CHAPTER FOUR

SUSCEPTIBILITY OF SHARKS, RAYS AND CHIMAERAS TO GLOBAL EXTINCTION

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Abstract

Marine biodiversity worldwide is under increasing threat, primarily as a result of over-harvesting, pollution and climate change. Chondrichthyan fishes (sharks, rays and chimaeras) have a perceived higher intrinsic risk of extinction compared to other fish. Direct fishing mortality has driven many declines, even though some smaller fisheries persist without associated declines. Mixed-species fisheries are of particular concern, as is illegal, unreported and unregulated (IUU) fishing. The lack of specific management and reporting mechanisms for the latter means that many chondrichthyans might already be susceptible to extinction from stochastic processes entirely unrelated to fishing pressure itself. Chondrichthyans might also suffer relatively more than other marine taxa from the effects of fishing and habitat loss and degradation given coastal habitat use for specific life stages. The effects of invasive species and pollution are as yet too poorly understood to predict their long-term role in affecting chondrichthyan population sizes. The spatial distribution of threatened chondrichthyan species under World Conservation Union (IUCN) Red List criteria are clustered mainly in (1) south-eastern South America; (2) western Europe and the Mediterranean; (3) western Africa; (4) South China Sea and Southeast Asia and (5) south-eastern Australia. To determine which ecological and life history traits predispose chondrichthyans to being IUCN Red-Listed, and to examine the role of particular human activities in exacerbating threat risk, we correlated extant marine species' Red List categorisation with available ecological (habitat type, temperature preference), life history (body length, range size) and human-relationship (whether commercially or game-fished, considered dangerous to humans) variables. Threat risk correlations were constructed using generalised linear mixed-effect models to account for phylogenetic relatedness. We also contrasted results for chondrichthyans to marine teleosts to test explicitly whether the former group is intrinsically more susceptible to extinction than fishes in general. Around 52% of chondrichthyans have been Red-Listed compared to only 8% of all marine teleosts; however, listed teleosts were in general placed more frequently into the higher-risk categories relative to chondrichthyans. IUCN threat risk in both taxa was positively correlated with body size and negatively correlated albeit weakly, with geographic range size. Even after accounting for the positive influence of size, Red-Listed teleosts were still more likely than chondrichthyans to be classified as threatened. We suggest that while sharks might not have necessarily experienced the same magnitude of deterministic decline as Red-Listed teleosts, their larger size and lower fecundity (not included in the analysis) predispose chondrichthyans to a higher risk of extinction overall. Removal of these large predators can elicit trophic cascades and destabilise the relative abundance of smaller species. Predator depletions can lead to permanent shifts in marine communities and alternate equilibrium states. Climate change might influence the phenology and physiology of some species, with the most probable response being changes in the timing of migrations and shifts in distribution. The synergistic effects among harvesting, habitat changes and climate-induced forcings are greatest for coastal chondrichthyans with specific habitat requirements and these are currently the most likely candidates for extinction. Management of shark populations must take into account the rate at which drivers of decline affect specific species. Only through the detailed collection of data describing demographic rates, habitat affinities, trophic linkages and geographic ranges, and how environmental stressors modify these, can extinction risk be more precisely estimated and reduced. The estimation of minimum viable population sizes, below which rapid extinction is more likely due to stochastic processes, is an important component of this endeavour and should accompany many of the current approaches used in shark management worldwide.

1. INTRODUCTION

Humans have depended on marine resources since prehistory (Walker and Deniro, 1986), with the commonly held belief until even recent times that it was beyond human capability to cause the extinction of marine species. This is summarised by two of the foremost thinkers of the eighteenth and nineteenth centuries, Jean Baptiste de Lamarck and Thomas Huxley, who reflected a widespread belief that the high fecundity and wide distributions of marine fishes made the seas an inexhaustible source of food and wealth, and that people could use but a small fraction of the total resources available using fishing methods employed at the time (Garibaldi and Caddy, 2004; Sims and Southward, 2006). Even only a decade ago, a survey of marine scientists revealed that nearly one-third believe marine extinctions are currently not a serious problem (Roberts and Hawkins, 1999).

In the past decade, it has become clear that marine biodiversity worldwide is under increasing threat, primarily as a result of over-harvesting, pollution and the direct and indirect impacts of climate change (Gardner *et al.*, 2003; Harley *et al.*, 2006; Harvell *et al.*, 2002, 2004; Hutchings and Reynolds, 2004; Jackson *et al.*, 2001; Jones *et al.*, 2004; Lotze *et al.*, 2006; Pauly *et al.*, 2002; Roberts, 2002). At present, around 40% of the world's human population lives within 100 km of the coast (Martinez *et al.*, 2007) and this proportion is increasing. With the median global human population predicted to increase to over 9 billion by 2050 (McMichael, 2001) and more people choosing to live along the coastal fringes, marine habitats are likely to suffer increasing degradation and over-exploitation (Worm *et al.*, 2006). As a corollary, anthropogenic stresses and climatic changes have reduced the resilience of ecosystems in many locations around the globe by slowly degrading habitats and directly harvesting species, causing many ecosystems to switch unexpectedly into alternate states (Folke *et al.*, 2004; Hughes *et al.*, 2003; Nystrom *et al.*, 2000; Scheffer *et al.*, 2001; Worm *et al.*, 2006). Stressors can operate singly or synergistically at multiple scales (Brook *et al.*, 2008), resulting at times in large shifts in species composition. Familiar examples include regime or phase shifts on coral reefs (Aronson *et al.*, 2004; Bellwood *et al.*, 2004; Hawkins and Roberts, 2004; McManus and Polsenberg, 2004), in kelp forests following declines in canopy-forming species (Steneck *et al.*, 2002, 2004), and the abandonment of many coastal and oceanic fisheries (Dulvy *et al.*, 2004b, 2006; Jennings and Kaiser, 1998; Pauly *et al.*, 2002; Roberts, 2002, 2003; Worm *et al.*, 2006). Indeed, despite having sometimes wide geographic distributions and unique regional histories, many marine systems have experienced long periods of slow degradation followed by rapid acceleration in collapse of the biological communities they support (Lotze *et al.*, 2006). This has been largely attributed to the global colonisation by European nations and then the subsequent increase in industrial fishing efficiency (Christensen *et al.*, 2003; Mullon *et al.*, 2005; Roberts, 2003). These rapid changes since the 1950s have been scrutinised intensely over the past decade (Essington *et al.*, 2006; Hilborn *et al.*, 2003; Hutchings, 2000; Hutchings and Reynolds, 2004; Jackson *et al.*, 2001; Jennings and Kaiser, 1998; Myers and Worm, 2003, 2005) to the extent that the sustainability of current and future fisheries is now seriously called into question (Pauly *et al.*, 1998, 2002; Roberts, 2002).

The total world catch from wild marine stocks has increased from 19.3 million tonnes in 1950, peaking in 2000 at 86.4 million tonnes and then slightly declining to 84.5 million tonnes in 2004 (Food and Agriculture Organization of the United Nations, 2005). The majority of the world's fish stocks have been as intensively fished as deemed possible, even to the extent that target populations have been severely reduced and many fisheries have been abandoned (Hilborn *et al.*, 2003). One of the most infamous examples of such depletions is that of Atlantic cod (*Gadus morhua*) (Hutchings, 1996; Myers *et al.*, 1997); and examples of fisheries abandonment include those targeting whales (Baker and Clapham, 2004) and herring (Engelhard and Heino, 2004). These have most often been associated with decline in abundance across entire species' ranges, or a decreased reproductive capacity through the excessive removal of large, mature females (McIntyre and Hutchings, 2003; Scott *et al.*, 1999) or immature stages (Hutchings and Myers, 1994; Myers *et al.*, 1997).

Population declines have also had a number of ripple effects including changes to ecosystems and shifts in fishing to other economically lucrative target species. For example, once cod stocks declined around Newfoundland, the shellfish (shrimp, lobster and crab) populations increased substantially due to a reduction of predators (Bundy, 2001; Worm and Myers, 2003). For mixed-species fisheries, it has commonly been seen through time series of harvesting that population reductions occur selectively for larger individuals first, causing a decline in the size of individuals caught (Jackson *et al.*, 2001; Pitcher, 2001) before leading to an overall decline in catches. This results in smaller species being caught, with the fishery remaining economically viable only because there is a shifting focus towards species lower down the food web (Jennings *et al.*, 1999; Pauly and Palomares, 2005; Pauly *et al.*, 2001). Fisheries harvests are linked to the majority of recorded marine extinctions; around 55% of 133 extinctions have been attributed principally to direct and indirect harvesting by industrial fisheries (Hilton-Taylor, 2000; Lotze *et al.*, 2006; Roberts, 2002). Of course, a large proportion has been initiated by subsistence, artisanal and recreational fishing, but these have generally been responsible for local and regional, rather than range-wide extinctions (Dulvy *et al.*, 2003).

