CONE SNAILS

A SIGNIFICANT BIOMEDICAL RESOURCE AT RISK

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“Cone snails may contain the largest and most clinically important pharmacopoeia of any genus in nature. To lose them would be a self-destructive act of unparalleled folly.”

Eric Chivian - Center for Health and the Global Environment, Harvard Medical School.
Nobel Peace Prize 1985

Abstract

Gastropod molluscs of the genus *Conus* (cone snails) occur throughout the world's tropical coastal waters where they capture their prey of fish, molluscs or worms using a complex battery of neurotoxins. Although these toxins are of major importance to biomedical science, the conservation status of *Conus* has been largely ignored. I assessed 632 species of *Conus* to the standards of IUCN Red List of Threatened Species. This revealed 10.6% of species globally are either threatened or near threatened with extinction, with a further 13.8% data deficient but with indicators that suggest substantial cause for concern. Hotspots of endemism, particularly along the Eastern Atlantic found 42.9% of 98 species there at risk. This includes Cape Verde where 53 of 56 species are endemic and mostly restricted to single islands, and where all three critically endangered and four of eleven globally endangered species occur. The rapid transition of the Cape Verdean economy from services to tourism was found to have placed many *Conus* species at risk from habitat disturbance and marine pollution. Although the Red List yields valuable data, it is primarily focussed on species nearing extinction. However, many wide-ranging species, exposed to considerable anthropogenic impacts, may, through remoteness and/or depth, remain unnoticed and unrecorded for years, invisible to the Red List as their populations decline. To identify such species I explored the overlap of *Conus* with biogeographic data of human impacts and future threats from ocean acidification and thermal stress. This revealed a further 67 species occurring in high impact zones deserving further status consideration, and pinpointed regions with high concentrations of endemic taxa under potential threat. This reinforced the benefits of approaching threat assessment from a holistic standpoint in addition to the forensic scrutiny offered by the Red List, allowing proactive conservation management to complement its traditional reactive role.

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Declaration

For Chapter 3, volunteer undergraduate and master students assisted in the primary collection of data from literature and websites under my direction and supervision. All this data was subsequently reviewed and edited by me.

For Chapter 5, Bethan O'Leary provided technical assistance in the modelling of data with Geographical Information Systems under my direction using my data.

I declare that the work contained in this thesis is my own and has not been submitted for any other degree or award. The contributions of co-authors to papers accepted or prepared for submission are detailed in the preface to their respective chapters. All data analysis and writing of this thesis is my own work.

Howard Peters

Chapter 1. Introduction

Across the world's oceans marine life is under stress; from coastal margins to the abyssal plain, humankind continues to render incalculable harm to habitats and organisms that have evolved over millions of years (Allsopp et al, 2009; Roberts, 2012). The demographic challenges for many maritime nations are formidable. In the Philippines, the global centre of marine biodiversity (Bellwood & Hughes, 2001), the human population grew from 48 million in 1980 to 92 million in 2010 and is expected to reach 140 million by 2040 (NSO, 2013). Here, as throughout much of the developing world, a weak economy combined with open-access policies towards marine resources have driven landless rural populations to the coast (Cruz-Trinidad et al, 2001) where they vie with one another for dwindling stocks (McManus, 1997). With the decline in edible fish populations, important new contributions to the earnings of many subsistence fishers can be derived from gathering other marine taxa, but not just for food.

1.1 Marine molluscs

Globally molluscs represent around 60% of all described marine invertebrates (Gosliner et al, 1996). They are primarily gathered as foodstuff; however, they also provide income from their shells. It is unknown what percentage is taken exclusively for sale to shell dealers, but from Cebu in the Philippines alone it has been estimated that between 24 and 25 tonnes of mollusc shells and shell-craft are exported daily (Floren, 2003), and with beached 'dead' shells invariably damaged by wave action, almost all specimens of merchantable quality are gathered live from wild populations (Grey et al, 2005).

For many, the idea of seashell collecting appears to be a harmless pastime and even among the scientific community there is no unified voice warning against the risks of overexploitation. Witness the conflicting messages of the American Malacological Society (AMS) in their proclamation: "The conservation of mollusks is a major concern to the AMS. The AMS policy concerning molluscan conservation prohibits the sale of shell or shell products at our meetings...." (AMS, 2012). Nevertheless, in one of their leading publications, 'The Mollusks – a Guide to their Study, Collection, and Preservation', there are detailed instructions on how to dredge for shells and kill the animals with procedures in preparing shells for presentation. The three chapters devoted to marine shell collecting run to 1,400 col cms compared to just 10 col cms on ‘Ecological Considerations’. On the subject of habitat destruction wrought by dredging for shells, the publication is silent (Sturm et al, 2006).

Worldwide there are numerous examples of catastrophic effects on molluscs of over-extraction. For example, the white abalone (*Haliotis sorenseni*) of California and Mexico where populations have declined to just 0.1% of their pre-exploited numbers owing to failure of management to protect this food stock (Hobday et al, 2001). From the ornamental shell trade, the giant triton (*Charonia tritonis*) has fallen into global decline and become extinct in many parts from over-gathering (Moore & Ndobe, 2008).

Shell collecting is only one of a number of threats faced by tropical marine molluscs. Considered to be of even greater impact is the loss and damage to habitat from trawl and dredge fishing (Skilleter & Warren, 2000). In many regions and in shallow waters close to the shore, blast fishing, and coral mining, although much of it illegal, has increased as a result of human migration to the coast (Steenbergen, 2013). Loss of habitat results in the displacement of living coral-associated molluscs by bivalve crevice dwellers that prefer dead coral heads (Zuschin et al, 2001) with a reduction in marine diversity. Pollution, both seaborne and from coastal development, also plays a major part. Marine molluscs including the gastropods accumulate toxins discharged into the marine environment from industrial and domestic effluents, such as lead, cadmium and mercury, that are not only injurious to human health (Noël et al, 2011), but also present a danger to the molluscs themselves (Sarkar et al, 2013). Other pollutants affecting survival of molluscs include pesticides (Ray et al, 2013) and plastic litter (Aloy et al, 2011).

Research on the conservation status of marine molluscs is limited. There have been some studies at a regional and national level on the effect of shell collecting (Dias et al, 2011; Newton et al, 1993), and of the status of individual species (Guerra-García et al, 2004), however, conservation research papers on the potential extinction risk to marine invertebrates in general, and molluscs in particular, are sparse possibly owing to the generally held belief that marine taxa are less at risk of extinction owing to their wide distribution and high fecundity (Reynolds et al, 2005; Roberts & Hawkins, 1999). However, this may be at variance with reality: the limpet *Lottia alveus*, was found from Labrador to Long Island, New York, before its demise in the 1930s from loss of the eelgrass *Zostera* that it inhabited (Carlton et al, 1991).

Régnier et al. (2009) determined from the 2007 IUCN Red List, updated by their own research, that there are 532 species of mollusc that have gone extinct during the Anthropocene, of which just one is a marine species. Even though primarily terrestrial or freshwater, this constitutes a tally greater than all other documented recent extinctions combined. With a considerable taxonomic bias in conservation assessment favouring higher terrestrial fauna particularly mammals, but with only 3% of molluscs having been assessed, and even fewer insects (Gerlach et al., 2012), extinction rates must be significantly in excess of these numbers (Régnier et al, 2009). For marine invertebrate species, the data is even more impoverished, with extinction rates for molluscs seriously lacking in research.

The marine gastropod mollusc genus *Conus* (cone snails) occurs mainly in shallow tropical waters around the world, often but not always coincidental with coral reefs. The exceptional species richness of *Conus* makes the genus of particular importance to marine biodiversity, but as is the case for many gastropods, their shells are actively sought after and traded by collectors and dealers. However, cone snails differ from most other marine gastropods in their importance to biopharmaceutical research through the neurotoxins the snails deploy in the capture of prey. Ziconotide, the first approved drug from a marine mollusc, is derived from the venom of *Conus magus* and is used to control pain in patients tolerant to opioids (Staats et al, 2004). The use of 'conotoxins' as the basis for treatment of other medical conditions continues to be actively researched (Livett et al, 2006). The venom of every species of *Conus* is probably unique (Olivera et al, 1999), and extinction represents a potential loss of source biota. However, despite their medical, scientific and commercial value, there has been almost no research into the conservation status of *Conus* or the long-term impact on pharmacology from a decline in its diversity.

Marine molluscs have been shown to be an excellent indicator group for other species, particularly in the selection of marine protected areas, where variations in mollusc species richness between populations within prospective reserves were shown to reflect the richness of other taxa with which they coexisted (Gladstone, 2002). In that light, *Conus* with a global distribution, wide bathymetric profile and sensitivity to the major threats previously described, also offers an ideal research subject as an indicator for determining extinction risk to other shallow-water tropical gastropods.

1.2. Research objectives

My research aim was to critically assess the status of the genus *Conus*, in order to identify any species threatened with extinction.

The objectives I set out to determine were:

1. The conservation status of *Conus* and those species at risk of extinction, if any
2. The principal causes of threats to any species that may be at risk
3. The biogeography of endemic clusters and commonality of any threats between species
4. Means to arrest decline of any species at risk
5. Methods to improve effectiveness of global and regional species assessments
6. Whether there is evidence to refute the view that marine taxa are less at risk than terrestrial.

In Chapter 2, as an introduction and literature review, I explore the reasons behind the importance of cone snails and why such an exceptional genus of marine molluscs contributes to marine biodiversity, medicine and trade. I describe the genus' evolution, reproduction, distribution and predatory skills, and their historical association with humans. I review the market in cone snails, in particular shell-collecting and biopharmaceuticals together with general threats that they and other tropical gastropod molluscs face from habitat loss, pollution and over-gathering.

In Chapter 3, I explain how I employed IUCN Red List assessment methodology to identify *Conus* species threatened with extinction. The Red List is the global standard for extinction risk evaluation. To answer the principal thesis aim of determining species at risk, I analyse and present the results of my global assessment and reports details of threatened, near threatened, and data deficient species, together with the rationale in support of their categorisation. Cape Verde species are identified as subjects for further research and analysis that are then described in Chapter 4.

In Chapter 4, I explore why Cape Verde's cone snails are of great conservation concern. I examine the Red List assessments of all 53 endemic species in detail, and analyse the threats, current and projected, at locations where cone snails occur. I review each island's economic and structural development plans together with government statistics on the growth in visitor numbers. From this a picture emerges of the severity of threat faced by *Conus* and other shallow water marine taxa around the archipelago.

In Chapter 5, I revisit the Red List assessment to review its strengths and to test its focus on individual species extinction when compared to a holistic approach. I examine the effects of current anthropogenic impacts and future threats from changes to ocean chemistry at a global level. As well as supporting the rationale of species already categorised as threatened by the Red List, other species not considered threatened, according to Red List criteria, are proposed as candidates for conservation. Furthermore, I provide powerful evidential data to assist in the resolution of data deficient species. In support of the Red List, I offer this as a new tool for determining threat that is particularly appropriate for wide-ranging genera such as *Conus*.

Conus is an exceptional genus: a major contributor to marine biodiversity, an important source of compounds for biomedical research, a cash source for some of the world's poorest fishers, and an item of pleasure to thousands of people through the beauty of its shells. However, it also constitutes a finite resource. In common with marine molluscs around the world cone snails face an uncertain future from thermal stress and changes to ocean chemistry, and although it is not yet fully understood how these will affect the long-term survival of taxa such as *Conus*, or whether some species can adapt, the prognosis is not encouraging (Parker et al, 2013). Nevertheless, even without the spectre of global extinction, cone snails are today facing a multitude of other more immediate threats. My research identifies species threatened with extinction with others approaching that status. By shining a light on limitations of the IUCN Red List process to identify all potential species at risk, it reinforces the need for urgent planning to protect this most important genus for future generations.

NOTE: The data for this thesis is derived from the results of my assessment of 632 species of *Conus* for the IUCN Red List of Threatened Species. These data form an integral part of my PhD, however, owing to the exceptionally large body of work it is not practical to bind this into the thesis as a hard copy appendix. It is freely and publicly available at www.iucnredlist.org.

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Chapter 2. *Conus*: an exceptional genus of marine gastropod mollusc.

Preface

Through the ages, natural products, especially extracts of plants, have formed the basis of folk medicines and remedies around the globe, and for the past 70 years the pharmaceutical industry has realised the potential of such organisms in the development of novel drugs (Fenical, 2006). The discovery of penicillin by Fleming in the 1920s was followed by other antibiotics during the 1940s based on terrestrial biota, but in the 1950s several nucleosides that are used in anti-viral agents were isolated from the Caribbean sponge *Tethya crypta* by Bergmann *et al* (Kijjoa & Sawangwong, 2004). It has been suggested that the discovery in the late 1960s of the muscle-regulating compounds, prostaglandins, in high concentrations in gorgonians was the trigger for the sudden growth in interest in marine natural products (Carté, 1996). More recent discoveries, especially among sessile reef invertebrates such as soft corals, as well as sponges (Porifera *spp*), have also lead to increased interest in marine resources (Kijjoa & Sawangwong, 2004). Fruits of this research are not confined to pharmaceuticals; starting in 1985, collaboration between the cosmetics corporation Estee Lauder and Sea Grant of California, resulted in the development of anti-allergenic agents suitable for skin lotion from the Caribbean sea-whip *Pseudopterogorgia elisabethae* (Fenical, 2006; Look et al, 1986). This success in prospecting for marine taxa for potential new pharmaceutical agents has led to research on other marine phyla of which the Mollusca is one. From this, it is the venom of the gastropod molluscs of the genus *Conus* that holds out one of the great promises for biomedical research (Chivian & Bernstein, 2008).

2.1. Cone snails of the genus *Conus*

Cone snails are carnivorous marine gastropod molluscs of the genus *Conus* that occur in tropical coastal waters around the globe. At over 630 extant species, *Conus* is the largest genus of any marine invertebrate (Terlau & Olivera, 2004). However, its taxonomic unity is open to challenge with many species displaying characteristics that suggest alternate generic groupings based on the morphology of their shells and radulae. There are currently active exchanges among taxonomists concerning a proposal to create 80 new cone snail genera within four families (Tucker & Tenorio, 2009). However, this has not been embraced by all experts and the taxonomic identity within this thesis follows the Linnaean genus. The family *Conidae,* to which *Conus* belongs is of the superfamily *Conoidea* previously known as *Toxoglossa*, or 'poison tongue', owing to the venom apparatus deployed in capture of prey. The *Conoidea* also includes the families *Terebridae* or auger snails and *Turridae* or turrid snails.

2.2. Biogeography

2.2.1. Evolution, radiation and speciation

Figure 1. Pliocene fossil France, 2.6 to 5.3 mya. *C. mercatii* Brocchi, 1814. *Image: H Peters*

In evolutionary terms *Conus* is a recent arrival, first appearing during the Lower Eocene of 50 mya (Kohn, 1990) with the earliest known fossils found in England and France – *C. concinnus* and *C. rouaulti* respectively (Röckel et al, 1995). From 23 mya, in the latter half of the Cenozoic and during the Miocene, there was an acceleration of species diversification that was largely tropical in nature, with radiation of scleractinian corals and a growth in the complexity of tropical reef ecosystems (Rex et al, 2005; Veron, 1995) including gastropods and, latterly, *Conus* (Kohn, 1990). However, it was only during the later Pleistocene of 0.01 to 2 mya that the fossil record shows a very rapid increase in speciation of the *Conidae* (Röckel et al., 1995).

2.2.2. Distribution

Conus occurs in four distinct biogeographical realms: the Eastern Atlantic, Western Atlantic, Indo-Pacific and Eastern Pacific with only four species having managed to break the natural barriers that are now present to migrate between them (Duda & Kohn, 2005). The largest diversity occurs within the Indo-Pacific with approximately 390 species with a further 31 species along the western coast of the Americas from California in the north to Ecuador and the Galapagos in the south. In the Atlantic there are approximately 98 species along the western flank of Africa including its islands and a further 113 in the Western Atlantic from the Carolinas south to Brazil including all the Caribbean and the Gulf of Mexico (IUCN, 2013). These numbers are continually being revised as new species are regularly described and others synonymised. The greatest concentration of species richness is to be found within the Coral Triangle of Southeast Asia (Wells, 2000). A few species of *Conus* also live in warmer sub-tropical waters but diversity in the higher latitudes is low with only single species often occurring in some regions including the Mediterranean, Easter Island, and the northern ranges of California and the Carolinas (IUCN, 2013; Kohn & Perron, 1994).

2.2.3. Endemism

Endemism for marine species like *Conus* occurs most commonly in isolated island groups where the original dispersal was assisted by a pelagic larval stage or by transport on rafting matter. For example, there is a single species, *C. jourdani,* off the remote island of St Helena in the mid-Atlantic that is endemic to the island (Peters et al., 2013). Endemics may also be found where non-reversing currents transport water away from the tropics towards higher latitudes, such as from the Leeuwin Current in Western Australia (Roberts et al., 2002). *Conus* endemics are found throughout the genus' range but in particular off the islands of the Western Atlantic, and in their extreme off Cape Verde where 94.6% of *Conus* species are endemic (Peters et al. in press 2013). Endemic *Conus* species are also found along the coasts of West Africa and Brazil where large plumes of freshwater from major river systems act as barriers to biogeographic expansion.

2.2.4. Habitat and bathymetry

The majority of cone snails inhabit shallow warm waters surrounding coral reefs and mangroves typically at depths from the inter-tidal to thirty metres although some species prefer the soft-sediment of bays and deeper parts of the continental shelf (Röckel et al, 1995). Here deep-water species occur to depths of hundreds of metres (Kohn & Perron, 1994) with some being recorded down to 1,100 m (Röckel et al, 1995). Microhabitats include sand and sandy-mud, rocky reefs, sub-tidal reef platforms with living and dead corals, inter-tidal limestone benches (i.e. the smooth remains of reef structures from earlier geological period when sea levels were higher), beachrock (i.e. structures lithified through the precipitation of carbonate cements) with sand or algal turf or boulders with sandy layers (Kohn, 1968, 1983).

2.3. Morphology

Shells of *Conus*, as the name implies, are broadly of conical form with the sides of the aperture parallel (Röckel et al, 1995). However, there are many variations to this generalised description with some species being distinctly conical while others are of a much narrower profile and almost cylindrical (Fig. 2). Some species possess convex sides giving an ovate appearance. These are the principal outlines but there are many intermediary forms. The 'spire' of the shell for some species is distinctive and for those, such as the spectacular *C. milneedwardsi,* may comprise almost 50% of the total shell length, whereas in others it may be so low as to be almost flat. The outline of the spire can be concave, convex or domed with shoulders in a variety of forms including coronate. The size of *Conus* shells are equally varied with some species measuring less than 10 mm while others can exceed 200 mm.

Figure 2. Variations in colour and form. Top row left to right: *C. striatus* Linnaeus, 1758; *C. bullatus* Linnaeus, 1758; *C. eburneus* Hwass in Brugiére, 1792; *C. imperialis* Linnaeus, 1758; Bottom Row: *C. figulinus* Linnaeus 1758; *C. kintoki* Habe & Kosuge, 1970; *C. generalis* Linnaeus, 1767; *C. circumcisus* Born, 1778; *C. quercinus* Lightfoot, 1786. *Image: H.Peters*

The characteristics of cone snails that make them so attractive to many shell collectors are the extraordinary range of patterns and colours they exhibit, both within and between species. These colours are built up through differing layers, with overall appearance determined by the shell's opacity and especially through the layer on the surface or 'last whorl' (Röckel et al, 1995).

The form of the shell is the leading visual indicator to determine species. Pattern and especially colour are less reliable indicators on their own owing to wide variations within species (Röckel et al, 1995). Live animals are covered by a periostracum, a thin organic layer of sclerotized protein or conchin that is secreted by the snail and envelopes the last whorl of the shell. With *Conus* the periostracum is usually opaque and can have ridges and/or be tufted (Röckel et al, 1995). Cone snails, in common with most prosobranchs, have an operculum. This is a calcareous plate positioned on the posterior end of the dorsum of the foot and is employed to secure the aperture when the animal has retreated into its shell. In *Conus* this is small and insignificant in appearance.

2.4. Life cycle

2.4.1. Reproduction and larval development

Cone snails are separated by sex and fertilisation is accomplished internally (Kohn & Perron, 1994). Most species of *Conus* deposit a thin-walled capsule of eggs on the underside of a hard surface with each capsule containing a few dozen to tens of thousands of eggs, although at least one species, *C. figulinus* (Fig. 2) deposits within a sandy substrate (Kohn & Perron, 1994). Larvae hatch about two weeks after spawning (Kohn, 1959) following which metamorphosis takes place after varying periods that can be from less than one day to 50 days or more (Perron, 1981). Most larvae are planktotrophic, i.e. feed on plankton during the larval stage, but some such as *C. pennaceus* (see larval dispersal below) are lecithotrophic and obtain nourishment through their egg sac (Perron, 1981). Metamorphosis, where the larvae undergo transformation to juvenile form may occur intracapsulate, i e. within the egg capsule or extracapsulate, i.e. after hatching (Röckel et al, 1995) (Fig. 3).

2.4.2. Larval dispersal

The geographic range of *Conus* is influenced by the mode of larval dispersal (Kohn, 1990). Developmental mode varies by species from large eggs and non-planktonic embryos through to small eggs and long-term planktonic veligers with varying intermediate modes (Perron & Kohn, 1985). Those *Conus* species that are lecithotrophic, where there is an absence of a planktonic feeding stage, are generally restricted to the seas abutting continental island groups such as the Philippines or land masses such as Asian coastal waters and on the Caribbean continental shelf (Kohn & Perron, 1994). By contrast those that are planktotrophic, with a pelagic larval stage, are also found among the archipelagos of the Pacific Plate and other isolated oceanic locations where any other dispersal mechanism would be less possible (Perron & Kohn, 1985). However, species with a planktonic larval stage do not always disperse widely (Levin, 2006).

Rafting is an alternative means of transport for lecithotrophic larvae although *Conus* is evidently unsuited to it in the Indo-Pacific (Paulay & Meyer, 2006) as only one non-planktotrophic species: *C pennaceus*, is found outside continental island groups and large land masses (Perron & Kohn, 1985). There appears to be no correlation between the distance of dispersal of planktotrophic species and the duration of the planktonic stage, however, habitat depth may influence distribution patterns (Perron & Kohn, 1985).

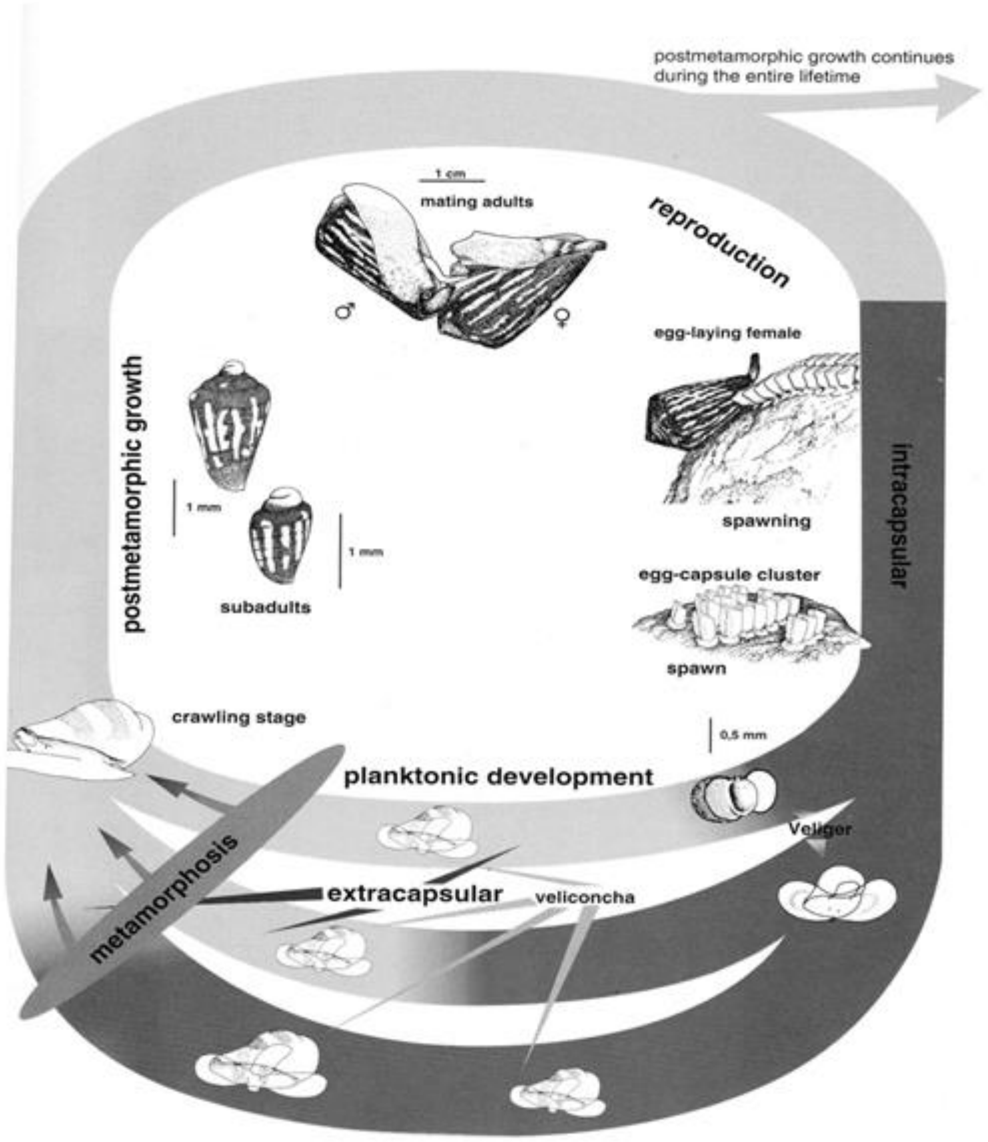

Figure 3. Life cycle of *Conus* (Röckel *et al,* 1995) *© Verlag Christa Hemmen*

2.5. Diet and Predation

2.5.1. Diet

Cone snails are predatory gastropods that can generally be classified as vermivorous, molluscivorous or piscivorous species according to their prey although some species have a mixed diet (Duda et al, 2001). Cone snails generally feed at night (Kohn, 1959). The diet of all species is not known but it is thought that there are around 50 species of fish-hunters (Olivera, 1999; Röckel et al, 1995) and a further 80 that prey on molluscs (Livett et al, 2004) with the majority consuming worms, in particular polychaetes, which for some species are the exclusive source of food (Kohn, 1959). All cone snails use venom to immobilize their prey. The diversity of toxins employed by a particular species in the capture of prey is reflected by the degree of specialisation in its diet; among the specialists are *C. leopardus* that preys only on hemichordates (Remigio & Duda, 2008) and *C. marmoreus* that only feeds on other *Conus*. Even more specialised is *C. chaldeus* that feeds only on a single species of nereid *Platynereis dumerilii* (Kohn, 1959). These highly specialised cone snails possess a less diverse array of toxins compared to species with a broader dietary range where the venom is of greater complexity (Remigio & Duda, 2008). It is thought that the diversity of venom peptides across the genus has evolved through evolutionary processes as a result of genetic mutations enforced by a rapid change in prey (Olivera, 1997). Even though venom has adapted for each species to target specific quarry, cone snails have been shown to be remarkably adept at modifying their venom components to suit the availability of prey species. Conopeptides from *C. miles*, a species that preys exclusively on polychaetes, have been subject to fractionation using high-performance liquid chromatography (HPLC) (Mebs, 2001). Fractions obtained from the process injected into fish resulted in paralysis, indicating that even venom synthesised for invertebrate prey such as polychaetes has the potential to be re-assigned to other species (Mebs, 2001), although the degree to which *Conus* species with greater specialisation are able to adapt their prey preference has not yet been explained. However, this potential adaptability has probably contributed to the rapid speciation and success of the genus.

2.5.2. Predation

To detect and distinguish the presence of prey, cone snails possess chemoreceptors associated with the osphradium, an organ situated in the mantle cavity at the base of the siphon used for food recognition and possibly to detect predators and also potential mates (Taylor & Miller, 1989). The envenomation mechanism is highly sophisticated and consists of a duct and bulb for the synthesis and storage of the venom and a sac for the generation and storage of hollow radulae that have evolved into specialized harpoons deployed in delivery of the venom (Shaw, 1914). The formation of radula teeth takes place in the long posterior arm of the sac and the fully formed teeth are stored in the short anterior arm (Marsh, 1977). The method of envenomation is dependent upon the target. Some fish-hunters such a *C. tulipa* and *C. geographus* engulf fish in their rostrum or proboscis, stinging them when the prey is secure (Terlau et al, 1996) whereas others bury themselves in the sand and lure passing fish by shaking their extended proboscis (Olivera et al, 1985).

