing when $F = 0.2$, 27% of spawning aggregations are lost (in comparison with 2% with uniform fishing and $F = 0.2$). It appears then, that fishing on spawning areas is much more disruptive than fishing uniformly even though total population sizes are comparable.

Given that fishing targeted on spawning aggregations causes aggregations to move, fishermen might be expected to update their fishing effort in response to this movement. Interestingly, updating the location of fishing effort every 50 years (Figure 5.3) causes more aggregations to collapse at higher fishing effort, but offers better protection at lower fishing effort. With higher fishing effort the selective pressure to move spawning location is high, and therefore spawning aggregations move before fishing effort is redistributed. Therefore, when effort is redistributed infrequently, more populations collapse via competition with neighbouring aggregations. At lower fishing effort, or when effort is redistributed more frequently, aggregations are not given enough time to move away from fishing effort before effort redistribution. Spawning aggregations are therefore less likely to be forced closer to each other and therefore the rate of collapse is lower (Figure 5.3). This is the case even though updating the location of fishing more frequently increases total catch and decreases population size as individuals are exposed to fishing pressure for a longer period. These results are not obvious prior to running the simulations and are possible because of the explicit spatial and temporal design of the IBM. Similar insight would be difficult or impossible to reproduce using population models.

5.5.3 UNIFORM FISHING WITH 50% MPA

By fishing uniformly with an MPA protecting 50% of the modelled area a portion of both spawning and feeding areas is protected. Again, mean population size and aggregation persistence decrease with fishing effort, although they are always higher relative to uniform fishing without an MPA, and the total population does not collapse even at $F = 0.9$. However, at this fishing pressure, the spawning aggregations are completely contained within the MPA (i.e. all aggregations in fished areas collapse and catch is only maintained via spillover from the MPA). Catch is maximised at $F = 0.7$ at half of the catch without an MPA which is unsurprising considering that half of the area is lost to fishing. ‘Overfishing’ again causes a decrease in catch with $F = 0.8$ and $F = 0.9$, but to a much lesser extent to that which occurs without an MPA.

By updating the location of the MPA, previously protected spawning aggregations at higher population size can be fished, and previously fished aggregations can be protected and allowed to recover. Updating the location of the MPA every 50, 10 and 2 years always leads to an increase in relative catch when compared to the static MPA (Figure 5.5). When updating every 2 years, maximum catch is higher that the catch obtained with a static MPA with $F = 0.7$ and roughly equivalent to the catch obtained with uniform fishing with $F = 0.7$. The advantage of a static reserve, however, is that some spawning aggregations will always be protected from fishing pressure. When the MPA is updated every 50 years, more spawning aggregations are lost compared with the static MPA at all fishing pressures, although updates every 10 or 2 years fair somewhat better and can outperform a static MPA at lower fishing pressures. This enhanced protection at lower fishing pressures when updating every 10 and 2 years occurs because aggregations are not fished for long enough to collapse, and therefore recover when the MPA is relocated. At higher fishing pressure, however, the populations do have time to collapse and because relocation of the MPA allows the exploitation of aggregations in both halves of the area the resulting number of surviving aggregations is lower. It is interesting to note that although the mean population size decreases when the MPA location is updated, there is not a huge difference between population sizes with different frequencies of update. This is in contrast to the large difference in spawning aggregation survival.

5.5.4 EVOLUTION OF DISPERSAL

Fisheries-induced evolution in size or age at maturation has the potential to reduce productivity and sustainability of fish stocks (Law and Grey 1989, Law 2000, Heino and Godø 2002, Olsen *et al.* 2004), and MPAs are predicted to protect against such evolution if located on feeding grounds or exacerbate it if located on spawning grounds (Baskett *et al*. 2005, Dunlop *et al*. 2009, Miethe *et al*. 2010a). Recommendations for preventing evolution in size at maturation may therefore be incompatible with the protection of spawning aggregations which maximised catch in this model. The impact of fishing on the evolution of dispersal distance is less well explored. However, several studies predict that MPAs may select for lower movement by increasing the fitness of less mobile individuals which remain within the MPA (Travis and Dytham 1998, Baskett *et al*. 2007, Miethe *et al*. 2009, Miethe *et al*. 2010b). In the model presented here, the evolutionary effects of fishing on dispersal are not straightforward. In the long-term (Figure 5.6), the norm is for evolution to a greater dispersal distance (mean individual step-length, *d*) with increased fishing pressure, even when MPAs protect spawning aggregations. This can be explained by considering what happens to the environment experienced by surviving individuals following fishing effort. If fishing effort is strong then the population size and the number of surviving spawning aggregations is reduced. This reduces competition between individuals from different spawning aggregations when they mix during feeding time. Given that there remains a strong selective pressure to disperse away from crowded spawning aggregations following spawning, this usually results in a long-term evolutionary increase in dispersal distance. The exception to this occurs when $F = 0.9$ with uniform fishing and a 50% MPA. Here, fishing pressure is obviously so strong that it is an advantage to reduce dispersal to increase the probability of remaining within the MPA, thereby reducing exposure to fishing. With lower fishing effort the selective pressure is not strong enough to reduce dispersal in the same way and an advantage remains in dispersing to areas outside the MPA which are less densely populated.

In the short-term, however, a contrasting picture emerges (Figure 5.7). Within such a short timescale spawning aggregations are generally unlikely to have collapsed and therefore selection for increased dispersal is not as strong. For protection of spawning aggregations and uniform fishing with a 50% MPA, selection towards lower dispersal distance is now seen, as predicted by previous studies. There is also an apparent slight increase in dispersal distance when protecting feeding grounds. Although an increase in dispersal to avoid fishing following spawning might be expected when feeding grounds are protected, the increase observed here is too small to be conclusive. The levels of evolution in either direction may be more pronounced with different life-history parameterisations e.g. a reduction in competitive strength, or costs to movement, but a detailed evaluation of evolutionary change with alternative life-histories is beyond the scope of this study.

5.5.5 FURTHER CONSIDERATIONS

It has previously been assumed from traditional spillover studies that MPAs are likely to be inadequate tools in the protection of mobile fish species (Kramer and Chapman 1999, Gell and Roberts 2003). However, such studies only consider non-directional movement across MPA boundaries. Adult movement is very important for many marine species and therefore needs to be incorporated more realistically into MPA models (Gerber *et al*. 2003). Some population studies of migratory species indicate that MPAs may play a role in enhancing yields and preventing collapse (e.g. Apostolaki *et al*. 2002, Stefansson and Rosenberg 2005, Stefansson and Rosenberg 2006, Röckmann *et al*. 2007, West *et al*. 2009) but simplify migration and do not account for the response of individual spawning aggregations to fishing pressure. The individual based model predicts that, indeed, yields may be maximised and global populations protected when MPAs are used. In addition, spawning aggregations are more comprehensively protected from collapse when MPAs are introduced, although collapse cannot be completely prevented in any of the MPA scenarios if very high fishing pressure takes place. The results from this model therefore suggest that MPAs are a useful tool in the management of highly mobile migratory species, especially given that the additional benefits that MPAs may bring such as protection of habitat (Kaiser *et al.* 2002) or preventing the disturbance of spawning aggregations by trawling (Morgan *et al.* 1997) have not been considered.

Two options for the implementation of MPAs in addition to uniform fishing are presented in this model; static MPAs or updating MPA location periodically. From a management point of view, a static MPA may be easier to implement and at high fishing pressure will protect the largest number of aggregations. However, there will be a significant cost in terms of total catch. It is also worth considering the resulting distribution of spawning aggregations following exploitation with static versus updated MPAs. With a static MPA and high uniform fishing pressure, most or all remaining spawning aggregations are located within the MPA, whereas with an updated MPA remaining aggregations are more evenly spread. Given that, from a genetic point of view, individuals in aggregations nearer to one another are likely to be more closely related (e.g. genetic isolation by distance in Atlantic cod; Hutchinson *et al*. 2001, Pogson *et al*. 2001) it may be that a greater proportion of the total genetic diversity is maintained with regularly updated MPAs as opposed to a static MPA, even if the overall number of aggregations is reduced. Furthermore, if, for example, a static MPA is located at the northern range of a species distribution and aggregations in the southern range collapse, genetic diversity which may help species adapt to warming waters with climate change may be lost.

Although the movement and behaviour modelled in the IBM is representative of that exhibited by many commercial migratory species, life-history and fishing has deliberately been simplified to explore general trends in the response of populations to extreme fishing scenarios. It is, however, worth considering what the possible effects of including more detail would be on the model results. For example, no age-structure is included in the IBM. Doing so would likely have an effect on results of updating the location of the MPA with uniform fishing. In the model, updating the MPA every 2 years leads to maximum yield, but if individuals do not mature until a later age then 2 years may not be a sufficient period to protect aggregations, yield may be lower and collapse of aggregations higher. There may also be differences in the migration strategy between juvenile and adult fish (Righton *et al*. 2007). Additionally, inclusion of age-structure would allow an evaluation of the effects of fishing on evolution of age at maturation, something which has not been possible in this study. It should also be noted that the mechanism of evolution represented in the model is a simplification of reality. Increasing model complexity to allow mixing of alleles between both male and female parents, and allowing for the possibility for novel alleles to arise via mutation, would allow for a more detailed study of the genetic effects of fishing on exploited populations.

Apart from the distribution of fishing effort, the model is also environmentally homogeneous. In reality, water temperatures (Planque and Fredou 1999, O'Brien *et al*. 2000), currents (Lough *et al*. 1989, Pepin and Helbig 1997, Rindorf and Lewy 2006), and sediment types (Lough *et al*. 1989, Link and Demarest 2003, Wieland *et al*. 2009) may constrain spawning locations or determine recruitment success. An obvious impact of including such habitat constraints is the response of aggregations to fishing pressure on spawning grounds. Because there are no constraints in the model, aggregations are able to fragment and move away from sites of fishing pressure. This may not be possible if there are habitat constraints, and an increase in the rates of aggregation collapse would therefore be expected.

The IBM also ignores the potential impact of individuals straying between spawning grounds. Tagging studies show that approximately 5% of North Sea cod (Heath *et al*. 2008) and 6-28% of Icelandic plaice (Solmundsson *et al*. 2005) stray to areas other than their original spawning location. Juvenile thornback rays also migrate to non-natal grounds in order to spawn (Chevolot *et al*. 2006a). It is unclear whether straying would be able to prevent collapse of exploited aggregations (such analysis is worthy of further exploration) but it is likely to allow some level of genetic mixing between aggregations and may aid recovery of aggregations (and the formation of new aggregations) following fishing pressure.

The fisheries scenarios described here are deliberately simple and represent extremes of exploitation and protection scenarios. For example, in reality, fishing pressure is likely to be heterogeneous in both time and space. However, given that optimal fishing strategies (in terms of maximising catch etc.) are likely to be dependent on the exact life-history of the species concerned, exploration of more complicated fishing strategies is beyond the scope of this study. Despite the omissions described above, the IBM provides interesting insight into the effects of fishing pressure on migratory aggregative spawning fish species.