Physical changes that largely degrade fish habitats can result from either natural sources (e.g. severe storms—Cheal *et al.*, 2004; Kaufman, 1983; earthquakes—Noerenberg, 1971; freshwater inputs and disease—Dulvy *et al.*, 2003) or anthropogenic sources (e.g. land reclamation, coastal development, alteration of freshwater flow and other habitat destruction). Such natural changes can compound the severity of population declines arising from fisheries exploitation. The effects of habitat change will usually alter the abundance and distribution of affected species, and can act differently on different age or developmental groups. These effects can also be location- and species-specific, typically affecting critical habitat requirements (e.g. nursery areas), meaning that attributing observed declines to particular sources can be difficult. Furthermore, the amount of habitat change is mostly related to proximity to land and to human population pressures. Therefore, freshwater and estuarine species are predicted to receive the greatest threats (Musick *et al.*, 2000b). The effects of pollution are closely related to, and often found in association with, other habitat changes. Common pollutants include sewage effluent, organic and inorganic compounds, heavy metals and nutrients that potentially affect all trophic levels. Other biological threats include introduced species, parasites and disease.

Introduced organisms can outcompete or eat native prey, or they can act as vectors for the transmission of diseases and parasites, thus increasing extinction risk (Dulvy *et al.*, 2003). This risk is further heightened as climate change and other habitat degradation provide more suitable habitats for invading non-indigenous species (Harvell *et al.*, 1999; Ruiz *et al.*, 2000).

One taxonomic group of marine fishes that has come under increasing scrutiny in terms of extinction risk from these processes is Chondrichthyes (sharks, rays and chimaeras). These species are typically large predators in all major marine systems and have life history strategies that are likely to predispose them to extinction under rapid environmental change. Chondrichthyan fishes are subject to the range of human-derived threats, from targeted and indirect fishing pressure to other impacts (e.g. habitat change and pollution) across their entire range (Cadet *et al.*, 2003; Cheung *et al.*, 2007; Dulvy *et al.*, 2008; Ferriti *et al.*, 2008; García *et al.*, 2008; Stevens *et al.*, 2000, 2005; Walker, 1998). But are chondrichthyans any more or less susceptible to rapid environmental change than other marine biota? We explore this complex question by describing the life history strategies adopted by chondrichthyans in relation to the different threats they face today.

1.1. Aims

The overall aim of this chapter is to review the available evidence for and against the posited higher susceptibility of marine shark populations to threatening processes, relate this to other fish taxa that are conservation-listed, and identify areas (regional and topical) requiring more knowledge in this regard. We also tackle the question of whether chondrichthyans should be treated as a specific case in fisheries research and management, or whether they respond in much the same way as all other marine taxa challenged with the additional pressure imposed by human activities. It is not our intention to provide an exhaustive review of all chondrichthyan fisheries (target, by-catch or otherwise) (for some reviews, see Camhi *et al.*, 1998; Fowler *et al.*, 2005; Garcia and de Leiva Moreno, 2003; Hilborn *et al.*, 2003; Kroese and Sauer, 1998; Mullon *et al.*, 2005; Rose, 1996; Sims, 2008; Stevens *et al.*, 2000; Walker, 1998); rather, we contextualise the current extinction risk within this taxon with respect to one of its principal sources of mortality by highlighting specific fishery examples. Nor is our goal to provide a complete overview of chondrichthyan life history (see Cailliet *et al.*, 2005; Compagno, 1990; Cortés, 2000; Dodd, 1983; Frisk *et al.*, 2001; Smith *et al.*, 1998; Wourms, 1977 for more comprehensive compilations and reviews); our coverage of ecological, life history and human-relationship traits is undertaken to examine the relative susceptibility of this taxon to particular extinction drivers. Specifically, our review encompasses five main, inter-related topics: (1) a description and discussion of chondrichthyan life history traits that are thought to predispose species within this taxon to population declines and possible extinction; (2) a broadly comprehensive review of the past and present threats faced by sharks and rays; (3) a quantification of threat risks faced by chondrichthyan and teleost species based on correlations of World Conservation Union (IUCN) Red List categories (www.iucnredlist.org) and a series of life history, ecological and human-relationship attributes; (4) an overview of the ecosystem role of chondrichthyans as predators and implications of their loss to marine biological communities and (5) an appraisal of the future of chondrichthyan species richness and abundance, with emphasis on research priorities.

2. CHONDRICHTHYAN LIFE HISTORY

Chondrichthyes are cartilaginous fish that include sharks and rays (Class Elasmobranchii) and chimaeras (Class Holocephalii) (for a detailed review of current classification, see Compagno *et al.*, 2005). Modern chondrichthyans are derived from over 400 million years of evolution (Compagno, 1990), and there are presently thought to be over 1100 species (Compagno *et al.*, 2005). However, not all species have been described, and there are new species being described regularly. For examples of recent new descriptions, see Last *et al.* (2008). The taxon has survived and re-radiated after two major mass extinction periods: the Permian–Triassic and Cretaceous–Tertiary transitions (Carroll, 1988). Although chondrichthyans are generally large in size compared to the average teleost (Compagno, 1981), their historically low economic value to fisheries (see Section 3.1) has stymied the impetus to collect information describing their biology, ecology and role in ecosystem dynamics (Cailliet *et al.*, 2005). At present there is a paucity of essential biological parameters required for both conservation and resource management, with the information currently available derived largely from commercially important or by-catch species (Cailliet *et al.*, 2005; Walker, 1998; Wood *et al.*, 2007).

2.1. Niche breadth

Chondrichthyans are found throughout all of the world's oceans (Compagno, 1990), although they essentially adopt a single trophic mode—predation—and have radiated to fill a range of habitat types. Around 50% of extant species live in coastal and shelf waters (to around 200 m), ~35% in deeper water (200–2000 m), and the rest are either oceanic (~5%), live in freshwater (~5%) or occur within several of these habitats (~5%) (Compagno, 1990; Compagno *et al.*, 2005). Although some are obligate freshwater species (~35 species), we focus on marine species that live either partially or totally in the marine environment. Within these habitats, some have wide distributions, while others are endemic to specific habitats.

They also have a range of foraging niches including benthic or pelagic specialisation such as whitetip reef sharks *Triaenodon obesus* (Stevens, 1984) and salmon sharks *Lamna ditropis* (Kubodera *et al.*, 2007), respectively. Some are opportunistic predators (e.g. tiger sharks *Galeocerdo cuvier*—Simpfendorfer *et al.*, 2001), and other are the ocean's largest filter feeders (e.g. basking sharks *Cetorhinus maximus*—Sims, 2008).

During their evolution, chondrichthyans have adopted alternative life histories from that of most other marine fishes (Compagno, 1990; Holden, 1974). The general category into which these life histories fall has been summarised as '*K*-selected' (Cortés, 2002; Fowler *et al.*, 2005) where individuals are long-lived, slow-growing and late-maturing, and have low production and low mortality rates (Cailliet *et al.*, 2005; Musick *et al.*, 2000a; Stevens *et al.*, 2000), although there are a few exceptions, such as spot-tail *Carcharhinus sorrah* and sharpnose *Rhizoprionodon taylori* sharks (Simpfendorfer, 1999; Stevens and Wiley, 1986). There is now a general consensus in the literature that these traits, in combination with their main role as predators (Camhi *et al.*, 1998), make chondrichthyan populations highly susceptible to over-exploitation (Cortés, 2002; Fowler *et al.*, 2005).

2.2. Age and growth

The measurement of growth, survival and reproductive potential can provide important information on rates of population change (Hilborn and Walters, 2001; Sinclair *et al.*, 2006; Walters and Martell, 2004), and ultimately risk of extinction (Dulvy and Reynolds, 2002; Hutchings, 2002; Reynolds *et al.*, 2005; Smith *et al.*, 1998). Various methods have been used to calculate or estimate age in chondrichthyans, including measurement of growth bands in vertebrae or other hard structures, bomb carbon dating, tag recapture and captive growth experiments (Cailliet and Goldman, 2004). Some species live >50 years (Beamish and McFarlane, 1987; Bradshaw *et al.*, 2007; Pauly, 2002; Wintner, 2000). Age and growth patterns have been validated for around 120 species (Cailliet and Goldman, 2004; Haddon, 2001) and show a wide range of growth coefficients from 'slow-growing' species such as *Leucoraja ocella* [$K = 0.06$ (von Bertalanffy growth constant); Sulikowski *et al.*, 2003] to relatively rapid-growing species like *C. sorrah* ($K = 1.17$; Davenport and Stevens, 1988). Chondrichthyans also vary widely in age at maturity (Cailliet and Goldman, 2004), from 1 year in the brown smoothhound shark (*Mustelus henlei*) that can live up to 13 years (Yudin and Cailliet, 1990), to bull sharks (*Carcharhinus leucas*) that can live for >32 years and not reach sexual maturity until 13 years (Wintner *et al.*, 2002). The distribution of the age at maturity among species appears bimodal, with one peak at 5–6 years and second at 15–25 years (Cailliet and Goldman, 2004). Growth rates also vary extensively within species depending on local water temperature and productivity (Barker *et al.*, 2005; Francis, 1997).