Once the target has been identified, the snail loads a single tooth from its radula sac through the pharynx and engages it in the proboscis (Le Gall et al, 1999). After loading, the radula tooth is armed by pressure applied through the venom duct by a bulb on its end which injects the venom through the hollow harpoon-like tooth (Le Gall et al, 1999). The proboscis with the tooth towards its end is then held against the prey (Schulz et al, 2004; Stewart & Gilly, 2005). The tooth stalls for 4-5 milliseconds against a constriction in the proboscis while it is primed with venom, then is explosively propelled into the prey. In the final millisecond the tooth travels at considerably more than 3 ms^{-1}. This is one of the fastest capture events in nature such that experimental video recording at 1,000 frames/s has been found to be incapable of freezing images of toxin delivered at peak velocity (Salisbury et al, 2010; Schulz et al, 2004). Once prey has been stung and venom injected, envenomation takes hold within 50 milliseconds, and where the prey is fish, the snail retains a grip on the base of the tooth to inhibit escape of the prey (Schulz et al, 2004). A tooth is used just once and usually swallowed along with the prey to be regurgitated with bones, scales etc. a few hours later (Olivera et al, 1985). Piscivorous and vermivorous cone snails most commonly employ only a single tooth (Stewart & Gilly, 2005) whereas with molluscivorous species multiple teeth may be used (Kohn, 2003). If the prey is an opisthobranchiate mollusc with an internal shell it is swallowed whole and the shell later regurgitated, whereas for mollusc prey with a large outer shell the cone snail removes the prey through the aperture of its shell (Kohn, 1959).

Observations have shown that some molluscivorous species of *Conus* can swallow prey whose body volume is up to 85% and weight up to 50% of their own, with digestion taking several days (Kantor, 2007). All cone snails, with the single known exception of *C. californicus* (see below), swallow their prey whole, excluding its shell. In order to provide adequate capacity in the body cavity of the shell to accommodate the whole meal in addition to the animal, as the snail ages and grows it thins its interior whorls through dissolution. Concurrently, the last whorl and the spire of the shell thicken to enhance structural strength. The snail dissolves approximately 25% of its secreted shell material during its life and in so doing contributes 70% of its internal living space (Kohn et al, 1979).

C. californicus, the exception to the solitary feeding method described above, is a temperate water species that has a wide ranging diet comprised of fish, molluscs, worms and, unusually, small crustaceans. These snails have been observed in cooperatives of up to ten individuals attacking prey larger than their individual body capacities, devouring together just the soft tissue of the prey (Biggs et al, 2010).

The venom of cone snails is a complex of between 50 and 200 different peptides each of only 10 to 35 amino acids in length that is distinct for each species (Olivera et al, 1999). These toxins act as a combination drug strategy or a 'cabal', first immobilising the prey then disrupting its neuromuscular transmission (Olivera, 1997). In fish-hunting cone snails paralysis of prey is achieved by the injection of several classes of toxins. This prevents closure of the sodium (Na) channel allowing massively elevated sodium ion flux into the nerve and at the same time blocking the potassium (K) channel, thereby inhibiting the outflow of potassium ions causing an uncontrollable firing of nerves, leading to massive hyperexcitability. In fish envenomated by most pisciverous species of *Conus* this results in rigidity of the fins and total paralysis (Imperial et al, 2007).

The use to which *Conus* venom is employed is complex and not fully understood. Only a fraction of venom can be accounted for in the capture of prey, and it is suggested that other constituents are for defensive purposes and to deter competitors (Olivera et al, 1999). For prey capture purposes the results demanded of the venom vary even between species with similar dietary preferences; fish-hunting cone snails that use a 'harpoon-and-line' strategy, such as *C. striatus*, are not affected by the resultant fin rigidity or violent jerking of their prey, however, those that employ a 'net' strategy and engulf their prey before envenomation, such as *C. geographus* (see above), appear to pre-sedate their prey and once captured subsequently envenomate without promoting a violent reaction that could otherwise damage their proboscis (Olivera et al, 1999).

2.6. Utilisation and trade

2.6.1. Conus shells as objects of commerce and utility

There are examples of cone shells being collected for ornamentation from the earliest civilisations. A necklace of *Conus* shells, unearthed from archaeological digs in the world's first known urban settlement of Uruk in the Tigris-Euphrates valley of ancient Mesopotamia, dates from 5,000 ybp (Terlau & Olivera, 2004). In the New World, an archaeological dig of prehistoric Hopi Indian graves in Arizona yielded rattles made from *C. fergusoni, C. princeps* and *C. regularis,* which were still used for the same purpose until quite recently (Fewkes, 1896). On Ujae, in the Marshall Islands of the Pacific, adzes made from *Conus spp* dating from the third century AD have been discovered together with sliced apices from *C. leopardus* and *C. literatus* fashioned into amulets and earrings for insertion into grossly distended earlobes (Weisler, 1999). From Pompeii (destroyed AD 79) a *C. textile* was unearthed from the volcanic debris together with other exotic species (Dance, 1966). It is believed that *Conus* shells or their disc-shaped ends were used for currency in East Africa before the arrival of Arab traders (Harding, 1961).

The striking patterns on cone shells and their wide range of colours and shades continue to attract serious collectors today with rare examples in perfect condition changing hands for high prices (Rice, 2007). Specialist publications, shell clubs and the Internet are all devoted to fulfilling the demands of a truly global market, and consequently great pressure is placed on a natural resource of finite supply. As in philately, the high end of shell collecting is dominated by serious amateur and professional collectors with dealers willing to pay thousands of dollars for scarce specimens (Dance, 1966; Rice, 2007). More commonly, however, cone shells are traded by the hundreds for just a few dollars each to satisfy the tourist market or for manufacturing into jewellery and household ornaments (Fig. 4) (Floren, 2003). There are few if any reliable statistics on the quantities of *Conus* species collected and most of the import/export data that do exist are consolidated into categories such as shellcraft, ornamental shells, mother-of-pearl, and waste fragments, rather than distinguished by any form of shell genus or species (Floren, 2003).

Figure 4. A contemporary use for cone snail shells. *C. leopardus* Röding, 1798, fashioned into salt and pepper shakers.
Image: H Peters

Specimen shells for the collector market are categorized and priced according to scarcity, size, quality and coloration. Shell size is important and there is keen competition to lay claim to the largest known specimen of a species. Scarcity may result from over-gathering or because a species has restricted range or occurs in a degraded habitat or at extreme depth (Newton et al, 1993; Peters et al, 2013). From shallow waters, artisanal fishers typically gather cone shells by gleaning or shallow-water diving, while deeper dwelling species are normally brought to the surface as fishery by-catch.

In the same way that prices of mollusc shells can become inflated through scarcity of supply, they can also collapse from sudden finds, especially for hitherto rare species. The cone snail ‘Glory of the Seas’ *C. gloriamaris* achieved almost mythical status owing to its great beauty and extreme rarity (Terlau & Olivera, 2004). By 1949, almost 200 years since its discovery, only twenty-two specimens were known from collections and in 1957 one was sold to an American collector for $2,000 (equivalent to $16,000 in 2013). Nine years after this record price still only fifty shells had been recognised (Dance, 1966), but then in 1969 three Australian scuba divers discovered 68 specimens at Guadalcanal, Solomon Islands (Cross & Fair, 1970; Gibbins, 1970). Further finds were subsequently made and today *C. gloriamaris* typically changes hands for between $100 and $200 dependent upon size and quality, although outstanding specimens are still able to command well in excess of that (Rice, 2007).

Shell quality is measured according to the 'Hawaiian Malacological Society International Shell Grading Standard' or HMS-ISGS. The approach, first proposed in March 1973 by Leehman and Lillico in Hawaiian Shell News (Leehman & Lillico, 1973; Tunnell et al, 2010), being upgraded and clarified in 1977. It has now been universally adopted by shell dealers worldwide and includes an official classification, summarised as 'Dead' for beached, faded and badly chipped specimens; F (Fine): major chips and other blemishes; F+: more than one flaw but reasonably good condition; F++: not more than one flaw and overall presentation very good; G (Gem): a live-taken fully adult shell in perfect condition and of excellent colour. Other grades, such as F+++ and G- are also used by some dealers. 'Dead' shells and those that fall below the standards described are classified as 'commercial' quality and are used in gift packets at minimal cost or broken down for jewellery or other artworks. 'Dead' shells may at times be offered as specimen shells where the species is very rare and few other examples are available.

Unusual characteristics such as colour variations, albinism and, in particular, 'sinistral' forms (i.e. left-handed) command a premium, with extremely rare colour variations having a significant effect on price. Colour may be influenced by environmental conditions, for example, iron in the water from shipwrecks will sometimes impart a bluish tinge to the shell (Cross & Fair, 1970). The presence of an operculum, although insignificant in *Conus* may also increase value. Other aspects that affect price are clarity of the pattern and lack of flaws or irregularities such as growth marks. However, some patterns may be so distorted that they attract buyers seeking 'freaks' who will pay for their uniqueness.

2.6.2. Cone snail toxin, a danger to humans but a biomedical resource

To arrest the progress of fish, venom needs to act with exceptional rapidity. For some piscivorous and molluscivorous *Conus* the toxicity of their venom is so potent that they can be seriously injurious or even lethal to people, although it is suggested that in stinging humans the snail is acting defensively (Olivera, 1999). *C. geographus* is one of the most venomous cone snails from which a sting can result in cerebral oedema, disseminated intravascular coagulopathy, coma, respiratory arrest and cardiac failure leading to death within an hour (Fegan & Andresen, 1997). These symptoms, similar to the effects of curare poisoning, occur as the venom blocks the nicotinic acetylcholine receptors at the neuromuscular junction, causing asphyxiation resulting from failure of the diaphragm muscle (Livett et al, 2006). There is no anti-venom for *Conus* toxin. In his work Amboinsche Rariteitkamer, published in 1705 three years after his death, Rumphius writes about a Moluccan woman killed while handling a *C. textile* "... the [cone snail] can stick out a little tongue, that is white, edged with red, and in it is a small bone, or thorn, which will hurt you, if stung by it.... she felt a slight itching in her hand, which gradually crept up her arm and through her entire body; and so she died from it instantaneously." (Rumf & Beekman, 1999). By contrast Sir Edward Belcher survived his sting from *C. aulicus*, reported, again from the Moluccas in 1847 – "...he compares the sensation he experienced to that produced by the burning of phosphorus under the skin. The instrument which inflicted the wound, in this instance, I conceive must have been the tongue which is.......armed with two ranges of sharp-pointed teeth." (Adams, 1848).

Biomedical research of 'conotoxins' has gained traction during the past 25 years, but today less than two per cent of toxins has so far been characterised (Kaas et al, 2010). Nevertheless, even with a relatively small number of toxins explored, their capability to target a broad range of highly-specific cellular receptor sites with subtle variations in sequencing holds unparalleled promise for both their diagnostic and human therapeutic potential (Terlau & Olivera, 2004). It has been suggested that the analgesic properties of *Conus* venom were first aroused by the reported painless deaths of its early victims (Livett et al, 2006). The first approved product derived from a *Conus* toxin is Prialt® (Ziconotide), an N-type calcium channel blocker developed from the snail *C. magus* for the treatment of severe chronic pain and the prevention of stroke (Staats et al, 2004). This ability to provide effective relief from intractable pain without the side-effects of dependency and tolerance characteristic of opiates, and with far superior potency (Garber, 2005), opened the window to a raft of other therapeutic possibilities for *Conus* toxins. Current research and development potential for other toxins lies in the diagnosis and treatment of conditions as diverse as cancers, hypertension, epilepsy, arrhythmia, asthma, multiple sclerosis, and diabetic neuropathy (Livett et al, 2004; UN, 2007).

2.6.3. Cone snail toxin as a biological weapon

Although treated with some bemusement and disbelief within the cone shell collecting community (Tenorio pers. comm. 2012) and also by the author, the potential to derive biological weapons from conotoxin is of sufficient concern to grant it inclusion on the Core List of Biological Agents for Export Control by the Australia Group. There are 41 members of the Australia Group including the US, UK and Japan but excluding Russia. All participating states are parties to the Chemical Weapons Convention (CWC) and the Biological Weapons Convention (BWC), and “strongly support efforts under those Conventions to rid the world of Chemical and Biological Weapons” (Australia Group, 2012; Patočka & Středa, 2006). Other agents of concern to the Australia group include Botulinum toxins, Ebola virus and Ricin (Australia Group, 2012).

2.6.4. Cone snail flesh as food

Cone snails are not generally associated with human food consumption; however some species are used for food in a number of Pacific islands. Also, in the Visayas, Central Philippines *C. magus*, *C. radiatus* and *C. furvus* among others are cooked in coconut milk with herbs and spices to make a broth (Chadwick & Olivera, 2009), where the author also witnessed the consumption of these species at a festival.

2.7. Threats to *Conus*

2.7.1. Habitat loss and pollution

It is to the misfortune of *Conus* that many species occur in shallow water around coastlines that are becoming increasingly affected by development, industrialisation and agriculture (IUCN, 2013). Most often these are also in the waters of developing countries where control on effluent disposal, dumping of chemicals and over-application of pesticides and fertilisers is seldom enforced (IUCN, 2013). In many areas where *Conus* occurs, the removal of mangroves has deprived coastlines of a natural barrier to land-borne discharges (Valiela et al, 2001), while increased human migration to coastal areas has increased levels of sewage and other domestic waste. In areas opened up to tourism and other construction projects, there are reports of increasing removal of sand from the littoral zone for the purposes of construction (Lopes, 2010). Where destructive fishing methods such as blast fishing are employed, including most of Southeast Asia, there are consequences for marine invertebrates, including mollusc assemblages that occur in the vicinity (Pet-Soede & Erdmann, 1998).

2.7.2. Shell gathering

Shell-gathering, once the preserve of children and dedicated 'conchologists' now attracts a global audience, swollen by international mass tourism to previously inaccessible tropical shorelines (Newton et al, 1993) and expanded by web-marketing (www.conchology.be). Unlike the taking of wild animal pelts, shell collecting has not yet attracted the opprobrium of the general public and is generally perceived as benign. This attitude is supported by an almost total lack of regulatory controls in the trade in mollusc shells (www.cites.org). However, the reality is very different, with gathering of shells in some parts of the world now approaching industrial levels that cannot be sustained without serious impact on populations, especially among endemic species with highly restricted geographical ranges (Floren, 2003). Cone snails are particularly attractive to collectors owing to the size and diversity of the genus, their wide range of colours and patterns, the mystique of certain rare species and the quest for the finest or largest specimen. Endemism among *Conus* is common within isolated groups, with many species also occurring in shallow waters where they can be easily gleaned (Peters et al, 2013). Here they may live within a highly restricted range, even a single bay (IUCN, 2013).

2.7.3. Bioprospecting

The stratospheric costs associated with drug development, together with the massive economic potential of the few products that make it to human trials, demand that pharmaceutical companies treat all aspects of their research with utmost secrecy (Kesselheim & Mello, 2007). This limits available information on source biota and in particular any quantitative data on species taken for research. In 2003 Chivian *et al.* drew attention to the possibility that researchers in the biomedical industries could be purchasing hundreds of thousands of cone snails taken from the wild (Chivian et al, 2003). This was vigorously refuted by representatives of research groups who estimated that typically ten to twenty specimens only were sacrificed to describe the conotoxins employed by any one species. Additionally, they estimated that there were probably only twenty research groups working on *Conus* at the time of writing (Duda et al, 2004). In response, (Chivian et al, 2004) revealed that information they had received from a university researcher declared one kilogram of *Conus* venom duct had been supplied that they estimated would have required about 10,000 snails to produce. This wide discrepancy of views underscores the paucity of reliable information on the true extent of sourcing of *Conus* for the biomedical industry.

Reliance on supplies of living *Conus* for the extraction of duct venom has implications for human safety in gathering as well as security of supply and the impact on species populations. To reduce this dependence on securing large numbers of wild-caught cone snails, recent advances have been made in milking venom. This is performed in a manner similar to extraction of venom from snakes, albeit conducted underwater (Bingham et al, 2010). The technique requires a suitably-sized prey fish, e.g. a goldfish (*Carassius auratus auratus*) to be positioned in front of the captive snail to encourage the extension of the snail's proboscis. The decoy fish is then substituted with a surrogate constructed from a tube covered with a membrane fashioned out of a condom incorporating a fresh fish fin. The snail harpoons the surrogate and the venom can be captured. The snail is then fed the original live fish as reward (Hopkins et al, 1995). Venom extraction by milking is time-consuming and requires dedication to animal husbandry but in return offers a viable alternative to a continuous re-supply from the wild.

Further techniques to reduce the dependence on wild caught specimens include polymerase chain reaction (PCR) sequencing of DNA fragments that requires just one specimen (Livett et al., 2006). This further demonstrated that there are variations in expression of conotoxins across individuals of the same species, and that each toxin has multiple peptide subsets for each *Conus* species, with a conservative estimate of over 25,000 subsets across the genus (Livett et al., 2006). This increases source material for biomedical research even further from the estimated 50,000 toxins across the genus (Craig et al, 1999).

At the 10th meeting of the Conference of the Parties of the Convention on Biological Diversity (UNEP/CBD, 2010) held in Nagoya, Japan, October 2010, a landmark agreement was reached to combat biopiracy or the unlawful taking of biological material for research (UNEP/CBD, 2010). This addressed the issue of approval for bioprospecting from the source country through the establishment of documented authorisation channels with simplified access procedures. Non-monetary benefits must also be shared, such as knowledge acquired locally during research being acknowledged in any subsequently published papers. Ratification from participating countries was still awaited at time of writing. Uptake of the scheme should in the future clarify the rules and responsibilities for field researchers. However, agreement through international consensus does not always translate to action on the ground as witnessed by the wholesale disregard of agreements on high seas fishing (Baird, 2004) despite the UN Convention on the Law of the Sea (UNCLOS). In developing countries with long coastlines in remote areas where enforcement is weak or non-existent, biopiracy will inevitably continue to raise its head.

2.7.4. Elevated sea surface temperature and ocean acidification

Among marine invertebrates generally, rising ocean temperatures have been shown to affect patterns of spawning, planktonic duration and availability of prey species, with the risk that some planktotrophic larvae may not emerge in the water column concurrently with their planktonic food thereby disrupting the entire food-web, with shallow water taxa most at risk (Przeslawski et al., 2008); this includes many species of *Conus*.

Ocean acidification, resulting from combustion of fossil fuels and deforestation, has led directly to a reduction in ocean pH levels through dissolved atmospheric carbon dioxide (Doney et al, 2009). For shell-forming molluscs and other calcifying species the effect is reduced calcification and growth rates, with mollusc larvae especially at risk owing to their composition from amorphous calcium carbonate, a form of $CaCO_3$ with enhanced dissolution characteristics, rather than the less soluble crystalline structured form present in mature individuals (Parker et al, 2013). There is also the likelihood of indirect consequences on food and habitat: many molluscs, including species of *Conus*, prey on other molluscs and also inhabit tropical reefs (Röckel et al, 1995), where scleractinian corals are, like the molluscs themselves, composed of calcium carbonate. The rate of ocean acidification is expected to rise throughout the century but to-date there is little known about the ability of organisms to adapt to the changing chemistry of their environment (Doney et al, 2009), although there is an extensive and growing body of work on the predicted effects. A recent meta-analysis on the effects of changing ocean chemistry on molluscs paints a bleak picture particularly for gastropods but especially for their larvae, where the rate of development and larval size were both negatively impacted, with increased exposure to predation and starvation (Parker et al, 2013).

It is against this backdrop that I embarked on my research to determine the true risk to *Conus*.

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Chapter 3. *Conus*: first comprehensive conservation Red List assessment of a marine gastropod mollusc genus

3.1. Preface

Conus is an exceptionally large genus of marine gastropod molluscs with in excess of 630 species that continually expands as new species are described. Cone snails occur in shallow waters across the tropical regions of the world most often at depths where their habitats are threatened by anthropogenic stressors and where they may be easily gathered. Cone snails have significant commercial value both for their shells and in the biomedical potential of their toxins, and yet their conservation status is virtually unknown, either for the genus as a whole or for individual species.

The aim of this chapter was to determine the extent to which cone snails are threatened and reasons behind the threats. I explored the distribution of every *Conus* species that had been verified as taxonomically valid, determined their bathymetric profile and preferred habitats, and any commercial interests in the species either for collecting as a marine curio or as a potential scientific resource for toxin characterisation and biomedical research, together with their considered rarity in the wild. I examined the threats confronting each species from anthropogenic and natural causes including proximity to large towns and cities, tourism, coastal development and pollution, and any protection afforded including marine protected areas within their area of occupancy.

The methodology I employed followed the standards and procedures of the IUCN Red List of Threatened Species (IUCN Standards and Petitions Subcommittee 2010). From the results, I also identified centres of endemism with the species at risk within those areas. With this research I laid the groundwork for future decadal monitoring addressing one of the primary objectives of the Red List. This, the first global marine gastropod mollusc assessment undertaken for the IUCN and only the fourth for a marine invertebrate, makes a major contribution to this open-access resource.

This paper was written to the style of PLoS One to which it was submitted and accepted for publication, subject to minor additions but without changes to the original text. For consistency and ease of reading, citations have been changed to follow the standard for the thesis (author and year, rather than code) with figures and tables inserted close to their first reference in the text, rather than as separate files as in the publisher’s version.

I declare that the work submitted is my own. The contribution by co-authors was as follows:

Callum Roberts & Julie Hawkins: Supervision, review and editing.

Kent Carpenter: Red List workshop support and assistance with map production for IUCN Red List.

3.2. References

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Conus: First Comprehensive Conservation Red List Assessment of a Marine Gastropod Mollusc Genus

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ABSTRACT

Marine molluscs represent an estimated 23% of all extant marine taxa, but research into their conservation status has so far failed to reflect this importance, with minimal inclusion on the authoritative Red List of the International Union for the Conservation of Nature (IUCN). We assessed the status of all 632 valid species of the tropical marine gastropod mollusc, *Conus* (cone snails), using Red List standards and procedures to lay the groundwork for future decadal monitoring, one of the first fully comprehensive global assessments of a marine taxon. Three-quarters (75.6%) of species were not currently considered at risk of extinction owing to their wide distribution and perceived abundance. However, 6.5% were considered threatened with extinction with a further 4.1% near threatened. Data deficiency prevented 13.8% of species from being categorised although they also possess characteristics that signal concern. Where hotspots of endemism occur, most notably in the Eastern Atlantic, 42.9% of the 98 species from that biogeographical region were classified as threatened or near threatened with extinction. All 14 species included in the highest categories of Critically Endangered and Endangered are endemic to either Cape Verde or Senegal, with each of the three Critically Endangered species restricted to single islands in Cape Verde. Threats to all these species are driven by habitat loss and anthropogenic disturbance, in particular from urban pollution, tourism and coastal development. Our findings show that levels of extinction risk to which cone snails are exposed are of a similar magnitude to those seen in many fully assessed terrestrial taxa. The widely held view that marine species are less at risk is not upheld.

Keywords: cone snail; marine conservation; gastropod; extinction; endangered species; coral reef

1. Introduction

Extinction risk of marine organisms has attracted little attention compared to that of terrestrial taxa, with a widely held view that such risk is inconsequential due to high dispersal ability and large geographic ranges (Harnik et al., 2012; Roberts & Hawkins, 1999) especially when taking reference from the fossil record (Harnik et al., 2012; McKinney, 1998). These beliefs are particularly prevalent when considering marine invertebrates, where a decline in abundance of the important phylum *Mollusca* has been overshadowed by the collapse in many exploited vertebrates, especially finfish (McManus, 1997). This is primarily due to their relatively minor contribution to human protein requirements and the generally held belief that molluscs possess greater resilience to extinction through their perceived wide distribution and a likelihood of hidden pockets of survivors (Jamieson, 1993). Marine invertebrates in general are seriously under-represented within the IUCN Red List (IUCN, 2013). Only cuttlefish, lobsters and scleractinian corals have been fully assessed and published (Carpenter et al., 2008; IUCN, 2013). Although limited research on the impact of habitat loss and fishing pressure on marine gastropod molluscs has been undertaken on a regional scale including for shell fisheries (Newton et al. 1993; Queensland Government 2007), there have been no comprehensive assessments of trends in species abundance, commercial and environmental impacts and extinction risk to any genera with a global biogeographical distribution.

Cone snails of the genus *Conus* offer an excellent opportunity to explore global threats to marine molluscs owing to their exceptional diversity (Bouchet, 1990), wide distribution, high degree of endemism, varied depth distribution (Röckel et al., 1995), and an established global market in their trade from amateur shell collectors to commercial traders (Rice, 2007). In addition, cone snails are used in some communities in the Pacific as an occasional foodstuff (Chadwick & Olivera, 2009) but, more importantly, they are actively targeted by international drug companies and researchers as a potential pharmacological resource (Garber, 2005).

Cone snails constitute the family *Conidae,* which together with the *Turridae* (turrid snails) and *Terebridae* (auger snails) comprise the superfamily *Conoidea* otherwise known as *Toxoglossa* (‘poison tongue’) owing to the venom apparatus they deploy for immobilising prey (Taylor, Kantor, & Sysoev, 1993). The *Conoidea* form part of the order *Neogastropoda* in the sub-class *Prosobranchia* of the class *Gastropoda* of the phylum *Mollusca* (Röckel et al., 1995).

Cone snails live throughout the world’s tropical coastal waters with a steep latitudinal diversity gradient away from the tropics, extending into cooler regions that include southern California, northern Gulf of Mexico, Florida and the Carolinas, North Africa, the Mediterranean, South Africa, Australia, southern Japan and China (Kohn & Perron, 1994). Distribution varies widely with some species occurring across the entire tropical Indo-Pacific but others restricted to a single bay or seamount (Monteiro et al., 2004; Röckel et al., 1995).

The genus *Conus* is taxonomically challenging. Although morphological characteristics of the shell remain the initial means of species identification (Röckel et al., 1995), more recently, other traits have also been employed to differentiate among species, in particular the radular teeth used in the capture of prey, whose shape and structure not only reflects the dietary preferences of the species (Tenorio et al., 2012) but may also be specific to a single species (Franklin et al., 2007). Separation of species through DNA sequence variations provides even greater reliability, but more recently, character-based DNA barcoding has been highly effective in distinguishing among closely-related species (Zou et al., 2011). For this assessment we relied upon expertise from taxonomists in *Conus* to create a dataset of valid species.

The fossil record indicates that the first *Conus* appeared in a sea that covered what is now England and France during the Lower Eocene around 55mya (Kohn, 1990). During subsequent radiations the genus expanded around the globe and by the Holocene had formed into four biogeographical regions: Indo-Pacific (IP), Eastern Pacific (EP), Western Atlantic (WA), and Eastern Atlantic (EA). Although widening of the Atlantic during the Cretaceous and Cenezoic has today created an impermeable barrier to *Conus* crossing the ocean, there have been some migrations in the past, as witnessed from the fossil record and more recently by *C. ermineus* extant in both the EA and WA and *C. chaldeus, C. ebraeus* and *C. tessulatus* found in both the IP and EP (Duda & Kohn, 2005).

The majority of the 632 species of *Conus* assessed (53.6%) occurs in the infralittoral zone of 5 m deep or less, with most of the remaining species (27.7%) at 50 m deep or less. However, there are some species such as *C. teramachii* that live in deeper parts of the continental shelf extending to 1,000 m where they may be brought to the surface as bycatch of demersal fisheries. The bathymetric ranges of individual species vary considerably with some shallow water species living within a one or two metre depth range and some deep-water species being found within a 500 m range or more (Röckel et al., 1995).

Microhabitats vary by species and most often consist of sand or mud into which the cone snail may burrow, but may also include inter-tidal limestone benches (the smooth remains of reef structures from earlier geological periods when sea levels were higher (Kohn, 1983)) with sand or algal turf, sub-tidal reef platforms with living and dead corals, or boulders with sandy layers (Kohn, 1968). They may also be found among coral rubble and occasionally among mangroves and sea-grasses.