5.5.6 CONCLUDING REMARKS

This novel IBM, which includes movement and behaviour impossible to replicate using population models, clearly highlights the potential for fishing pressure to have a large impact (and for MPAs to have a protective benefit) on the distribution and persistence of spawning aggregations, in addition to the impacts on population size and catch. It is important to aim to protect as many genetically distinct populations of commercially exploited fish as possible, especially considering that loss of genetic variability may have a negative impact on the response of species to environmental change. Strikingly, strategies which maximise global population sizes in the model do not necessarily correspond to strategies which maximise aggregation persistence (Figure 5.3) and persistence of aggregations may be dramatically different even though global population sizes remain similar (Figure 5.5). Large-scale indications of population health (such as global population size) are therefore clearly not sufficient to protect aggregations. Given that, in the North Sea, ICES stock assessment rectangles are now known to contain genetically isolated sub-populations (Hutchinson *et al.* 2001) this brings into question the suitability of using data collated over such large areas to protect genetic diversity.

6

6

SUMMARY AND POTENTIAL MODEL ENHANCEMENTS FOR REAL-WORLD APPLICATIONS

6.1 SUMMARY OF PREVIOUS CHAPTERS

Using two different modelling approaches, this research has examined the consequences of migratory behaviour and aggregation on the persistence of populations, fisheries yield, and evolution of dispersal distance under exploitation and environmental change. Although largely theoretical in nature and therefore potentially applicable to a wide variety of species, both marine and terrestrial, modelled movement has been characterised principally from migratory commercial fish species such as the Atlantic cod, *Gadus morhua*. The fact that fish migrate has been known for centuries (Kurlansky 1997, Metcalfe 2006), and mark recapture studies have shown that individuals may perform seasonal homing migrations to specific areas (Robichaud and Rose 2004, Wright *et al*. 2006, Righton *et al*. 2007). However it is only recently that new technological advances in the form of data storage tags and genetic analysis have allowed greater insight into the movement and structure of populations (Ruzzante *et al*. 2000, Hutchinson *et al*. 2001, Knutsen *et al*. 2003, Hunter *et al*. 2004a, Righton *et al*. 2007, Righton and Mills 2008). That populations have such fine structure brings into question current large-scale management measures (Hutchinson *et al*. 2001, Andrews *et al*. 2006) and new models are therefore required in order to explore what impact this newly discovered behaviour and structure might have on management and protection, including the use of marine protected areas (MPAs). Historically, most models of MPAs have not accounted for seasonal migration, or do so very simply (Gerber *et al*. 2003). This research has attempted to address new questions about migration and aggregation, including increasing the realism with which movement behaviour is modelled.

Chapter 2 introduced a theoretical fish population, exhibiting different propensities for migration between a protected spawning area and an exploited feeding area. The use of an MPA was analysed to determine whether it is sufficient to protect against the collapse of an overexploited population in the presence of environmental stochasticity. It concluded that MPAs can be useful as a protective tool, enhancing persistence and yields when compared with a non-MPA scenario, but that they may be unable to fully protect populations with a high propensity for migration. In such cases, combining an MPA with a harvest control rule may help reduce the probability of collapse. These conclusions, however, were based on the stochastic results of the model. The deterministic outcome is different, highlighting the impact that stochasticity may have on modelled results (West *et al*. 2009).

The movement modelled in Chapter 2 (and West *et al*. 2009) still represents a large simplification of the behaviour of migratory species. Population models are limited in their ability to reconstruct the complex spatio-temporal behaviour revealed by modern tagging methods. Therefore, Chapter 3 introduces an individual based model (IBM) designed to represent migratory behaviour more accurately within a spatially explicit framework. By designing the model using characterisations of movement exhibited by many commercially important migratory fish species, a system was constructed where the population-level response to simple individual behaviour was the formation of discrete breeding aggregations.

In Chapter 4 the model framework developed in Chapter 3 was used to explore questions about the response of breeding aggregations to environmental change. It was discovered that population-level movement occurs on a much longer timescale than the movement of individuals. The consequence of this is that breeding aggregations may be unable to respond to rapid environmental change in the form of range expansion, although there may be a rapid evolutionary response in dispersal distance at the individual level. Competition between aggregations at different distances from the expanding margin may even lead to the collapse of aggregations. Crucially, the slow response to environmental change occurs within an homogeneous environment, highlighting the potential for behavioural constraints to affect population persistence.

In Chapter 5 the model developed in Chapter 3 was used to explore the response of spawning aggregations to different forms of fisheries exploitation, including the use of MPAs. It was demonstrated that fishing may lead to the collapse and fragmentation of aggregations, with potential consequences for the protection of genetic diversity. MPAs can be used to prevent such collapse and may enhance yields. Fishing pressure may also induce evolutionary changes in dispersal distance. It was also determined that population-scale measures of population health such as global population size may not expose the collapse of individual spawning aggregations.

The content of these chapters addresses previously under-investigated questions in animal movement behaviour and exploitation. It can be concluded that an understanding of the behaviour of individuals is of critical importance when considering the effects of exploitation or environmental change on population persistence, and the way in which such populations should be managed. This has been demonstrated with relatively simple caricatures of behaviour and life-history (albeit with significant advances in the realism of modelled migration in comparison with previous models). However, in order to tailor recommendations to specific real-world scenarios, such as the plight of Atlantic cod or European plaice, *Pleuronectes platessa*, it is likely that the parameterisation and design of these models needs to be enhanced.

6.2 POTENTIAL MODEL DEVELOPMENTS FOR REAL-WORLD SCENARIOS

6.2.1 STRAYING

Straying occurs when individuals do not return (either as adults or juveniles) to their natal spawning areas to spawn. Tagging studies have shown that around 5% of North Sea cod (Heath *et al*. 2008) and 6-28% of Icelandic plaice (Solmundsson *et al*. 2005) may stray to areas other than their original spawning grounds, and juvenile thornback rays, *Raja clavata*, also migrate to non-natal grounds in order to spawn (Chevolot *et al*. 2006a). It has been proposed that the slow recovery of Newfoundland cod following their collapse in 1992 (Hutchings and Myers 1994) may be due to the strong homing behaviour exhibited by individuals and only a low level of straying (Robichaud and Rose 2001). A decline in genetic diversity from overexploitation in the Flamborough Head cod stock was followed by increases in diversity attributed to increased gene flow from immigrant individuals from neighbouring stocks (Hutchinson *et al*. 2003). One possible mechanism for straying is that of learning the behaviour of other individuals. For example, it has been shown that immature cod follow older 'scouts' to spawning locations (Rose 1993). Similar phenomena are shown in Atlantic herring, *Clupea harengus*, (McQuinn 1997) and other fish species (Brown and Laland 2003). Other potential mechanisms could include density-dependent effects or just randomly straying by 'getting lost'. By facilitating genetic mixing and the potential colonisation of new spawning areas, straying behaviour may be important when considering a stock's resilience to, and recovery from, exploitation, or the impacts of environmental change on stock persistence and distribution. Previous models which have considered straying have imposed straying rules onto the population by assigning individuals as strayers (Andrews *et al*. 2006, Heath *et al*. 2008). However, understanding the biological basis for straying may be crucial when designing fisheries management and conservation plans. It is possible that exploitation may change the benefit of straying behaviour, leading to evolutionary changes with a resultant impact on resilience (similar to fisheries-induced evolutionary impacts on size- and age-at-maturation (Law and Grey 1989, Law 2000, Heino and Godø 2002, Olsen *et al*. 2004)). Modifications to the IBM could allow further analysis of different straying mechanisms as adaptive traits rather than imposed behaviours. An initial exploration into the ability of the IBM to model straying is presented in Section 7.6.

6.2.2 AGE-STRUCTURE

The addition of age-structure into the model could be an interesting addition for a number of reasons. Firstly, in the context of straying, incorporating age-structure would allow an exploration of age-dependent straying (e.g. at a juvenile stage only), and would allow older fish to be defined as 'scouts' which lead younger fish to spawning aggregations (Rose 1993). Even ignoring straying behaviour, including age-structure would enable differentiation between migratory strategies based on age. For example, immature juveniles may be less likely to undergo migrations to spawning grounds than mature adults (Righton *et al*. 2007). Secondly, the introduction of age-structure allows additional model parameterisation of life-history traits such as the age at which individuals are likely to become mature, age-dependent fecundity, and vulnerability to natural mortality. For example, in both Chapter 2 and Chapter 5, individuals need only to survive fishing for one year before reproducing and reproductive success is not age-dependent. Reproducing later in life in an age-structured system may affect the protective benefit of MPAs, especially if they are not static (Beverton and Holt 1957, Hastings and Botsford 1999, Hart 2006, and see Chapter 5). Statistics such as weight-at-age and fishing pressure-at-age may also be important when undergoing analysis of real-world fisheries yields. Different fish species may have very different life history characteristics which can only be modelled with consideration of age-related parameters. For example, in fish such as cod in the North-east Atlantic, the majority of individuals are mature by around the age of four (ICES 2009) and release millions of eggs. In comparison, thornback rays do not reach usually reach maturity until the age of six (Gallagher *et al*. 2005) and may only release tens or hundreds of eggs (Ellis and Shackley 1995). Such differences in life-history mean that different species may react differently to fishing or environmental change. Finally, in the models presented in this thesis, where evolutionary analysis has been limited to changes in dispersal distance, an introduction of age-structure would allow analysis of evolution of age at maturation. Fisheries-induced evolution of age at maturation may reduce the sustainability and productivity of fish stocks (Law and Grey 1989, Law 2000, Heino and Godø 2002, Olsen *et al*. 2004), and MPAs may be used as a tool to prevent this (Baskett *et al*. 2005, Miethe *et al*. 2010a), but relatively few studies have looked at the benefits of MPAs in the context of migratory species (Dunlop *et al*. 2009, Miethe *et al*. 2009, Miethe *et al*. 2010b).