2.3. Reproduction and survival

Chondrichthyan reproduction has evolved to be specialised and highly efficient (Carrier *et al.*, 2004). It generally involves considerable parental investment to produce relatively few large, well-developed young that have a high natural probability of survival (Hamlett and Koob, 1999; Holden, 1974). This is in contrast to teleost fishes that typically produce thousands to tens of millions of tiny eggs annually, although only a few young survive to maturity. This is primarily due to density feedback mechanisms that permit increasing fertility and juvenile survival to compensate for adult population decline (Hilborn and Walters, 2001).

Chondrichthyan reproductive parameters are still relatively unquantified for most species although there have been a number of detailed reviews (Budker, 1958; Carrier *et al.*, 2004; Dodd, 1983; Wourms, 1977). Chondrichthyan reproductive strategies tend to proceed along a single path, with all species having internal fertilisation. However, there is still a large diversity among chondrichthyans in terms of egg production, ovulation cycle, gestation period and mating systems (Carrier *et al.*, 2004). Once fertilisation has occurred females retain the eggs during the most vulnerable stages of development. Although energy-expensive, the production of well-developed embryos with access to energy reserves allows for highly efficient energy transfer from mother to offspring. Depending on how long embryos are retained, chondrichthyan species are divided into oviparous (egg-laying) and viviparous (live-bearing) forms (Carrier *et al.*, 2004). Oviparous species retain their eggs for a short time and then deposit or attach the eggs to benthic structures. The embryos continue to develop by consuming a yolk sac within the egg case and then hatch fully developed. Viviparous species will retain their embryos internally in one of the five uteri. There are various forms of vivipary employed. These include placental vivipary where the embryo is attached by a placenta, ovovivipary where the development of unattached embryos within the uterus is sustained by food supplied by large egg yolks; oophagy where embryos ingest infertile eggs; embryophagy where embryos consume smaller embryos; and hysteritrophy where fluids secreted by the uterus sustain the embryo.

Depending on the species, females can bear from one or two young in sand tiger sharks *Carcharias taurus* and manta rays *Manta birostris* (Robins and Ray, 1986; Springer, 1948), to 300 young in whale sharks *Rhincodon typus* (Joung *et al.*, 1996). Gestation rates are unknown for most species, but measured times range from around 3 months for *Dasyatis* sp. rays (Hamlett and Koob, 1999) to more than 22 months for the ovoviviparous spiny dogfish which has the longest gestation period known for any living marine vertebrate (Pratt and Casey, 1990). Breeding does not always occur annually in females and some species have one or more ‘resting’ years between pregnancies.

Following their high initial investment in pup production, many sharks and rays subsequently give birth in sheltered coastal or estuarine nursery areas where predation risk to pups (primarily from other sharks) is presumably reduced (Branstetter, 1990). Other species deposit eggs in locations where they are most likely to survive undamaged until the pups emerge. There is no known post-birth parental care. Nevertheless, it is thought that most chondrichthyans have relatively low natural mortality compared to teleosts (e.g. Bradshaw *et al.*, 2007; Cortés and Parsons, 1996; Grant *et al.*, 1979; Gruber *et al.*, 2001; Heupel and Simpfendorfer, 2002; Walker and Hislop, 1998; Waring, 1984).

Recently, there has been an increase in the development and use of demographic and population models to describe and predict the status of chondrichthyan populations (Cortés, 2007). Modelling approaches range from empirically derived age-based demographic models to recruitment models used to estimate survival and productivity, or to characterise vulnerability to exploitation (e.g. Au and Smith, 1997; Cortés, 1995, 2002; Frisk *et al.*, 2001, 2005; Gruber *et al.*, 2001; McAuley *et al.*, 2007; Punt and Walker, 1998; Simpfendorfer, 1999; Sminkey and Musick, 1996; Smith *et al.*, 1998; Walker, 1992; Xiao and Walker, 2000).

3. PAST AND PRESENT THREATS

Harvest of shark and ray populations has been proposed as the current greatest threat to their diversity and abundance, with risk from commercial and industrial fisheries far out-weighing that of artisanal and subsistence harvests (Baum *et al.*, 2003; Dulvy, 2006; Dulvy and Reynolds, 2002; Dulvy *et al.*, 2008; García *et al.*, 2008; Robbins *et al.*, 2006; Stevens *et al.*, 2005; Worm *et al.*, 2005). In comparison, the effects of habitat change and degradation, pollution and invasive species on this taxon are poorly understood (Stevens *et al.*, 2000). In this section, we provide an overview of current and past fishing effects on shark populations by industrial fishing, within single and mixed-species fisheries, by targeted or indirect harvesting, as by-catch in fisheries directed to other species and other threats including beach meshing, habitat loss and pollution.

3.1. Fishing

Chondrichthyans are a diverse taxonomic group that have radiated into specialised and opportunistic top predators. Whether chondrichthyan fisheries are sustainable has been debated and reviewed extensively over the last three decades (Holden, 1973; Stevens *et al.*, 2000; Walker, 1998). Over the last decade or so in particular, there has been much controversy regarding the causes of collapsing fisheries (Hutchings and Reynolds, 2004; Myers and Worm, 2005; Reynolds *et al.*, 2005) and the global state of shark populations (Baum *et al.*, 2005; Burgess *et al.*, 2005a; Dulvy *et al.*, 2008; Ferriti *et al.*, 2008; Robbins *et al.*, 2006; Stevens *et al.*, 2000; Walker, 1998). There has also been much discussion and supposition regarding the impact of shark and ray removal on the marine ecosystems that support them (Coll *et al.*, 2006; Jackson *et al.*, 2001; Stevens *et al.*, 2000; Ward and Myers, 2005; Worm *et al.*, 2006). Some have gone so far as to suggest that many of the world's shark populations are teetering on the brink of extinction, with catastrophic ecosystem change predicted as the logical corollary (Baum *et al.*, 2003; Myers and Worm, 2003; Worm *et al.*, 2006). Although there is some support for this contention (Aires-da-Silva *et al.*, 2008; Simpfendorfer *et al.*, 2002) others strongly disagree with this outlook, and identify problems in data quality and interpretation (Burgess *et al.*, 2005a,b; Hampton *et al.*, 2005; Hilborn, 2007; Polacheck, 2006; Walters, 2003), and the use of other data sources (Sibert *et al.*, 2006) (see also Section 3.1.3.2). The debate thus far has been confined mainly to large pelagic fisheries, but there is increasing concern for deepwater species living in presumably relatively stable environments that have already become subject to new and increasing exploitation as pelagic and coastal fisheries fail to meet the economic demand for fish products (Camhi *et al.*, 1998; García *et al.*, 2008; Roberts, 2002). Furthermore, local fishing has also been suggested as the main driver for population reductions in and around conservation areas (Robbins *et al.*, 2006), which highlights a number of management difficulties associated with the design and implementation of marine protected areas.

The global catch of chondrichthyans (including sharks, rays and chimaeras—Fig. 4.1) has increased from approximately 270,000 tonnes in the 1950s to around 810,000 tonnes in 2004, with a peak catch of 881,000 tonnes in 2003 (Food and Agriculture Organization of the United Nations, 2005). This accounts for approximately 1% of the current total landings of all marine fish (Food and Agriculture Organization of the United Nations, 2005). The greatest period of increase during that time was between the 1960s and 1970s when catches rose by 40%. More recently, from 1996 to 2004, the annual catch has exceeded 800,000 tonnes. FAO fishery statistics show that in 2004, 20 countries shared over 75% of the total catch, with Indonesia (15%), India (7.5%), Spain (6.5%), Taiwan (5.5%) and Mexico (4%) sharing approximately 40% of the total catch (Food and Agriculture Organization of the United Nations, 2005) (Fig. 4.2). The current status of regional fisheries harvesting chondrichthyans are reviewed in greater detail by Fowler and Cavanagh (2005). However, recent research has indicated large potential errors in FAO reporting based on market estimates of shark fins (Clarke *et al.*, 2006), from which global fin trade is estimated to be up to four times higher.

Figure 4.1 Examples of legal and illegal harvest of sharks. (A) Blue sharks (*Prionace glauca*) being landed at a port in Portugal (photo credit: N. Queiroz, CIBIO, Portugal, and the Marine Biological Association of the UK). (B) Dried shark fins (unidentified species) confiscated by the Australian Customs Service from an illegal fishing boat found within the Australian Fishing Zone in the Arafura Sea (photo credit: M. G. Meekan, Australian Institute of Marine Science). (C) Whole shark carcasses (mainly silky sharks *Carcharhinus falciformis*, blue sharks and dusky sharks *Carcharhinus obscurus*) (photo credit: W. White, Commonwealth Scientific and Industrial Research Organisation, Australia).