Figure 1. Diet and toxicity. Left: *C. geographus* Linnaeus, 1758; piscivorous, 65-165mm; intertidal to 20m; significant fatality risk to humans. Centre: *C. textile* Linnaeus, 1758; molluscivorous, 40-150mm; intertidal to 50m; handle with extreme caution. Right: *C. betulinus* Linnaeus, 1758; vermivorous, 55-177mm; intertidal to 20m; minimal risk to humans; note operculum. All species Indo-Pacific. Image: H. Peters

Cone snails are generally nocturnal in their feeding habit (Kohn, 1959) and group-specific in their preference for worms, molluscs or fish (Fig. 1) although some species have a mixed diet (Duda et al., 2001). The smallest groupings by diet are the obligate piscivores with around 50 species (Olivera et al., 1999; Röckel et al., 1995), and obligate molluscivores with approximately 80 (Livett et al., 2004). The majority of *Conus* are vermivorous with polychaetes representing the largest dietary component, that can be the exclusive source of food for some species (Röckel et al., 1995). All cone snails use venom to immobilize their prey. The diversity of venoms employed by a particular species in the capture of prey is a reflection of the degree of specialisation in its diet (Remigio & Duda, 2008).

From the earliest civilizations, people have prized cone shells for their exceptional beauty, with examples discovered among prehistoric artefacts used for personal adornment extending back 5,000 years (Terlau & Olivera, 2004). Their striking patterns and wide range of colours and shades continue to attract collectors today with rare examples in perfect condition changing hands for thousands of dollars with common and abundant species traded for cents to a dollar or two each (Rice, 2007).

Over millions of years *Conus* has evolved a battery of peptide toxins (conopeptides / conotoxins) for immobilizing prey (Olivera, 1997). The venom of each species is a cocktail mixed from between 50 and 200 different peptides each of only 10 to 35 amino acids in length and is generally targeted at voltage-gated or ligand-gated ion channels (Terlau & Olivera, 2004). These conopeptides have become a focus for biomedical research worldwide (Garber, 2005). Indeed, with the probability that there are on average over 100 distinct toxins for each species (Terlau & Olivera, 2004), as a whole, the *Conidae* can probably synthesize in excess of 50,000 toxins with little, if any, replication (Craig et al., 1999).

Cone snails are therefore important to: a) biodiversity; they have evolved into one of the largest of all marine genera, b) biopharmaceutics; they offer unparalleled opportunities in the development of novel drugs, and c) economics; their shells provide income to poor fishing communities through sales to tourists, traders and a global business in the specimen shell trade.

Habitat loss is considered by many malacologists to be the primary risk factor facing tropical marine mollusc species (Bouchet pers. comm. 2011) and there is plenty of hard evidence to support this view. In Queensland, Australia, for example, abundance and species richness of mollusc assemblages have been shown to be adversely affected by removal of subtropical mangrove forests, with population declines of 83% recorded (Skilleter & Warren, 2000). In San Diego, Southern California the endemic horn snail, *Cerithidia fuscata,* that lived along intertidal mudflats was last seen in 1935 after pollution and dredging had driven it to extinction (Carlton, 1993). Where coral cover has been extensively damaged or degraded through pollution, sedimentation, coastal development and destructive fishing, as witnessed throughout much of the tropics, coral-associated molluscs such as the *Conidae* are being usurped by bivalve crevice dwellers (Zuschin et al., 2001).

In this paper we report one of the first comprehensive extinction risk assessments of a taxonomically well-resolved marine taxon. Our research assesses the extinction risk to the global populations of *Conus*, examining each species' distribution, current and projected threats from disturbance to habitats, pollution, coastal development, and shell gathering. We have examined where possible the effects of fragmentation on populations and the likely impact of demersal fisheries on deeper water species. The assessment enables us to reappraise whether marine taxa are less extinction prone than terrestrial. In addition, our aim is to provide data in support of conservation measures for those species at the greatest risk of extinction over the short to medium term.

2. Methods

2.1. Red List Assessment

We used the assessment standards and procedures of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species to assess extinction risk to 632 species of *Conus*. This is the world's leading resource for describing the global conservation status of plants and animals and uses a standard methodology to classify species into one of nine categories, together with a codified set of criteria (IUCN Standards and Petitions Subcommittee, 2010). The assessment includes examination of the effects of both ecological change and commercial exploitation on the subject taxa. Data derived during the research and discovery process for each species is compiled to a standard format together with maps, images and other supporting documentation.

Following taxonomic review, we divided valid species into 12 biogeographical working sets for detailed assessment. A comprehensive assessment was not possible for those species where data was substantially absent. For example, species endemic to areas of protracted civil unrest such as the Horn of Africa may not have been researched in the field for many years. Coincidentally, these regions are not generally subject to intensive coastal development, harbour works and refineries and so may offer a degree of protection to marine taxa. Similarly, species occurring in deep water, where recovery is most commonly through fisheries by-catch, often suffer a paucity of data including extent of distribution and habitat types. Furthermore, bathymetry data will often rely on the questionable estimation of fishers. Wherever possible for deep-water *Conus*, we have focussed our attention on the level of demersal fishing in the area, including destructive methods such as dredging that may seriously affect mollusc assemblages.

Most *Conus* species, however, occur in shallow water where impacts such as coastal development, pollution and habitat destruction can be more easily recorded. Such threats can give rise to population fragmentation leading to a serious decline in abundance which may be difficult to quantify until it has become extreme. However, indicators including market prices for specimen shells provide a useful guide to increasing scarcity. Knowledge voids are common for *Conus* but where they occur we have, where possible, used estimation or inference using suboptimal data permitted under Red List standards (IUCN Standards and Petitions Subcommittee, 2010). Despite this, 13.8% of *Conus* species were found to be so deficient in data we were unable to make an assessment with any degree of reliability.

2.2. Key indicators of risk

2.2.1 Distribution

A key indicator of potential risk to a species is the size of its geographical distribution. The Red List standard assessment uses two measures: Extent of Occurrence (EOO) and Area of Occupancy (AOO). EOO for marine species is the area within a polygon drawn around the boundary of the species' range, excluding land areas. This will include areas which may not be physically occupied by the taxon, e.g. deep water, but which could contribute to larval dispersal. AOO is the physical area within the EOO in which the taxon is known to occur. For shallow water species, this may be calculated from the perimeter of an island or length of coastline, extended by the width of habitat calculated from the known or inferred bathymetric range of the species over the area under review. However, for 'linear' habitats such as rivers and coastlines, IUCN suggests that their standard habitat width of 2 km should be used in computing AOO (IUCN Standards and Petitions Subcommittee, 2010) and we have adopted this approach in the assessment for *Conus*. It should be noted that both the AOO and the EOO are only of major significance in assessing the level of threat if the species has a restricted range.

2.2.2. Number of Locations

It is possible that a catastrophic event could have a profound effect on the population size of some species. Although marine molluscs are resilient in being able to endure physical forces such as extreme weather events, small populations may be extirpated as a result of sudden habitat loss caused by catastrophic events such as major oil spills. The 'location' count indicates the number of areas in which a single catastrophic event could affect all individuals of the taxon present, events that may cumulatively drive a species into extinction. The value of this measure is another key factor in determining the level of risk a global population faces.

2.3. Literature search

We conducted a comprehensive search through published papers and other literature for data relating to *Conus* species' populations, depth, distribution, habitats, trade in animals and shells, use for foodstuff, pharmaceuticals, etc., together with any conservation measures in place, including indirect conservation as may be offered by marine protected areas. We sought information on current and possible future threats, including coastal development for tourism, industry or port construction, nutrient loading from agricultural run-off, pollution from domestic and industrial effluent, intensive trawling, siltation from land-based sources, dredging for shipping channels and mineral extraction. Data on activities such as these can often only be found in trade publications, contract award notifications etc.

We also examined the market in shells to determine 'collectability', pricing fluctuations, scarcity and demand. Some shells with exceptional colour and form will achieve iconic status, and if they are also rare like *C. gloriamaris* or *C. milneedwardsi*, it adds to their cachet. Species that live within a highly restricted range, within a single bay for example, are often at heightened risk from human activity. This particularly applies to shallow water species which may be gathered as curios in areas where new beach tourism projects are being developed or planned. We synthesised distribution data including observed fragmentation, location counts, marketability, population declines and threats for each species to apply one of the nine categories listed below.

2.4. Assessment categories

There are three categories of extinction risk: Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) that broadly define 'extremely high', 'very high, or 'high' risk of extinction respectively. In addition, there are two extinct categories, Extinct (EX) and Extinct in the Wild (EW), and three other categories: Near Threatened (NT) for species that will be elevated to a threatened category in the short term unless the potential risk is removed; Data Deficient (DD) where there is insufficient data to determine a category, and Least Concern (LC) where current and projected population levels indicate the species is not at risk. As this was a comprehensive assessment, we did not use the category Not Evaluated (NE), where the species has been recorded but no assessment has been carried out.

For *Conus*, the criteria in support of the selected category are primarily derived from a range of variables based on estimated population size and/or level of decline together with species range size and location count.

2.5. Synthesis and pre-publication checks

Following our research and assessment, the results were reviewed by a panel of fourteen international experts, each with specialist knowledge of the *Conus* species within their allotted biogeographical working sets. The review took the form of a five day synthesis workshop with teams comprising leading academics together with renowned specialists from the commercial sector with comprehensive field knowledge of species' distribution, scarcity and threats, and facilitators experienced in Red List standards and procedures. This peer-review process confirmed or modified findings of the original assessment authors, and allowed inclusion of supplementary field-based knowledge from the participating experts. All reports were checked for consistency by the Mollusc Specialist Group of the IUCN Species Survival Commission before final approval and submission for publication through the IUCN Red List Unit.

3. Results

3.1. Global threats

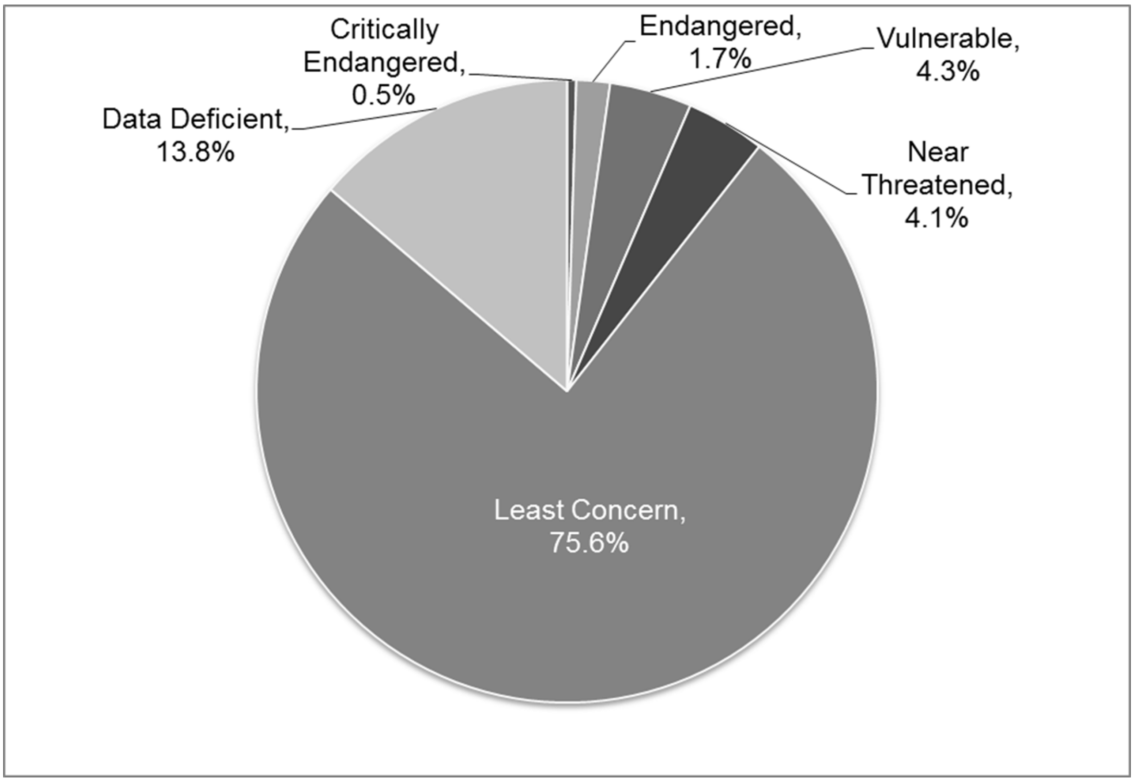


Figure 2. Global extinction risk to *Conus*. The percentage contribution for each assessed category to the global diversity of 632 spp of *Conus*. These are represented by 3 Critically Endangered species; 11 Endangered; 27 Vulnerable; 26 Near Threatened; 87 Data Deficient, and 478 of Least Concern.

Three of 632 *Conus* species assessed were considered to be Critically Endangered (CR), 11 Endangered (EN) and 27 Vulnerable (VU), which together represent 6.5% of all global species (Fig. 2), with a further 26 species (4.1%) categorised as Near Threatened (NT). Over one in ten of all *Conus* species is therefore considered at risk or may become so in the near future. Eighty-seven species (13.8%) were categorised as Data Deficient (DD) of which 75 (86.2%) occur in the Indo-Pacific.

Table 1. Threatened *Conus* of the Eastern Atlantic (EA).

Critically Endangered (CR)		**Endangered (EN)**		**Vulnerable (VU)**	
Cape Verde	*C. lugubris*	Cape Verde	*C. ateralbus*	Angola	*C. allaryi*
Cape Verde	*C. mordeirae*	Cape Verde	*C. crotchii*	Angola	*C. cepasi*
Cape Verde	*C. salreiensis*	Cape Verde	*C. cuneolus*	Angola	*C. xicoi*
		Cape Verde	*C. fernandesi*	Cape Verde	*C. decoratus*
		Senegal	*C. belairensis*	Cape Verde	*C. felitae*
		Senegal	*C. bruguieresi*	Cape Verde	*C. fontonae*
		Senegal	*C. cloveri*	Cape Verde	*C. regonae*
		Senegal	*C. echinophilus*	Cape Verde	*C. teodorae*
		Senegal	*C. hybridus*	Senegal	*C. cacao*
		Senegal	*C. mercator*	Senegal	*C. guinaicus*
		Senegal	*C. unifasciatus*	Senegal	*C. tacomae*

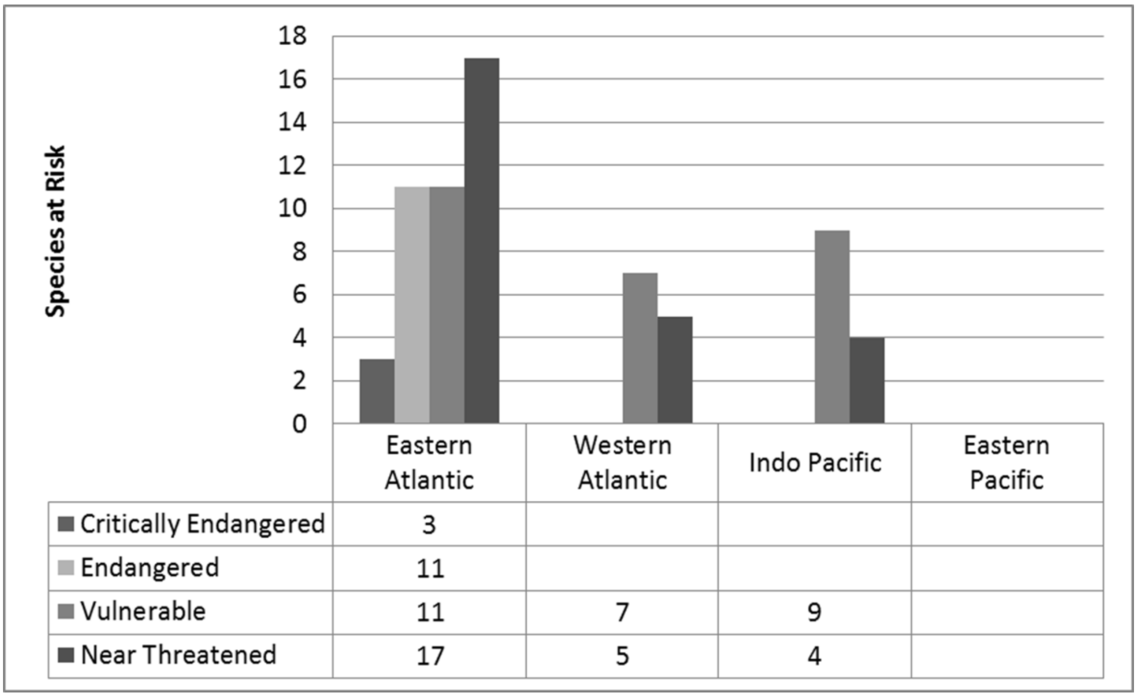
Table 2. Threatened *Conus* of the Western Atlantic (WA).

Vulnerable (VU)	
Aruba	*C. hieroglyphus*
Florida	*C. anabathrum*
Florida	*C. stearnsii*
Bahamas	*C. richardbinghami*
Brazil	*C. henckesi*
Martinique	*C. hennequini*
Venezuela	*C. duffyi*

Table 3. Threatened *Conus* of the Indo-Pacific (IP).

Vulnerable (VU)	
Oman	*C. ardisiaceus*
Oman	*C. melvilli*
S Red Sea	*C. cuvieri*
Mascarenes	*C. julii*
Réunion	*C. jeanmartini*
SE South Africa	*C. immelmani*
W Thailand	*C. rawaiensis*
Australia	*C. compressus*
Australia	*C. thevenardensis*

All 14 CR and EN species occur in the waters off Cape Verde and Senegal, West Africa (Table 1). Of the 27 assessed as VU, eight are from Cape Verde and Senegal with three from Angola (Table 1), seven from the Western Atlantic (Table 2), and nine from the Indian Ocean, including two from Western Australia (Table 3). Only three threatened species occur east of longitude 60 (Oman to Mascarenes): *C. rawaiensis* from Western Thailand and *C. compressus* and *C. thevenardensis* from Western Australia – all VU. According to this assessment procedure, there are no threatened species in the Pacific (Fig. 3). Of the 26 Near-Threatened species (NT), Cape Verde and Senegal are again over-represented with 14 of the 17 species from the Eastern Atlantic. Of the remainder in this category, five are from the Western Atlantic, one from the Western Indian Ocean, and three from the Pacific (Fig. 3).



	Eastern Atlantic	Western Atlantic	Indo Pacific	Eastern Pacific
■ Critically Endangered	3			
■ Endangered	11			
■ Vulnerable	11	7	9	
■ Near Threatened	17	5	4	

Figure 3. Number of Conus species at risk by ocean basin for each threatened category. There are no species at risk in the Eastern Pacific.

3.2. Analysis by Region

Marine molluscs that are wide-ranging are likely to be more resilient against threats than those that are range-restricted, with dispersed populations providing a reservoir for re-colonization in the event of local extirpations (Roberts & Hawkins, 1999). The Eastern Atlantic species occupy a limited length of coast with few islands when compared to the Western Atlantic and, more particularly, the Indo-Pacific. It is also intersected by large rivers draining the tropical land mass of Africa which render substantial areas of coastal water unsuitable for many marine molluscs. Conversely, islands of the tropical Indo-Pacific and Caribbean contribute substantial areas of shallow water habitat suitable for taxa such as *Conus* and do not generally suffer any significant flux of freshwater. Fig. 4 shows the percentage distribution of species' range sizes within each of the four oceanic regions. This graphically illustrates that wide-ranging *Conus* species, i.e. AOO > 2,000 km^2, are uncommon within the Eastern Atlantic compared to the other regions.

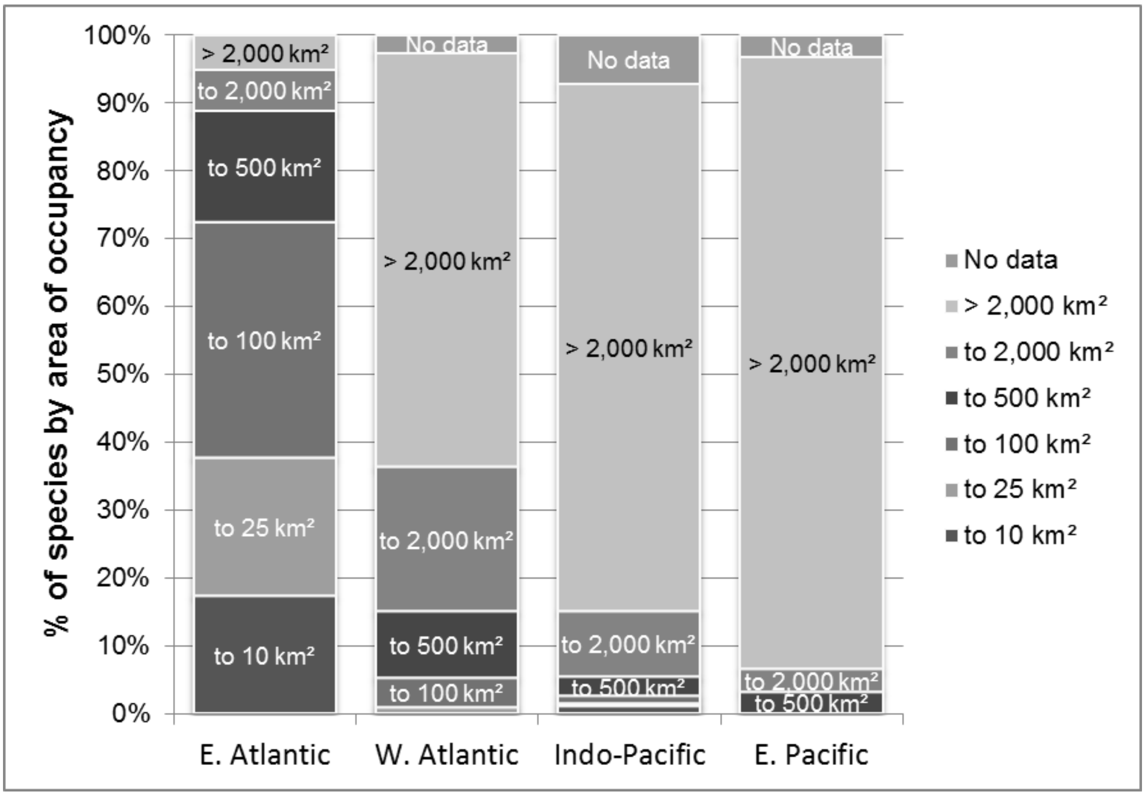


Figure 4. Contribution of range-restricted species to *Conus* biodiversity within each ocean basin. This illustrates by region the percentage of total species by area of occupancy, with wide-ranging species, i.e. > 2,000km^2 being minimal in the Eastern Atlantic but the major contributor to the Indo-Pacific and Eastern Pacific *Conus*. The abbreviated key describes the band sizes, e.g. to 10 km^2 = 0-10km^2, to 25 km^2 = 11-25km^2, to 100km^2 = 26-100km^2, etc.

3.2.1 Eastern Atlantic

Ninety-eight species of *Conus* occur along the Eastern Atlantic seaboard from the Mediterranean and Morocco south to Namibia, with associated island archipelagos including the Canaries, Azores, and Cape Verde (plus one: *C. ermineus*, that also occurs in the Western Atlantic and was included in that region). There is one species from the island of St Helena, *C* *jourdani*, within this grouping although no live specimens have been observed and it is categorised as DD. With three CR, 11 EN and 11 VU species, representing 25.5% of the Eastern Atlantic species, and a further 17 species NT (Table 1), 42.9% of Eastern Atlantic *Conus* are considered at risk of extinction or liable to become so. This exceptional concentration of threatened species is found nowhere else across the genus' wide distribution and the disproportionate contribution of species from Cape Verde and Senegal demands further explanation.

Cape Verde is home to 8.9% of all *Conus* species. With 53 species endemic from a total of 56 present in the archipelago, endemism is exceptionally high at 94.6%. Forty-three species are each restricted to a single island. All three CR species are found in Cape Verde, *C. lugubris, C. mordeirae,* and *C. salreiensis,* together with four EN and five VU (Table 1). There are also 12 NT species. With 24 species in either a threatened or near-threatened category, Cape Verde has 45.3% of its *Conus* diversity at risk compared to 7.4% for the remainder of the world. Angola and Senegal contribute the next largest numbers of endemic *Conus* species with 22 and 13 respectively, which together with 53 species endemic to Cape Verde account for 89.8% of all 98 species within the Eastern Atlantic. Senegal contributes seven EN and three VU species with Angola contributing three VU (Table 1).

3.2.2. Western Atlantic

We assessed 113 species of *Conus* from the Western Atlantic where they occur from the Carolinas and Bermuda south to Brazil and throughout the Gulf of Mexico and Caribbean. Species are widely variable in their distribution across the region. There are six threatened species, all categorised as VU (see Table 2), representing 5.3% of the total and a further four NT, together resulting in 8.8% of *Conus* species within this region considered at immediate or potential risk.

3.2.3. Indo-Pacific

We assessed 390 species of *Conus* from the Indo-Pacific where they occur across the tropics and subtropics, from East Africa south to South Africa and north to the Red Sea and the Persian Gulf and across the whole of the Indian Ocean and the Western and Central Pacific, south to Australia and New Zealand, north to Japan, east to French Polynesia and Easter Island and northeast to Hawaii.

Only nine species were found to be VU. All occur within the Indian Ocean with six species from the western flank: two from Oman, one from the southern Red Sea, two from the Mascarenes and one from South Africa. From the eastern flank there is one species from Thailand and two from Western Australia. There are also four NT species including one from Oman with the other three being the only *Conus* species potentially at risk in the Pacific – one each from Queensland, the Philippines and the Marquesas.

3.2.4. Eastern Pacific

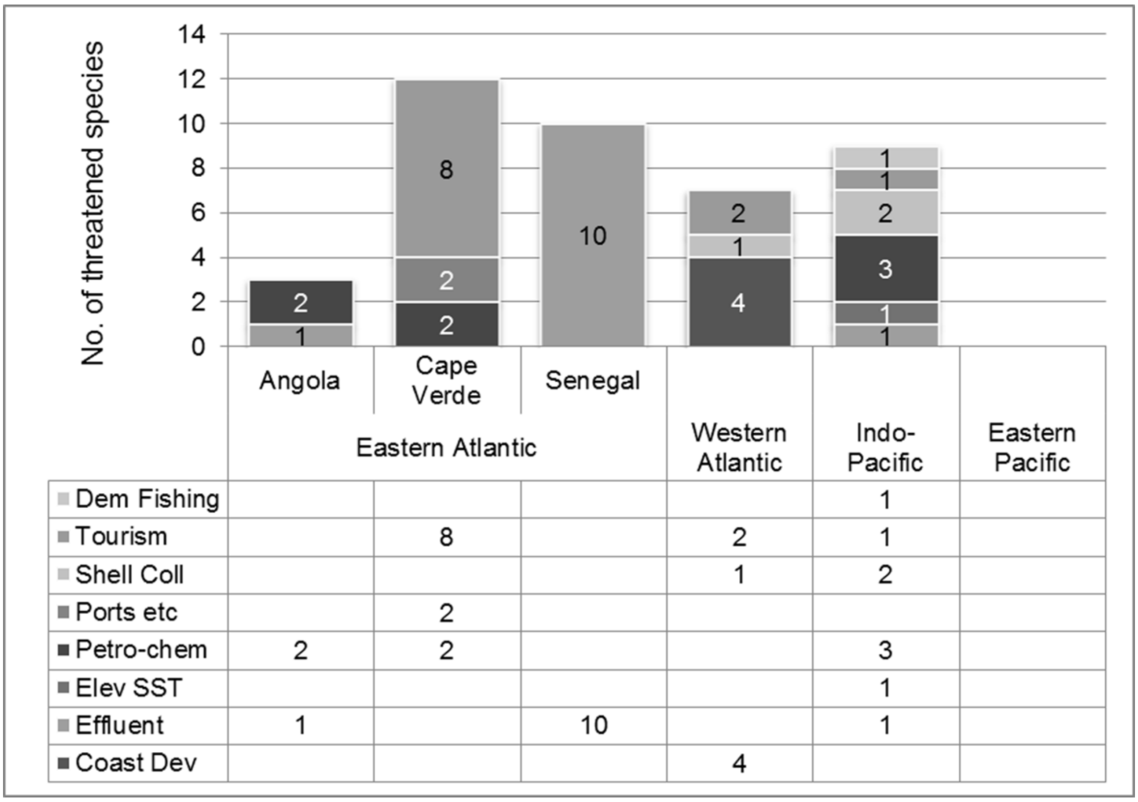
We assessed 31 species of *Conus* from the Eastern Pacific where they occur from Southern California south along the Pacific coast of Meso-America to Southern Ecuador including the Galapagos and other island groups of the region.