6.2.3 ENVIRONMENTAL HETEROGENEITY

Environmental homogeneity has been maintained throughout the IBMs in order to investigate the effects of animal behaviour on the model outcomes without possible interference from environmental factors. Real-world processes may be affected by a variety of different environmental parameters. Environmental factors such as temperature (Planque and Fredou 1999, O'Brien *et al*. 2000), sediment type (Lough *et al*. 1989, Link and Demarest 2003, Wieland *et al*. 2009), and currents (De Veen 1978, Lough *et al.* 1989, Pepin and Helbig 1997, Rindorf and Lewy 2006) may influence recruitment success, the distribution of recruits, and migration pathways. Growth, survival and distribution in larvae and juveniles may be affected by habitat factors including temperature and food availability (Houde 1989, Blaxter 1992, James *et al*. 2003, Blanchard *et al*. 2005). Temperature may also play a role in the distribution of adults as it influences growth rate (de Cárdenas 1996, Clark *et al*. 2003), metabolic rate (Claireaux *et al*. 2000), and maturation (Yoneda and Wright 2005a), although evidence suggests that adults may tolerate suboptimal temperatures (Neat and Righton 2007). Adult growth is also determined by food availability (de Cárdenas 1996, Clark *et al*. 2003, Yoneda and Wright 2005a). Bigger females produce more eggs of larger size (Pitcher and Hart 1982, Kjesbu 1996), and in order to reach spawning condition, cod rely on reserves of energy acquired during the non-spawning period (Fordham and Trippel 1999). The availability of food may therefore play a large role in individual reproductive success. The population model of Chapter 2 incorporated one form of environmental heterogeneity in a simplified manner in the form of stochastic recruitment, and showed that variability may have a large impact on conclusions drawn from the modelling process. The IBM models a homogeneous environment and, whilst there is no explicit environmental influence on recruitment, some variability does occur due to annual differences in the location of individuals during spawning time which impacts on spawning success. Incorporation of more detailed environmental heterogeneity, and relating this heterogeneity to success in recruitment, mortality and fecundity in order to replicate observed levels of variability, is needed if the model is to be extended to provide advice for the fisheries management of specific species and environmental change scenarios.

6.2.4 INCLUDING MALES

Another extension to the IBM could be the inclusion of males in addition to females. In addition to allowing the inheritance of genes to be modelled more realistically, males may have different life-history characteristics to females and may have different habitat requirements. For example, in female cod, temperature may be important on the maturation of gonads, with low temperature leading to postponed spawning (Yoneda and Wright 2005a). In males, maturation of the gonads does not appear to be dependent on temperature (Yoneda and Wright 2005b). Female fecundity prior to their first spawning season may also not be dependent on the amount of food available, with surplus energy instead invested in somatic growth. This will affect body size and the probability of survival, and will therefore influence fecundity in the following season (Yoneda and Wright 2005a). Males, in contrast, appear to maximise current reproductive potential (Yoneda and Wright 2005b). These sex-related differences may reflect the influence of body size on reproductive potential because, whereas fecundity in females is related to size (Pitcher and Hart 1982, Kjesbu 1996), spawning success is not necessarily related to size in experimental studies on males (Rakitin *et al*. 2001). Males and females may also differ in the timing of arrival and departure from spawning grounds, and in their distribution at spawning time (Morgan and Trippel 1996, Robichaud and Rose 2003). Such differences between males and females mean that they may react differently to exploitation and environmental change.

6.3 CONCLUDING REMARKS

In this research fish migration and aggregation, previously under-investigated behaviours, have been explored in the context of fisheries management and environmental change. Although both the population and individual based models are simplifications of real-world systems they provide important insight into the likely impacts of movement behaviour on the response of populations to changes in their environment and exploitation, including the likely success of marine protected areas. General conclusions are that:

- Movement at a population-level is typically much slower than movement at the individual-level for individuals undergoing migration and aggregation. This is due to inertia caused by a combination of homing behaviour and density dependence which restricts how quickly populations can move. As a result, breeding aggregations may be vulnerable to collapse via fishing or environmental change;
- Marine protected areas can be a useful tool in the management of migratory species by preventing population and aggregation collapse. They may also enhance fisheries yields. Despite high rates of movement, seasonally migrating fish may spend periods in spatially restricted areas, i.e. aggregations, which can be effectively protected. MPAs are, however, unlikely to provide complete protection unless combined with other forms of management as seasonal migration will also cause individuals to move into fished areas;
- Measures of population health on a large scale may be insufficient to indicate problems at a smaller scale such as the collapse of breeding aggregations. Current management areas, such as those used by ICES, may therefore need revising in order to account for newly-discovered stock structure. Alternatively management measures

could be designed that are more regionally focused so that migrations of fish can more easily be taken into account.

- Evolution in individual dispersal distance is a likely outcome following environmental change and exploitation. The rate and direction of evolution may depend on the rate of environmental change and the type and strength of exploitation. Such evolutionary change may impact stock structure and aggregation persistence.
- Including sources of stochasticity in models, for example uncertainties inherent in fish recruitment, is important when considering the efficacy of fisheries management measures. Deterministic fisheries models which do not account for environmental variability can result in misleading and over-optimistic results.
- In order to extend these conclusions to, and provide management advice for, specific real-world systems, several modifications to the individual based model could be made. These include the incorporation of straying, age-structure, male individuals and environmental heterogeneity.

7

APPENDICES

7.1 A DESCRIPTION OF THE DETERMINISTIC MODEL EQUILIBRIA OF CHAPTER 2

If a deterministic model is considered in the absence of migration or an MPA (i.e. there is no division of area into MPA and fishery), then the results will be identical to those of Kot (2001). By adding an MPA, the results of the deterministic model will be identical to those of Pitchford *et al*. (2007). In both cases there is an unique stable equilibrium at the maximum sustainable yield (MSY).

In the model of an MPA system (Equations 2.7 to 2.10) seasonal migration was added, which results in three possible stable equilibrium scenarios that apply in different regions of phase space and have different nullclines. These scenarios differ in the amount of catch taken in each half time-step, i.e. whether the full quota, $2c$, can be taken. The solutions to the nullclines are shown below.

For Scenario 1 where the full quota ($2c$) is taken in each half time-step, the model equation for the X population for a complete time-step is

$$\begin{aligned} N_{X,t+1} = {} & -(-KN_{X,t} + 2K\mu N_{X,t} - K\gamma N_{Y,t} + 2K\mu\gamma N_{Y,t} - K\mu^2 N_{X,t} - K\mu^2\gamma N_{Y,t} \\ & + K\gamma N_{X,t} - 2K\gamma\mu N_{X,t} + K\gamma^2 N_{Y,t} - 2K\mu\gamma^2 N_{Y,t} + K\gamma\mu^2 N_{X,t} \\ & + K\mu^2\gamma^2 N_{Y,t} - rKN_{X,t} + rN_{X,t}^2 + 2rN_{X,t}\gamma N_{Y,t} - rK\gamma N_{Y,t} \\ & + r\gamma^2 N_{Y,t}^2)/K. \end{aligned} \tag{7.1}$$

Equation 7.1 is formed by starting with Equation 2.9, and replacing $N_{X,t+½}$ terms with Equation 2.7 and the recruitment term with Equation 2.6. The model equation for the Y population for a complete time-step is

$$\begin{aligned} N_{Y,t+1} = {} & N_{Y,t} - 2\mu N_{Y,t} - \gamma N_{Y,t} + 2\mu\gamma N_{Y,t} + \mu^2 N_{Y,t} - \mu^2\gamma N_{Y,t} - 4c + 2c\mu + N_{X,t}\gamma \\ & - 2\gamma\mu N_{X,t} + \gamma^2 N_{Y,t} - 2\mu\gamma^2 N_{Y,t} + \gamma\mu^2 N_{X,t} + \mu^2\gamma^2 N_{Y,t}. \end{aligned} \tag{7.2}$$

Equation 7.2 is formed by starting with Equation 2.10, and replacing $N_{X,t+½}$ terms with Equation 2.7, $N_{Y,t+½}$ terms with Equation 2.8, and D_Y terms with $2c$.

Setting $N_{X,t+1}$ equal to $N_{X,t}$ leads to a quadratic equation in $N_{X,t}$:

$$\begin{aligned} & -rN_{X,t}^2 + (-K\gamma - 2K\mu - K\gamma\mu^2 + K\mu^2 - 2r\gamma N_{Y,t} + 2K\gamma\mu + rK)N_{X,t} \\ & \quad - r\gamma^2 N_{Y,t}^2 + (K\gamma\mu^2 + K\gamma - 2K\mu\gamma - K\gamma^2 + 2K\mu\gamma^2 - K\mu^2\gamma^2 + rK\gamma)N_{Y,t} \\ & \quad = 0. \end{aligned} \tag{7.3}$$

The X nullcline is therefore the solution of the quadratic formula

$$X = (-b - \sqrt{b^2 - 4ad})/2a\ , \tag{7.4}$$

where,

$$a = -r \, ,$$

$$b = -K\gamma - 2K\mu - K\gamma\mu^2 + K\mu^2 - 2r\gamma N_{Y,t} + 2K\gamma\mu + rK \, ,$$

and

$$d = -r\gamma^2 N_{Y,t}^2 + (K\gamma\mu^2 + K\gamma - 2K\mu\gamma - K\gamma^2 + 2K\mu\gamma^2 - K\mu^2\gamma^2 + rK\gamma)N_{Y,t} \, .$$

Setting $N_{Y,t+1}$ equal to $N_{Y,t}$ and solving the equation, the Y nullcline is obtained:

$$Y = -(-2\gamma\mu N_{X,t} - 4c + 2c\mu + N_{X,t}\gamma + \gamma\mu^2 N_{X,t})/(-2\mu - \gamma + 2\gamma\mu - \gamma\mu^2 + \gamma^2 - 2\mu\gamma^2 + \mu^2 + \mu^2\gamma^2). \tag{7.5}$$

Repeating this analysis for Scenarios 2 and 3 reveals that the X nullcline is unchanged, but the Y nullclines are given by

$$N_{Y,t+1} = \gamma N_{X,t} - 2\gamma\mu N_{Y,t} + \gamma^2 N_{Y,t} - 2\mu\gamma^2 N_{Y,t} + \gamma\mu^2 N_{X,t} + \mu^2\gamma^2 N_{Y,t} - 2c \Rightarrow$$

$$Y = -(N_{X,t}\gamma - 2\gamma\mu N_{X,t} - 2c + \gamma\mu^2 N_{X,t})/(-2\mu\gamma^2 + \mu^2\gamma^2 + \gamma^2 - 1) \, , \tag{7.6}$$

for Scenario 2, and

$$N_{Y,t+1} = 0 \Rightarrow$$

$$Y = 0 \, . \tag{7.7}$$

for Scenario 3. These nullclines correspond to those plotted in Figures 2.3 and 2.4.

To determine the dividing line, $S_{1,2}$, between the regions of phase space in which Scenario 1 and 2 apply, $N_{Y,t+1}$ for Scenario 2 is subtracted from $N_{Y,t+1}$ for Scenario 1, and solve to obtain

$$S_{1,2} = 2c/(-\mu + \gamma\mu + 1 - \gamma) \, . \tag{7.8}$$

For the dividing line, $S_{2,3}$, between the regions of phase space in which Scenario 2 and 3 apply, $N_{Y,t+1}$ for Scenario 3 is subtracted from $N_{Y,t+1}$ for Scenario 2, and solve to obtain

$$S_{2,3} = -(\gamma N_{X,t} - 2\gamma\mu N_{X,t} + \gamma\mu^2 N_{X,t} - 2c)/\gamma^2(1 - 2\mu + \mu^2) \, . \tag{7.9}$$

These dividing lines are shown in grey in Figures 2.3 and 2.4.