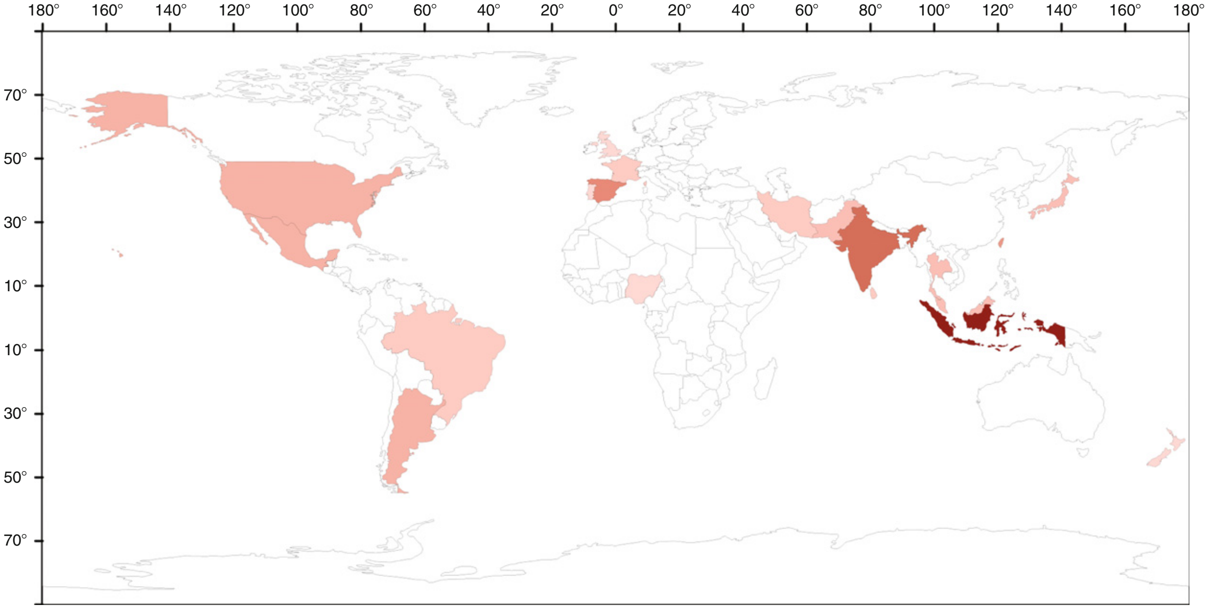

Figure 4.2 Global distribution of the relative shark catch for the top 20 countries listed by the Food and Agriculture Organization of the United Nations (FAO) in 2004. These 20 countries shared over 75% of the total catch in 2004, with Indonesia (15%), India (7.5%), Spain (6.5%), Taiwan (5.5%) and Mexico (4%) sharing approximately 40% of the total catch (www.fao.org).

These catches deliver products to a global and growing market for their meat, fins, cartilage, skin (leather), oil, teeth, gill rakers and jaws (Rose, 1996). Unfortunately, records of how and in what quantities these resources are used are poor, and for most catches they are entirely unquantified. Fresh shark meat is consumed locally near landing ports, but due to the need for expedient processing and cold storage it has little export value relative to most teleost fisheries (Camhi *et al.*, 1998). On the other hand, dried shark meat and fins are easily processed and supply distant markets (Fig. 4.1). This has led to a large demand that has continued to grow since the mid-1980s, especially for dried fin that is the main ingredient in popular Asian soups (Clarke *et al.*, 2006; Marshall and Barnett, 1997; Rose, 1996).

The biological and social effects of fishing exploitation are well documented (Dulvy *et al.*, 2000, 2004b; Hawkins and Roberts, 2004; Hutchings and Reynolds, 2004; Jackson *et al.*, 2001; Jennings and Kaiser, 1998; Jennings *et al.*, 1999; Kitchell *et al.*, 2002; Pauly and Palomares, 2005; Robbins *et al.*, 2006; Stevens *et al.*, 2000; Worm *et al.*, 2006). In addition to the obvious reduction in abundance brought about by unsustainable harvesting, chondrichthyan species might also experience changes to their life history traits (e.g. age at maturity and size distribution) and demography following harvest (Frisk *et al.*, 2005; Stevens and Davenport, 1991).

Currently, it is thought that sustainable and economically viable shark and ray fisheries can be maintained if carefully managed, especially for species with relatively high productivity rates (Walker, 1998) such as gummy (*Mustelus antarcticus*) and blue sharks (*Prionace glauca*) (Fig. 4.1). Presently, both industrial and small-scale commercial operations frequently raise concern regarding their sustainability, and with an increased demand for shark fin products it has been suggested that shark and ray catches are in reality three to four times higher than those reported (Clarke *et al.*, 2006). This highlights the potential threats from illegal, unreported and unmanaged (IUU) fishing (see Section 3.1.4). It is worth noting that most industrial shark fisheries are unmanaged with the exception of those from a few countries such as Australia, New Zealand, Canada and USA (Fowler *et al.*, 2005).

3.1.1. Definitions

From the perspective of providing objective insight into the global status of harvested chondrichthyans and to place this deterministic driver of population reduction into the context of extinction biology, we must be clear about what we mean by ‘extinction’. In his classic paper, Caughley (1994) differentiated the two main paradigms in conservation biology that are still relevant today: (1) the declining population paradigm, which refers to factors that depress the demographic rates of a species and cause its population to decline, and (2) the small-population paradigm, which refers to small populations that have already declined due to some (deterministic) perturbation and are thus more susceptible than large populations to extinction via chance events. This distinction is important because semantic labelling of a fishery's status, with similar terms used with different meanings, does not necessarily indicate heightened extinction risk.

A large number of individuals are typically required to ensure that a species will persist with high certainty, given the substantial evidence demonstrating that small and isolated populations are most vulnerable to extinction (Berger, 1990; Brook *et al.*, 2002; Spielman *et al.*, 2004). Small populations have a relatively higher extinction risk than large populations for three main reasons. Firstly, due to demographic fluctuations resulting from random variation in survival and fertility. Secondly, through environmental variation in resource or habitat availability and quality, competitive interactions or predation, and catastrophic mortality events (e.g. disease epidemics, severe storms). Finally, with decreasing genetic heterozygosity, inbreeding depression and genetic drift (Gilpin and Soulé, 1986; Shaffer, 1981), the eventual fate of all closed, finite populations is extinction through genetic erosion (Frankham *et al.*, 2004).

As populations decline they become more susceptible to demographic variance in vital rates, stochastic variation in environmental conditions, Allee effects, inbreeding depression and loss of genetic diversity (Caughley, 1994; Frankham, 1995; Melbourne and Hastings, 2008; Traill *et al.*, 2009). A minimum viable population (MVP) size is defined as the smallest abundance required for an isolated population to persist at a defined 'high' probability (usually set at >95%) for some (mostly arbitrary) set period into the future (Shaffer, 1981; typically 100 years or 40 generations—Traill *et al.*, 2007). Population-specific MVP sizes can be estimated empirically using population viability analyses (PVA) that calculate the probability of an initial population persisting in spite of demographic, environmental and genetic stochasticity and natural catastrophes (Shaffer, 1981). PVA models can be constructed by empirical simulation, experiments or long-term monitoring (Traill *et al.*, 2009); however, such models generally require good demographic and/or census data to provide reliable estimates (Traill *et al.*, 2007). Other MVP methods use genetic data to estimate the minimum population size that will maintain evolutionary potential—the population size required at equilibrium to balance the loss of quantitative genetic variation with the gain from mutation (Franklin and Frankham, 1998). Once a fishery (or some other deterministic driver) reduces a population to below its MVP size (Shaffer, 1981), then the reduced population becomes subject to a host of population-specific threats, most of which are stochastic (Traill *et al.*, 2007).

This important concept appears to have had little adoption or tractability in fisheries science, perhaps mainly because so few chondrichthyans have associated good census or demographic data. As an example, the spiny dogfish (*Squalus acanthias*) has declined by >78% in the north-eastern Atlantic in about three generations, which is sufficient to warrant *Endangered* status under the IUCN's Category A. Yet the entire population of *S. acanthias* numbers in the millions (Reynolds *et al.*, 2005), which exceeds all cross-taxonomic estimates of MVP size (Traill *et al.*, 2007, 2009). Therefore, this species, and perhaps many other chondrichthyans that have declined due to fishing harvest (Reynolds *et al.*, 2005) still have a relatively low risk of extinction.

Instead, the fisheries literature is replete with subjective terms that are used to refer to a fished population's status, with little differentiation between local, global, biological and economic 'extinction'. Terms such as 'over-exploited', 'over-harvested', 'depleted' and 'collapsed' are often only arbitrarily or not explicitly defined, so confusion is common (Hilborn, 2007; Jennings, 2007). For example, a fishery has been labelled 'collapsed' when its catch in any year falls below 10% of the highest recorded catch (Worm *et al.*, 2006), yet this definition is uncoupled from the concept of distance to a population's MVP. Likewise, terms adopted by the FAO like 'depleted' are reserved to describe the point at which harvest rate exceeds the maximum biological productivity (or maximum sustainable yield, MSY; Fig. 4.3), but this relationship depends on the underlying model chosen to represent the relationship between population rate of change and density (Fig. 4.4), which can vary considerably and is rarely evaluated specifically (Bradshaw, 2008; Brook and Bradshaw, 2006). The term 'collapse' has been defined loosely as when high catches continue for some time after 'depletion' has occurred, usually followed by low catch rates and abandonment of the particular fishery (Cooke, 1984), with some definitions based again on arbitrarily set magnitudes of decline (e.g. >90% relative to baseline abundance; Worm *et al.*, 2006). This is a result of socio-economic factors related to profitability (Hilborn *et al.*, 2003; Musick, 2005).