No species were assessed as threatened or near threatened in the Eastern Pacific.

3.3. Threats

The nature of threats to those species of *Conus* at risk of extinction are varied and depend primarily, but not exclusively, on the proximity and nature of human habitation and development adjacent to coastlines where the molluscs occur. This alone, however, will not normally create a scenario for species extinction. Wide-ranging species are capable of maintaining their viability through resilience from multiple sub-populations. Although most threatened *Conus* species are range-restricted, this is not always the case: two species from the USA, *C. anabathrum* and *C. stearnsii* occur along the west coast of Florida where their ranges are substantially fragmented by shoreline development. However, restricted range, coupled with shallow water habitat, magnifies the impact of stressors such as coastal development or pollution. Of the 41 *Conus* species globally assessed as threatened with extinction, 32 (78.0%) occur within an AOO of 250 km^2 and a minimum depth of 5 m or less. In the Eastern Atlantic, of the 25 threatened species, this rises to 100%.

Threats to those *Conus* species assessed within one of the three threatened categories can be classified into four causal groups (Fig. 5): 1. pollution, either from proximity to actual or potential petro-chemical spills, or urban and industrial effluent; 2. disturbance to habitat from coastal development either resulting from human population increases, e.g. sea defences, residential and commercial structures, including aquaculture facilities, and port construction, or tourism infrastructure. Also included in this group is damage to habitat caused by damaging and extensive demersal fishing; 3. shell gathering, and 4. environmental change e.g. elevated sea-surface temperatures. There will frequently be a combination of causes, for example tourism infrastructure may also increase shell gathering. Similarly, the proximity of shanty towns devoid of planning regulations poses an elevated risk of effluent discharge into the marine environment. Finally habitat destruction from sand removal, beach nourishment works and recreational use of the sea may all result in disturbance to local mollusc populations.



	Angola	Cape Verde	Senegal	Western Atlantic	Indo-Pacific	Eastern Pacific
	Eastern Atlantic					
■ Dem Fishing					1	
■ Tourism		8		2	1	
■ Shell Coll				1	2	
■ Ports etc		2				
■ Petro-chem	2	2			3	
■ Elev SST					1	
■ Effluent	1		10		1	
■ Coast Dev				4		

Figure 5. Main threats to *Conus* by ocean basin. The number of *Conus* species at risk (consolidation of CR, EN and VU) indicating primary causes of endangerment, being demersal fishing, tourism, shell collecting, ports and harbours, petro-chemical spills, elevated sea-surface temperatures, effluent discharge and runoff, and coastal development.

Cape Verde is experiencing a major structural change from a largely services and fisheries based economy supported by development aid and remittances from its diaspora to one of beach tourism (AfDB et al., 2012). This is accompanied by a myriad of threats from road and resort construction, unlawful removal of beach sand for cement (Irwin & Wilson, 2011) and casual shell gathering by tourists. All three CR species occur in Cape Verde where their populations are already reduced. *C. lugubris* and *C. mordeiiri* live in areas where habitat has already been lost to development and *C. salreiensis* which is restricted to a single bay has had observable declines in population since a harbour was constructed. Each is found in an area along a shallow coastal strip of less than 11 km in length. Harbour expansion and the accidental discharge of engine fuel increase the pressures on small, range-restricted *Conus* populations such as *C. fernandesi, C. fontonae* and *C. regonae*. With so many *Conus* species occupying highly restricted ranges within the archipelago, modest threats such as these could have a profound impact.

Around the Dakar peninsula, Senegal, it has been observed that species restricted to its highly polluted coastal waters are showing a marked decline in abundance coupled with an overall diminution of shell size including *C. echinophilus, C. hybridus, C. mercator* and *C. unifasciatus*. In common with many maritime cities in developing countries, Dakar suffers from a burgeoning population with largely inadequate waste-processing infrastructure. South in Angola, *Conus* species categorised as at risk face similar threats to those in Senegal.

In the Western Atlantic some disturbance to *Conus* can be traced to human migration to the Florida coast. Tourism and retirement have driven large-scale construction projects for condominiums and other coastal infrastructure leading to significant loss of habitat for *C. anabathrum* and *C. stearnsii.* Tourism also represents the underlying risk to the Vulnerable species *C. hennequini* in Martinique and *C. hieroglyphus* in Aruba. Shell collecting in the Bahamas threaten *C. richardbinghami*. General coastal development in Bahia, Brazil threatens *C. henckesi* where it occurs only off two small islands. The Venezuelan government has voiced plans for substantial development on the islands of Los Roques which will place the shallow water species, *C. duffyi* at risk.

The *Conus* species of the Indo-Pacific are at less risk. In the north-western Indian Ocean, the Persian Gulf, the southern Red Sea including the Gulf of Aden and the Horn of Africa, civil wars, poverty, piracy and the security situation offer some degree of protection from coastal development. However, there are still concerns from oil spillage in the region and two scarce species from Oman, *C. ardisiaceus* and *C. melvilli* together with *C. cuvieri* from Djibouti are categorised as VU. In Southern Natal and the Mascarene islands of Mauritius and Réunion respectively, *C. immelmani* and *C. julii*, have both declined in numbers almost certainly from over-collecting, with *C. jeanmartini* also from Réunion being subject to intensive trawling in its deep-water habitat.

In the Eastern Indian Ocean, *C. rawaiensis* occurs only in an area estimated at less than 35 km^2 in a single location off the western shores of Thailand in a region zoned for tourism. In Western Australia, an extreme localized warm-water event in 2011 from La Niña, in the region around Geraldton to Shark Bay including the Abrolhos Islands, resulted in a catastrophic decline of marine molluscs including *Conidae*. *C. compressus*, a restricted range species, possibly suffered a 50% decline in abundance. Also in Western Australia, *C. thevenardensis*, already rare, is subject to a range of threats including a large oil installation, tourism and dredging.

3.4. Other Red List categories

The results for the three threatened categories paint an incomplete picture. There are also 87 species assessed to be Data Deficient and 26 as Near Threatened, together representing 17.9% of the global diversity. Many of the Data Deficient species are considered to be scarce in the wild even though the causes and extent of the threats they face cannot yet be determined with sufficient accuracy. Over one quarter of these (26.1%) are found in deep-water below 100 m, against a global proportion of 13% for all *Conus* species. Specimens may be brought to the surface from these depths as by-catch from fisheries. However, demersal gear such as dredges may also contribute substantially to the endangerment of the species recovered through destruction of their habitat, especially for those that are also of restricted range. Occurrence in deep water does not automatically result in a DD categorisation. Despite paucity of data, taxa with a known distribution greater than 2,000 km^2 but with no known threat would normally be assessed as Least Concern. At the other extreme, there are also a number of DD species where there is an almost total absence of recent sightings but extinction cannot be proven, i.e. there is reasonable doubt that the last individual has died (IUCN, 2012). This is exemplified by species such as *C. jourdani* from St Helena which is only known from 'dead' shells washed onto the beach in one small bay; *C. bellulus* and *C. luteus* which have not been reported since the 1970s; *C. splendidulus* which has not been seen in 20 years and *C. sauros* which is possibly extinct. The plight of the DD and NT species are at risk of being ignored because they are not in a threatened category.

4. Discussion

It is widely believed that extinction risk in the sea is less likely than in the terrestrial environment and that this is supported by the fossil record (McKinney, 1998; Roberts &

Hawkins, 1999). This view is based largely on perceived high fecundity, greater dispersal ability and geographic range size (Roberts et al., 2002). With 6.5% of *Conus* species at risk globally this would appear to follow this perception, however, in regions offering reduced dispersal opportunity, such as the whole of the Eastern Atlantic, 25.5% of species are threatened. Cone snails here have a similar level of extinction risk to species in well-assessed terrestrial taxa, such as freshwater invertebrates (34% of 7,784 species assessed at risk), lepidoptera (from 8.5% of butterflies in Europe to 17% in the U.S. at risk), European terrestrial molluscs (20% at risk) (Darwall et al., 2012; Gerlach et al., 2012) and bryophyte flora from the Canaries (21% at risk) (González-Mancebo et al., 2012). Contributing to the pattern seen, many cone snails have limited dispersal ability, small geographic ranges and/or are rare. The level of extinction risk is similar in other well assessed marine taxa, including corals (27% of species at risk) (Carpenter et al., 2008; Kemp et al., 2012) and scombrid and billfish (11% of 61 species at risk) (Collette et al., 2011). Given the rapid escalation of threats to the marine environment (Roberts, 2012), if the pattern seen in these groups is typical of marine species generally, then there is a high risk that extinctions will soon become common in the sea, just as they now are on land.

Our global assessment of the conservation status of all 632 cone snails shows that three-quarters (75.6%) of species are classified as Least Concern under IUCN Red List standards. However, beneath this relatively optimistic result lies a picture of substantial regional variations with indicators signalling wider concerns. In the Eastern Atlantic along the shores of Senegal, Cape Verde and Angola, species restricted in their range and subject to the effects of industrialisation and urbanisation face an elevated risk of extinction. Endemism for marine species occurs most commonly in isolated island groups where the original dispersal was assisted by a pelagic larval stage or by transport on rafting matter (Devantier, 1992). Endemics may also be found where there may be non-reversing currents transporting water away from the tropics towards higher latitudes (Roberts et al., 2002). All Cape Verde endemic *Conus* have a non-planktonic larval stage having lost the ability during speciation to feed during larval dispersal (Cunha et al., 2005). This conforms to the hypothesis that non-planktonic, i.e. lecithotrophic, species of *Conus* commonly originate from planktotrophic species (Duda & Palumbi, 1999). All three species assessed as Critically Endangered occur in the waters off Cape Verde where they are exposed to habitat degraded through coastal development primarily driven by tourism. Similarly, of the 11 Endangered species, four are found in Cape Verde with the remaining seven occurring off the coast of Senegal, in particular the Dakar peninsula, where high levels of pollution from industrial and residential effluent is thought to be the driver of declining abundance and observable reductions in body size. A further 11 species (40.7%) of the 27 assessed as Vulnerable occur in Cape Verde, Senegal and Angola, making West Africa home to 61% of the 41 *Conus* species threatened with extinction. Of the remaining 16 species categorised as Vulnerable, seven are found in the Western Atlantic where they are primarily exposed to coastal development, tourism and shell collecting. The remaining nine occur in the Indian Ocean where petrochemicals, shell-collecting and elevated sea-surface temperatures represent the principal causes of decline.

4.1. Threats

4.1.1. Overfishing

The effect of overfishing on the abundance of fish stocks has been extensively reported in both the scientific and general press over many years (Myers et al., 1997; Thurstan et al., 2010). However, threats to invertebrates from fishing are seldom equated with extinction, especially marine molluscs. Although extremely unusual, near-extinctions in this group have occurred in the recent past; for example in the white abalone *Haliotus sorenseni* from southern California and Baja California by the mid-1990s had been fished to the edge of extinction (National Marine Fisheries Service, 2008). Once counted in the millions there are now probably less than 1,600 individuals remaining.

Amongst marine molluscs, most species are sought by shell collectors (Rice, 2007). Although this does not threaten the survival of the vast majority of molluscs, shell collecting has undoubtedly caused the decline and endangerment of some species, particularly ‘trophy’ shells. Throughout the Indo-Pacific, the spectacular giant triton (*Charonia tritonis*), has been extensively fished and in many areas has been extirpated (Moore & Ndobe, 2008). Similarly, although primarily removed for its adductor muscles, the giant clam (*Tridacna gigas*) the largest of all bivalve molluscs, has met the same fate (Wells, 1997). In Zanzibar, East Africa, the cowries *Cypraea tigris, C. histrio* and *C. lynx* were found to be up to 18 times less abundant in exploited tourist areas (Newton et al., 1993). We identified three rare species of *Conus* threatened by shell collecting: *C. richardbinghami* from the Bahamas and *C. immelmani* and *C. julii* from the Mascarenes. Taxa already facing pressures from factors such as pollution may be pushed further towards extinction by gathering for shells, yet warning indicators such as sudden price inflation on the shell market may not alone warrant inclusion to a threatened category.

4.1.2. Bioprospecting

Conus is exceptionally important to biomedical science, although there is dispute about the number of animals taken for their bioactive compounds. To protect their intellectual property, pharmaceutical companies are silent on the issue, but researchers are adamant that volumes are negligible. In their dialogue in *Science* Chivian et al. (2003; 2004) raised important concerns about the quantity of cone snails taken from the wild, indicating that thousands were then collected to satisfy research demands (Chivian et al., 2003, 2004). This was forcefully rebutted by Duda et al. (2004) who reviewed recent conotoxin research from which they determined that a maximum of 20 research groups were working on *Conus* toxins at that time, and that any single characterisation required fewer than 21 animals to be sacrificed (Duda et al., 2004). Regardless of where the true determinant lies, balancing the legitimate needs of medical research without further compromising natural resources is essential. Fortunately, alternative, more sustainable options are now available including milking venom without killing the animal (Hopkins et al., 1995), polymerase chain reaction (PCR) sequencing of DNA fragments that requires just one specimen (Livett et al., 2006) and more recently digital marine bioprospecting using massive parallel deep sequencing of transcriptomes that requires only minute samples of bioactive material (Urbarova et al., 2012).

4.1.3. Habitat loss

It has been shown that habit loss leads to declines in species richness, reduced biomass and loss of complexity (Airoldi et al., 2008; Munday, 2004), often accompanied by colonisation by species that inhibit recovery (Thrush & Dayton, 2002). Virtually all of the world's 'trawlable' area of continental shelf has already been altered, and about half the area of all the continental shelves is hit by trawls every year (Watling & Norse, 1998), changing the structure and function of habitats, destroying assemblages and resulting in homogenisation of the seabed (Gray et al., 2006). Of 133 marine species that have been recorded as having gone extinct either regionally or globally, 37% were attributed entirely or in part to habitat loss (Dulvy et al., 2003). Extinctions of marine gastropod molluscs from loss of habitat are set to continue and include the horn snail *Cerithidea fuscata* from southern California last seen in 1935, the eelgrass limpet *Lottia alveus alveus* from the northwest USA last collected in 1929, and from the 19th century the rocky shore limpet '*Colisella' edmitchelli* also from southern California and the periwinkle *Littoraria flammea* from China; all driven to extinction through loss of habitat from anthropogenic causes, with the possible exception of the eelgrass limpet that lost its habitat from a slime mould that may have been introduced from ships' ballast (Carlton, 1993; Roberts & Hawkins, 1999).

Our assessment found that with the exception of three species made vulnerable by shell collecting (see above), all 38 other *Conus* species threatened with extinction are impacted to some degree by habitat loss, either directly from coastal and port development or indirectly from pollution or from human exacerbated natural occurrences such as El Niño/La Niña–Southern Oscillation (ENSO) warm-water events (Fig. 4).

4.2. Red List comparatives

Our *Conus* assessment is the first global study for the IUCN Red List for any marine gastropod mollusc genus and one of the few for marine invertebrates. Other marine invertebrates that have been the subject of a global assessment include 845 reef-building corals, 247 lobsters and 195 cuttlefishes (Kemp et al., 2012). Data Deficiency is a common thread throughout each of these studies with 17%, 35% and 76% of species for each respective grouping (Kemp et al., 2012) compared to 14% for *Conus*. Preliminary results available for oceanic squid show that 57% of this group are of Least Concern with the remaining 43% Data Deficient. As with the data deficient cone snails, many of these cephalopods are deep-water species that have only been captured on a few occasions (Kemp et al., 2012).

Of the 845 corals that have been globally assessed 27.3% fall into a threatened category with a further 20.8% near threatened, although prior to the massive bleaching event of 1998 it has been estimated that 95.3% of non-DD species would have been categorised as Least Concern (Carpenter et al., 2008). The exceptional ENSO event which resulted in this bleaching largely devalues any post-event comparison, although it has been shown that La Niña can impact some mollusc assemblages through stress, changes in productivity and availability of dietary preferences (Riascos et al., 2007). In Australia, the La Niña event of 2010-11 gave the highest monthly Southern Oscillation Index values on record accompanied by elevated sea-surface temperatures in Western Australia (Australian Government, 2012). In the region around Geraldton to Shark Bay including the Abrolhos Islands, this coincided with an estimated 50% mortality in molluscs that included *Conus compressus* (H. Morrison pers. comm. 2011). Scleractinian corals and molluscs, including *Conus,* also share the threat of ocean acidification with the prospect of arrested development in their aragonite-forming structures (Doney et al., 2009; Rodolfo-Metalpa et al., 2011). Of all the threats faced by these fauna this is the most intractable and one that could even determine their continued existence.

For freshwater molluscs, Red List assessments have been completed for 1,500 of the 5,000 described species (Darwall et al., 2012; IUCN, 2013). Results show that out of 7,784 freshwater invertebrates assessed to date, gastropods are the most threatened group with a threat range of 33% (if no DD species are threatened) to 68% (if all DD species are threatened) (Darwall et al., 2012). In common with *Conus*, the threatened species include range-restricted habitat specialists that are particularly at risk from loss of habitat and pollution.

4.3. Further Research and Conservation Priorities

As a global assessment for conservation has not been undertaken on any other marine gastropod mollusc it is not possible to explore relationships between different gastropod genera to identify commonality of risks. Further research is urgently needed to address this issue.

One of the primary sources of information on species distribution, habitats, populations and threats for our Red List assessment has been the specimen shell trade. In many parts of the developing world, trade in shells provides valuable additional revenue to some of the poorest families living along tropical coastlines. Research is needed to assess the threat from rare shell collecting towards mollusc population decline to determine what measures should be taken to enable this activity to continue sustainably while at the same time allowing for protection of vulnerable species.

The need to identify conservation strategies for all species at risk is compelling, although for developing nations, snail conservation is unlikely to become a driver for environmental improvements. In the absence of in situ conservation measures, captive breeding programmes may ultimately be necessary, such as those undertaken for tree snails of the genus *Partula* from the Pacific Islands (Tonge & Bloxam, 1991). At present, except possibly for species such a *C. pennaceus* and *C. textile* that emerge as mature veligers, this is not a viable option, as the complexity of plankton essential for developing larvae cannot be easily replicated (Livett et al., 2004).

Over half (53.6%) of all *Conus* species occur at depths of 5 m or less where they are susceptible to gleaning, and nearly three-quarters (74.5%) occur at or above recreational SCUBA diving depths of 30 m or less. Marine Protected Areas (MPAs) offer one of the few sanctuaries, but regional authorities need encouragement to strengthen enforcement and to erect prominent signage against shell gathering within MPAs.

Cape Verde presents a special case in *Conus* conservation. With 45.3% of its species at risk there is a strong argument for legislating against export of both animals and shells, and with manageable borders the country is ideally suited to export controls. This small archipelago also signals a warning to other nations developing their coastal infrastructure: new roads bring visitors to areas previously protected by their isolation, and illegal sand removal for construction from beaches and shallow water of the littoral zone (Lopes, 2010) pose a constant threat to habitat. Regional authorities should be required to undertake environmental impact assessments that take account of these issues when planning new developments.

The toxins that make *Conus* so successful are generally unique to each species (Livett et al., 2006) and any extinction in the genus could in turn deprive science of a potential pharmacological resource. The extraordinary number of species and the global distribution of these tropical snails make them an important contributor to marine biodiversity, and with the appeal of their shells they help support some of the world's poorest people.

Finally, there exists a well-defined community of cone snail aficionados who together are highly influential in the trade in cone shells. This includes leading academics as well as collectors and dealers. A positive first step from our Red Listing is that following a preliminary presentation of our findings at their international convention, a core of members has been motivated to explore a voluntary embargo in trade of Critically Endangered species and to consider this also for other *Conus* species at risk (Monteiro et al., 2012).

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Chapter 4. The endemic *Conus* of Cape Verde: a special case for conservation

4.1. Preface

The result of the global assessment described in Chapter 3 identified Cape Verde as the most important global centre of endemism for *Conus* species, with 53 of its 56 species assessed occurring only in the archipelago. With 45.3% of its endemic species threatened or near threatened with extinction and with all three critically endangered species occurring there, Cape Verde is an important indicator for other regions of the world where economic development goals may compromise a crucial environmental heritage.

In this chapter, to understand the reasons behind the high incidence of threatened species, I examine more closely the distribution of endemic cone snails around the archipelago. Most species are restricted to a single island with some occurring only in one or two bays, but with all species living in shallow water where they may be exposed to shoreline development, sand excavation, pollution and casual gathering for shells. I examine the rapid economic changes occurring across Cape Verde together with island development plans that could set the scene for mass species extinction.

This paper has been written to the style of Biological Conservation to which is has been submitted for review. For consistency and ease of reading, figures have been inserted close to their first reference in the text rather than separated as in the publisher's version.

I declare that the work submitted is my own. The contribution by co-authors was as follows:

Callum Roberts & Julie Hawkins: Supervision, review and editing.

The endemic *Conus* of Cape Verde: a special case for conservation

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Abstract

Cape Verde in the Eastern Atlantic is typical of many island groups in supporting a wealth of endemic species, both terrestrial and marine. Marine gastropod molluscs of the genus *Conus* occur in coastal tropical waters throughout the globe, but in Cape Verde their endemism reaches its apogee with 53 species out of 56 occurring nowhere else, 44 of which are restricted to a single island and frequently to a single bay. However, Cape Verde is rapidly moving to a tourism-based economy with a projected boom in infrastructure development often coincidental with the shallow-water habitat of many range-restricted *Conus*. Our conservation assessment of all *Conus* to standards of the International Union for the Conservation of Nature (IUCN) Red List of Endangered Species, finds that 45.3% of Cape Verde's 53 species are threatened or near-threatened with extinction compared to 7.4% of 579 species in the rest of the world. The three species determined to be critically endangered and at the cusp of extinction are only found in Cape Verde. Our results explain the current and projected threats to all the endemic *Conus* of Cape Verde and we explore conservation options available including a restriction on exports.

Keywords: Red List, endemism, mollusc, threatened, tourism, pollution, marine

1. Introduction

Small islands and archipelagos, isolated by distance and ocean currents, support centres of endemism in both their terrestrial and marine taxa (Roberts et al., 2002). However, these endemism 'hotspots' are often subject to threats from natural and anthropogenic sources that can have a disproportionate impact on the biodiversity they support. Cape Verde in the tropical Eastern Atlantic, with a high degree of endemism among its flora and fauna typifies such small oceanic archipelagos. Here endemism reaches its apogee in the venomous marine gastropod genus *Conus*. Fifty-six species of *Conus* occur in Cape Verde, fifty-three of which are endemic, with just three, *C. ermineus, C. genuanus* and *C. tabidus*, occurring elsewhere in the Atlantic (Monteiro et al., 2004). Such a high concentration of endemic marine species of the same genus is exceptional and may be unsurpassed (Duda & Rolán, 2005). Other Macaronesian island groups are largely devoid of *Conus* (Monteiro et al., 2004).

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Figure 1. Map of Cape Verde.

Cape Verde is a horseshoe-shaped archipelago of ten volcanic islands and eight islets (Fig. 1) 570 km west of Senegal. It is the most southerly of the Macaronesian islands. The Canary Current flowing south-west from Morocco brings nutrient rich waters to the region attracting both artisanal and international fishing fleets. The six islands to the north: Santo Antão, São Vicente, Santa Luzia, São Nicolau, Sal and Boavista comprise the Windward group (Ilhas do Barlavento); those to the south: Brava, Fogo, Santiago and Maio comprise the Leeward group (Ilhas do Sotavento). With the exception of Santa Luzia, all the islands are inhabited. There is a shallow seamount, the João Valente Shoals, between Boavista and Maio with a platform at 14 m that is probably a guyot (Ramalho, 2011). Shallow water at 20 m also separates the islands of São Vicente and Santa Luzia with its islets of Ilhéu Raso and Ilhéu Branco to the south-east. These islands were probably linked during the Holocene and subsequently separated by sea-level rise (Ramalho, 2011).

Service industries account for 80% of the country's economy, with agriculture and fisheries constituting only 8.2% (AfDB et al., 2012). Cape Verde has few natural resources apart from marine products and services and the land is generally unsuited to agriculture, requiring nearly 90% of food to be imported (AfDB et al., 2012). Tourism is now considered the primary economic force and is responsible for 26% of GDP and 95% of service exports, and apart from attracting foreign investments it also drives the construction sector (AfDB et al., 2012) including a new harbour on Porto Grande, São Vicente, together with international airports on Boavista and São Vicente to augment those already on Sal and Santiago.

Cone snails of the genus *Conus* occur within tropical and subtropical coastal waters throughout the world where for over 55 ma they have evolved into more than 630 species (Kohn, 1990). Those in the waters off Cape Verde form part of the Eastern Atlantic (EA) group of 98 species found from the Mediterranean south along the West African coast to Angola. The arrival of *Conus* in the EA is uncertain. Migration from the Indo-Pacific by way of the Western Cape is today impeded by the Benguela cold current and upwelling that formed after the Miocene (Duda & Kohn, 2005). Similarly the Atlantic forms a barrier to dispersal of larvae from the Caribbean and Gulf of Mexico, although the occurrence of *C. ermineus* on both flanks of the Atlantic, including Cape Verde, indicates that this may have been achievable in the past , however, phylogeny now suggests that *Conus* arrived from the Tethys Sea prior to its closure (Duda & Kohn, 2005).

Cytochrome c oxidase subunit I (COI) sequencing of Cape Verde *Conus* indicates that speciation originated from two ancestral lines (Duda & Rolán, 2005) that resolved into two clades with morphological attributes of small-shelled (typically < 35 mm mean size) and large-shelled (typically ≥ 35 mm mean size) species. The former first arrived on Cape Verde 16.5 mya during early formation of the archipelago, with the latter 4.6 mya (Cunha et al., 2005). Evidence that some speciation may have occurred quite recently is supported by near identical COI sequences between species (Duda & Rolán, 2005). Small-shelled species occur across the archipelago with the more recently arrived large-shelled species confined to the eastern islands of Sal, Boavista, Santiago and Maio (Cunha et al., 2005; Monteiro et al., 2004).

Unlike many cone snails, all endemic Cape Verde larvae are lecithotrophic and obtain nourishment through an egg sac during their pre-metamorphic phase (Kohn & Perron, 1994; Perron, 1981). This has resulted in low larval production and limited dispersal ability but accelerated speciation, and probably accounts for the unusual diversity of species in the archipelago where the majority are restricted to single islands or even single bays (Cunha et al., 2005). Rises in sea level have isolated most of the island assemblages and driven allopatric speciation (Cunha et al. 2005; Cunha et al. 2008).

This high degree of endemism among Cape Verde *Conus* with a hereditary loss of functionality to freely disperse, low larval production and confinement to a highly restricted range, has set the scene for an elevated threat of extinction. With a government policy of promoting inward investment in tourist infrastructure and services particularly along shorelines (SDTIBM, 2013a, 2013b) pressures can only increase. From examination of species distribution, bathymetry, and anthropogenic forces including plans for coastal development, we have been able to define the level of risk to all *Conus* species, offer guidance for their protection, and help inform future policy on Cape Verde marine management.

2. Methods

2.1. IUCN Red List assessment

We used the assessment standards and procedures of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN Standards and Petitions Subcommittee 2010) to assess the extinction risk to 632 species of *Conus* including 53 species endemic to Cape Verde (IUCN, 2013; Peters et al., 2013). This utilizes a standard methodology for the assessment process and defines the status of each species into risk categories together with a codified set of criteria in support of the result. In particular, the assessment includes examination of the effects of both ecological change and commercial impact on the subject species.

There are three categories that define the level of threat: Critically Endangered (CR), Endangered (EN) and Vulnerable (VU). These broadly define 'extremely high', 'very high, or 'high' risk of extinction. In addition, species approaching a threatened status in the immediate future are categorized as Near Threatened (NT) and those with insufficient data to determine a category are categorized as Data Deficient (DD). Species whose population levels are not considered to be at risk are listed as Least Concern (LC).