Although analytically intractable, the stability of the equilibrium points was confirmed by numerical simulation, and validated by calculation of the eigenvalues of the Jacobian matrix at each equilibrium point. For example, when γ = 0.8, there are two stable equilibria located in the regions of phase space corresponding to Scenarios 2 and 3. For the upper equilibrium point, a Jacobian matrix is constructed of the form

$$J = \begin{pmatrix} \frac{\partial f}{\partial X} & \frac{\partial f}{\partial Y} \\ \frac{\partial g}{\partial X} & \frac{\partial g}{\partial Y} \end{pmatrix},$$

where $N_{X,t+1} = f(N_{X,t}, N_{Y,t})$ and $N_{Y,t+1} = g(N_{X,t}, N_{Y,t})$. Solving

$$\frac{\partial f}{\partial X} = -\frac{-K + 2K\mu - K\mu^2 + K\gamma - 2K\mu\gamma + K\mu^2\gamma - rK + 2rN_{X,t} + 2r\gamma N_{Y,t}}{K} \tag{7.10}$$

$$\frac{\partial f}{\partial Y} = -\frac{-K\gamma + 2K\mu\gamma - K\mu^2\gamma + K\gamma^2 - 2K\mu\gamma^2 + K\mu^2\gamma^2 + 2rN_{X,t}\gamma - rK\gamma + 2r\gamma^2 N_{Y,t}}{K} \tag{7.11}$$

$$\frac{\partial g}{\partial X} = \gamma - 2\gamma\mu + \gamma\mu^2 \tag{7.12}$$

$$\frac{\partial g}{\partial Y} = \gamma^2 - 2\mu\gamma^2 + \mu^2\gamma^2, \tag{7.13}$$

the position of the upper equilibrium point is found numerically at $N_{X,t}$ = 64.85077 and $N_{Y,t}$ = 35.34738. Substituting these values along with the values of the other parameters into the Jacobian matrix obtains

$$J = \begin{pmatrix} 0.23071326 & 0.184570608 \\ 0.648 & 0.5184 \end{pmatrix},$$

which has eigenvalues of 0 and 0.7491132600. These eigenvalues are <1, confirming that the equilibrium point is stable. Analysis of the lower equilibrium point when γ = 0.8 confirms that this is also stable.

It is important to note that, although the deterministic results of the model displayed here and in the model of Pitchford *et al*. (2007) can tell us something about the existence and relative position of equilibrium points, stochastic analysis of these systems is necessary to fully understand the dynamics of the system.

7.2 A COMPARISON OF THE STOCHASTIC RECRUITMENT SIMULATED IN THE MODEL OF CHAPTER 2 WITH FISHERIES DATA

In the default stochastic model recruitment values, R_{st}, are drawn at random from a normal distribution centred on R with a coefficient of variation, CV_R, of 0.6. This realistically simulates the phenomenon in fisheries of highly variable year-on-year recruitment success. Figure 7.1 shows an example of the variability generated from the stochastic recruitment function. Also plotted are lagged recruitment/spawning stock biomass data for cod, *Gadus morhua*, in the North Sea, Eastern Channel and Skagerrak (ICES Subarea IV, VIId and IIIa) and plaice, *Pleuronectes platessa*, in the Eastern Channel (ICES Subarea VIId) (calculated from raw data in ICES 2007c), linearly scaled to reflect the range of model data. The output from the model clearly falls within the variability exhibited in these real-world systems.

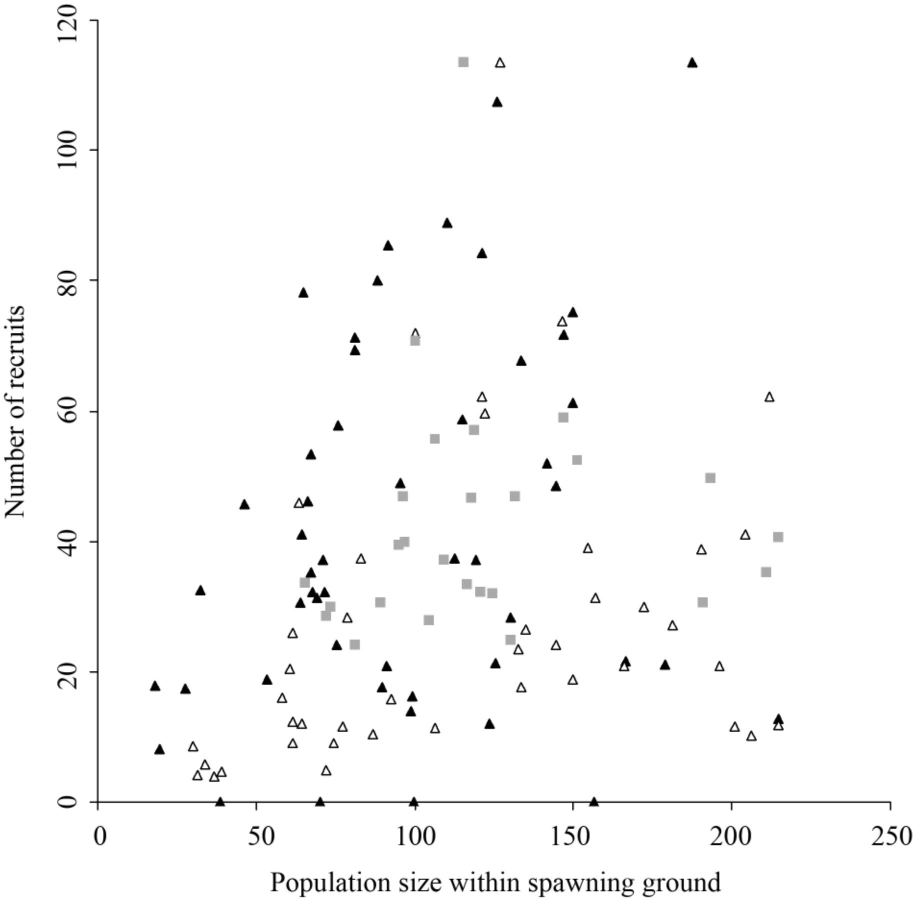

FIGURE 7.1. RECRUITS PLOTTED AGAINST SPAWNERS FOR MODELLED AND REAL DATA. BLACK TRIANGLES SHOW THE NUMBER OF RECRUITS PLOTTED AGAINST THE NUMBER OF INDIVIDUALS SPAWNING FROM THE STOCHASTIC RECRUITMENT FUNCTION USED IN THE MODEL. THE OPEN TRIANGLES AND GREY SQUARES SHOW ONE-YEAR LAGGED AND SCALED RECRUITMENT DATA (YEAR-OLD RECRUITS IN YEAR *n*+1 VS. SPAWNING STOCK BIOMASS IN YEAR *n*) FOR COD IN THE NORTH SEA (YEARS 1963-2004) AND PLAICE IN THE EASTERN CHANNEL (YEARS 1957-2005) RESPECTIVELY (CALCULATED FROM RAW DATA IN ICES 2007C). NOTE THAT IT IS POSSIBLE TO OBTAIN ZERO VALUES IN THE MODEL RECRUITMENT FUNCTION BUT THIS DOES NOT OCCUR IN THE REAL DATA, ALTHOUGH THIS DOES NOT AFFECT THE QUALITATIVE RESULTS OF THE MODEL (SEE SECTION 7.3).

7.3 ALTERNATIVE PARAMETERISATION OF THE MODEL OF CHAPTER 2

This section presents the results of alternative parameterisations of the model. In summary, the alternative assumptions and parameterisations detailed below have the potential to change the quantitative outcome of the model, but the qualitative outcome remains, i.e. as γ is increased the probability of population collapse generally increases.

7.3.1 INTRODUCING DIFFUSIVE MOVEMENT

An alternative method of modelling movement within a fish population is that of diffusive movement between areas. This type of non-directional movement is what is commonly investigated in traditional spillover studies. A modification of the model with the MPA can be used to assess the additional impact of diffusive movement on population persistence. Equations 2.7 to 2.10 become:

$$N_{X,t+½} = (1-\mu)(N_{X,t} + \gamma N_{Y,t}) - \lambda M(N_{X,t}, N_{Y,t}) \tag{7.14}$$

$$N_{Y,t+½} = (1-\mu)(N_{Y,t} - \gamma N_{Y,t}) + \lambda M(N_{X,t}, N_{Y,t}) - D_{Y,t} \tag{7.15}$$

$$N_{X,t+1} = (1-\mu)(N_{X,t+½} - \gamma N_{X,t+½}) - \lambda M(N_{X,t+½}, N_{Y,t+½}) + R(N_{X,t}, N_{Y,t}) \tag{7.16}$$

$$N_{Y,t+1} = (1-\mu)(N_{X,t+½} + \gamma N_{X,t+½}) + \lambda M(N_{X,t+½}, N_{Y,t+½}) - D_{Y,t+½} \tag{7.17}$$

where:

$$M(N_{X,t}, N_{Y,t}) = ((1-\mu)(N_{X,t} + \gamma N_{Y,t})) - ((1-\mu)(N_{Y,t} - \gamma N_{Y,t}) - D_{Y,t}) \tag{7.18}$$

$$\begin{aligned} M(N_{X,t+½}, N_{Y,t+½}) = {} & ((1-\mu)(N_{X,t+½} - \gamma N_{Y,t+½})) \\ & - ((1-\mu)(N_{Y,t+½} + \gamma N_{Y,t+½}) - D_{Y,t+½}) \end{aligned} \tag{7.19}$$

are the differences between the surviving population sizes in the two areas in each half time-step. A proportion λ of this difference moves from the more populated area to the less populated area at the end of each half time-step.

Figure 7.2 shows the effect of introducing diffusive movement into the model. This additional form of movement clearly increases the population's susceptibility to collapse. However, the qualitative results of the model do not change i.e. as γ is increased the probability of collapse generally increases.