Even the word 'extinction' can have different meanings. 'Local' or 'population' extinction is often referred to as 'extirpation'. This differs from 'global' extinction in that only a proportion of the total number of individuals of that species is removed, usually, a sub-population that is geographically or genetically distinct from others (Sodhi *et al.*, 2007). This is further complicated because it is nearly impossible to observe local extinctions directly, especially in the marine environment where most species' behaviours go unnoticed. Thus extinctions can only be truly determined from successive surveys that fail to identify a species' presence (Fagan and Holmes, 2006; Sodhi *et al.*, 2007). There are also a number of alternative methods can be used to infer extinction including correlative approaches based on life history and ecological information, time-series to estimate changes in abundance; or demographic analyses based on age- or stage-structured models of vital rates (Dulvy *et al.*, 2004a). These approaches all focus on individual species.

Extirpations can change the local biological community (see Section 5), or lead to trophic replacements (Jackson *et al.*, 2001). Local extinctions can

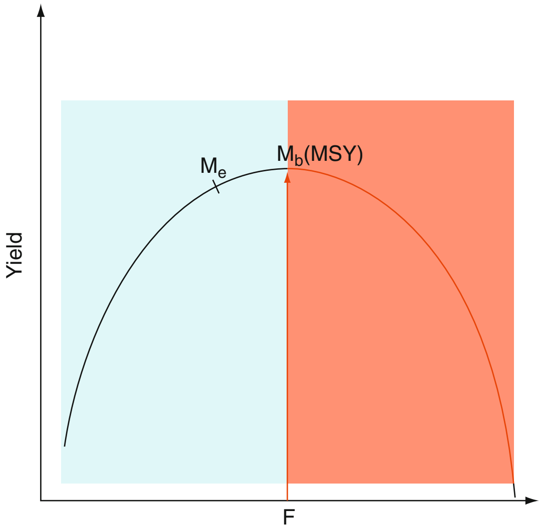

Figure 4.3 The classic trade-off between recruitment and fishing rate (F) showing the fishing rate where maximum biological productivity (M_b) occurs, also known as maximum sustainable yield (MSY). Also shown is the fishing rate where economic benefit (M_e) is maximised, which is inferior to M_b because it takes into consideration the long-term sustainability of the fishery (i.e. sustained fishing at M_b will tend to result in long-term declines in catch rates) (Hilborn and Walters, 2001).

also lead to increased fragmentation and genetic isolation, which are known to increase extinction risk especially for weakly dispersing and specialist species (Brook *et al.*, 2008; Purvis *et al.*, 2000b). Another concern for range-restricted species is density depensation, or Allee effects, that cause a reduction in the growth rate of small populations as they decline via reduced survival or reproductive success (Courchamp *et al.*, 2008; Mullon *et al.*, 2005). We want to avoid potentially subjective terms (Jennings, 2007) and focus instead on how deterministic decline due to harvesting can change chondrichthyan susceptibility to extinction. In the following sections, we document several chondrichthyan fisheries with the view to assess the degree of population decline that could lead to higher extinction risk.

3.1.2. Targeted fisheries

Commercial fisheries targeting sharks started as early as the late eighteenth century, with basking sharks (*C. maximus*) being the earliest-known target species (McNally, 1976). Although this fishery started from artisanal operations, it grew quickly in response to increasing consumer demand (McNally, 1976). From the 1920s, commercial fisheries targeting sharks grew steadily (Bonfil, 1994; Gauld, 1989), with overall shark landings

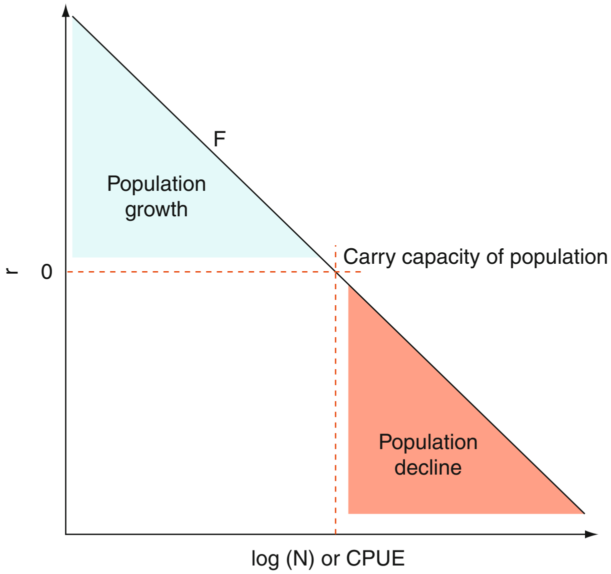

Figure 4.4 A simple linear relationship between the rate of population change ($r = \log_e(N_{t+1}/N_t)$), and measure of abundance ($\log_e N$ or catch-per-unit-effort, CPUE) and fishing rate (F). This particular population dynamical model represents the classic logistic rise to an environmentally determined (temporally averaged) carrying capacity and has formed the basis for fisheries models for the past 50 years (e.g. Beverton and Holt 1957, 1993; Fox, 1970); however, many non-linear forms of the relationship between r and N exist and should also be considered when the true relationship is unknown (Bradshaw, 2008; Brook and Bradshaw, 2006; Turchin, 2003).

increasing by 2% each year since 1985 (Food and Agriculture Organization of the United Nations, 2005).

More recently, directed shark fisheries have clearly reduced target population sizes. These fisheries usually focus on one or two primary species and are often managed using conventional single-species modelling approaches. It has been suggested that shark populations can withstand only modest levels of fishing without large reductions in population size (Camhi *et al.*, 1998; Cortés, 2000; Musick, 1999b; Musick *et al.*, 2000a). Brief periods of high harvest rates are usually followed by severe declines in catch rates in fished shark populations (Camhi *et al.*, 1998), usually associated with a fishery's closure and a long, slow period of recovery, or continued low catches at a fraction of those obtained during the initial period (Gauld, 1989; Hurley, 1998; Schindler *et al.*, 2002; Sminkey and Musick, 1996). Due to this predominant historical pattern, intensive and careful management is recommended at the inception of any shark fishery (Musick *et al.*, 2000a). However, the majority of shark fisheries (e.g. see Kroese and Sauer, 1998) are unmanaged (Walker, 1998). These are likely to cause rapid population declines (Bonfil, 1994), with slow or little recovery, or fishery abandonment due to economic or market constraints (Musick, 2005).

Although many shark species and their fisheries have traditionally been of low economic value compared to dedicated teleost fisheries, the economic impact of population reductions can be similar because recovery time and associated economic downturns usually last much longer (Musick and Bonfil, 2005). Often-cited examples of reduced or abandoned shark fisheries are the various basking shark fisheries (Anonymous, 2002; Kunzlik, 1988; Parker and Stott, 1965), the porbeagle shark (*Lamna nasus*) fishery in the Northeast Atlantic (Department of Fisheries and Oceans, 2001; Gauld, 1989), the tope or 'soupfin' shark (*Galeorhinus galeus*) fisheries off California and Australia (Olsen, 1959, 1984; Ripley, 1946; Walker *et al*., 1995) and the spiny dogfish (*S. acanthias*) fisheries in the North Sea and off British Columbia, Canada (Anderson, 1990) (Fig. 4.5). Although the history and status of targeted shark fisheries are reviewed in detail elsewhere (Camhi *et al*., 1998; Fowler *et al*., 2005), we have provided a brief overview of examples of both abandoned and apparently sustainable shark fisheries below.

3.1.2.1. Basking shark **C. maximus** Dedicated fishing for basking sharks has been noted across northern Europe since the mid-1700s (International Council for the Exploration of the Sea, 2007), with the oldest confirmed fishery records available from west Ireland in the late eighteenth century. This was most likely an artisanal net fishery spanning several decades and becoming a commercial enterprise with rising demand for shark liver oil. This led to notably large declines by 1830 and fishery abandonment in the second half of the nineteenth century. Basking sharks were not targeted again until 1947, at which point a new localised fishery started near Achill Island (Ireland), where 900–1800 sharks were taken each year from 1950 to 1956 (Fig. 4.5). Catches started to decline after 1955, from 1067 per year between 1949 and 1958, to 119 per year between 1959 and 1968, and then to 40 per year for the remaining 7 years of the fishery that ended in 1975. Toward the end of the fishery, even increasing shark oil prices and capital investment did not reverse the steady decline in catches. A total of 12,360 individual fish were caught over the life of the fishery, with 75% caught in the first 6 years (McNally, 1976). Today, basking sharks are often sighted around shelf fronts, although total population sizes are unknown (Sims, 2008; Sims and Quayle, 1998; Sims *et al*., 2005). Over the same period as the Irish fishery and beyond its end, a Norwegian fleet was also fishing for basking sharks over a large area of the northeast Atlantic. Catches were high (>1000 sharks per year, and >4000 in some years) between 1959 and 1980. Since 1981, landings have declined and not exceeded 1000 sharks per year (Kunzlik, 1988). This decline has been attributed to an ageing fleet, a decline in value of basking shark liver oil (Kunzlik, 1988), or possibly a change in the species' distribution to areas of higher productivity (Sims and