Following taxonomic validity checks, we determined conservation status by examining each species' distribution and bathymetric profile with evidence of abundance, sub-populations and habitat preferences. We examined commercial activities in species including shell trading, pharmaceutical research, etc., together with conservation measures in place, in particular marine reserves within the species' area of occupancy. We considered the potential impact of current and future threats to each species including coastal development, harbour works, nutrient loading from agricultural run-off, residential and industrial pollution, demersal fishing, beach and foreshore alterations e.g. sand excavation for construction, dredging for shipping channels and mineral extraction. Trade publications, local newspapers, government notices, contract notifications and other 'grey' literature provided a major source of data.

2.2 Demographic data

We examined published statistical data by the Cape Verde National Institute of Statistics (INE, 2012) on annual visitor numbers to explore trends in tourism. We also reviewed hotel occupancy for each island published for 2011, the last full year for which data were available.

2.3. Marine Protected Areas

The Second National Environmental Action Plan (PANA II) is an umbrella programme for environmental management for the years 2004-2014 developed by the Cape Verde Ministry of Environment, Agriculture and Fisheries (PANA II, 2004; UNDP, 2009). By reference to PANA II together with local development plans, we considered the implementation of marine protected areas (MPAs) and the protection they offered to shallow water marine taxa such as *Conus* when viewed alongside zoning for tourism projects.

By synthesizing all the data above we were able to determine current and future impacts on *Conus* species as a direct result of economic expansion.

3. Results

3.1. Summary of threats

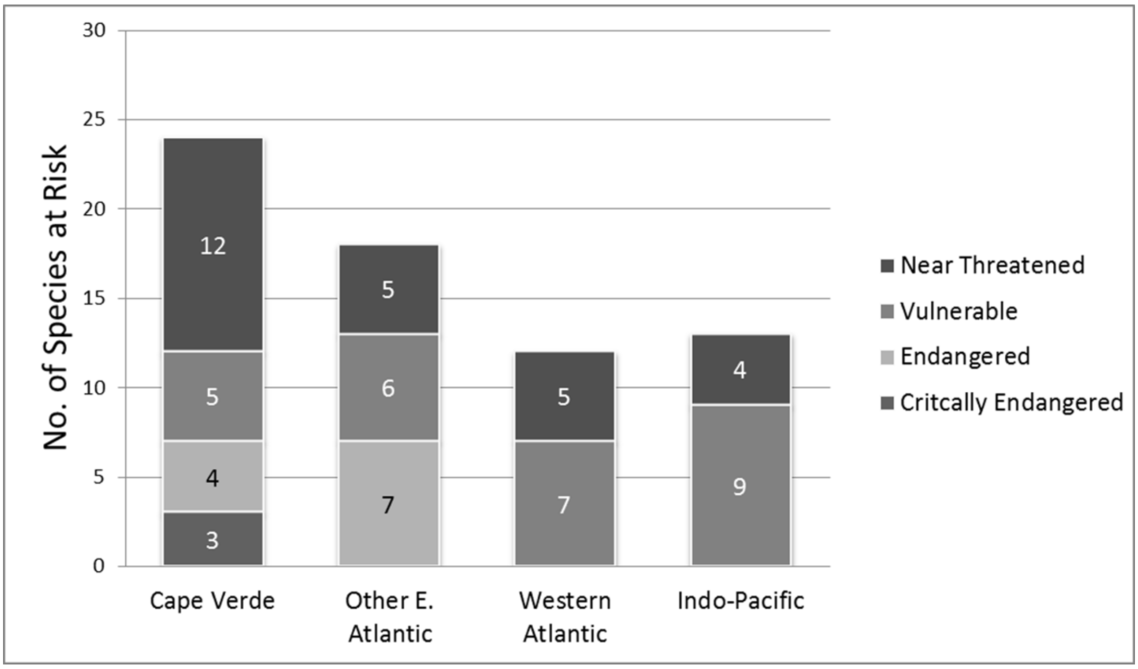

Figure 2. Number of threatened and near threatened *Conus* species that occur in each global region (Peters et al., 2013) **illustrating the extent of concentration within Cape Verde.**

Figure 2 illustrates the disproportionate contribution of threatened and near-threatened *Conus* species from the Eastern Atlantic and in particular Cape Verde to the global total for the genus. Of 632 *Conus* species assessed, all 3 Critically Endangered (CR), 4 of 11 (36.4%) Endangered (EN), and 5 of 27 (18.5%) Vulnerable (VU) occur in Cape Verde. A further 12 species (46.2% of the global total of 26) were assessed as Near Threatened (NT). Over one-third (35.8%) of the *Conus* species at risk globally (including NT) are from within the Cape Verde endemic pool. Of the 53 species of Cape Verde, 45.3% were found to be at risk compared to 7.4% for the rest of the world.

Table 1. Distribution of Cape Verde *Conus* across the archipelago

01. S Antão	**02. S Vicente only**	**04. S Vicente & S Luzia**	**05. S Nicolau**	**06. Sal**
C. fernandesi (EN)	*C. denizi* (NT)	*C. bellulus* (DD)	*C. kersteni* (NT)	*C. antoniomonteiroi* (LC)
	C. lugubris (CR)	*C. decoratus* (VU)		*C. ateralbus* (EN)
		C. graham (LC)		*C. cuneolus* (EN)
	03. S Luzia only	*C. navarroi* (NT)		*C. felitae* (VU)
		C. saragasae (NT)		*C. fontonae* (VU)
	C. curralensis (NT)			*C. longilineus* (LC)
				C. melissae (LC)
				C. miruchae (LC)
07. Boavista	**08. Boavista/Maio**	**09. Sal/Boa/Mao/S'ago**		*C. mordeirae* (CR)
				C. pseudocuneolus (LC)
C. atlanticoselvagem (NT)	*C. damottai* (LC)	*C. venulatus* (LC)		*C. regonae* (VU)
C. boavistensis (LC)	*C. irregularis* (LC)			*C. serranegrae* (LC)
C. borgesi (LC)	*C josephinae* (NT)			
C. crotchii (EN)				
C. delanoyae (LC)				
C. derrubado (NT)	**10. Maio**	**11. Santiago**	**12. Fogo**	
C. diminutus (NT)				
C. evorai (NT)	*C. calhetae* (LC)	*C. verdensis* (LC)	*C. furnae* (LC)	
C. fuscoflavus (LC)	*C. claudiae* (LC)			
C. luquei (NT)	*C. crioulus* (LC)			
C. messiasi (LC)	*C. fantasmalis* (LC)			
C. pseudonivifer (LC)	*C. infinitus* (LC)			
C. roeckeli (LC)	*C. isabelarum* (LC)			
C. salreiensis (CR)	*C. maioensis* (LC)			
C. teodorae (VU)	*C. raulsilvai* (LC)			
C. trochulus (NT)				
C. vulcanus (LC)				

Of the 53 species of *Conus* endemic to Cape Verde, 44 are restricted to a single island, and mostly within a small area of that island (Table 1). A further species, *C. atlanticoselvagem*, is found on the João Valente Shoals between Boavista and Maio. Distribution of species is weighted towards the east with the southern group having disproportionately fewer species than those in the northern islands (Fig. 3). Species richness is greatest on the three islands of

Sal, Boavista and Maio which together are home to 41 of the 53 species endemic to Cape Verde.

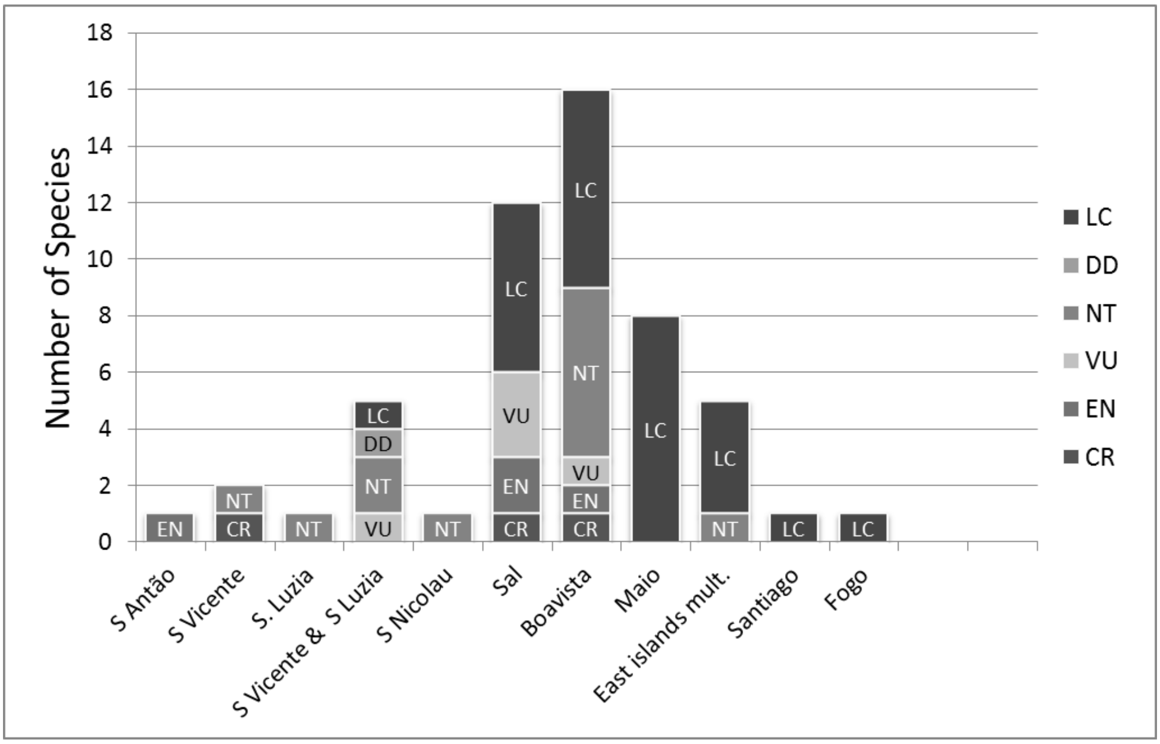

Figure 3. Number of *Conus* species occurring on each Cape Verde island by category of threat. Most species are endemic to a single island. The islands are listed clockwise around the archipelago with the islands of S. Antão and Fogo at the north-western and south-western extremities respectively. The 'Eastern islands multiple' are a consolidation across several islands: three species that occur on both Boavista and Maio, one occurring on Sal, Boavista, Maio and Santiago, and one occurring on Sal, Boavista and Santiago. Only one species (*C. atlanticoselvagem*, classified as NT) occurs between two islands (Boavista and Maio) and this has been allocated to Boavista. Key: CR Critically Endangered, EN Endangered, VU Vulnerable, NT Near Threatened, LC Least Concern, DD Data Deficient.

3.2. Tourism

Tourism has been earmarked as the 'engine of growth' for the Cape Verde economy (African Development Bank, 2009). To-date most tourism has been focused on Sal and Boavista, but with four international airports in operation there is intent to expand to other islands in the archipelago. In the 10 years from 2002 to 2011 the number of visitors to Cape Verde (Fig. 4) increased steadily from 152,032 to 475,294 (312.63%) and hotels from 93 to 195 (209.68%) (INE, 2012), indicating larger hotels under construction. It is projected that tourism revenues will increase by an average of 12% annually from 2012 to 2015 (IMF, 2012). There are indications that the government would like to see tourism numbers climb to one million visitors annually by 2020 but many believe this would be unsustainable socially and environmentally, requiring substantial inward migration to service such numbers (Baker, 2009).

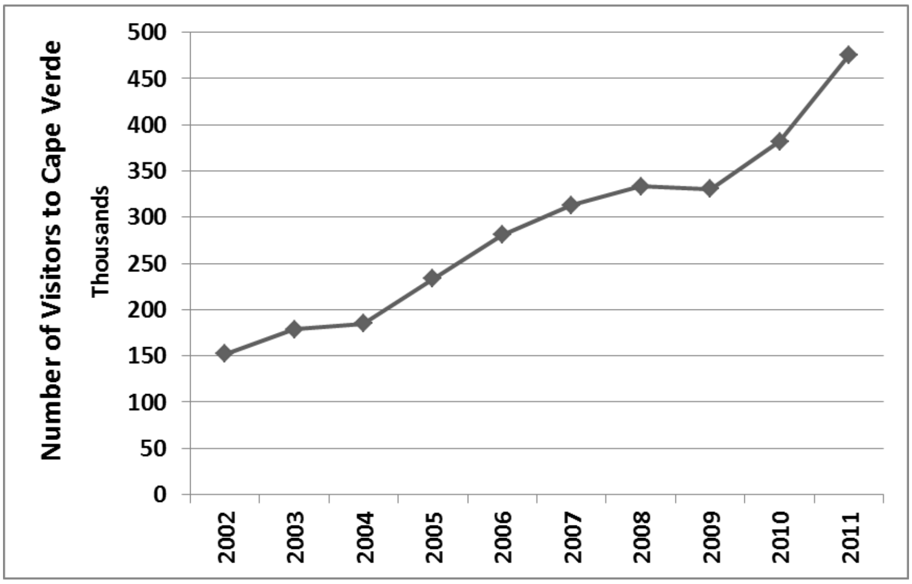

Figure 4. Visitors to Cape Verde for 10 years to 2011. Source: Instituto Nacional de Estatística Cabo Verde.

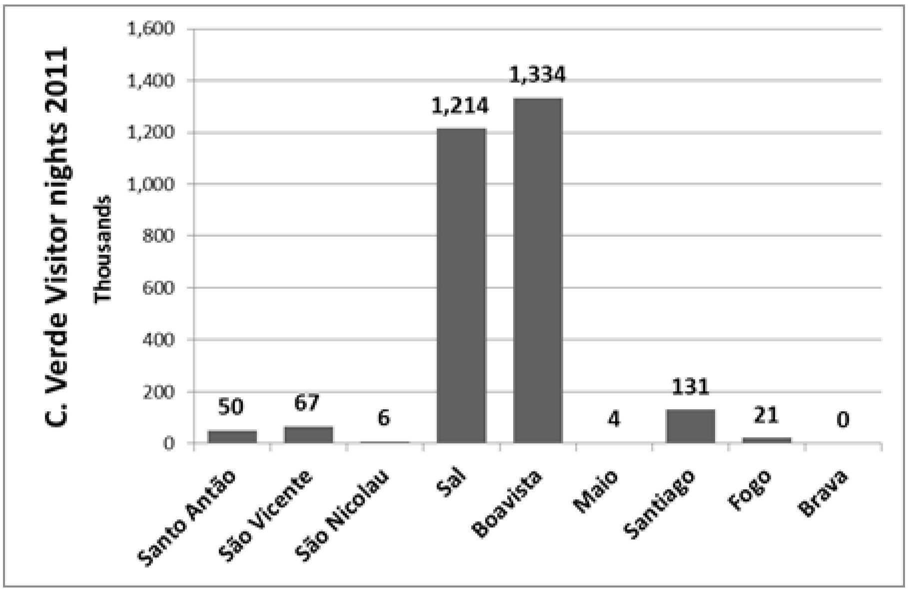

Figure 5. Nights spent by visitors to Cape Verde in 2011 by island. Source: Instituto Nacional de Estatística Cabo Verde.

The uneven distribution of tourists around the islands is illustrated by the number of visitor nights spent on each island, (Fig. 5) where 90% of total nights are spent on the islands of Sal and Boavista (42.94% and 47.18% respectively) with the remaining 10% across the remainder of the archipelago (INE, 2012). In addition, plans to develop the islands as a stopover for large cruise liners are well advanced with construction of deep-water facilities at Porto Grande, Mindelo on São Vicente (NL Agency, 2012). Although this venture will not generate direct expansion of shore-based accommodation, it will undoubtedly put further pressure on coastal intrusion and disturbance to shallow-water marine habitats.

3.3. Habitat disturbance by recreational users

With the exception of *C. atlanticoselvagem*, all Cape Verde endemic *Conus* occur within snorkel depth and only seven descend deeper than 5 m, with none below 15 m. This narrow bathymetric range biased towards the shallows combined with a restricted geographic distribution places all species of Cape Verde *Conus* at risk from over-gathering for shells.

3.4. Coastal Pollution and shoreline disturbance

Pollution from the dumping of waste, effluent and oil in the waters off Cape Verde have been measured and reported as increasing in all municipalities (PANA II, 2004). Furthermore, there is a complete lack of waste collection and no effective regulation to compel boats to segregate oil from other effluents (PANA II, 2004). The practice of discharging urban wastewater into the marine environment is increasing, and there are no contingency plans for handling pollution events (PANA II, 2004). In addition, development in the interior of the islands has led to deposition of sediment in coastal areas and the widespread excavation of sand from the marine environment for construction (de Carvalho & Araújo 2006; UNDP 2009) with ineffective enforcement and few alternatives (UNDP, 2009). From further afield, oil spills from offshore drilling in Mauritania can be transported by the Canary Current and carried ashore in Cape Verde, as proven by Mauritanian fish traps finding their way onto Cape Verde beaches (FAO/UNEP, 2007).

3.5. Status by island

3.5.1. Santo Antão

Status of island-endemic *Conus* species: CR: 0; EN: 1; VU: 0; NT: 0; LC: 0; DD: 0

Santo Antão is the most westerly of the Windward group of islands. At present the island is relatively undeveloped with only 514 hotel beds delivering 50,429 tourist nights in 2011 (INE, 2012), just 1.8% of total occupancy (Fig. 5). Where beaches do exist, it has been reported that sand has been illegally extracted for the construction industry (Irwin & Wilson, 2011). There is no international airport on Santo Antão and visitors have to travel by ferry from São Vicente. Santo Antão hosts a single species of *Conus*: *C. fernandesi* (EN), a recently described and scarce species that occurs along just one kilometre of coast, off Porto Novo and close to the small but busy ferry port, where it is at risk from the accidental discharge of oil and other pollutants.

3.5.2. São Vicente and Santa Luzia

Status of island-endemic Conus species: CR: 1; EN: 0; VU: 1; NT: 4; LC: 1; DD: 1

Fourteen kilometres to the east of Santo Antão lie the islands of São Vicente and Santa Luzia separated by an eight kilometres wide shallow-water channel. Santa Luzia is uninhabited and designated as a nature reserve which requires a permit to visit. By contrast, the port in São Vicente has been targeted for major expansion to service large cruise ships calling at the island capital of Mindelo. Costing €30m, the cruise terminal will have a 250 m long deep-water quay with associated infrastructure suitable for the largest liners (Macauhub, 2012). The port is managed by ENAPOR, the Cape Verdean port authority, headquartered at Mindelo (ENAPOR, 2013). Statistics indicate that São Vicente has not benefitted from any significant increase in tourism over the past 11 years with 66,650 tourist nights representing just 2.4% of occupancy across the archipelago in 2011 (Fig. 5). There is an international airport near Mindelo that currently serves a single flight per week to Lisbon.

There are eight species of *Conus* endemic to the two islands, five of which occur on both. Of the three island-specific species, *C. curralensis* (NT) is restricted to Santa Luzia with *C denizi* (NT) and *C. lugubris* (CR) restricted to São Vicente. With the exception of *C. lugubris* all São Vicente *Conus* occur off the island's east coast. *C. lugubris*, however, is limited to the north shore of the island with its center of population located in the Baía de Salamansa. Most of the shallow water, rocky habitats occupied by this species have been disturbed, and most, if not all of their populations are thought to have been extirpated. No specimens of *C. lugubris* have been collected since the 1980s. *C. decorates* (VU), occurs along the southeast coast of São Vicente where it is subject to disturbance from beach tourism, fishers and shell collectors. It is also found along three kilometres in the southwest of Santa Luzia where populations are considered scarce. A further population at Salamansa in the north of São Vicente has been lost. Other species endemic to both islands include *C. bellulus* (DD) with habitats of five kilometres and three kilometres length respectively and *C. grahami* (LC). *C. bellulus* has not been recorded for several years and has probably always been scarce. There are two other NT

Conus: *C. navarroi* and *C. saragasae*. As with *C. curralensis* and *C denizi* both occupy highly restricted ranges in shallow water where they are at risk from pollution, over-gathering and habitat loss, although not yet at a level where they are at immediate risk.

3.5.3. São Nicolau

Status of island-endemic *Conus* species: CR: 0; EN: 0; VU: 0; NT: 1; LC: 0; DD: 0

São Nicolau, lies to the east of Santa Luzia and has so far been largely overlooked as a tourist resort. However, its attractive beaches and potential for diving mean that this is likely to change (Irwin & Wilson, 2011), although the beaches have been heavily affected by sand removal for construction that has impacted coastal habitats (Lopes, 2010). There is a domestic airport that connects to other islands in the archipelago.

The island is home to a single *Conus*, *C. kersteni,* endemic to the southwest. This has been assessed as NT on a precautionary basis owing to its highly restricted range.

3.5.4. Sal

Status of island-endemic *Conus* species: CR: 1; EN: 2; VU: 3; NT: 0; LC: 6; DD: 0

Sal lies to the northeast of the Cape Verde archipelago and north of Boavista. It has an international airport. After Boavista it is the most popular tourist destination to Cape Verde with a 450% increase in visitor accommodation between 1999 and 2011 and occupancy in 2011 of 1.2m tourist nights (Fig. 6) (INE, 2012). Recent years have witnessed a boom in construction of resort hotels, golf courses and marine and boating facilities.

Baía da Murdeira is being developed as part of a major expansion of tourism in Sal with large-scale infrastructure projects including a €2bn, 425 ha construction, consisting of 5,000 residential units, five-star hotels, two golf courses and a 75-berth marina managed by Cape Verde Developments. Although there are reports that the development has stalled (www.diarmaidcondon.com), it indicates the intent of the local authorities to pursue tourism aggressively. Although Baía da Murdeira has been classified as a marine protected area (MPA) it is also reported that no enforcement is in place and that its future is uncertain (UNDP, 2009).

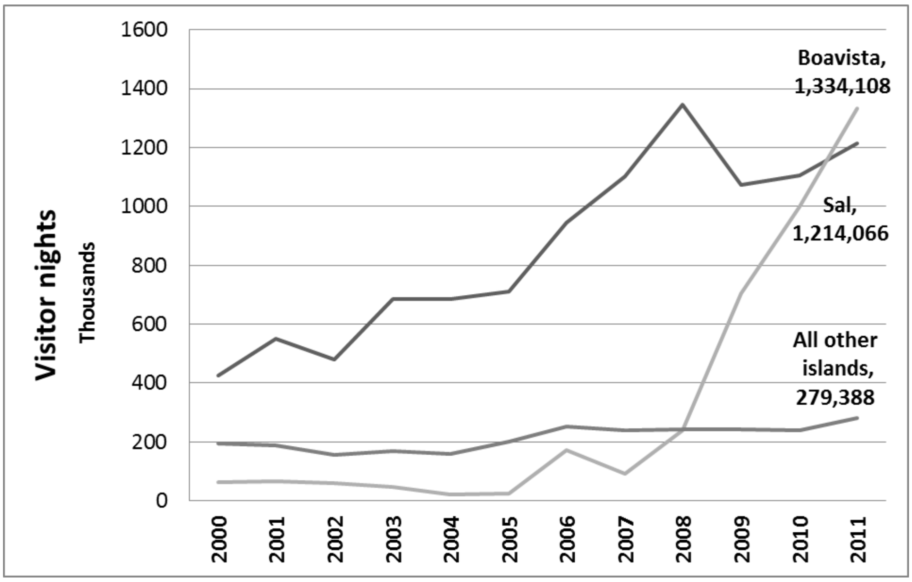

Figure 6. Nights spent by visitors to Cape Verde for 12 years to 2011. This illustrates the increasing importance of the islands of Sal and Boavista for tourism. Source: Instituto Nacional de Estatística Cabo Verde.

The Port of Palmeira in the northwest of Sal handles the third highest volume of goods in Cape Verde of which oil is an important constituent. There is substantial boat traffic from fishery and other vessels (ENAPOR, 2013).

Twelve species of *Conus* are endemic to Sal. These include one CR, *C. mordeirae*; two EN, *C. ateralbus* and *C. cuneolus;* and three VU, *C. felitae, C. fontonae* and *C. regonae*. All six threatened species occur along the western coast of the island, where all three CR and EN species together with *C. felitae* are principally located along the shoreline of Baía da Murdeira. The ranges of *C. ateralbus* and *C. cuneolus* also extend two kilometres to the south into Baía do Algodoeiro, while *C. cuneolus* also occurs along the southern bay of Santa Maria. North of Baía da Murdeira, *C. fontonae* occurs in Baía da Fontona to the south of the port of Palmeira, and C. *regonae* has its habitat extending to the north and south of the port. Both of these range-restricted shallow water species are threatened because of risk to their habitat from marine pollution in particular the accidental discharge of oil from boat traffic including tankers and other commercial vessels using the port of Palmeira (IUCN, 2013).

All six endangered species occur within snorkel reach at depths from approximately one to five metres, with only *C. ateralbus* also found in water to 15 m.

C. mordeirae, with its population restricted to the bay that bears its name, has been observed to be in decline, with the highest density of taxa occurring adjacent to resort developments.

Similarly, *C. felitae* occurs solely in the north of the bay where plans have been mooted to extend development. Under such eventuality and in the absence of special conservation measures, this species may require re-categorisation from VU to CR.

3.5.5. Boavista

Status of island-endemic *Conus* species: CR: 1; EN: 1; VU: 1; NT: 6; LC: 8; DD: 0

Boavista is the most easterly island in the Cape Verde group and also the most popular tourist destination with large-scale projects under construction for golf courses, apartments, hotels and condominiums. The scope of this development is described in the reports of the Sociedade de Desenvolvimento Turistico das Ilhas de Boa Vista e Maio, SA, a government organization established to exercise control and grant permits within the development zones (SDTIBM, 2013a) in response to concerns raised by the World Wildlife Fund (WWF) and others (Irwin & Wilson, 2011). Nevertheless, development continues apace along the entire west and south coasts from Sal Rei to Santa Monica and beyond, including recent plans for 11,641 rooms at Praia da Chave, 4,370 rooms at Morro de Areia, and 28,650 rooms at Praia de Santa Mónica (SDTIBM, 2013a). There is an international airport near Rabil to the south of Sal Rei.

Boavista is home to the greatest diversity of *Conus* with 21 species of which 15 are endemic to the island. All three threatened species occur off the west coast: *C. salreiensis* (CR) is only found in the northwest of Boavista in the bay at Sal Rei and its adjacent islet. Harbour construction in the early 1990s impacted abundance and it is now mainly found off the islet where it is at risk from pollution and human disturbance (IUCN, 2013). *C. crotchii* (EN) occurs from Morro de Areia south to Santa Monica in the centre of the new tourism zone where paved roads and resort hotels are under construction. There is a high risk of damage to habitat during the construction phase and of continuing disturbance thereafter from holidaymakers. *C. teodorae* (VU) also occurs around Sal Rei continuing north to Baía Teodora for 4.5 km. Around the southern half of its range it is subject to the same pressures as *C. salreiensis*.

There are seven NT species found off Boavista of which five are endemic to the island: *C derrubado* restricted to just five kilometres of coast in the north; *C. diminutus* which is found along two 2 kilometre sites in the west; *C. evorai* and *C luquei* which occur off Baía das Gatas in the northeast with another population of *C. evorai* at the islet off Sal Rei; and *C. trochulus* which with *C. josephinae* occurs along the western shores of Boavista adjacent to part of the development zone and continuing north to Sal Rei. There is a sub-population of *C. josephinae* also on Maio. With the exception of C. *trochulus* and *C. josephinae,* all these NT species have highly restricted ranges, and although not at immediate risk as they are sufficiently remote from main centres of tourism, they may become threatened in the future. *C atlanticoselvagem* (NT) occurs on the João Valente Shoals which are only visited by lobster fishers, and although within SCUBA depths the shoals do not at present attract divers. However, its solitary site and the potential for over-gathering or habitat degradation have placed this species as a candidate for future review (IUCN, 2013).

3.5.6. Maio

Status of island-endemic *Conus* species: CR: 0; EN: 0; VU: 0; NT: 0; LC: 8; DD: 0

Maio is a teardrop shaped island lying to the east of Santiago where it is the most easterly of the Leeward group (Ilhas do Sotavento). Despite its extensive beaches it has escaped the recent influx of visitors, however, that is about to change. New zones have been established for tourism development, including: Sul da Vila do Maio on the south coast of the island, from Praia Preta east to Ponta do Poça Grande with planning for 5,067 rooms; Ribeira D. João on the east coast that continues north from Ponta do Poça Grande to Ponta Vento for 8,278 rooms; and Pau Seco on the west coast that is expected to account for 4,148 rooms although zoning has not yet been completed (SDTIBM, 2013b). The airport at Vila do Maio at present only serves inter-island flights.