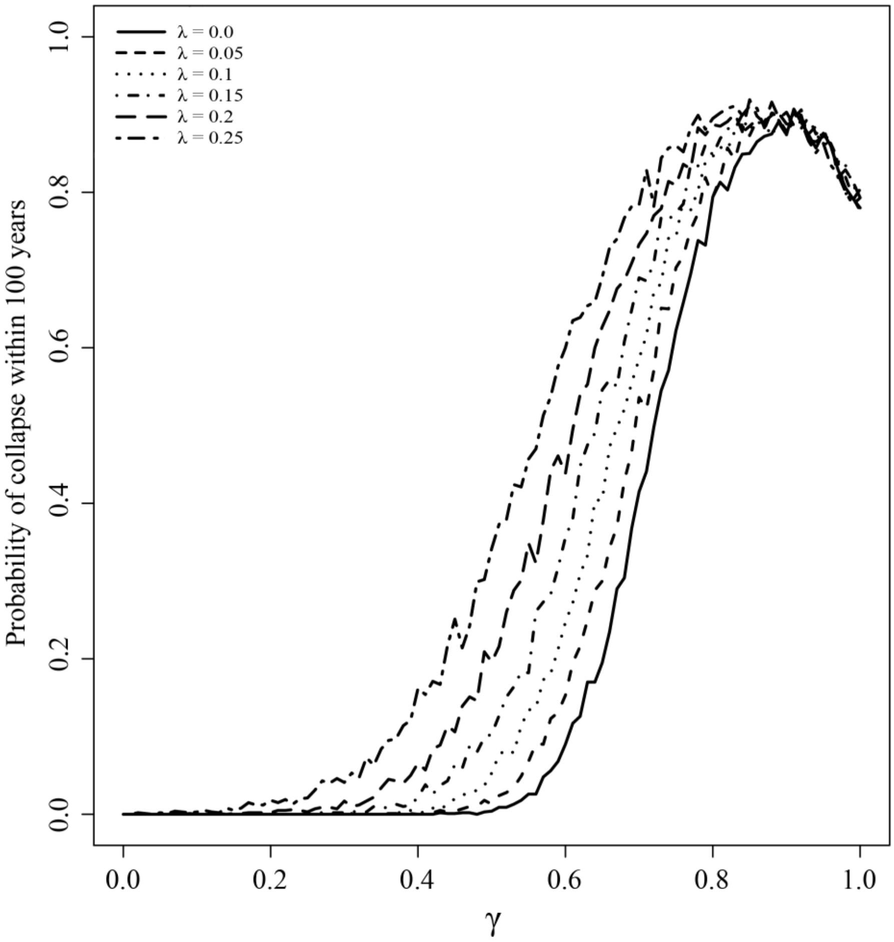

FIGURE 7.2. THE EFFECT OF VARYING λ ON THE PROPORTION OF EXPLOITED POPULATIONS GOING EXTINCT WITHIN 100 YEARS, FROM 1000 SIMULATIONS OF THE MODEL. THE LEGEND IN THE UPPER LEFT CORNER OF THE GRAPH SHOWS THE VALUES OF λ ASSOCIATED WITH EACH LINE ON THE GRAPH. $\lambda = 0$ (I.E. NO DIFFUSION) GIVES THE SAME RESULT AS THE DEFAULT MODEL WITHOUT DIFFUSIVE MOVEMENT.

7.3.2 ALTERNATIVE RECRUITMENT FUNCTIONS

In addition to the logistic recruitment function, other recruitment functions such as the Ricker and Beverton-Holt functions can be used to calculate the number of recruits produced. When using the Ricker function instead of Equation 2.6 the function becomes:

$$R(N_{X,t}, N_{Y,t}) = \max[(N_{X,t} + \gamma N_{Y,t})\exp(a(1 - (N_{X,t} + \gamma N_{Y,t})/B), 0] . \quad (7.20)$$

When using the Beverton-Holt function instead of equation 2.6 the function becomes:

$$R(N_{X,t}, N_{Y,t}) = \max[((N_{X,t} + \gamma N_{Y,t})f)/(1 + (((f - 1)/G)(N_{X,t} + \gamma N_{Y,t}))), 0] .$$

(7.21)

Figure 7.3 shows the difference between the three recruitment functions. Only one parameter set is used for each model and the parameters were chosen so that all models intersected at the peak of the logistic function (see Figure 7.3, inset). For the Ricker model, *a* = 0.3, *B* = 30.207. For the Beverton-Holt model, *f* = 2, *G* = 33.333. Using these parameters it is clear that the logistic model results in the most severe density-dependent overcompensation, the Ricker model has reduced overcompensation and the Beverton-Holt model has no overcompensation. Thus, as expected, the result is obtained that the logistic model leads to the highest probability of collapse, followed by the Ricker and Beverton-Holt models. A full investigation of recruitment parameters for different real-world species is beyond the scope of this paper (a change in the *a*, *B*, *f* and *G* parameters for the models will lead to different extinction probabilities) but the qualitative results are the same regardless of the choice of recruitment function – namely that high γ leads to a higher probability of collapse. Different parameter choices do not change these qualitative results.

7.3.3 STANDARD DEVIATION OF SAMPLES

The stochastic sampling method is that of a constant coefficient of variation (CV_R), i.e. the standard deviation, σ, around *R* decreases as *R* decreases. Alternatives to decreasing σ include using a constant σ, σ_{const}, for all values of *R* and decreasing σ with increasing *R*. To illustrate the example of decreasing σ with increasing *R* the following function (Minto *et al*. 2008) is used to calculate σ:

$$\sigma_R = \surd(\exp(u + vR)) \quad (7.22)$$

where *u* and *v* are parameters. In the examples, *u* = 8 and *v* = -0.02 or -0.04

Figure 7.4 shows the effect of changing the standard deviation, *σ*, used when sampling from the logistic function. The way *σ* changes with population size in the different simulations is also shown (Figure 7.4, inset). Although the quantitative results change depending on the assumptions made, the qualitative results stay the same, i.e. high *γ* leads to a higher probability of extinction.

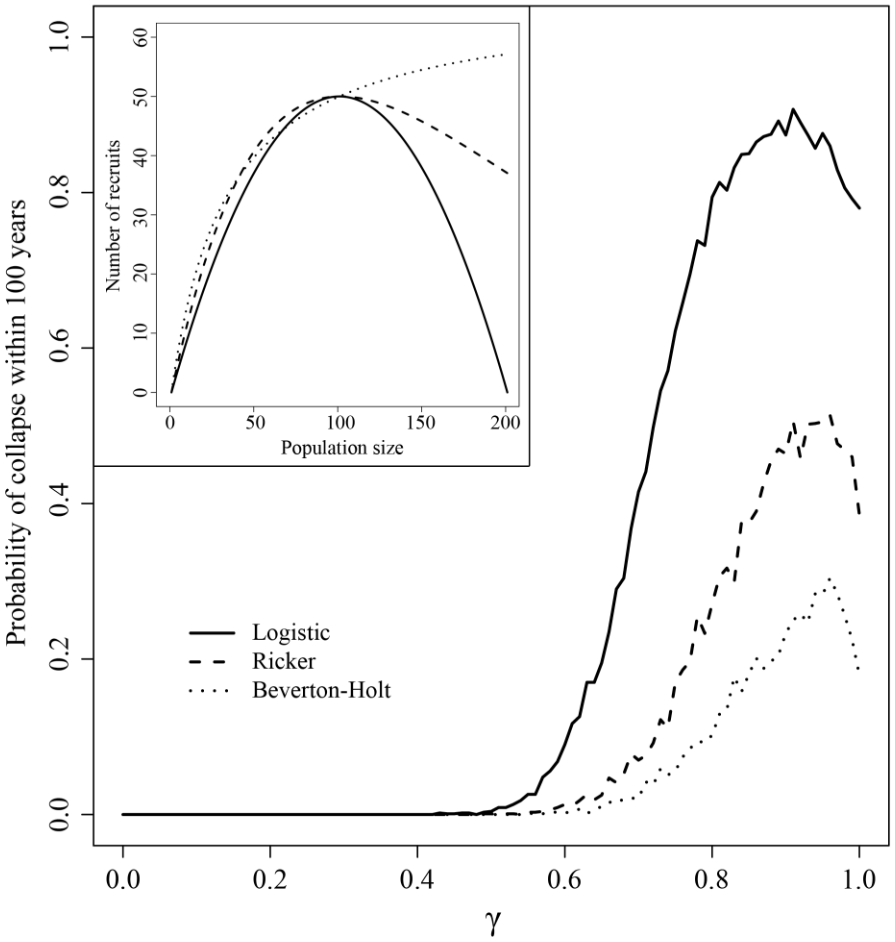

FIGURE 7.3. PROPORTION OF EXPLOITED POPULATIONS GOING EXTINCT WITHIN 100 YEARS USING ALTERNATIVE RECRUITMENT FUNCTIONS, FROM 1000 SIMULATIONS OF THE MODEL. SOLID LINE: LOGISTIC FUNCTION (DEFAULT MODEL); DASHED LINE: RICKER FUNCTION; DOTTED LINE: BEVERTON-HOLT FUNCTION. THE RICKER AND BEVERTON-HOLT FUNCTIONS WERE PARAMETERISED TO INTERSECT THE LOGISTIC FUNCTION AT ITS PEAK (SEE INSET).

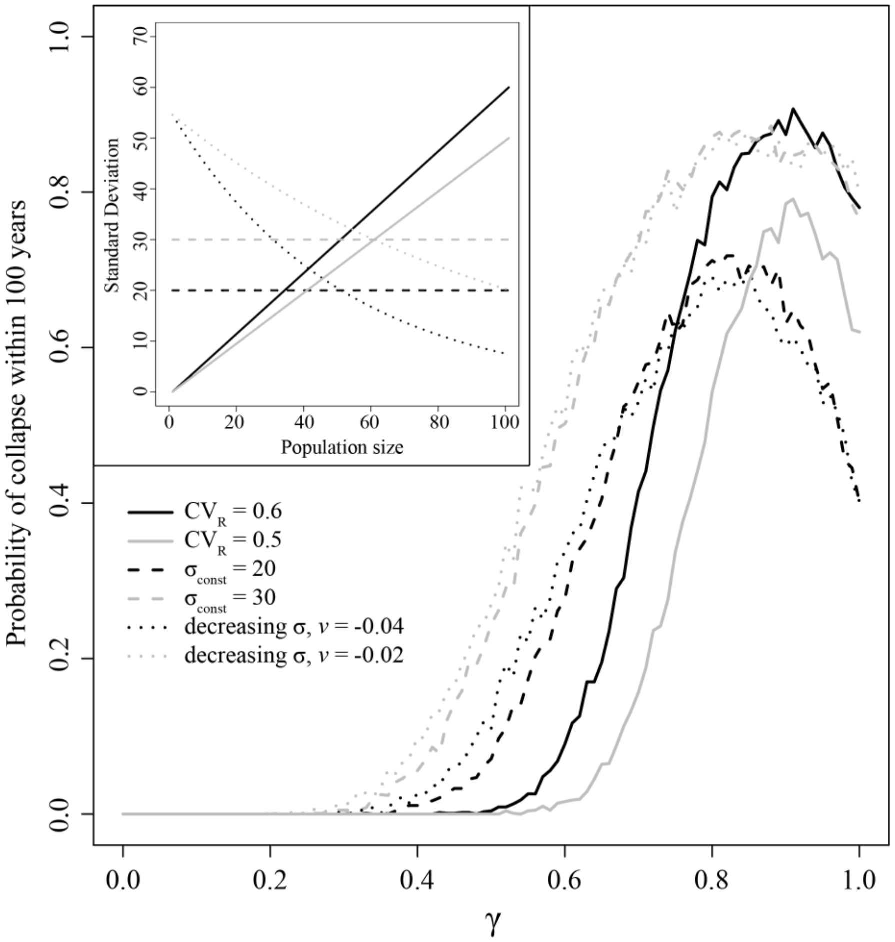

Figure 7.4. Proportion of exploited populations going extinct within 100 years using alternative standard deviations, σ, when sampling, from 1000 simulations of the model. Solid black line: $CV_R = 0.6$ (default model); solid grey line: $CV_R = 0.5$; dashed black line: $\sigma_{\text{const}} = 20$; dashed grey line: $\sigma_{\text{const}} = 30$; dotted black line: decreasing σ, $u = 8$, $v = -0.04$ (σ calculated from Equation 7.22); dotted grey line: decreasing σ, $u = 8$, $v = -0.02$ (σ calculated from Equation 7.22). σ against population size for each of the simulations is also shown (see inset).