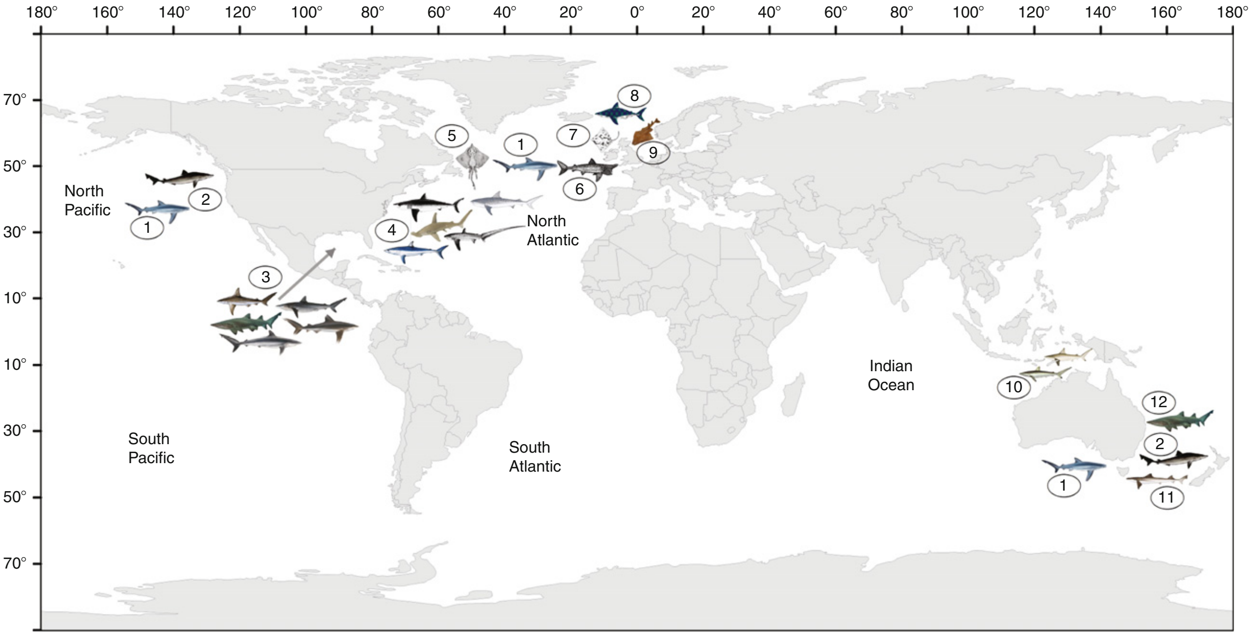

Figure 4.5 Location of fisheries and target chondrichthyan species mentioned in the text (coverage is not intended to be inclusive of all shark fisheries). (1) Blue shark *Prionace glauca* high-seas fisheries; (2) tope, school or 'soupfin' shark *Galeorhinus galeus* fisheries off California, south-eastern Australia and New Zealand; (3, 4) Gulf of Mexico and south-eastern USA coastal and pelagic shark fisheries (including dusky *Carcharhinus obscurus*, sandtiger *Odontaspis taurus*, oceanic whitetip *Carcharhinus longimanus*, sandbar *Carcharhinus plumbeus*, silky *Carcharhinus falciformis*, great white *Carcharodon carcharias*, hammerhead *Sphyrna lewini, S. mokarran* and *S. zygaena*, thresher *Alopias vulpinus* and *A. superciliousus*, short-fin mako *Isurus oxyrinchus*, and tiger sharks *Galeocerdo cuvieri*); (5) barndoor skate *Dipturus laevis* off New England and Canada in the western Atlantic ground fishery; (6) basking shark *Cetorhinus maximus* fisheries in the north-eastern Atlantic; (7) Irish Sea common skate *Dipturus batis* fishery; (8) porbeagle *Lamna nasus* fishery in the North Atlantic; (9) angel shark *Squatina squatina* in United Kingdom waters; (10) blacktip *Carcharinus tilstoni* and *C. limbatus* and spot-tail *C. sorrah* shark fishery in the Arafura-Timor Seas, northern Australia; (11) gummy shark *Mustelus antarcticus* catches increasing to offset declines in school shark catches in south-eastern Australia; (12) grey nurse shark *Carcharias taurus* rapid decline in eastern Australia due to spear-fishing, recreational fishing by-catch, commercial by-catch and beach meshing. Bold numbers and zone demarcations refer to Food and Agriculture Organization of the United Nations (FAO) Fishing Areas (www.fao.org).

Reid, 2002). Overall in the north-eastern Atlantic between 1946 and 1997, including the target fishery in Scottish waters, records indicate 105,730 basking sharks were captured and traded (Sims, 2008). However, due to a large fishing area and location uncertainty, it has been difficult to detect and evaluate temporal trends in the catch data. Since 1978, management of basking shark fishing in European Community waters (UK and Ireland) has been by a total allowable catch quota system initially set at 400 tonnes, but now the quota has been reduced to zero (Sims *et al.*, 2005). There still appears to be incentive to continue the fishery due to the high prices paid for large basking shark fins in Singapore (Camhi *et al.*, 1998) and other Asian markets.

3.1.2.2. Tope, school or soupfin shark G. galeus

Although there are numerous fisheries for tope ('school' or 'soupfin' shark) around the world, the most infamous fishery occurred off the Californian coast in the early to mid-1900s (Holden, 1974; Ripley, 1946; Fig. 4.5). The fishery only lasted 8 years and was abandoned in the mid-1940s (Ripley, 1946). It is still uncertain whether populations have recovered more than 50 years later (Camhi *et al.*, 1998). Shark landings from 1930 to 1936, of which tope comprised a high proportion (around 80%), were relatively low and stable at around 270 tonnes per year. The fishery then expanded enormously following the establishment of a new market for liver oil in 1937, with catches peaking at 4185 tonnes in 1939. This new market demand also pushed prices from some US $50 per tonne in 1937 to US $2000 per tonne in 1941. Tope landings were declared independently of the general take from 1941, with annual declines from 2172 tonnes in 1941 to 287 tonnes in 1944. Catch-per-unit-effort (CPUE) in one region declined from 34.4 fish/1000 m of gillnet fished for 20 h in 1942, to 4.8 fish/1000 m/20 h in 1945 (Roedel and Ripley, 1950).

Not all targeted *G. galeus* fisheries have caused large population declines. In southeast Australia (Fig. 4.5), exploitation of school sharks began in the 1920s, but production increased greatly during the war years. Catches reached 2000 tonnes live weight in 1949 (Walker *et al.*, 1995) due to demand for shark liver oil. Catches remained relatively high between 1949 and 1957 as the fishery spread from inshore to offshore waters (Olsen, 1959; Walker *et al.*, 1995). In 1964, decline of the liver oil market led to development of the shark meat market and a switch to gillnetting. This new market allowed production to increase rapidly, peaking in 1969 at 3158 tonnes, although the proportion of gummy shark (*M. antarcticus*) in the catch was also increasing. Following a ban on the sale of large *G. galeus* in 1972 because of reported high mercury concentration in the meat, catches declined for about 10 years and gummy sharks took over as the principal target species in the fishery (Stevens *et al.*, 1997). With relaxation of mercury laws in the early 1980s, catches again increased, reaching

3060 tonnes in 1986. However, concerns of population reduction prompted by a measured 84% reduction of mature biomass resulted in the implementation of a dedicated fishery management plan in 1988 (Stevens *et al.*, 1997, 2000) and ongoing research initiatives (Punt and Walker, 1998; Punt *et al.*, 2000; Walker, 1992; Walker *et al.*, 1998). In New Zealand, *G. galeus* have been harvested since the late 1940s and have followed a similar trend to the Australian fishery. With the demise of the liver oil fishery in the 1950s, a market for the flesh developed with a small export market to Australia. Catches peaked at 5000 tonnes live weight in 1984 (Francis, 1998).

3.1.2.3. Northern Territory, Australia shark fishery Many dedicated shark fisheries tend to be small and target highly productive species (Stevens *et al.*, 2000; Walker, 1998). An example of one such fishery is the north Australian shark fishery in the Northern Territory (Fig. 4.5). This is a small tropical shark fishery with only 13 licences and only 7–9 vessels operating currently. Target species are primarily the Australian blacktip (*Carcharhinus tilstoni*) and spot-tail sharks (*C. sorrah*), but frequent switches to teleosts such as grey mackerel (*Scomberomorus semifasciatus*) occur. A variety of secondary shark species are also caught including tiger (*G. cuvier*), pigeye (*Carcharhinus amboinensis*) and hammerhead sharks (*Sphyrna* spp. and *Eusphyra blochii)* (Field *et al.*, 2008). The fishery has developed slowly from 1984 to its present management system (Australia Department of Environment and Heritage, 2005) with an annual shark catch that peaked in 2004 at 1089 tonnes (Northern Territory Department of Primary Iindustry Fisheries and Mines, 2005). It has remained relatively stable ever since. An increase in CPUE and in proportional catch of non-primary target species from 2000 to 2003 prompted questions regarding the industry's future sustainability (Australia Department of Environment and Heritage, 2005). Due to market demand, grey mackerel currently dominates the catch in terms of single-species catch, and there has been a reduction in fishing effort to prevent rapid changes or growth of new fisheries enabled by technological advantages (Northern Territory Department of Primary Iindustry Fisheries and Mines, 2005). Research projects to address concerns of sustainability were implemented in 2004 to include stock monitoring (Northern Territory Department of Primary Iindustry Fisheries and Mines, 2005), risk assessment (Pillans, 2007) and observation and tagging studies (Field *et al.*, 2008).