There are eight species of *Conus* endemic to Maio with a further four that occur on neighboring islands. With the exception of *C. josephinae* (NT) on Boavista (see above), all other species are LC. However, in the light of recent development plans it may be necessary to review these assessments over the short term.

3.5.7. Santiago

Status of island-endemic *Conus* species: CR: 0; EN: 0; VU: 0; NT: 0; LC: 1; DD: 0

Santiago is the largest island in the archipelago with the capital, Praia, the most populous. The island is less suitable for beach tourism.

Two species of *Conus* occur in Santiago, *C. verdensis* which is endemic to the island, and *C. venulatus* which also occurs on Sal, Boavista, and Maio. None of these species is currently at risk.

3.5.8. Fogo

Status of island-endemic *Conus* species: CR: 0;   EN: 0;   VU: 0;   NT: 0;   LC: 1;   DD: 0

The island of Fogo lies to the west of Santiago, and is an active volcano that rises steeply to 2,890 m. It supports a resident population of 39,000 mainly employed in agriculture. The tourism sector is small as there are no suitable white sand beaches. It is reported through the Verdean press (www.asemana.publ.cv – article 55183) that the black lava beaches have been extensively excavated for building material. There is an airport on the island with flights from Praia the capital and excursions from Sal.

Fogo is home to a single *Conus* species, *C furnae*, which is not currently under threat.

3.5.9. Brava

The island of Brava lies at the western extremity of the Leeward group (Ilhas do Sotavento). There are no *Conus* species reported to occur off this island.

3.5.10. Other species

Status of non-island-endemic *Conus* species: CR: 0;   EN: 0;   VU: 0;   NT: 1;   LC: 3;   DD: 0.

In addition to those described in each of the island analyses (above), there are four species that occur on Boavista and Maio: *C. damottai, C. irregularis, C. josephinae* and *C. venulatus,* with the latter also present on Sal and Santiago. All are LC with the exception of *C. josephinae* which is described under 'Boavista'.

3.6. Marine Protected Areas

Most of the designated protected areas on Cape Verde are terrestrial, including national parks, and although there are plans to extend marine reserves these have not yet come to fruition (UNDP, 2009). Those reserves within the marine environment, although established in law, are generally unenforced and offer limited protection to taxa such as *Conus* (UNDP, 2009). Although 27 MPAs have been created these include 'salt-marsh protected landscapes' and 'integrated natural reserves', all of which suffer from a general lack of management capability (UNDP, 2009). Marine reserves currently include a number of islets (ilhéus): Ilhéu dos Pássaros off the northwest coast of São Vicente; the island of Santa Luzia with the islets of Branco and Raso off the southeast coast; Baía da Murdeira on the west coast of Sal with 2,067 hectares, Praia do Morro on the west coast of Maio, Ilhéu de Baluarte off the east coast of Boavista, Ilhéu de Curral Velho off the south coast of Boavista, Ilhéu de Sal-Rei off the west coast of Boavista, and Ilhéus do Rombo off the north coast of Brava (de Carvalho & Araújo 2006; UNDP 2009). The Baía da Murdeira which is exclusively marine has an uncertain future owing to unresolved building rights (UNDP, 2009).

There are competing interests: the islet of Sal-Rei, a valuable refuge for the Critically Endangered *C. salreiensis*, is also a protected area. In the rationale for conservation status, its stated goal is the protection of migratory bird species and marine turtles, but "in the long term, the goal is to guarantee the offers of tourism products (sic) by tour operators" (de Carvalho & Araújo, 2006). In their consolidation report on the status of protected areas, UNDP (2009) reports that the protected area agenda is pursued by a few individuals with little influence or effect, and there is insufficient political will to make a difference. Furthermore, there is limited general support for protected areas and existing partnerships achieve little.

4. Discussion

Cape Verde is a biological hotspot for both terrestrial and marine organisms and possesses an exceptional diversity of endemic taxa. Marine gastropod molluscs of the genus *Conus* are especially rich in endemic species on Cape Verde with 94.6% of 56 species that occur across the archipelago being unique to the islands. Furthermore, over three-quarters of these endemic species are found only on a single island often living within a single bay. Our research found that 12 species are threatened with extinction including three at the highest category of Critically Endangered, the only *Conus* with this status among the 632 species assessed worldwide (Peters et al., 2013). A further 12 species have been assessed as Near Threatened. The evolutionary transition of endemic *Conus* of Cape Verde from planktotrophic to lecithotrophic larvae limits opportunities for further migration and exposes the many species with highly restricted ranges to a heightened risk of extinction from external pressures. Species with reduced populations are subject to the 'Allee Effect' whereby sessile or semi-sessile organisms are unable to locate a mate (Berec et al., 2007) and where populations become so small, there is insufficient genetic diversity to ensure a continuing healthy population (Briggs, 1966). Even though there are many who consider marine taxa to be less susceptible to extinction risk than terrestrial species (Roberts & Hawkins, 1999), Cape Verde with 23% of all endemic *Conus* threatened with extinction is comparable to the 23% of island endemic birds that are globally considered to be threatened (Johnson & Stattersfield, 1990).

In common with many developing countries experiencing a transition to a modern market economy Cape Verde suffers from inadequate management of its natural resources. This is exemplified by the proliferation of unlawful waste disposal sites, indiscriminate use of fertilizers, dumping of effluents into the marine environment and the discharge of urban waste-water into the sea (PANA II, 2004). As Cape Verde expands its economy to encourage tourism, areas previously protected by their isolation will inevitably be targeted for development. This also brings other problems associated with development including illegal sand removal from beaches and the littoral zone for construction (Lopes, 2010) with uncertain consequences for shallow water species. Along the shoreline new port facilities and marinas increase boat traffic and elevate risks from oil-spills. New harbour construction has already resulted in the decline of *C. salreiensis* leading to its Critically Endangered status (IUCN, 2013). Disturbance to habitats from tourism infrastructure projects has had similar effects on the viability of *C. lugubris* and *C. mordeiri* (IUCN, 2013). Nine others are also threatened with extinction. With tourism comes shell gathering. In Cape Verde most *Conus* are small-shelled, which may offer some salvation as individually they are less attractive to casual gatherers, alternatively it may encourage necklace-stringing.

Our assessment has shown that range-restricted *Conus* occurring at shallow depths are at particular risk in areas of development whether for tourism or general urbanization. Although some species may be targeted by specimen shell collectors this is not yet believed to have had a major impact on the viability of most species (Tenorio pers. comm. 2011). However, rare species already facing pressures from other factors may be pushed further towards extinction by irresponsible gathering for shells.

In PANA II it is proposed that extraction of sand should be moved from the beaches to the seabed, which could aggravate the problem of disturbance to benthic organisms such as *Conus* still further (PANA II, 2004) . Nevertheless, PANA II incorporates proposed programmes of education and environmental awareness, dissemination of information concerning marine protection laws and instilling a sense of environmental responsibility on the populace (PANA II, 2004). All of this is to be welcomed as the United Nations Development Program report into the islands' protected areas shows a shortage of political will, lack of popular environmental awareness, and scarce financial resources (UNDP, 2009).

If threatened species of *Conus* are to be saved from extinction, direct and immediate action is needed now before the full effect of projected increases in tourist development are realized.

We propose that all existing legislation for environmental protection is fully enforced, including the control of visitor numbers to marine reserves, the closure of unlawful waste disposal sites that impact on the marine environment, prevention of dumping of pollutants into coastal waters, and a halt to the removal of sand from the foreshore and seabed. We recommend a ban on the export of all Cape Verde *Conus* animals and shells, except through special license and then only for scientific research. It is proposed that a field assessment of the population status of all species of *Conus* should be initiated urgently and followed through with monitoring programmes, and that in future all environmental impact assessments for development including harbours and marinas should take account of the risk to endemic taxa such as *Conus*.

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Chapter 5: Predicting species extinction risk from global models of anthropogenic impact

ABSTRACT

The International Union for the Conservation of Nature Red List of Endangered Species is the world's leading index of the conservation status of flora and fauna and is used to set conservation policy by governments and organisations around the world. It employs a robust, standardised approach to assess extinction threat based primarily on population dynamics and species range size, with the focus fixed firmly on taxa approaching the end-point of population decline. Used alone, I argue this enforces a reactive approach to conservation. Where population density is largely unknown across a broad geographical range, but a species is abundant in small isolated areas, its true status may not be recognised until only vestigial clusters remain, finally qualifying it under Red List criteria. Conservation, if even possible, is then reduced to attempted recovery. Alternatively, species not assessed as threatened, but occurring in areas with high levels of anthropogenic impact, could be considered instead as candidates for proactive conservation management. To explore this scenario I analysed geographic distribution and bathymetric data from the global Red List assessment of 632 species of the marine mollusc, *Conus*. I matched Red List distribution data with present human impacts, and predicted future thermal stress and aragonite saturation (a proxy for acidification) due to the combustion of fossil fuels. My results show 67 *Conus* species categorised by the Red List as 'least concern' have 70% or more of their area of occupancy in places subject to high and very high levels of human impact. Eighteen of these species living exclusively in high and very high impact regions have ranges of less than 100 km^2. From examining range-rarity scores I identified clusters of endemic species in areas subject to all three stressors of high human impact and projected reduced aragonite saturation levels with elevated thermal stress. I found that modelling impact data in this way reinforces Red List threatened status, highlights new candidate species for reassessment, contributes important evidential data to minimise data deficiency and identifies regions that would benefit from environmental management, encouraging a proactive stance towards conservation.

1. Introduction

Founded in 1948, the International Union for the Conservation of Nature (IUCN) was the world's first environmental organization and is the sole authority in biodiversity and conservation that has permanent observer status at the United Nations (www.iucn.org). It plays a lead role in forming conservation policy at government level within its member countries, and offers guidance in international initiatives including the Convention on Biological Diversity (CBD).

The IUCN Red List of Endangered Species was conceived in 1963 to evaluate the conservation status of species and to focus on those threatened with extinction. In 1994, standardised Categories and Criteria were introduced to closely define species extinction risk on which all assessments are now based. Three Red list 'threatened categories' indicate levels of extinction risk, namely: Critically Endangered, Endangered and Vulnerable with a fourth category, Near-Threatened for those species liable to qualify for a threatened category in the near future. The category, Data Deficient is for species with insufficient evidence to support a threatened listing, while Least Concern is for species at no present risk. This categorisation, supported by codified criteria, have enforced uniformity on the evaluation process and enabled the Red List to be used to monitor trends in species' status with the goal of "providing information and analyses in order to inform and catalyse action for biodiversity conservation" (IUCN, 2013). Today the Red List is universally considered to be the most authoritative global conservation database available and the benchmark against which other indices of threatened species may be measured (Hoffmann et al., 2008; Rodrigues et al., 2006). It also functions as a performance assessment indicator for countries to manage their wildlife, including their legal obligations under international treaties.

1.1. Measuring conservation success

Halting biodiversity loss and measuring success in conservation are of international importance to countries when managing their wildlife resources and controlling exploitation. Targets on biodiversity agreed under the CBD were adopted by the UN Millennium Development Goals resolution A/RES/55/2, for monitoring the changing status of species in the signatory countries (www.un-documents.net). The Red List Index (RLI), used to measure temporal changes in conservation status by calculating losses and gains in categories between assessments, was adopted by CBD to monitor national progress in halting biodiversity loss.

Movement of species between Red List assessment categories frequently occurs after further scientific knowledge comes to light. This may either reflect conservation success (or failure) or simply the fact that more research has been performed (Butchart et al., 2005). Although the Red List Categories and Criteria were designed for global assessments, there is the potential for greater flexibility in regional and national assessments where species categorised as Least Concern globally may be elevated to a threatened status at local level (IUCN, 2012). These National Red Lists (NRLs) are considered key components in monitoring changes to biodiversity. However, within them invertebrates are poorly represented and studies have shown that vertebrate data coverage is negatively correlated with species richness, indicating that countries with the highest and most threatened biodiversity have produced significantly fewer NRL assessments (Zamin et al., 2010) reflecting a lack of resources or commitment or both. To accurately and consistently determine the degree of success by countries in fulfilling their obligations towards biodiversity continues to be challenging.

1.2. End-point biodiversity loss

The success of the Red List is based on its identification of species close to their point of extinction with its lowest at-risk category of 'Near Threatened', defined as 'close to qualifying … a high risk of extinction within the near future' (IUCN, 2013). Threat categories are mainly based on geographic range and population dynamics, together with definable stressors. Through its Categories and Criteria, Red List assessments quantify these indicators and, supported by a written rationale, are considered to deliver a robust result. However, I argue that when used in isolation this can steer conservation effort towards adopting a reactive approach geared towards those species on the cusp of extinction. For many this may be too late for the genetic pool to recover, and may fail to retrieve a situation that listing was intended to avert. More widely distributed species, in particular, are at risk of being overlooked on the assumption that larger ranges offer greater survival opportunities. However, where there is widespread and continuing habitat degradation, as is common in both terrestrial and marine environments (Krauss et al., 2010; Waycott et al., 2009), fragmentation of occupied habitat may not become apparent or be observed for years or even decades. This is particularly true in deep water marine ecosystems. Even though such areas may eventually come to contain only residual populations of a species, under Red List criteria the extensive range may still be perceived as sufficient to confer a low-risk assessment. Red List criteria provide for estimates of population decline to be based on rates of habitat loss; for a species to be categorised as Vulnerable requires a minimum 30% loss of abundance calculated over 10 years or three generations, rising to 80% for Critically Endangered. Providing the rationale to support these criteria is often challenging with many taxa (Hare et al., 2011). In this paper I argue that use of geographic information on the distribution of human impacts, in conjunction with species' range maps, offers enhanced assessment results with the advantage that biodiversity loss would be flagged before the point that extinction looms.

Five criteria, A to E, are used to evaluate if a taxon belongs to one of the three threatened categories. Criterion A is based on the percentage decline in populations over 10 years or three generations, with larger declines reflecting a higher threat category; Criterion B on the biogeographical distribution of the taxon with reference to fragmentation, number of sub-populations, decline or fluctuations in occupancy and/or number of mature individuals, and/or habitat quality; Criterion C on the count of individuals in small populations with continuing declines, including within sub-populations; Criterion D on very small population counts of mature individuals and/or highly restricted Area of Occupancy; and Criterion E on quantitative analysis of extinction risk over a defined time period (IUCN, 2012). Criteria are therefore wholly quantitative and mostly rely on population levels and/or distribution, although in acknowledgement that populations are seldom measurable with accuracy, they may be estimated, inferred, projected or suspected rather than based on direct observation (IUCN Standards and Petitions Subcommittee, 2010).

Within the Categories and Criteria framework it is remarked that having species listed in non-threatened categories should not deter conservation action (IUCN, 2012). However, there can be no doubt that the purpose of the Red List is to focus conservation effort on threatened species and that species not categorised in such a manner are unlikely to garner the same support.

1.3. Marine taxa

The possibility of marine species extinctions through human activity is still believed to be unlikely even among some scientists (see Reynolds et al., 2005; Roberts & Hawkins, 1999 for counterarguments). This is reflected in the reluctance of the Convention on International Trade in Endangered Species (CITES) to list marine species, with Parties to the Convention arguing that marine taxa have greater resilience through their high fecundity, high dispersal and wide distribution (Vincent et al., 2013). Twenty-six years passed between the inaugural

CITES convention in 1976 when the coelacanth (*Latimeria chalumnae*) gained protection and the further addition of marine fish in 2002 (Vincent et al., 2013).

From studying the fossil record, Harnik et al., (2012) showed that for over 500 million years geographical range size was the most significant driver of marine species extinctions, and that where species had restricted ranges, greater abundance did not protect them from extinction. Extrapolating this concept to the present day, Harnik et al., (2012) found that the same pattern still holds true in contemporary extinctions. Today, habitat loss through anthropogenic impact is essentially the precursor of diminished range size and thereby likely to be a major driver of marine species extinctions (Roberts & Hawkins, 1999). Habitat degradation presents one of the greatest current threats to species diversity, both terrestrial and marine, resulting in changes in complexity and species composition, reductions in food resources, and expansion of colonizing species (Airoldi et al., 2008). Smaller, fragmented habitats that remain may be insufficient in size to support viable co-existing populations resistant to predation (Andren, 1988). With ecosystems such as coral reefs in decline around the world, loss of habitat and marine pollution have a direct effect on the organisms that exist in association with them (Munday, 2004; Roberts & Hawkins, 1999).

Large areas of the marine environment have been evaluated for anthropogenic impact across a broad range of existing and future threats (Burke et al., 2011; Halpern et al., 2008). The drivers of extinction: over-fishing, habitat loss and ecosystem breakdown are well-documented (Brook et al., 2008; Dulvy et al., 2003), but it is now believed by many that irreversible changes to ocean chemistry brought about by increases in atmospheric CO_2 from burning fossil fuels will in the future come to eclipse threats suffered today by many marine taxa (IGBP et al., 2013). In particular, calcium carbonate forming species are likely to be particularly affected, including the scleractinian corals, echinoderms and molluscs (Hoegh-Guldberg et al., 2007; Wittmann & Pörtner, 2013). Ocean acidification and thermal stress from greenhouse gas emissions have the potential to drive all calcium carbonate forming species, including the *Mollusca*, towards mass extinction, with their combined effect exacerbating the impact (Rodolfo-Metalpa et al., 2011). Today's prediction is that by the end of the 21st century acidification levels will be at their highest for 40 million years (Pelejero et al., 2010). Research suggests that in the Permian extinction, which ended the Paleozoic era 250 million years ago, depressed pH levels were a major contributing factor for up to 92% of marine species being lost (Knoll et al., 2007; Pelejero et al., 2010).

1.4. Cone snails as research subject

Marine gastropod molluscs of the genus *Conus* (cone snails) comprise one of the largest genera of marine invertebrates. They occur throughout the world's tropical seas where they live along coastal margins typically to 50 m depth but with some species found in deeper water to below 500 m (Peters et al., 2013). Cone snails occupy diverse habitats and are commercially valuable in niche markets (Floren, 2003). They capture their prey of fish, molluscs or worms using complex neurotoxins (Olivera, 1997). These toxins possess exceptional biomedical properties that are important in the research and development of novel drugs (Bingham et al., 2010). Additionally, cone shells are sought after by collectors and dealers and through this help support the livelihoods of the countless artisanal fishers who gather them (Floren, 2003; Hoorweg et al., 2006; Rice, 2007).

A comprehensive global Red List assessment of 632 species of *Conus* revealed large variations in species distribution patterns with hotspots of endemism (IUCN, 2013; Peters et al., 2013). This was particularly prevalent in the Eastern Atlantic where range-restricted species occur off the coasts of Angola and Senegal and most notably the islands of Cape Verde, where 53 of the 56 species are endemic with most restricted to a single island or bay. It is off Cape Verde and its eastern neighbour Senegal that 22 of the 41 threatened *Conus* species (53.7%) from the global assessment are found, including all 14 of those Critically Endangered and Endangered. By contrast, across the vastness of the Indo-Pacific, home to 61.7% of cone snail species, just nine are listed as threatened with none occurring east of Western Australia. However, it is within the tropical Indo-Pacific, particularly the Coral Triangle of Southeast Asia that the greatest concentration of *Conus* diversity occurs. Here also destructive fishing methods, pollution, agricultural runoff, mangrove clearance and urban and industrial effluents, have resulted in steep declines in the quality of shallow water marine habitats (Carpenter et al., 2008; Roberts et al., 2002). Nevertheless, within the Coral Triangle there is just a single example of a *Conus* species, *C. rawaiensis* from Malaysia, occupying a threatened category on the Red List. In the Philippines, the global centre of marine biodiversity, not a single species has been assessed as threatened, despite the archipelago having experienced some of the most severe reef degradation seen anywhere in the world (Burke et al., 2011).

To test my hypothesis that Red List criteria can overlook many species at extinction risk resulting from the effect of human impacts, I analysed Red List assessment data of 632 species of *Conus* to compare its outcomes with an alternative method of determining risk of biodiversity loss. Using anthropogenic impact data created by Halpern et al., (2008), and future predictions of thermal stress and decreasing aragonite ($CaCO_3$) saturation developed for the World Resources Institute 'Reefs at Risk Revisited' analyses (Burke et al., 2011), I identified areas of ocean occupied by cone snails that are subject to threat. Adopting a holistic approach, I overlaid global species' distribution data with impact data, then sought to uncover candidate species at risk that had escaped extinction threat categorisation through Red List assessment as well as contributing new evidence to allow data deficient species to be reappraised.

2. Methods

A series of global maps were used to examine the overlap of all 632 *Conus* species ranges with variations in level of human impact now and into the future and to measure the potential for biodiversity loss: a) *Conus* species distributions according to known geographic range and bathymetric occurrence using data from the IUCN Red List of Threatened Species (IUCN, 2013) in association with oceanographic data from the General Bathymetric Chart of the Ocean (GEBCO, 2013); b) current impact data from Halpern et al., (2008) and c) predicted future thermal stress and decreased aragonite saturation from the World Resources Institute (Burke et al., 2011). ArcGIS version 10.1 with Python version 2.7 (Environmental Systems Research Institute) was used to analyse the data. All data were standardised onto 1° grid cells and projected to world cylindrical equal area.

2.1. Species distribution and bathymetric data sources

Red List geographic distribution data are calculated from known or estimated range size using two classifications measured in km^2: Extent of Occurrence (EOO) and Area of Occupancy (AOO). EOO is the area within a polygon drawn around the boundary of the species' range. AOO is the physical area in which the taxon is known to occur within the EOO. Where a species occurs in shallow water and its habitat follows the coastline, as is common for many cone snail species, the AOO may be estimated from coastline length or island perimeter. IUCN Standards and Petitions Subcommittee, (2010) suggests a width in standard grid multiples of two kilometres for such 'linear' habitats. This was adopted by Red List assessors of *Conus*. Distribution maps published by the Red List extend the AOO in that they visually represent the biogeographical extent of each species populations without consideration to bathymetry.

Together with other data, the Red List assessment of *Conus* was compiled with known bathymetric distributions for each *Conus* species to allow depth profiling. Global bathymetric data (GEBCO, 2013) was applied to the AOO described by the published maps to position the precise occupancy ('Corrected AOO') of each species based on their known bathymetric distribution. From this, a composite map was produced showing the worldwide distribution of *Conus* species richness. The procedure may be conservative from the perspective of extinction risk assessment since it assumes a species inhabits all of the area within its bathymetric range.

2.2. Marine environmental threat data sources

To assess the present day distribution of human impacts in the sea, Halpern et al., (2008) used a standardised, quantitative scoring method for the estimation of human impact based on 17 ecosystem-specific drivers of change from anthropogenic forces. The Halpern et al., (2008) global model of human impacts, overlaid onto a one degree world grid, produced an average human impact score per grid cell in the range of zero to 50, which I classified according to the same impact categories as defined by Halpern et al., (2008):

Very low: < 1.4 Low: 1.4 - < 4.95 Medium: 4.95 - < 8.47 Medium high: 8.47 - <12
High: 12 - < 15.52 Very high: 15.52+

Although Halpern et al., (2008) admitted that some ecosystem data were variable in quality and that some historical effects may still continue even though their drivers were no longer present, they considered their results the best current estimate of anthropogenic impacts. Impacts were derived from a number of original sources but were classified into three major constituents: 1) pollution, including direct human, non-point inorganic, and nutrient input; 2) Fishing: commercial, artisanal, and demersal low and high by-catch, and 3) general impacts, including benthic structures (oil rigs), commercial fishing gear, ocean-based pollution (shipping lanes, ports), and species invasion (Halpern et al., 2008).

In an alternative model assessing threat to the global distribution of a marine ecosystem, Burke et al. (2011), applied data on multiple threats to coral reefs to determine their threat status. I assessed the compatibility of Burke et al.'s (2011) model with my cone snail distribution data to examine whether it could form a comparable threat model with Halpern et al., (2008). While base data were global in extent, Burke et al.'s (2011) model of combined threat was restricted to the extent of coral reefs. Cone snails are not restricted to coral reefs, with many species preferring deeper parts of the continental shelf below reef depths and in other areas not colonised by corals (Kohn & Perron, 1994). An initial data exploration revealed a substantial number of grid cells containing cone snails in areas excluded from the Reefs at

Risk model and therefore I did not consider this model to be applicable to cone snails. However, Burke et al., (2011) present a global dataset of projected ocean warming (based on predicted elevated sea surface temperatures) and acidification (using predicted aragonite saturation levels as a proxy) from greenhouse gas emissions for 2030 and 2050. I therefore applied these data to cone snails in order to explore potential future risks to habitats and their $CaCO_3$ (shell) forming ability for the 2030 and 2050 scenarios.

As ocean acidification increases, pH levels decline along with aragonite saturation, resulting in reduced coral growth and shell-building capacity. Future aragonite saturation was modelled by Burke et al (2011) on data developed at the Carnegie Institution Department of Global Ecology at Stanford University (Cao & Caldeira, 2008). Saturation states at various atmospheric CO_2 stabilisation levels were based on a global climate model with saturation of 380 ppm for 2005 and 450 ppm and 500 ppm for 2030 and 2050 respectively. These levels were chosen as being more optimistic for the years than the IPCC A1B "business as usual" scenario (Burke et al., 2011; Burke & Reytar, 2011). Converting saturation states to threshold scores was based on suitability for coral growth determined from Guinotte *et al.* (2003) with some minor adjustments to the ranges (Burke et al., 2011). I adopted the same scoring groups as Burke *et al.* 2011, with the exception that for the high score I subdivided it into High and Very High, as follows:

Low: >= 3.25 Medium: 3 - < 3.25 High: 2.6 - < 3 Very High: < 2.6

Future thermal stress was modelled by Burke et al., (2011) on data developed at the University of British Columbia using accumulated degree heating months (DHM) from the Geophysical Fluid Dynamics Laboratory general circulation models (Donner, 2009). The future thermal stress variable represents the frequency, as a percentage of years within a decade that the DHM exceeds the bleaching threshold represented by NOAA Bleaching Alert Level 2, i.e. conditions that can cause severe coral bleaching and/or mortality, adjusted for historical sea surface temperatures (SST). Burke et al., (2011) classified areas predicted to experience a Level 2 alert at a frequency of 25% to 50% during the decade as medium threat, with > 50% classified as high threat. For reporting and visual display purposes, scores were grouped by Burke et al., (2011) into the following impact categories, which I adopted with the exception of the high score that I subdivided into High and Very High, as follows:

Low: < 25% Medium: 25 - < 50% High: 50 - < 75% Very High: 75 - 100%

The average cell impact score for both future threats were calculated by intersecting the data sources with the 1° world grid. Cells identified with no impact score, caused by the proximity of land mass creating voids in the source raster data, were completed where possible by averaging the scores from surrounding marine cells.

2.3. Geographical Information Systems (GIS)

2.3.1. Species richness mapping

Spatial and temporal variability in biodiversity are important indicators of ecosystem function (Cardinale et al., 2006) and a proxy measure of susceptibility to disruption from anthropogenic forces in species-rich regions. To determine the composition of *Conus* species diversity within regions of exceptional richness a global species richness map was constructed using the bathymetrically corrected AOO maps for each of the 632 species.

2.3.2. Range-rarity mapping

There is a greater risk of extinction for species that are geographically restricted (Roberts et al., 2002). Areas with large clusters of such species, such as those typically found in and around islands and archipelagos isolated from continental land masses, can potentially experience higher rates of species loss (Roberts et al., 2002). To identify such areas, I calculated the reciprocal of each species' Corrected AOO to emphasise those species with the smallest range (Roberts et al., 2002). I mapped range rarity as a function of the sum of the range-rarity for all species present in each 1° grid cell. This score provides a measure of the range-rarity and an indicator to the degree of endemism in each grid cell. For ease of interpretation and reporting I multiplied all range-rarity scores by 10^4.

2.3.3. Determining species and regions at risk

To identify levels of threat from which to infer population declines, I examined current anthropogenic impacts and projected aragonite saturation and thermal stress (in 2030 and 2050 for both) for each 1° grid cell in which at least one *Conus* species was known to occur. From these data, I determined which taxa live predominantly in areas under greatest threat and which regions support the greatest concentration of threatened range-rare species in order to assess whether these data were also supported by Red List assessments.