7.3.4 Sampling distributions

Zero recruitment values can be obtained when randomly sampling from the normal distribution described in Chapter 2 and may affect the generality of the model conclusions. Zero values are unlikely with a high mean, R, but as the mean of the normal distribution approaches zero they become more likely. To assess the effect of this on the results two alternative distributions are also used, a truncated normal (bounded below at zero) and a Weibull distribution. Unlike the normal distribution described in Chapter 2, zero values of recruitment cannot occur when sampling from these distributions with a positive mean.

Figure 7.5 shows the effect of using these alternative distributions. The distribution parameters were chosen so that the standard deviation of the samples matched that of the normal distribution used in Chapter 2. The use of the truncated normal distribution results in a reduction in the probability of population collapse, whereas the Weibull distribution closely approximates that of the normal distribution. In all cases, however, the qualitative shape of the curve remains the same.

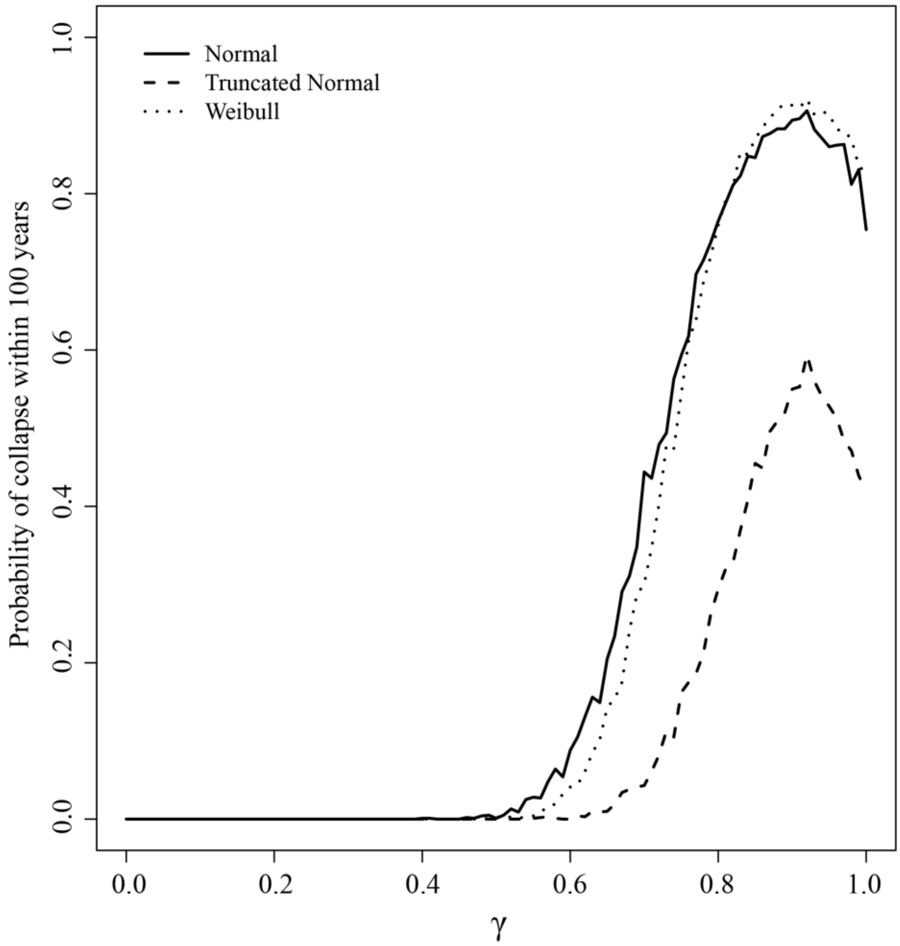

FIGURE 7.5. PROPORTION OF EXPLOITED POPULATIONS GOING EXTINCT WITHIN 100 YEARS WHEN USING ALTERNATIVE SAMPLING DISTRIBUTIONS, FROM 1000 SIMULATIONS OF THE MODEL. SOLID LINE: NORMAL DISTRIBUTION (DEFAULT MODEL); DASHED LINE: TRUNCATED NORMAL DISTRIBUTION; DOTTED LINE: WEIBULL DISTRIBUTION.

7.4 SENSITIVITY ANALYSIS FOR THE INDIVIDUAL BASED MODEL OF CHAPTER 3

The following describes the effect of changing the default parameters of the static model. It should be noted that whilst changing these parameters alters quantitative results such as the resultant number of breeding aggregations or value of *d*, the qualitative behaviour of the model is robust.

7.4.1 INITIAL MEAN STEP-LENGTH, *d*

In the default static model, *d* is equal to 2 for all initial individuals. Increasing initial *d* tends to reduce the number of breeding aggregations resulting from 2000 years of simulation, whilst decreasing *d* tends to increase the number of breeding aggregations. This is due to a change in the area of competition between breeding aggregations, especially early in the simulation when breeding aggregations are becoming established and are more readily outcompeted. Like the default model, the mean value of *d* in the population evolves over time to an equilibrium value. With increased initial *d* this equilibrium value tends to be slightly higher than the default model (because there are fewer breeding aggregations), whereas with decreased initial *d* the equilibrium tends to be slightly lower (because there are more breeding aggregations).

7.4.2 BREEDING RADIUS, *r*

At low *r*, following model initialisation with a random spread of breeding locations, it is much less likely that individuals will be able to breed with neighbours. Therefore, the number of breeding aggregations that result from a model with low *r* is reduced. Individuals within the breeding aggregations are also more tightly packed. There is an increase in the equilibrium value of *d* due to the reduction in the number of breeding aggregations. As *r* is increased, the number of individuals which are able to breed with neighbours after model initialisation increases. This results in a greater number of aggregations at the conclusion of the simulation, and a corresponding reduction in equilibrium *d*. As *r* is increased further breeding aggregations become more diffuse as individuals are able to breed over a wider area and therefore have to be less tightly packed. This reduces equilibrium *d* further as individuals are under less competitive pressure to move away from their breeding location. Reduced *d* allows aggregations to exist at closer distances, and the number of aggregations increases as a result.

However, at very large r individuals are able to breed over such a large area that the breeding aggregation structure begins to break down, i.e. individuals become so diffuse at breeding time that they do not form obvious aggregations.

7.4.3 RECRUITMENT LOCATION STANDARD DEVIATION, σ_r

At low σ_r, new recruits are more concentrated around their natal breeding location. This increases competition between individuals from the same breeding aggregation, which leads to an increase in equilibrium d. Increased d leads to increased competition between breeding aggregations, so the number of breeding aggregations is reduced. However, increasing σ_r to a higher value may also reduce the number of breeding aggregations. At high σ_r, the recruits are spread widely around their natal breeding location and competition between individuals from the same aggregation is therefore low. This leads to a decrease in the value of equilibrium d. However, because new recruits are more widely spread, competition between individuals from neighbouring aggregations increases, which leads to a reduction in the number of breeding aggregations. The expected number of breeding aggregations therefore follows an inverted ‘u’ shape with increasing σ_r.

7.4.4 BREEDING LOCATION STANDARD DEVIATION, σ_b

Reducing σ_b reduces the error associated with imprinting and results in breeding aggregations which are denser and take up less area. This results in an increase in the total number of breeding aggregations and a decrease in equilibrium d. Increasing σ_b results in breeding aggregations which are less dense and take up more area, and this results in a decrease in the total number of breeding aggregations and an increase in equilibrium d.

7.4.5 MEAN STEP-LENGTH STANDARD DEVIATION, σ_m

Changing σ_m has little effect on the number of breeding aggregations. However, reducing σ_m slightly reduces equilibrium d and increasing σ_m slightly increases equilibrium d. This is because the distribution of d within a population has positive skew (very small values of d are selected against more strongly than large values). Larger σ_m increases the standard deviation of inherited d, resulting in the generation of a larger number of extreme d values. This results in more positive skew and a slightly increased equilibrium d.

7.4.6 NAVIGATION ERROR, n

Reducing n (which increases homing accuracy) has little effect when compared with the default value, i.e. default individuals are usually capable of homing accurately to their breeding ground during the course of the breeding migration, and therefore reducing n has little impact on the population structure. Increasing n, however, decreases homing accuracy, i.e. some individuals are unable to return accurately to their breeding location. This increases the spread of breeding aggregations and reduces the number of aggregations. As the number of breeding aggregations decreases, equilibrium d increases. If n is increased further then eventually individuals reach a point where they can no longer navigate successfully back to their breeding location and the population collapses.

7.4.7 DENSITY-INDEPENDENT SURVIVAL PARAMETER, λ

Reducing λ increases density-independent mortality and leads to a smaller population size. This slightly decreases the number of spawning aggregations that successfully form immediately following initialisation, which results in an increase in equilibrium d. Increasing λ reduces density-independent mortality and leads to a larger population size. This slightly increases the number of spawning aggregations that form following initialisation and decreases equilibrium d.

7.4.8 DENSITY-DEPENDENT MORTALITY PARAMETER, μ

Reducing μ reduces competition between individuals and leads to a larger population size, initially leading to more spawning aggregations forming following initialisation. More aggregations and reduced selective pressure to disperse results in reduced equilibrium d. Increasing μ increases competition, leads to a smaller population size, increased equilibrium d and a reduction in the number of aggregations.

7.4.9 MOVEMENT MORTALITY PARAMETER, γ

Reducing γ reduces the cost of movement and leads to an increase in equilibrium d. This reduces the total number of breeding aggregations. Increasing γ increases the cost of movement and leads to a decrease in equilibrium d. The total number of breeding aggregations increases.

7.4.10 RECRUITMENT FUNCTIONS

Decreasing the *a* parameter and increasing the *b* parameter in the Ricker equation have the effect of increasing individual breeding success. This results in aggregations which are more densely populated, increasing competition and therefore increasing equilibrium *d*. The number of aggregations is reduced as a result. Increasing the *a* parameter and decreasing the *b* parameter decrease individual breeding success. This results in aggregations which are less dense with decreased competition and therefore equilibrium *d* decreases. Breeding aggregations are maintained when using Beverton-Holt or logistic functions in place of the Ricker function. The number of aggregations depends on the parameters used in these functions.