As with many shark fisheries, the history of shark harvest in northern Australia is more complex than the current industry's structure might suggest. From the early 1970s until mid-1986, a Taiwanese pelagic gill-net fleet operated in the waters around northern Australia targeting shark, longtail tuna (*Thunnus tonggol*) and mackerel (*Scomberomorus* spp.). Since it was largely unmanaged, the fleet's extent caused concern (Stevens and Davenport, 1991). The areas accessible to the Taiwanese fleet changed over the course of the fishery's lifetime following the implementation of the Australian Fishing Zone in 1979, limiting it to mainly offshore regions ranging from the North West Shelf to north of the Gulf of Carpentaria (Fig. 4.5). The catch was subsequently reduced from around 17,000 tonnes per year to an annual quota of 7000 tonnes. Before 1980, reporting of catch and effort was limited (Walter, 1981), but afterwards basic catch composition and effort data were collected under Taiwanese and independent logbook programmes. These records indicated that total catch composition by weight was approximately 80% shark, with blacktip (primarily *C. tilstoni* with an unknown proportion of *Carcharhinus limbatus*) and spot-tail (*C. sorrah*) sharks accounting for 60% of the total catch (Stevens and Davenport, 1991). During the early 1980s, fishing effort almost doubled, while CPUE decreased from 16 to 7 kg/km/h (Stevens and Davenport, 1991). Data from the Taiwanese fleet showed some signs of population reduction (Stevens and Davenport, 1991). Other data also indicated age structure changes; length-frequency distributions indicated fewer mature *C. tilstoni* were caught from 1981 to 1986, and there was also a decrease in the abundance of mature female *C. sorrah* and a decrease in median size of sharks caught for both *C. tilstoni* and female *C. sorrah*. Further restrictions were imposed in 1986, eventually leading to the decision by the Taiwanese to abandon the fishery for economic reasons. However, Taiwanese gillnetting continued outside the Australian Fishing Zone.

3.1.3. Mixed fisheries and by-catch

Although directed fishing can have severe effects on target species, possibly the greatest potential threat to chondrichthyans worldwide is indirect harvest, or in mixed-species fisheries where they represent 'by-catch' (Bonfil, 1994; Camhi *et al.*, 1998; Musick, 1999b; Stevens *et al.*, 2000, 2005; Walker, 1998). Sharks can be caught incidentally in trawl nets, gillnets, purse seines, and longlines, and mortality from these as by-catch might exceed that from directed fisheries (e.g. oceanic fisheries for tuna and billfishes, Bonfil, 1994; Francis and Griggs, 1997; Polacheck, 1989). In such cases, the fisheries can enter regional or international trade with little or no reporting or tracking of produce. This is of particular concern for small-scale commercial and artisanal fisheries, especially for trade in 'rare' species with small population sizes such as sawfishes (Camhi *et al.*, 1998) and possibly basking sharks (Magnussen *et al.*, 2007; Sims, 2008).

The two main problems with mixed-species fisheries that catch non-target species are the (1) low priority and economic value of secondary species catches and (2) limited or no reporting of captured and discarded by-catch species. Such fisheries can generally remain economically viable, at least over the medium term, because the primary species tend to be more productive than secondary species that can eventually sustain large population declines or be driven to extinction (Baum *et al.*, 2003; Casey and Myers, 1998; Essington *et al.*, 2006; Musick, 1999b; Myers and Worm, 2003; Stevens *et al.*, 2000). Poor catch recording of secondary species in fisheries in domestic and international waters severely limits our capacity to understand and manage by-catch (Alverson *et al.*, 1994; Nakano and Clarke, 2006). Even today most countries do not require by-catch data to be collected. The few data that are collected from either logbooks, landing statistics or observer programmes are limited in coverage, especially for high-seas fisheries, and are generally too imprecise even to identify reliably the species composition of the catch (Dulvy *et al.*, 2000; Nakano and Clarke, 2006). Although some shark by-catch is landed and reported officially, the majority is only estimated. As such, some have argued that by-catch might represent up to 50% of the total worldwide shark catch (Bonfil, 1994). These two components mean that large discrepancies and uncertainty in population trends impair management.

Mixed-species fisheries occur across a range of marine habitats, from coastal demersal to open-ocean pelagic regions, although historically deep-water habitats have likely escaped much of the exploitation pressure but are considered especially vulnerable in the future (García *et al.*, 2008). The constraints of deepwater fishing might have led to these habitats becoming conservation refuges for many shark species, given that up to 35% of all shark species primarily occupy deepwater habitats (Camhi *et al.*, 1998; García *et al.*, 2008; Stevens *et al.*, 2005). Many by-catch species are harvested mainly by trawlers across a broad range of life stages (Stevens *et al.*, 2000), and several examples exist of by-catch chondrichthyans showing signs of moderate to severe population decline.

3.1.3.1. Examples of mixed-species fisheries impacting chondrichthyans In the early 1980s, a severe decline in common skates (*Dipturus batis*) of the Irish Sea was reported, to the extent that the population was thought to be at the 'brink of extinction' (Brander, 1981). More recently, the barndoor skate (*Dipturus laevis*), a species that is taken as by-catch in the New England and Canadian Atlantic ground fish fisheries, has become the first well-documented example of localised extinction (Casey and Myers, 1998; Fig. 4.5), although non-peer-reviewed reports from Canada and USA concluded the populations have not even been severely reduced (Boelke *et al.*, 2005; Kulka *et al.*, 2002). Other large skate species might be potentially threatened with extinction (Dulvy and Reynolds, 2002), and several other studies have documented reduced diversity in demersal chondrichthyans (Aldebert, 1997; Jukic-Peladic *et al.*, 2001; Rogers and Ellis, 2000). In the north-western Mediterranean, there has been a clear decline of several shark species commercially captured by trawls due to increased fishing intensity and technological advances in fishing gear. This pattern has also been observed in some coastal areas around the United Kingdom (Fig. 4.5) where trawling has changed demersal fish assemblages by reducing the abundance of large sharks, skates and rays such as *D. batis* and the angel shark *Squatina squatina* (Rogers and Ellis, 2000). A similar decline in species richness and distribution has been reported for several large shark and rays species in the Adriatic between 1948 and 1998 (Jukic-Peladic *et al.*, 2001).

Pelagic fisheries using longlines, gillnets and driftnets also pose a large potential threat to chondrichthyans, some of which have been the focus of much research and concern over the last decade. In both the Pacific and Atlantic Oceans there have been large declines in many fish stocks caught in tuna and billfish longline fisheries associated with extensive by-catch (Christensen *et al.*, 2003; Schindler *et al.*, 2002). Pelagic longline fisheries worldwide remove up to 8 million sharks per year, or one-third of the world catch of all sharks and rays (Bonfil, 1994); however, the actual rate could be up to four times higher (Clarke *et al.*, 2006). One of the main by-catch species in the Pacific and Atlantic open-ocean fisheries (Fig. 4.5) is the blue shark (*P. glauca*) which accounts for around 50% of the total worldwide shark by-catch (Bonfil, 1994; Stevens *et al.*, 2000). This species has relatively high growth and fecundity compared to other chondrichthyans, and so is thought to be relatively resilient to current fishing pressure (Aires-da-Silva and Gallucci, 2007). Prior to the 1980s, there was little demand for blue sharks because of their soft muscle tissue and strong ammonia odour (Walker, 1998). As such, most blue shark by-catch was discarded or returned alive, which acted to reduce fishing mortality (He and Laurs, 1998).

With the expansion of the Asian fin market in the 1980s, there was a large increase in the demand for blue shark fins. This led to an increase in finning, the practice of removing the fins from a carcass and discarding the trunk overboard, sometimes with the de-finned shark still alive. Since dried fins do not take up much valuable space in freezers on ships or on land, they represent an economically attractive by-product. In the Hawaiian longline fishery where no sharks were reported being harvested solely for fins prior to 1990, up to 61,000 individual blue sharks were caught and finned in 1998 alone (McCoy and Ishihara, 1999). This increase in dedicated harvest caused population declines from the 1980s onward, although fisheries assessment to determine changes in catch rates have provided conflicting results. For example, it has been estimated that blue shark numbers in the Pacific have declined by 20% between 1982 and 1993, but no such trend was observed in Indian Ocean fisheries and only contrasting evidence of a decline in the Atantic Ocean (Aires-da-Silva *et al.*, 2008; Baum *et al.*, 2003; Nakano, 1996; Nakano and Clarke, 2005). Neither was there a decrease in blue shark catch rates observed in Australian longline fisheries (Stevens and Wayte, 1999). Recently however, these trends have been questioned and there now appears to be evidence of declines (Aires-da-Silva *et al.*, 2008; Baum *et al.*, 2003; Simpfendorfer *et al.*, 2002). Based on fishery-independent data from 1977 to 1994, Simpfendorfer *et al.* (2002) found evidence for an 80% decrease in the abundance of male, but not female, blue sharks, whereas an analysis of the US North Atlantic catch logbook data concluded an overall 60% decline in catches (Fig. 4.5; Baum *et al.*, 2003).