To understand which taxa were at greatest threat I calculated the percentage of occupancy for species within High and Very High impact cells. To identify regions supporting the highest concentrations of range-rare species that are also subject to high levels of threat and could therefore result in the greatest loss of *Conus* diversity within that area, I examined the top 10% of grid cells by summed range-rarity score overlaid with the highest score for all of current anthropogenic impact and projected 2050 aragonite saturation and thermal stress levels. From these cells, to identify species at greatest risk I examined taxa with a limited range size (< 100,000 km^2) categorised as Least Concern or Data Deficient on the Red List. The results indicated biogeographical regions that could benefit from long-term conservation planning.

3. Results

3.1. Species richness

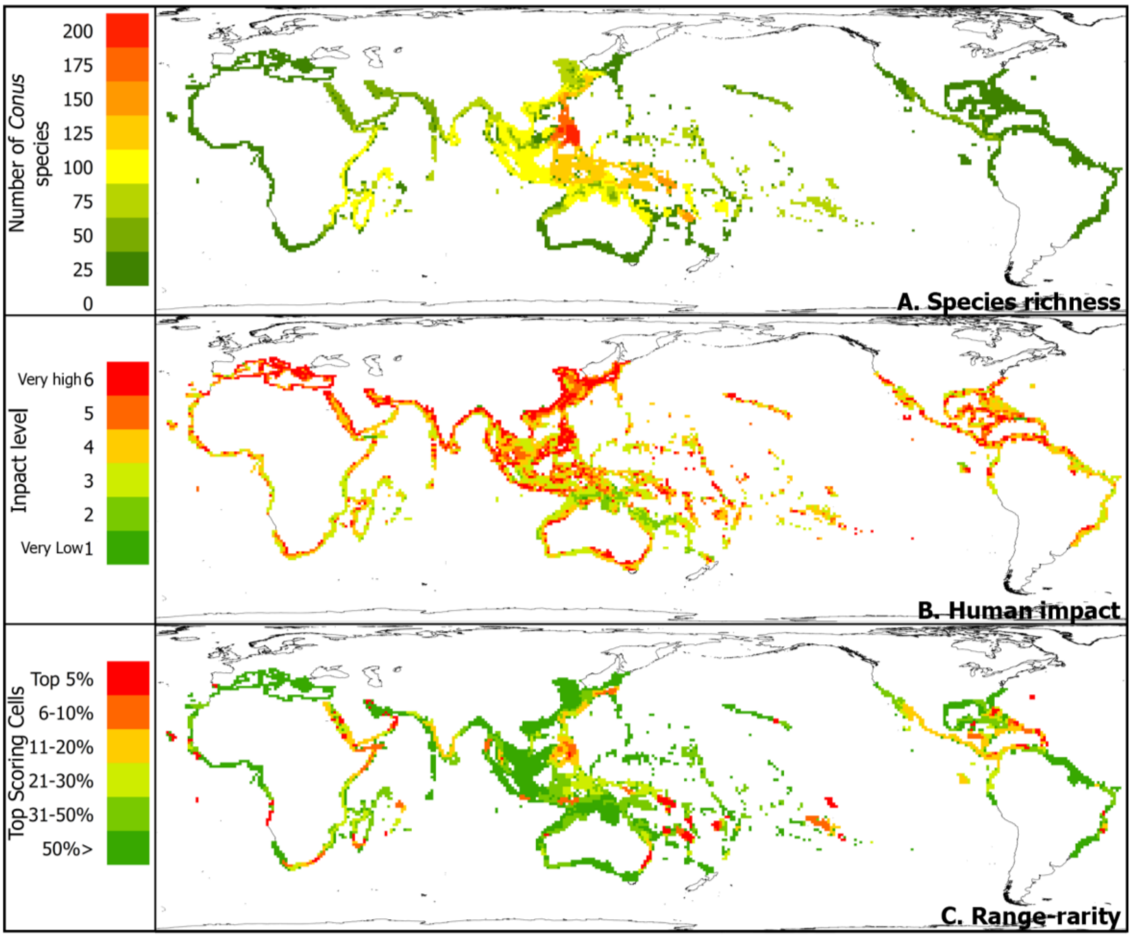

Figure 1. Distribution of cone snails classified according to (A) *Conus* species richness (total number of species per grid cell), (B) human impact levels in areas occupied by *Conus* species using data and scores from Halpern et al (2008) with scores 1. Very low: < 1.4; 2. Low: 1.4 - < 4.95; 3. Medium: 4.95 - < 8.47; 4. Medium high: 8.47 - < 12; 5. High: 12 - < 15.52; 6. Very high: 15.52+, and (C) range-rarity of *Conus* species displayed as percentiles of summed range-rarity scores (reciprocal of range size) for all of the species present in each grid cell.

A total of 632 species of cone snail were distributed across 4,033 1° grid cells, all within the tropics and subtropics to approximately 38° north and south (Fig. 1A).

Species richness was found to be highly uneven, being greatest across south-east Asia and the Coral Triangle, peaking in the Philippines, and then remaining high in an arc south to southeast through Indonesia, Papua New Guinea, Solomon Islands, New Caledonia, Vanuatu and east to Fiji (Fig. 1A).

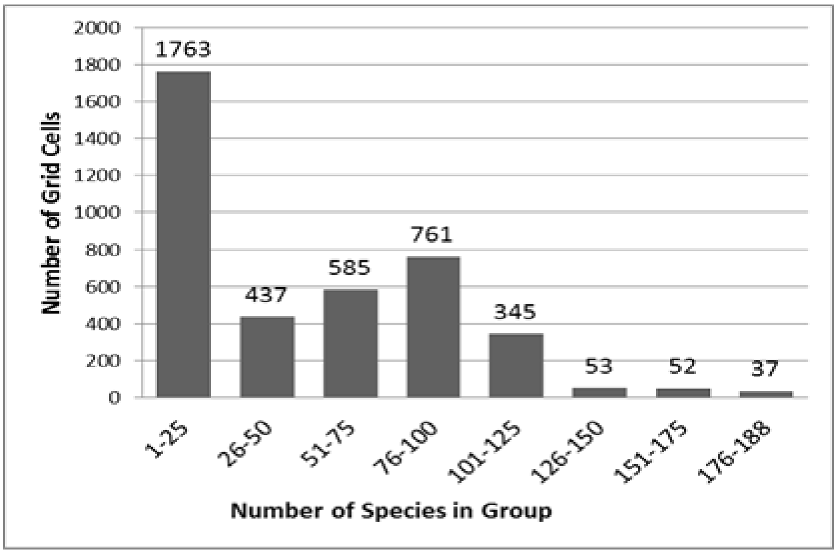

Figure 2. Number of 1° grid cells occupied by each of the species richness groups in Fig. 1A.

The highest levels of richness (containing 126 species and above) are geographically very restricted, occupying just 3.5% of the total area of *Conus* distribution. By contrast, low richness areas (25 species or less per grid cell) make up 43.7% of the total area occupied by *Conus* (Fig. 2). The cell with the highest richness is in the Philippines and contains 188 species.

3.2. Species' exposure to human Impacts

Current human impact scores from Halpern et al. (2008) for cells occupied by *Conus* species (Fig. 1B) illustrate the prevalence of High and Very High impact areas.

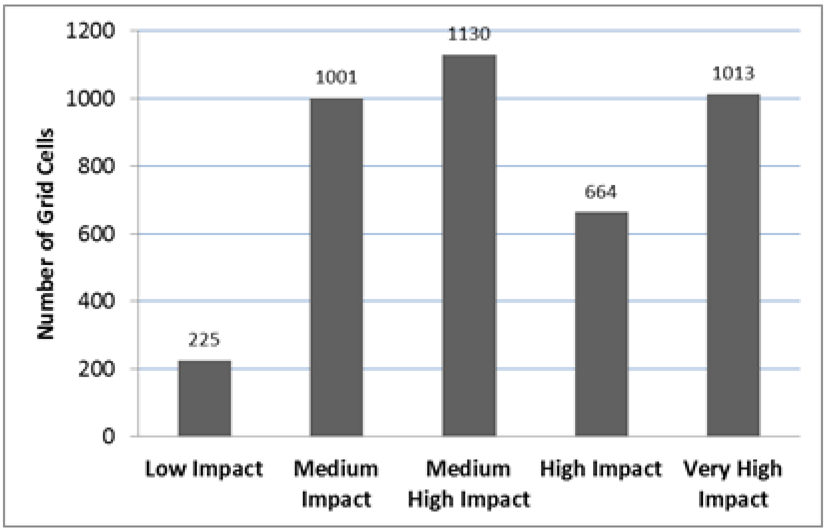

Figure 3. Analysis of 1° grid cells occupied by *Conus* species by predicted level of human impact (Halpern et al., 2008).

There were 664 High (16.5%) and 1,013 Very High (25.1%) impact cells. No cells occupied by cone snails were classified as Very Low impact and only 225 as Low (5.6%) (Fig. 3). Analysis of levels of impact across *Conus* species ranges indicates that, of 632 *Conus* species globally, 56 (8.9%) have ranges wholly within cells of High or Very High impact, i.e. they had no presence in any lower impact cells (Fig. 4).

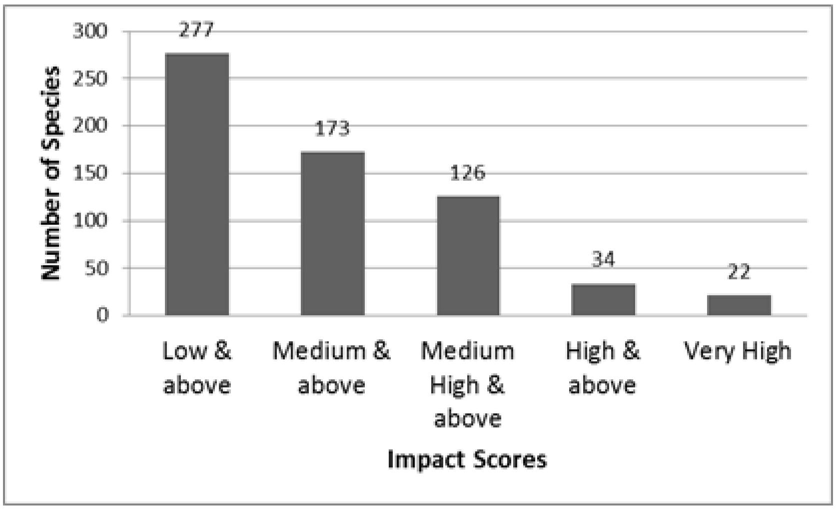

Figure 4. Exposure to human impacts for *Conus* species. This shows the number of species whose ranges entirely overlap cells of the stated level of impact (i.e. 22 species occur only in grid cells where human impact is Very High, etc.).

Figure 4 also shows the number of species that could potentially drift toward extinction as conditions deteriorate, starting with the 22 species where their entire population occurs in Very High impact areas. However, since range size is also a determining factor those with the smallest range would probably be extirpated before others under identical scenarios. Of the 56 species that wholly occupy High and Very High impact cells, 26 had a range of less than 10 km^2 (46.4%), 16 had one in the range 10-100 km^2 (28.6%), and 14 in wider ranges (25.0%). Table 1 lists these species sorted by range size and Red List status.

Thirty-nine of the 56 species that wholly occupied High and Very High impact cells (69.6%) are found in the Eastern Atlantic, ten in the Indo-Pacific and seven in the Western Atlantic. There was a mean occupancy of 2.3 cells, with 36 (64.3%) species each occupying just a single cell. This concentration in the Eastern Atlantic was in line with expectations since the region had been classified as a centre for Threatened endemic cone snails: of 98 species in the Eastern Atlantic, 42 (42.9%) had been assessed on the Red List as Threatened or Near Threatened, whereas outside the Eastern Atlantic, of the remaining 534 species only 25 (4.7%) had been assessed as such (Peters et al., 2013).

From the 56 species subject to High and Very High impact, 27 were already categorised by the Red List as Threatened or Near Threatened, however, eight were Data Deficient (DD), and 21 were Least Concern (Table 1). From the Eastern Atlantic, *C. pineaui* and *C. flavusalbus*, classified as Least Concern, have restricted ranges and occur solely in Very High impact areas (Table 1).

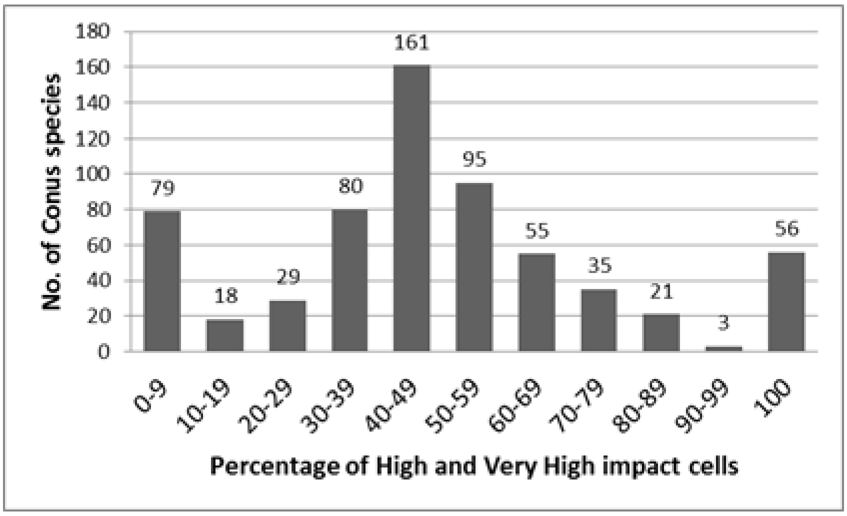

Figure 5. Percentage of the geographic range of each species, measured by cell, that lies in areas with High and/or Very High levels of human impact.

Most *Conus* species had at least part of their geographic range overlapping High and Very High impact cells. As the percentage of overlap increases, the risk of extinction can be expected to rise. Figure 5 shows the percentage overlap of *Conus*' ranges with High and Very High impact regions. Two hundred and sixty-five species (42%) have half or more of their range overlapping High and Very High impact regions. Of these, the 56 species discussed above are at the highest ranking of risk since they have 100% of their Corrected AOO in High and Very High impact cells (Fig. 5). However, I used the three groupings immediately below this level that together form 70% to 99% range (Fig. 5) to define a second ranking of 59 at-risk species (Table 2). Of these, one was categorised by the Red List as Threatened, 12 Data Deficient (DD), and 46 Least Concern (LC). There was no concentration of species in this ranking occurring in the Eastern Atlantic as there was in the first ranking of 56 species (Table 1) with just a single species represented. Of the other regions, 21 were from the Western Atlantic, one from the Eastern Pacific and 36 from the Indo-Pacific (Table 2).

Of the 115 *Conus* from the two rankings combined and described above with 70% or more of their cell occupancy in High and/or Very High impact regions, 87 (75.7%) are categorised on the Red List as either Least Concern or Data Deficient (Tables 1 & 2). Over half of these, 44 (50.6%) occur in the Indo-Pacific, followed by 23 in the Western Atlantic (26.4%), 19 in the Eastern Atlantic (21.8%), and one in the Eastern Pacific (1.1%) (Fig. 6). Although the Eastern Atlantic still garners the largest share of species which are highly range-restricted (i.e. those with a Corrected AOO of less than 10 km^2) and not listed within a threatened or near threatened category on the Red List, the total number of species potentially at risk in the Indo-Pacific is more than twice those from the Eastern Atlantic.

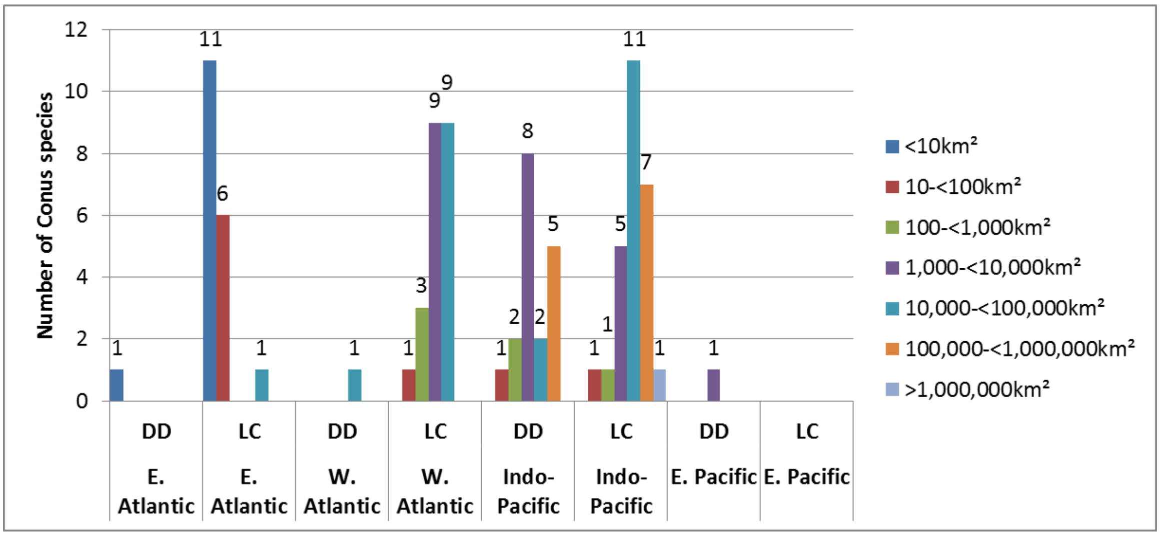

Figure 6. Eighty-seven species with 70% or more of their range overlapping cells in High and Very High impact areas and not listed within a threatened category on the Red List. Quantities are shown by oceanic region and Corrected Area of Occupancy.

3.3. Range-rarity and endemism

Cell range-rarity scores identify which geographic regions are likely to be home to the greatest density of endemic *Conus* at high risk of extinction from current and future impacts. Areas with range-rarity with very high values occur in the Eastern Atlantic including Cape Verde, Senegal and Angola. Other centres of endemism include the Eastern Cape, the Horn of Africa and the Arabian Gulf, New South Wales and various island groups of the Pacific Plate; also the Gulf of Mexico and the Caribbean (Fig. 1C). I found no correlation between range-rarity and species richness [Pearson $r^2=1$, $P>0.05$, $n=3055$]. Range-rarity is important since high densities of restricted-range species, subject to severe levels of anthropogenic threat, could result in exceptional biodiversity loss.

The cells with the top 10% range-rarity scores are shown on Figure 1C in red and orange. To identify centres of endemism I adopted these top 10% of cells as an arbitrary cut-off, (resulting in 411 of 4033 cells, the extra 8 cells due to equal range-rarity scores at the cut-off point). These cells, classified with scores from each of five threat scenarios are shown as: anthropogenic impacts (Fig. 7A), aragonite saturation at 2030 and 2050 (Figs. 7B & 7C), and thermal stress at 2030 and 2050 (Figs. 7D & 7E).

Cells that were void of data were assigned scores based on the average of the surrounding cells. However, although all cells for human impact data were successfully included within my analysis (Fig. 7A), 36 cells for projected aragonite concentration in 2030 and 2050, and seven cells for projected thermal stress in 2030 and 2050 out of the total 411 were excluded owing to all surrounding cells also being void.

The 411 cells in Fig. 7 A-E show those regions containing centres of endemism. The maps graphically illustrate the potential for a significant loss of regional biodiversity under each of the five threat scenarios, and in particular show the projected deterioration between the 2030 and 2050 scenarios for acidification and elevated sea-surface temperatures. Since the two 2050 scenarios are a progression of those from 2030, I restricted the following analyses to data from 2050 only.

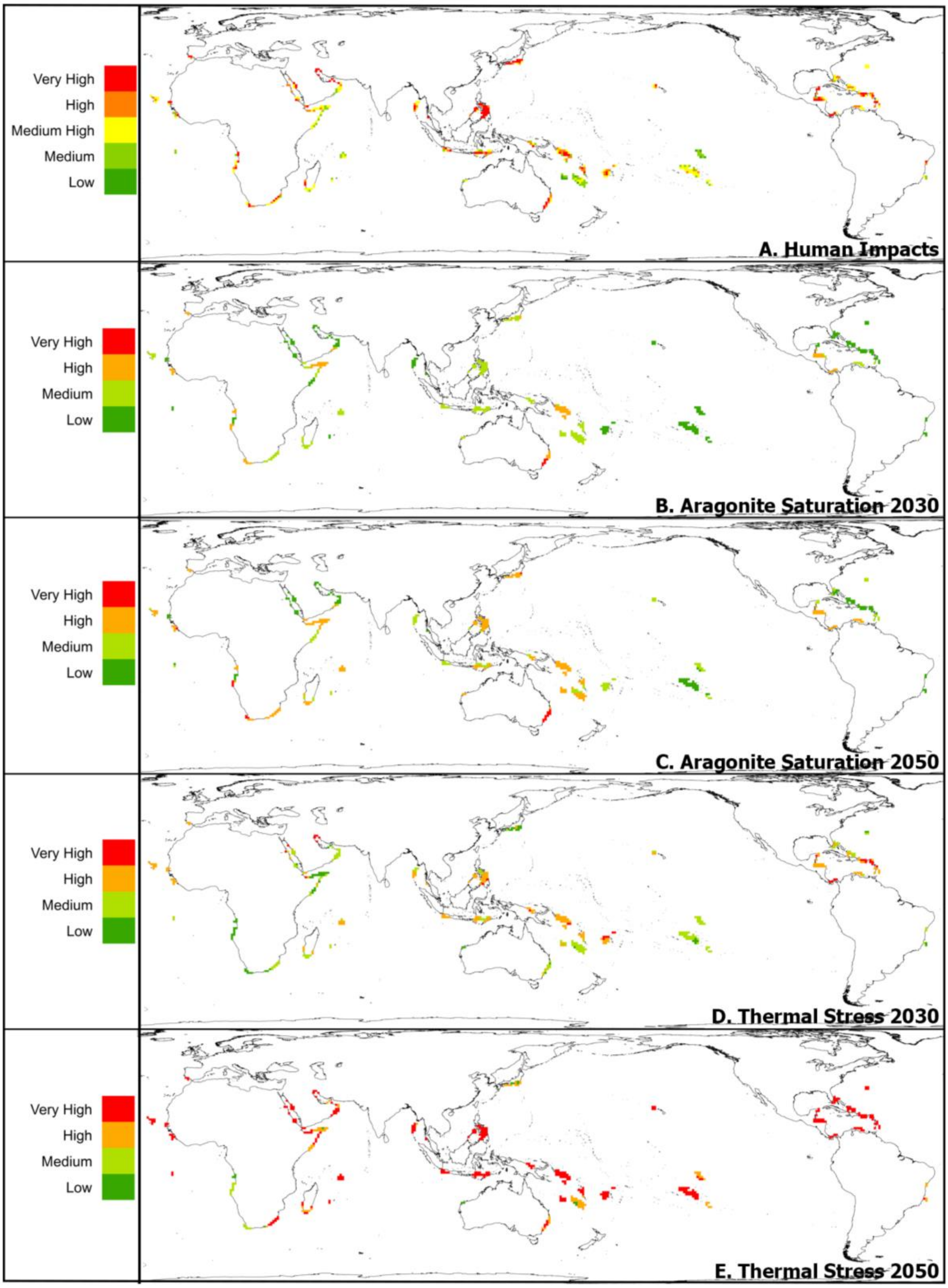

Figure 7. Distribution of centres of *Conus* endemism. This shows the cells containing the top 10% (n=411) of summed range-rarity scores classified under different threat scenarios: (A) anthropogenic impacts[1]; (B) aragonite saturation 2030 (450ppm)[2]; (C) aragonite saturation 2050 (500ppm)[2]; (D) thermal stress 2030[2]; (E) thermal stress 2050[2]. [1]Halpern et al., (2008), [2]Burke et al., (2011).

Cells with the highest range-rarity scores, although containing the largest numbers of endemic species, also contain species with wide ranges. Within the 411 top ten per cent of cells by range-rarity score, 594 *Conus* species were represented, being 93.4% of all 632 species. To target endemism more effectively I excluded from the 594 species those occurring across very wide ranges, that I defined as species with a Corrected AOO greater than 100,000 km^2 (an area the size of Iceland). This was based on the median AOO of those species at Least Concern. Although this reduced the species count from 594 to 364, the total number of cells that remained, 411, was not affected. An average of 8.3 species with a median of 6 resulted for each cell.

Regions with high levels of endemism are at much greater risk of multiple species loss. This is manifest in the Eastern Atlantic where the high incidence of endemism has resulted in a very high ratio of threatened species (Peters et al., 2013). Such regions would benefit most from targeted conservation. From the 364 species described above, I selected those where all or some of their populations occurred within highest scoring threat cells, i.e. High and/or Very High impact, for all three scenarios of: current anthropogenic impacts, aragonite saturation 2050 and thermal stress 2050.

The resulting number of species whose populations were at risk of regional extirpation or extinction was 57, of which 21 were from the Eastern Atlantic, nine from the Western Atlantic, 10 from the Indo-Pacific and 17 from the Eastern Pacific (Fig. 8; Table 3). *Conus* from the Indo-Pacific include six from the Philippines, and from the Western Atlantic there were eight from Colombia / Netherlands Antilles.

Thirty-seven of the 57 species had already been identified from the 115 species in Tables 1 & 2, leaving a further 20 species. This included 16 from the Eastern Pacific, three from the Indo-Pacific and one from the Western Atlantic (Table 3, marked with *).

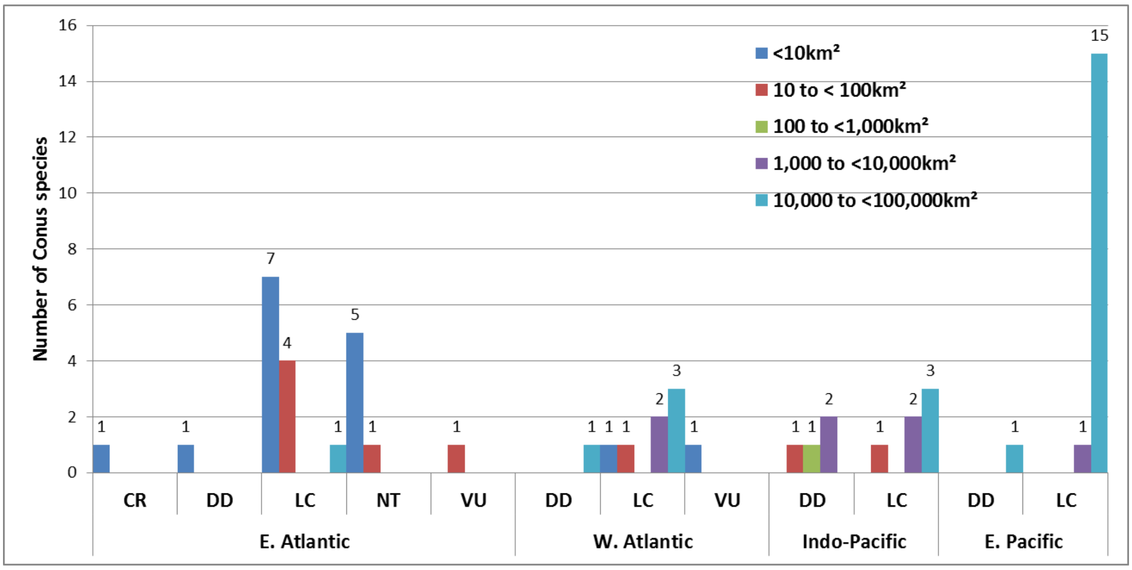

Figure 8. Centres of endemism at risk. Ocean basin analysis of 57 *Conus* species present in the top 10% of cells for range-rarity with a Corrected AOO < 100,000km^2, and where all or some of their populations occur in cells of High and Very High impact for all three scenarios: present day anthropogenic impact, aragonite saturation 2050 and thermal stress 2050.

4. Discussion

Geographical range size for all taxa, terrestrial and marine, is critical to species survival and in the marine environment it has been shown to have a significantly greater influence on extinction risk than abundance (Harnik et al., 2012). As marine species ranges contract through a combination of human impacts, thermal stress and altered ocean chemistry, the need to account for these forces in threat assessments becomes ever more pressing. Findings have confirmed my initial contention that the Red Listing process with its primary focus on taxa approaching extinction may obscure the status of many other species and centres of endemism that are also at potential threat.