7.5 VALUES OF RECRUITMENT AND MEAN STEP-LENGTHS RESULTING FROM THE INDIVIDUAL BASED MODEL OF CHAPTER 3

Individual mean step-length, *d,* is inherited with error in the IBM described in Chapter 3. An example of the distribution of mean step-lengths which results in the 2000th year of simulation of the static model (see Section 3.4.1), and has a final population size of 8817 individuals, is shown in Figure 7.6.

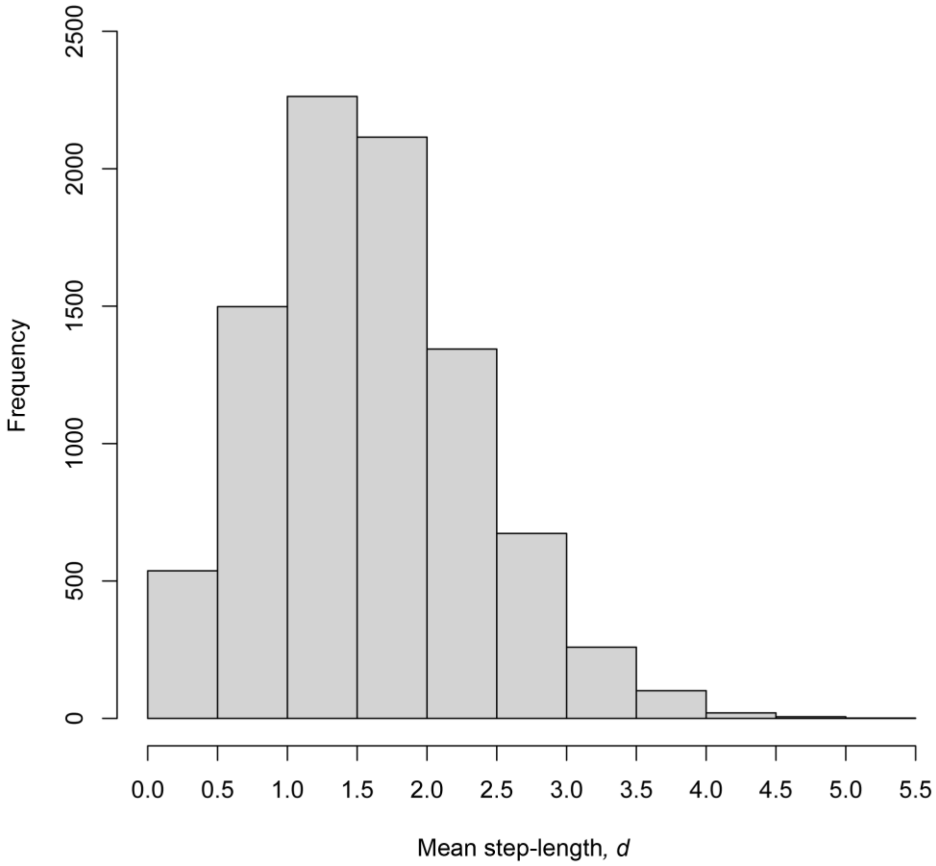

FIGURE 7.6. AN EXAMPLE DISTRIBUTION OF INDIVIDUAL MEAN STEP-LENGTH, *d*, AFTER 2000 YEARS IN THE STATIC MODEL.

A Ricker-type equation is used to calculate the number of recruits produced for each breeding individual (see Section 3.4.3). Using this equation, Figure 7.7 shows the number of recruits produced against neighbouring individuals within radius, *r*.

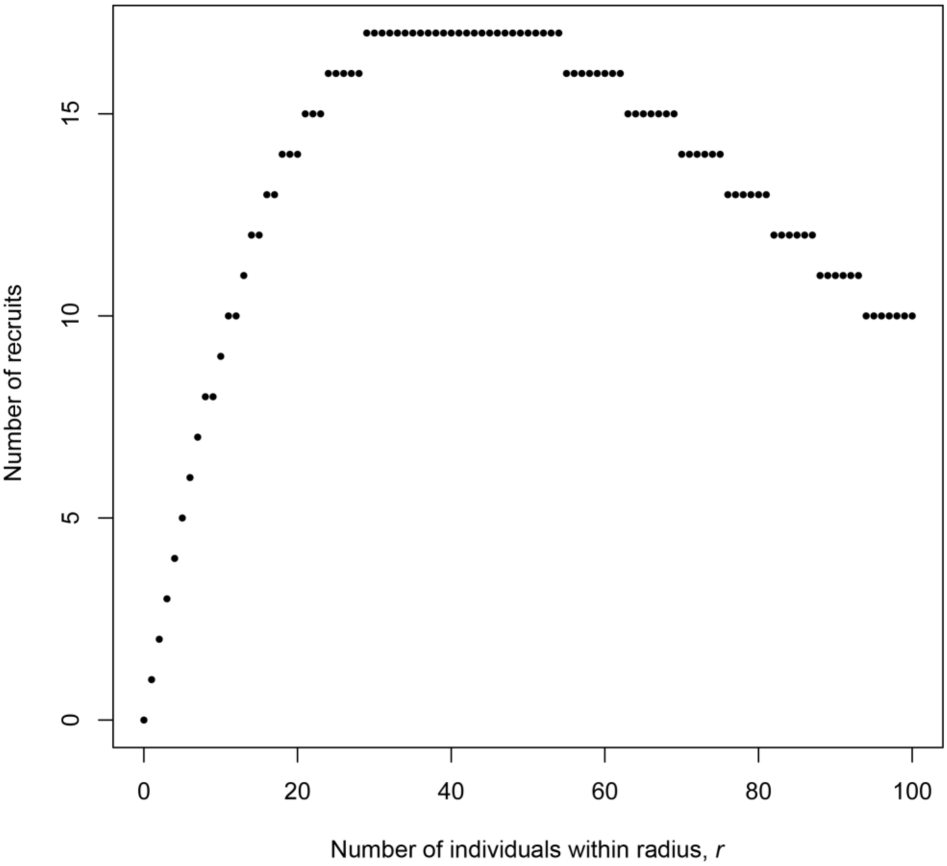

FIGURE 7.7. THE NUMBER OF RECRUITS PRODUCED AGAINST THE NUMBER OF NEIGHBOURING INDIVIDUALS WITHIN RADIUS, *r*, AT SPAWNING TIME.

Figure 7.8 shows an example of the actual distribution of recruits produced per individual that results from this equation in the 2000th year of simulation using the static model. It clearly shows that most individuals are optimally distributed at spawning time, resulting in maximum reproductive potential. The total number of recruits produced by the population is 134,714.

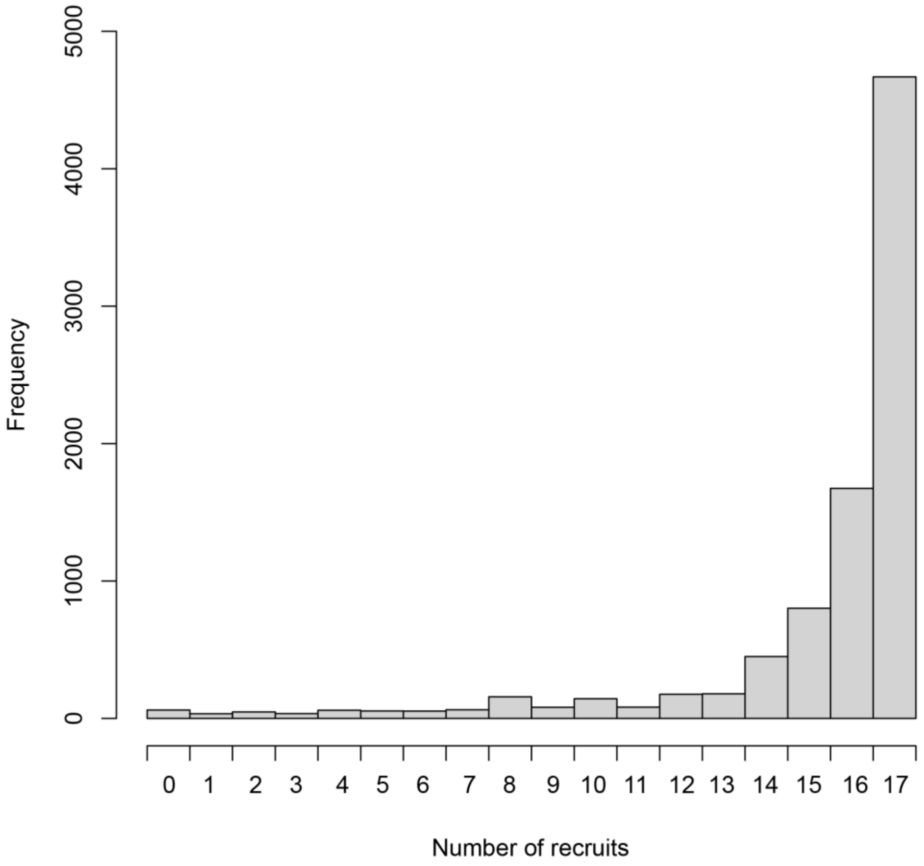

FIGURE 7.8. AN EXAMPLE OF THE DISTRIBUTION OF THE NUMBER OF RECRUITS PRODUCED PER INDIVIDUAL AFTER 2000 YEARS IN THE STATIC MODEL

7.6 MODELLING STRAYING – A PRELIMINARY EXPLORATION

Straying has the potential to occur in a number of different ways. Here, only one straying mechanism is explored, that of ‘learning’ the spawning site of another individual. Immature cod, *Gadus morhua*, have been shown to follow older ‘scouts’ to spawning locations (Rose 1993), in a similar way to that shown in Atlantic herring, *Clupea harengus*, (McQuinn 1997) and other fish species (Brown and Laland 2003). For the purposes of this initial exploration within the IBM, which does not include age-structure, the straying mechanism is simplified by allowing all individuals (i.e. not only juveniles) the potential to learn an alternative spawning location. In order to introduce straying behaviour into the IBM, the model presented in Chapter 3 has been modified to incorporate the following:

Tracking the movement of individuals

After running the model to produce a stable population of spawning aggregations, each individual is assigned a 'gene' (an identification number, acting as a mitochondrial lineage passing through the female line) which identifies it to a particular aggregation. This gene is then inherited by the individual's offspring. This allows genes to be tracked over time to explore the spatial spread and persistence of genes following straying.

Incorporating straying

Each year, immediately prior to the spawning migration (i.e. at t = 265), individuals are assigned as strayers with a pre-defined probability (i.e. there can be different straying rates). If an individual is a strayer then it 'learns' the breeding coordinates of the nearest individual (i.e. it inherits the x_{br} and y_{br} values of its nearest neighbour). This occurs even if the individual has strayed before, or if the learnt coordinates return the individual to the same spawning aggregation. If individuals are not assigned as strayers then they retain their own breeding coordinates.

Simulations using these modifications were run for 200 years with uniform fishing pressure from F = 0.5 to F = 0.8 to explore the spread and persistence of 'genotypes' with different straying rates. Other values of F were not included; F values lower than 0.5 do not cause significant reductions in spawning aggregation persistence, and F = 0.9 causes collapse of aggregations within 10 years (see Chapter 5). Straying rates of 1% to 20% were used to mimic the estimated straying rates of species such as cod and plaice, *Pleuronectes platessa* (Solmundsson *et al*. 2005, Heath *et al*. 2008).

7.6.1 INITIAL RESULTS

Figure 7.9 shows the spread of individuals with the same identification gene following the introduction of two different straying rates. Figure 7.9a shows that, after 10 modelled years when the straying rate is low (1%), individuals are mostly located in their historic spawning aggregation and only a few individuals have strayed (and survived) in neighbouring spawning aggregations. In comparison, in Figure 7.9b where the straying rate is higher (10%), more individuals have strayed and the pattern of individuals is similar to that achieved after 200 years for the lower straying rate (Figure 7.9c), although most are still located in the historical spawning aggregation. After 200 years with the higher rate of straying (Figure 7.9d), individuals are relatively evenly spread across all spawning aggregations and it becomes impossible to determine from which aggregations individuals historically originate.

Figure 7.10 shows that introducing straying always results in a greater persistence of the identification genes when compared to simulations where straying does not occur. With *F* = 0.5 with no straying, a mean of 2.2 genotypes are lost. In the five simulations only a straying rate of 15% completely preserved all genotypes. A straying rate of 20% produced a lower mean value at lower fishing effort although the sample size is not big enough to determine whether this difference is significant, and the results for 15% and 20% are similar overall. With *F* = 0.8 with no straying, only three genotypes remain and there are large differences in the preservation of genotypes with different straying rates, with 20% straying preserving most genotypes. However, even with 20% straying only 11 genotypes are preserved on average from an original value of 20.

Figure 7.11 indicates that, for *F* = 0.8, there may be an effect of straying on the number of spawning aggregations preserved. A straying rate of 15% seems to slightly increase persistence above that expected with the non-straying model, and mean population size, catch and dispersal distances also differ (Table 7.1). Other straying rates do not seem to affect spawning aggregation persistence to the same extent, but may still affect population sizes, catch and dispersal (Table 7.1). Data from other fishing pressures are not shown but show no apparent differentiation from the non-straying data.

FIGURE 7.9. POSITIONS OF INDIVIDUALS OVER TIME WITH THE SAME IDENTIFICATION GENE AND DIFFERENT RATES OF STRAYING: a) STRAYING RATE OF 1% AFTER 10 MODELLED YEARS; b) STRAYING RATE OF 10% AFTER 10 MODELLED YEARS; c) STRAYING RATE OF 1% AFTER 200 MODELLED YEARS; d) STRAYING RATE OF 10% AFTER 200 MODELLED YEARS.

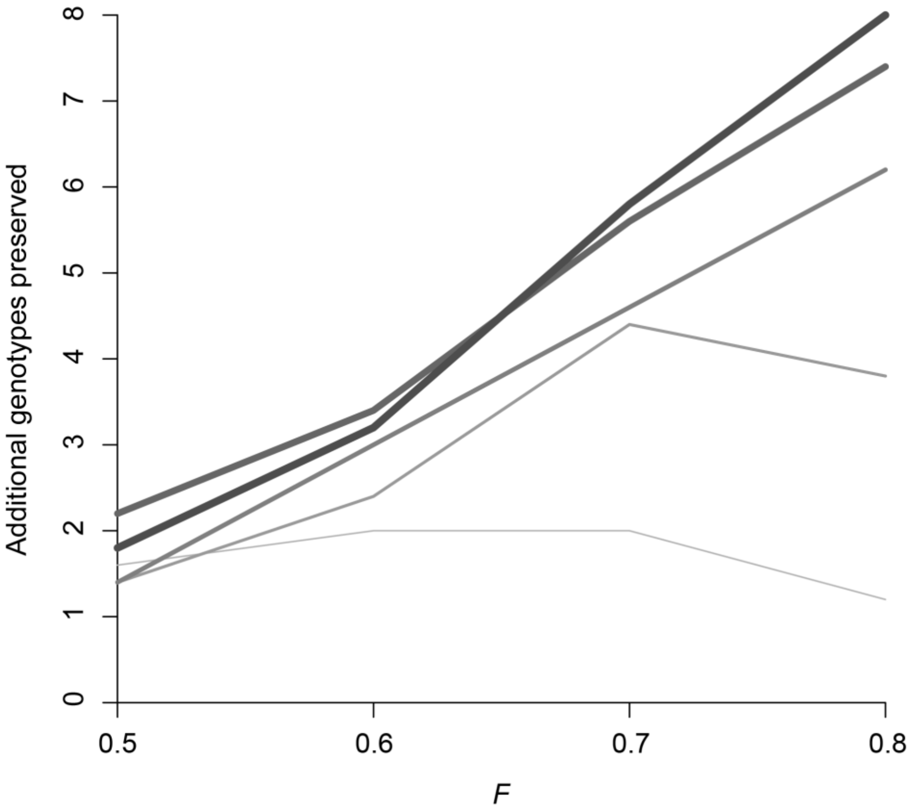

FIGURE 7.10. THE NUMBER OF ADDITIONAL GENOTYPES (MEANS OF FIVE SIMULATIONS ARE SHOWN) WHICH REMAIN, UNDER INCREASING FISHING PRESSURE, WHEN STRAYING OCCURS IN COMPARISON TO THE MODEL WITHOUT STRAYING. LINES OF INCREASING THICKNESS AND DARKNESS CORRESPOND TO STRAYING RATES OF 1%, 5%, 10%, 15% AND 20%. WITH *F* INCREASING FROM 0.5 TO 0.8, THE MEAN NUMBERS OF GENOTYPES PRESERVED IN THE NON-STRAYING SIMULATIONS ARE 17.8, 16.4, 12.8, AND 3.0 RESPECTIVELY.

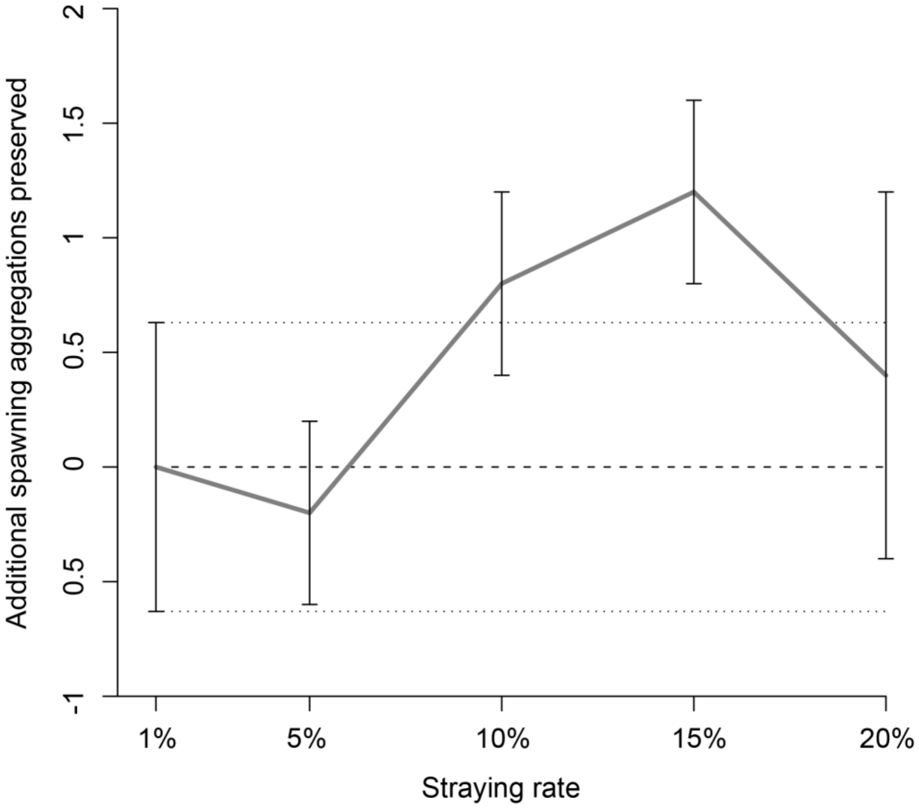

Figure 7.11. The number of additional spawning aggregations (means of five simulations are shown with standard deviations) which remain with *F* = 0.8 when straying occurs in comparison to the model without straying. The dashed line shows the mean of the non-straying simulations with dotted lines showing the standard deviation.

Straying Rate	**None**	**1%**	**5%**	**10%**	**15%**	**20%**
Mean population size	841 ±124	898 ±138	881 ±117	993 ±72	1033 ±34	962 ±69
Total catch	1151064 ±170762	1227032 ±186275	1204439 ±157204	1360414 ±97248	1411633 ±49385	1314645 ±95300
Mean individual step-length, *d*, at 200 years	3.72 ±0.22	3.76 ±0.26	3.75 ±0.30	3.34 ±0.12	3.24 ±0.11	3.59 ±0.34

Table 7.1. The means (and standard deviations) of the mean population size, total catch, and mean step-length, *d*, at 200 years (from five simulations) with different rates of straying and *F* = 0.8.

7.6.2 DISCUSSION

The results that have been presented show only an initial exploration into the effect of one possible form of straying on populations and genotypes. Despite this, this initial model shows that there is a clear effect of straying on the persistence of 'genotypes' in exploited populations with all straying rates able to protect some genotypes (Figure 7.10) even if historical spawning aggregations collapse, although protection may not be complete (genotypes are commonly lost with higher fishing pressure). These results are not unexpected, and whilst not that interesting in themselves, show that straying is an issue that is worth further exploration in the context of fisheries management and environmental change.

Although there is large variation in the results, Figure 7.11 and Table 7.1 indicate that there may be some effect of straying on spawning aggregation persistence, population size, catch, and dispersal. It tentatively appears that there may be a trend of increasing aggregation persistence, population size and catch, and decreasing dispersal distance with increased straying up to 15%. A straying rate of 20% bucks this trend, but it may be that very high straying rates are detrimental to the persistence of spawning aggregations containing fewer individuals, i.e. individuals from a smaller aggregation are likely to stray to non-natal spawning aggregations but, because there are less fish to 'learn' from, strayers from other aggregations are less likely to stray to the smaller aggregation. Further replicates may help to determine whether these trends are real or just a result of the variability in the model.

Only one possible straying permutation has been modelled here, that of 'learning' a spawning location from a neighbour. Additionally, for simplicity, the straying mechanism was implemented so that all individuals had the potential to stray, and would just 'learn' from their nearest neighbour. However, studies have suggested that in some species it may only be juveniles that stray and that they may learn from older 'scouts' (Rose 1993, McQuinn 1997, Brown and Laland 2003). The model could be readily adapted to account for this. Other potential mechanisms for straying which could be considered include straying as a result of competition at the natal spawning ground or more favourable conditions at potential spawning sites, or just randomly straying by 'getting lost'. These mechanisms could act on adults or juveniles, or both.

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