The Red List categorised a threat of extinction for twenty-five species of *Conus* in the Eastern Atlantic, seven species in the Western Atlantic, and six in the western Indian Ocean and the Gulf (IUCN, 2013; Peters et al., 2013). However, from the central Indian Ocean travelling east, just three species of *Conus* were classified within a threatened category: one species from Western Thailand, C. *rawaiensis*, and two from Western Australia, all assessed as Vulnerable (IUCN, 2013; Peters et al., 2013). No species from the Coral Triangle of Southeast Asia or from the entire Pacific are classified within a threatened category, despite the former being home to the world's greatest diversity of marine taxa (Barber, 2009; Veron et al., 2009). Whereas it is true that Indo-Pacific species are on average wider ranging than species from other ocean basins and therefore may be considered to have enhanced survival capability (Indo-Pacific species have a mean Corrected AOO of 933,971 km^2 ± SD: 1,705,500 (n=390), Eastern Pacific 91,277 km^2 ± SD: 72,367 (n=31), Western Atlantic, 90,751 km^2 ± SD: 212,276 (n=113) and Eastern Atlantic 3,627 km^2 ± SD: 18,965 (n=98)), the Indo-Pacific also has more range-restricted species (with a Corrected AOO of < 10,000 km^2, there are 97 species in the Indo-Pacific, 3 in the Eastern Pacific, 47 in the Western Atlantic and 93 in the Eastern Atlantic). This would indicate that there may be more species at risk in the Indo-Pacific than the Red List has revealed.

By examining overlap of *Conus* species ranges with anthropogenic impact data, I found 56 species of *Conus* occurring wholly in areas of High and Very High human impact, of which 21 were categorised on the Red List as Least Concern with a further eight as Data Deficient. Extending the approach to a second tier of exposure to human impacts - species with 70% to 99% of their range overlapping areas of High and Very High impact - I discovered an additional 59 species at risk, of which 46 had been categorised as Least Concern and 12 as Data Deficient in the Red List (Peters et al., 2013).

Geographic mapping of range-rarity scores for *Conus* revealed many centres of endemism. Some already face high levels of human impact, while others will come under increasing threat as the oceans warm and acidify. The importance of this analysis is that they highlight worrying gaps in the Red Listing process. Although Eastern Atlantic centres of endemism were reflected in Red List species assessments, it has flagged up other regions with the potential to drive extinction, and therefore of great conservation concern where timely intervention could yield large benefits. For example, it pinpoints the Philippines as being at risk. This is the global centre of *Conus* diversity (Fig 1A) and faces some of the most severe habitat degradation in the world from impacts of blast fishing, pollution and nutrient loading among others (Burke et al., 2011). The majority of cone snails in the Philippines live in association with coral reefs (Röckel, Korn, & Kohn, 1995) and it is precisely these areas that are subject to the most intense destructive forces. Nevertheless, the Philippines has no threatened *Conus* species on the Red List. This is also true for many regions of Southeast Asia where more than 100 species co-exist, including parts of Indonesia and the Solomon Islands. My exploration of range-rarity for pockets of endemism showed eight species from the Philippines occurring in cells at the highest risk within all three critical threat scenarios.

Other centres of endemism that emerge as candidates for early conservation intervention include south-eastern Australia and Eastern Pacific, which revealed a cluster of 17 species, all of which, with the exception of a single Data Deficient species, *C. kerstitchi* from Mexico, had been assessed as Least Concern on the Red List. Thirty-seven endemic species, including 17 from the Eastern Atlantic, identified at potential risk from both the current anthropogenic risk analysis and from the combined current and future impacts scenarios from ocean acidification and thermal stress, provide persuasive evidence for further investigation.

Data deficiency (DD) is a major hindrance to conservation. Lack of knowledge is often a function of rarity, in terms of both abundance and range size (Brito, 2010), denying many vulnerable species the opportunity for targeted and timely action. For cone snails, 87 species (13.8% of all 632 assessed) are categorised on the Red List as DD of which 75 (86.2%) occur in the Indo-Pacific. A recent analysis reveals how data deficiency can grossly devalue Red List statistics with 26% of marine invertebrates assessed as DD, including 76% of 195 cuttlefishes and 35% of 247 marine lobsters (Kemp et al., 2012). DD taxa are often species suspected of being at risk but they lack sufficient evidential data for categorisation to threatened status. Eighteen Indo-Pacific species of *Conus* assessed as DD had at least 70% of their habitat overlapping regions with High or Very High human impact.

Estimating population sizes for marine taxa is problematic, except in specific circumstances, such as those occurring exclusively in the observable littoral zone to 30 m depth. In the absence of population data, Red List criteria for threatened status are based on range size. Criterion B entry point provides for a listing of Vulnerable status if the AOO is < 2,000 km^2 together with two choices from a menu of three: severe fragmentation, declining AOO or EOO, and extreme fluctuations in AOO or EOO (unlikely for molluscs). For Endangered categorisation the AOO must be < 500 km^2 and for Critically Endangered < 10 km^2 (IUCN, 2012). For many marine taxa, estimating range sizes to this degree of precision can be daunting, and for shallow water species such as molluscs there is a tendency to over-estimate. Of 67 species of *Conus* categorised as Threatened or Near Threatened, 43 (64.2%) had been over-estimated on AOO compared with my results corrected according to their known depth range. Although some of this over-estimation probably resulted from the minimum grid size of 2 km with narrow linear habitats, it nevertheless indicates a trend. Species whose range sizes have been over-estimated may fall outside the criteria and escape being placed at risk.

This tendency to offer a more optimistic picture extends to the role of experts in reviewing draft assessments. This element is critical to the process and deservedly bestows authority on the Red List (Rodrigues et al., 2006). It is undertaken with rigour; however, it is also prone to human bias, especially with commercially exploited species. The author has witnessed during the *Conus* red listing workshop the reluctance of some experts to list species that are known to be rare even when they occur in habitats recognised to be under high levels of stress. On its own, this may be inconsequential, but with several years between assessments populations may collapse beyond recovery in the interim.

It has been argued that IUCN Red List standards and procedures are too prescriptive with excessive rigidity in the criteria used to determine the assessment category and that greater weight should be placed on qualitative judgements, such as examining current population stability, rather than quantitative scoring against historical abundance (Mrosovsky, 2003). Mrosovsky was excoriating in his critique of the Red List and, using turtles as examples, argued that the assessment process had often led to an over-pessimistic view of species' status that debased categorisation, with Critically Endangered in particular being overused or misused. I believe no standard system is perfect but some imperfection has to be weighed against a methodology that can also be applied, managed and implemented effectively by personnel unfamiliar with the taxa, and who can train and support those who are expert without an unwieldy and expensive bureaucracy. In this the Red List has been remarkably successful (Rodrigues et al., 2006). Whereas Mrosovsky argued that reliance solely on quantitative data resulted in species' extinction risk being overstated, my findings suggest that for some wider ranging species occurring over large areas with unknown quality of habitat, risk may be understated. Geographical data on human impacts can, I contend, add true value to assessment results that would otherwise be data poor. They enable early warnings to be sounded on potential population decline, particularly for range-restricted species and those in areas with high levels of endemism, and they uncover species and areas the Red List may fail to identify as threatened, also offering important evidential data to those assessed as Data Deficient. Reducing incidence of data deficiency in the Red List should be of concern to all assessors. For those species already listed as threatened, impact data reinforce existing categories and strengthen its rationale, and provide additional evidence for re-categorisation including upgrade from Near-Threatened to Threatened status.

Narrowly-restricted endemic species, as previously stated, are well represented among the 41 *Conus* species Red List assessed as threatened. In the Eastern Atlantic, with 53 out of 56 *Conus* species occurring in Cape Verde alone being endemic, 24 (45.3%) have been assessed as Threatened or Near-Threatened (Peters et al., 2013). This criteria-based evaluation of species approaching their end-point focusses only on those considered the most deserving cases where conservation is tinged with desperation. I believe that a broader perspective is needed to support and enhance the Red List; one that addresses potential biodiversity loss on a wider scale, and that can have greater consequences on natural resources and even, as in the case of *Conus*, on human health.

In this study I have explored the potential effect of human impacts across all 632 assessed species of *Conus.* By taking a holistic approach and using data to reveal species-rich areas under threat, I have demonstrated how new taxa can be recommended for re-assessment, data deficient species can be supported with evidence, species already listed as threatened can be given added rationale, and regional authorities can focus their attention on areas for proactive conservation management. As an example of this, my study revealed 17 species from the Eastern Atlantic that were Red List assessed as Least Concern occurring wholly in the highest impact zones. Eleven of these occurred in Cape Verde, of which eight represented the entire *Conus* diversity of the island of Maio, and were found nowhere else. Although Cape Verde is well represented with Red List threatened species, this data provides powerful ammunition in my proposal to restrict all trade in cone shells for the islands (Peters et al., 2013).

Finally, the author is a committed supporter of the Red List and considers it an essential tool in the armoury of conservation science. This study is intended to complement the proven methodology of the Red List, and enable a longer-term approach to be taken for the many species that could eventually qualify under Red List criteria if left unattended.

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Tables

Table 1. *Conus* species occurring wholly in 1° grid cells at High and Very High impact only, sorted by IUCN Red List threat category: CR Critically Endangered, EN Endangered, VU Vulnerable, NT Near Threatened, DD Data Deficient, LC Least Concern. Regions: EA Eastern Atlantic, IP Indo-Pacific, WA Western Atlantic. Sorted values represent the Corrected Area of Occupancy in km^2. Species marked with an * are those that wholly occupy Very High impact cells.

Region	Species	CR	EN	VU	NT	DD	LC
EA	*Conus verdensis*						0.19
EA	*Conus fantasmalis*						0.36
EA	*Conus furnae*						0.58
EA	*Conus grahami*						0.82
EA	*Conus flavusalbus* *						1.65
EA	*Conus filmeri*						3.13
EA	*Conus babaensis*						3.83
EA	*Conus infinitus*						4.72
EA	*Conus calhetae*						5.09
EA	*Conus crioulus*						6.06
EA	*Conus isabelarum*						8.78
EA	*Conus desidiosus*						15.5
EA	*Conus claudiae*						18.4
EA	*Conus raulsilvai*						19.8
EA	*Conus maioensis*						24.2
EA	*Conus pineaui* *						29.4
EA	*Conus anabelae*						35.2
EA	*Conus bellulus*					2.84	
EA	*Conus curralensis*				0.29		
EA	*Conus trencarti* *				0.35		
EA	*Conus dorotheae* *				0.61		
EA	*Conus saragasae*				0.86		
EA	*Conus kersteni*				1.46		
EA	*Conus navarroi*				2.28		
EA	*Conus denizi*				4.00		
EA	*Conus atlanticoselvagem*				14.8		
EA	*Conus allaryi* *			9.02			
EA	*Conus tacomae* *			12.0			
EA	*Conus decoratus*			15.1			
EA	*Conus xicoi* *			55.1			
EA	*Conus guinaicus* *			255			
EA	*Conus mercator* *		0.81				
EA	*Conus bruguieresi* *		7.13				

Contd.

Table 1 contd.

Region	Species	CR	EN	VU	NT	DD	LC
EA	*Conus hybridus* *		7.67				
EA	*Conus unifasciatus* *		10				
EA	*Conus belairensis* *		83.0				
EA	*Conus echinophilus* *		131				
EA	*Conus cloveri* *		223				
EA	*Conus lugubris*	1.60					
IP	*Conus andremenezi* *						2183
IP	*Conus escondidai* *					69.9	
IP	*Conus frausseni* *					122	
IP	*Conus sartii*					318	
IP	*Conus sculpturatus*					2083	
IP	*Conus wilsi*					2133	
IP	*Conus pauperculus*					2598	
IP	*Conus pseudokimioi* *					4649	
IP	*Conus terryni* *				66.5		
IP	*Conus rawaiensis* *			13.6			
WA	*Conus deynzerorum*						58.7
WA	*Conus pseudoaurantius*						1361
WA	*Conus cedonulli*						2924
WA	*Conus curassaviensis*				4.97		
WA	*Conus kirkandersi* *				124		
WA	*Conus hieroglyphus*			7.91			
WA	*Conus henckesi*			166			

Table 2. *Conus* species occurring in 1° grid cells with 70 – 99% of their occupancy in High and Very High impact, analysed by IUCN Red List threat category: VU Vulnerable, DD Data Deficient, LC Least Concern. Values shown represent the Corrected Area of Occupancy in km^2.

Region	Species	VU	DD	LC
EA	*Conus ventricosus*			15,398
EP	*Conus baccatus*			7,667
IP	*Conus taeniatus*			39.6
IP	*Conus aplustre*			324
IP	*Conus papilliferus*			2,854
IP	*Conus sukhadwalai*			4,875
IP	*Conus tuticorinensis*			8,668
IP	*Conus dondani*			9,659
IP	*Conus suduirauti*			12,845
IP	*Conus tisii*			13,366
IP	*Conus zapatosensis*			25,209
IP	*Conus madagascariensis*			25,757
IP	*Conus barbieri*			26,624
IP	*Conus thalassiarchus*			40,800
IP	*Conus zandbergeni*			41,693
IP	*Conus stupella*			47,646
IP	*Conus malacanus*			59,992
IP	*Conus pica*			60,434
IP	*Conus traillii*			70,356
IP	*Conus fulmen*			121,125
IP	*Conus insculptus*			223,312
IP	*Conus hirasei*			269,226
IP	*Conus otohimeae*			274,078
IP	*Conus kuroharai*			352,587
IP	*Conus spirofilis*			428,076
IP	*Conus sieboldii*			601,809
IP	*Conus roseorapum*			1,103,510
IP	*Conus scopulicola*		1,732	
IP	*Conus lentiginosus*		2,755	
IP	*Conus aculeiformis*		5,701	
IP	*Conus tuberculosus*		8,550	
IP	*Conus moncuri*		29,521	
IP	*Conus rizali*		37,216	

Contd.

Table 2 contd.

Region	Species	VU	DD	LC
IP	*Conus kiicumulus*		108,283	
IP	*Conus blanfordianus*		121,986	
IP	*Conus ikedai*		166,611	
IP	*Conus miniexcelsus*		203,986	
IP	*Conus habui*		227,437	
WA	*Conus exquisitus*			253
WA	*Conus boui*			643
WA	*Conus inconstans*			947
WA	*Conus sunderlandi*			1,437
WA	*Conus magellanicus*			3,294
WA	*Conus magnottei*			4,238
WA	*Conus anaglypticus*			4,491
WA	*Conus pealii*			7,628
WA	*Conus poulosi*			9,073
WA	*Conus roberti*			9,474
WA	*Conus pusio*			10,027
WA	*Conus penchaszadehi*			11,726
WA	*Conus havanensis*			12,248
WA	*Conus kevani*			13,171
WA	*Conus paulae*			17,633
WA	*Conus mazei*			30,619
WA	*Conus mappa*			57,439
WA	*Conus venezuelanus*			62,614
WA	*Conus nodiferus*			71,585
WA	*Conus honkeri*		11,809	
WA	*Conus stearnsii*	9,202		

Table 3. ***Conus*** **species within the highest 10% of range-rarity cells that are wholly within the High and Very High threat within all three of the threat scenarios of anthropogenic impact, thermal stress 2050 and aragonite saturation for 2050, analysed by IUCN Red List threat category: CR Critically Endangered, VU Vulnerable, NT Near Threatened, DD Data Deficient, LC Least Concern. Regions: EA Eastern Atlantic, IP Indo-Pacific, WA Western Atlantic. Sorted values represent the Corrected Area of Occupancy in km^2. * Indicates species NOT also included in Tables 1 & 2.**

Region	**Species**	**CR**	**VU**	**NT**	**DD**	**LC**
EA	*Conus lugubris*	1.60				
EA	*Conus decoratus*		15.05			
EA	*Conus curralensis*			0.29		
EA	*Conus saragasae*			0.86		
EA	*Conus kersteni*			1.46		
EA	*Conus navarroi*			2.28		
EA	*Conus denizi*			4.00		
EA	*Conus atlanticoselvagem*			14.8		
EA	*Conus bellulus*				2.84	
EA	*Conus verdensis*					0.19
EA	*Conus fantasmalis*					0.36
EA	*Conus grahami*					0.82
EA	*Conus infinitus*					4.72
EA	*Conus calhetae*					5.09
EA	*Conus crioulus*					6.06
EA	*Conus isabelarum*					8.78
EA	*Conus desidiosus*					15.5
EA	*Conus claudiae*					18.4
EA	*Conus raulsilvai*					19.8
EA	*Conus maioensis*					24.2
EA	*Conus ventricosus*					15,398
EP	*Conus kerstitchi**				94,371	
EP	*Conus baccatus*					7,667
EP	*Conus gladiator**					13,855
EP	*Conus diadema**					23,815
EP	*Conus nux**					28,668
EP	*Conus brunneus**					40,391
EP	*Conus bartschi**					43,779
EP	*Conus orion**					52,088

Contd.

Table 3 contd.

Region	Species	CR	VU	NT	DD	LC
EP	*Conus scalaris**					56,927
EP	*Conus vittatus**					61,988
EP	*Conus tiaratus**					63,510
EP	*Conus princeps**					66,675
EP	*Conus lucidus**					74,060
EP	*Conus patricius**					74,236
EP	*Conus dalli**					77,976
EP	*Conus mahogany**					83,185
EP	*Conus purpurascens**					99,114
IP	*Conus escondidai*				69.9	
IP	*Conus frausseni*				122	
IP	*Conus sculpturatus*				2,083	
IP	*Conus pseudokimioi*				4,649	
IP	*Conus terryni*					66.5
IP	*Conus andremenezi*					2,183
IP	*Conus baeri**					7,835
IP	*Conus rufimaculosus**					10,941
IP	*Conus iodostoma**					46,586
IP	*Conus stupella*					47,646
WA	*Conus hieroglyphus*		7.91			
WA	*Conus honkeri*				11,809	
WA	*Conus curassaviensis*					4.97
WA	*Conus deynzerorum*					58.7
WA	*Conus velaensis**					4,752
WA	*Conus poulosi*					9,073
WA	*Conus penchaszadehi*					11,726
WA	*Conus kevani*					13,171
WA	*Conus paulae*					17,633

Chapter 6. Discussion

6.1. Summary of thesis aims and results

In this study I set out to develop a profile of the gastropod mollusc genus *Conus*, the largest of the marine invertebrates, and an exceptional source of biomaterials for research and development of novel drugs. I aimed to identify species threatened with extinction, determine their biogeography and establish causes behind any population declines. I sought to describe centres of endemism where taxa, restricted by natural barriers from further migration and reduced to small isolated populations, may finally have reached the 'end of the line', and to propose conservation initiatives for their protection. I also sought to understand whether the methodology employed by the IUCN Red List and used in my study offered a sufficiently comprehensive means to evaluate the true potential threat to these species.

In Chapter 1 for the introduction, I placed my research into context, identifying the broader issues that generated the inspiration to embark on this study. I set out my research aims and objectives and briefly described the functions of the chapters that followed.

In Chapter 2, I reviewed the historical significance of cone snails, their emergence during the Lower Eocene and their radiation across all of today's tropical seas. I described their success in speciation resulting from their extraordinary battery of complex toxins and adaptability to exploit new prey, and the contribution they make to marine biodiversity. I examined their lifecycle and the important worldwide trade in their shells that brings pleasure to thousands and sustains many poor fishers in developing countries. Finally, I reviewed their potential as one of the world's most important source biota in the development of powerful new drugs that bring relief to thousands of sufferers, with the expectation of further advances against other pernicious medical conditions in the future.

In Chapter 3, using the standard categories and criteria of the IUCN Red List of Threatened Species I assessed the conservation status of 632 species of *Conus* and compiled source data for further research. I examined commercial and environmental stressors and analysed the distribution, bathymetry and impact on species' habitats from anthropogenic pressures across four separate biogeographical regions: Eastern Atlantic, Western Atlantic, Indo-Pacific and Eastern Pacific. I identified 67 species threatened or near-threatened with extinction, with the major hotspot in the Eastern Atlantic, where 42.9% of the 98 species fell into these categories.

Of 41 species categorised as threatened globally, 19 (46.3%) were exposed to pollution, either from effluent or petro-chemical discharges. A further 17 (41.5%) were affected by coastal development, tourism, ports and harbours, with three (7.3%) targeted by shell collectors. There was a single species affected by commercial fisheries and another by elevated sea surface temperatures following an extreme La Niña event.

In Chapter 4, I focussed on the results of my assessment of the 53 endemic cone snails of Cape Verde, where 24 species are threatened or near-threatened with extinction. The assessment had shown 45.3% of the archipelago's *Conus* diversity at risk compared to 7.4% for the rest of the world. All three critically endangered species occur in Cape Verde together with four of eleven endangered species and nearly half of the globally near-threatened *Conus*. Drilling down into the biogeography, I explored the environmental challenges facing the country's marine habitats where cone snails occur, and the impact from tourism now at the heart of its economy. I scrutinised the structural development plans for the islands and their potential effect on shallow water mollusc assemblages including *Conus*. The results revealed that where tourism infrastructure and port development projects overlapped with endemic *Conus* many species were destined for extinction. While illegal extraction of sand and gravel from the foreshore and shallows for construction continued, and waste processing remained inadequate, the future looked bleak for these small-shelled, range-restricted snails. Consequently I proposed a ban on all trade in cone shells and a tightening of environmental regulations.

In Chapter 5, I projected distribution and bathymetry data for all 632 species of *Conus* derived from the Red List assessment with global data of anthropogenic impacts and future threats from aragonite saturation levels and thermal stress. I sought to test whether extinction-focussed Red List evaluation criteria had resulted in some species being overlooked. Results revealed that of those species with 70% or more of their occupancy in places with the highest levels of human impact, 67 species had been categorised as Least Concern on the Red List. Nineteen of these species had a range of less than 100 km^2 and therefore immediate potential candidates for status reassessment. Where clusters of endemic species are at risk, the threat to biodiversity is greatly increased. By analysing range-rarity scores I identified hotspots of endemism occurring in regions not only exposed to high levels of anthropogenic impact now, but also projected to suffer the worst effects of ocean acidification and elevated sea-surface temperatures by 2050. This revealed 20 more species not list as threatened as further candidates for re-evaluation. Gradients in environmental threat projected across regions populated by species under evaluation disclosed taxa not classified as threatened under Red List criteria as suitable for reassessment. This model enhances the rationale for species already listed with threatened status and offers important supporting data to help lift species out of the Data Deficient category. The results can also describe all-important data for planning long-term conservation initiatives.

Although conservation must be the final goal for all threat assessments, its planning, implementation and monitoring are often fraught with bureaucratic and financial obstacles. Prevention is better than cure, and with Red List methodology centred on species nearing extinction, timelier warnings from broader-based assessments such as those I described could offer a pre-emptive approach to conservation to complement the reactive approach implied by the Red List.

Most marine species are unfavourably compared to terrestrial taxa in the league table of extinction risk owing to a general supposition of high fecundity and wide dispersal (Roberts & Hawkins, 1999; Vincent et al., 2013). This hypothesis however is far from assured, with 25.5% of cone snails from the Eastern Atlantic threatened, they find similar footing with island endemic birds with a global total of 23% at risk (Johnson & Stattersfield, 1990), European terrestrial molluscs with 20% at risk (Darwall et al., 2012; Gerlach et al., 2012) and bryophyte flora from the Canaries with 21% at risk (González-Mancebo et al., 2012) among others. The suggestion that marine taxa are less at risk than terrestrial taxa is spurious.

6.2 Future Research

Since this is the first IUCN Red List assessment of a marine gastropod mollusc, there are no data available from which to develop a comparative study against other Gastropoda to determine whether the risk to *Conus* is atypical. Species of particular relevance for comparison would be the *Volutidae* (volutes) that are also predatory and have a distribution profile not dissimilar to the *Conidae*.

Although there has been some research on the effect of gathering 'trophy' shells from tropical waters (Newton et al., 1993; Queensland, 2007), such studies are few and localized. Not surprisingly, there is a general reluctance in the shell trade and among amateur collectors to acknowledge the impact of their pursuit. Whereas it may be true that many species with an ocean-wide distribution are presently at minimal risk from this activity, unquestionably some local extirpation results from over-gathering (Newton et al., 1993) and the issue becomes increasingly pressing in centres of endemism. Shell collectors and traders are an important source of information on gathering pressure and without their comprehensive knowledge on distribution, abundance and threats gained from personal observation, the assessment of *Conus* for the Red List would have been impoverished and resulted in a larger proportion of species categorised as Data Deficient. Further research is now urgently needed on the effects of shell collecting on species abundance and diversity and the vexed question as to whether this problem can mainly be levelled at tourism or whether demand from ‘conchologists’ including traders also plays a significant part.

Prospecting for cone snails for bioactive compounds has been difficult to quantify owing to the secrecy surrounding intellectual property, although I do not believe it constitutes the same level of threat as shell collecting. However, lack of evidence is not proof of innocence, and pending further research on this subject at least, the jury is still out.

Mollusc shells can be considered as any other commodity in that there is a structured market in their trade. For a separate study, I have extracted the wholesale prices of cone shells together with a number of species-specific attributes, including size and quality of shell, from eight trade catalogues published at irregular intervals over 42 years to 2007 (Rice, 2007). I index-linked the low, high and median prices for all *Conus* species for all editions to the 2007 price levels of the final edition. Using the free market principle that where there is insufficient supply, the seller will “increase the price until equilibrium is once more attained” (Smith, 1776), further research should now be initiated to identify those species which show the greatest monetary gains and whether their perceived scarcity of supply is a reflection of their status in the wild, or from other factors such as inaccessibility from deep water, etc. Market analysis and price variability could introduce a novel and rapid means of determining changes in availability, increasing scarcity and possible rapid declines in abundance of species at risk.

6.3. Conclusions

The vast majority of cone snails occur in developing countries where financial and administrative considerations are unlikely to permit the introduction of complex conservation initiatives, particularly where livelihoods are concerned. Owing to the degree of taxonomic knowledge required, any partial ban on trade, for example with just species listed as threatened, would be too onerous to enforce. Similarly, a global ban on export through CITES of all species, even if feasible, could not be warranted owing to the high proportion that are not under threat. However, where there are clusters of threatened endemic species, in places such as Cape Verde, an export ban on animals and shells could be both realistic and achievable.

Loss of habitat and environmental degradation and pollution are the primary drivers of extinction risk to *Conus*, so species already under threat are not well served by the added pressure of shell collecting. The gathering of 'trophy' shells and marine curios is not confined to cone snails. The best opportunity for protection is through education supported by fully enforced marine protected areas (MPAs). To target protection at species at highest risk, I would propose the publication of guidelines for the specimen shell trade to include sustainable rates of off-take and species that should be avoided. For countries where the primary threat to endemic *Conus* is from casual shell gathering or from disturbance directly or indirectly related to tourism, my proposal would be to extend the programme to local environmental agencies. Assistance could be offered in the development of guidelines that warn of the consequences of shell collecting and habitat disturbance for dissemination through travel agents, hotels, tour operators and dive centres.

There is an established community of cone shell enthusiasts whose interests encompass every facet of the genus and who are keen collectors with sizeable private collections. Many are leading academics who have spent a lifetime in the research of cone snails including biopharmaceuticals, but there are also a number of international shell traders whose taxonomic knowledge is often greater than that of the academics. The distinction between these groups is blurred as many leading dealers are also academics with a body of published works. The principal voice of the global cone shell community is the online magazine, the Cone Collector (www.theconecollector.com), which in addition to publishing, also holds biennial conferences. My research enabled me to invite leading academics and major international shell dealers to peer review the Red List assessment at my synthesis workshop in Chicago. This in turn led to an invitation to present the preliminary findings at the Cone Collector convention in La Rochelle, France in 2013 and resulted in the first tentative steps with dealers and collectors to propose a moratorium on trade in species at highest risk, starting with the Critically Endangered but with possible extension to other endangered species at a later date. To my knowledge, this is the first time such a group has shown support for a voluntary code in conservation for an invertebrate.

Cone snails have been remarkably successful in their dispersal and speciation over a relatively brief evolutionary timeframe. Despite their low public profile they are of considerable importance to marine biodiversity, biomedical research, and as a source of additional income for countless impoverished fishers in developing countries around the world. However, the challenges they confront now from habitat loss, pollution and shell collecting may be eclipsed in future by thermal stress and acidification of the oceans. My research has identified species facing the threat of extinction and regions where trade in shells should be curtailed and conservation measures put in place for their protection. In support of the Red List, I have also explored new methods to identify species worthy of consideration for threatened status before populations reach critical levels. This should also provide evidence to lift some Data Deficient species into a more appropriate Red List category from where they can be formally monitored. In summary, I hope my research will help promote planned, proactive conservation of cone snails in place of inaction or crisis management.

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