Newer techniques have been used to determine the status of blue sharks (Aires-da-Silva and Gallucci, 2007; Clarke *et al.*, 2006; Schindler *et al.*, 2002; Simpfendorfer *et al.*, 2002) that link life history traits and vital rates to harvest scenarios. These modelling approaches use stochastic age-structured population models to assess population dynamics. By estimating the intrinsic rate of population increase, blue shark populations are at risk of declining once 20% of the original biomass is removed, and juveniles are more at risk if heavily harvested (Aires-da-Silva and Gallucci, 2007). Furthermore, sexual segregation gradients have also been reported for this and other shark species that would exacerbate over-exploitation for some populations (Mucientes *et al.*, 2009). Overall, evidence from market surveys (Clarke *et al.*, 2006) suggests that populations are currently at or just over the MSY for this species. Therefore, the strength of evidence at present shows that most blue shark populations are currently stable; however, some have declined and harvest rates require careful management and monitoring, particularly when there is the possibility of sexual segregation of populations and a likelihood of destabilising population structures (Mucientes *et al.*, 2009).

3.1.3.2. Chondrichthyan decline controversies For other harvested chondrichthyan species caught in coastal and oceanic fisheries, there have been population declines (Aires-da-Silva *et al.*, 2008; Cavanagh, 2005; Cortés *et al.*, 2002; Musick *et al.*, 1993, 2000b; Simpfendorfer *et al.*, 2002; Stevens *et al.*, 2000). Some studies even suggest that several species are close to extinction (Baum *et al.*, 2003, 2005; Myers and Worm, 2005; Worm *et al.*, 2005). In these cases, the conclusion of high, imminent extinction risk has generated extensive debate (Baum *et al.*, 2005; Burgess *et al.*, 2005a,b), especially with respect to the status of species such as tiger (*G. cuvier*), great white (*Carcharodon carcharias*), requiem (*Carcharhinus* spp.), hammerhead (*Sphyrna lewini, Sphyrna mokarran, Sphyrna zygaena*), shortfin mako (*Isurus oxyrinchus*), oceanic whitetip (*Carcharhinus longimanus*), thresher (*Alopias vulpinus* and *Alopias superciliousus*), and porbeagle sharks (*L. nasus*) (Fig. 4.5). Some of the differences in opinion expressed to date might have arisen in part from competing views of fisheries biologists and conservation ecologists (Hilborn, 2007); however, we attempt in the following to provide a neutral summary of the contentious issues around the reported species declines, to which almost all agree are real, even though the magnitude remains under debate.

Although some mention of species decline had been made previously (Cortés *et al.*, 2002; Musick, 1999a; Musick *et al.*, 1993), it was not until Baum *et al.* (2003) published their report of severe declines of some shark species in the Northwest Atlantic that serious concerns regarding extinction risk in sharks were raised and received broad national and international media attention. The logbook data set on which their analyses were based covered the US pelagic longline fishery targeting tuna and billfish from 1986 to 2000, encompassing a total of 214,234 longline sets (mean = 550 hooks/longline). This data set was proposed to be one of the longest time series for shark harvest ever analysed, with six species or species groups recorded from 1986 onward, and eight species from 1992 onward. Their results presented strong evidence that hammerhead, great white and thresher sharks had suffered the greatest declines, with reductions of over 75% in relative abundance over the past 15 years. Tiger, coastal requiem (carcharhinid), blue and oceanic whitetip sharks were also substantially reduced by 65%, 61%, 60% and 70%, respectively, and shortfin mako sharks declined moderately. These trends were then extrapolated to the entire region of the North Atlantic. Further evidence in support of large shark declines came soon after from the Gulf of Mexico, where longline records showed declines of 99% and 90% for oceanic whitetip and silky sharks (*Carcharhinus falciformis*), respectively, between 1954–1957 and 1995–1999 (Baum and Myers, 2004). A number of other coastal shark species in the region have apparently declined due to high harvest rates, including sandtiger (*Carcharhinus taurus*) and dusky (*Carcharhinus obscurus*) sharks (Fig. 4.5). These populations declined because of catches persisting until the late 1980s, and showed only modest signs of recovery after 10 years (i.e. a few generations) of regulation. The more productive sandbar shark (*Carcharhinus plumbeus*), although reduced in population size, continues to sustain fisheries (Musick, 1999a; Musick *et al*., 1993).

The above-mentioned studies, among others (Dulvy *et al*., 2008), have had a large influence on recent conservation decisions to list many shark species under the Convention on International Trade in Endangered Species (CITES) and the World Conservation Union's (IUCN) Red List. However, the methods on which the conclusions were based have since been called into question (Baum *et al*., 2005; Burgess *et al*., 2005a,b; Worm *et al*., 2006). According to Burgess *et al*. (2005a), the weaknesses of the Baum *et al.* studies are related to the nature of logbook reporting, choice and size of data sets used, the temporal and spatial context of the data, and the standardisations made.

One of the greatest concerns raised regard coverage and quality of the data set, in addition to assumptions and standardisation of catch data, to provide indices of relative abundance based on small sample sizes (Burgess *et al*., 2005a; Hilborn and Walters, 2001). Use of the US pelagic longline logbook data set was considered problematic for two main reasons. Firstly, another 25 data sets were available for the region from other sources, including from US observers on US and Japanese boats, Canadian observers on Canadian and Japanese boats, and from other scientific and recreational surveys. Although, Burgess *et al.* (2005a,b) recognised that the US pelagic longline data set gives the best temporal and spatial resolution, they contended that other data sets and studies were not used or cited; for example, stocks assessment of coastal shark populations from the northwest Atlantic and the Gulf of Mexico were not discussed (Cortés *et al.*, 2002). Apparent oversight of these additional lines of evidence that provide mixed support for and against the conclusion of severe declines in some species were identified as a shortcoming (Burgess *et al.*, 2005a,b). However, some of these additional data sets were not freely available (Baum *et al.*, 2005). Furthermore, other originally unused data sets have been considered by Shepherd and Myers (2005) and in some unreported studies (Baum *et al.*, 2005), and all of these support the initial conclusions.

Secondly, the data sets used (Baum *et al.*, 2003) might not adequately represent the large, less common coastal species relative to pelagic species, and catches might not reflect the true status of the coastal sharks (Burgess *et al.*, 2005a). Also less commonly caught species were not considered, despite other studies showing no evidence of decline in species such as sandbar sharks (*C. plumbeus*) (Burgess *et al.*, 2005a). Baum *et al.* (2005) conceded that their data set does not allow modelling of individual coastal shark species and that trends can vary among species; however, they made no inferences about individual trends in abundance. The capacity for species misidentification in the logbook data might also have inflated catches reported for some species, if indeed this was systematic. For example, Burgess *et al.* (2005a) contended that oceanic whitetip and other sharks bearing white skin patches are often reported as 'white sharks', which could be mistaken for *C. carcharias*, the great white shark. Other species misidentifications were thought to be likely with any large 'brown' sharks often reported as 'tiger' sharks, and shortfin makos as 'blue' sharks. However, the degree of potential misreporting was not determined by either grouping.

Concerns were also raised over the particular spatial analyses used and interpretation of results for a number of studies reporting severe declines (Baum *et al.*, 2003; Myers and Worm, 2003). Walters (2003) questioned the interpretation of widespread declines due to errors which can lead to overestimated reduction by summing and averaging catch data over broad areas without taking local 'weighting' into consideration (Hilborn and Walters, 2001; Walters, 2003). Burgess *et al.* (2005a) also identified that changes in fishing practices, target species, gear and management policy during the period over which the data were collected invalidated some of the temporal comparisons in catch composition. There were changes in the type of hooks and leaders used over the data set interval, with newer gear possibly reducing shark by-catch, especially for larger species. Finally, there was likely to be high error associated with data standardisation used to control for environmental heterogeneity, including oceanographic conditions and habitat type (Burgess *et al.*, 2005a).

Even after debating the data sets and methods used (Baum *et al.*, 2005; Burgess *et al.*, 2005a,b), there remains some contention over the original conclusion of near extinction for many large sharks. Regardless of the debate, however, the overarching trends on which there is agreement indicate that there have been general declines in many of the fished shark species in the north-western Atlantic. The debate is instead centred on the magnitude of the declines, and there is new agreement that to resolve the aforementioned problems, more research and monitoring are required. All parties also agree that a precautionary approach is most certainly advisable, given the signs that a problem exists. One view is that this must be based on stock assessments that rely on a range of data sets including catch rates, size and age composition, tagging returns, and other measurements of ecological and life history traits.

3.1.4. Illegal, unreported and unregulated (IUU) fishing

Although sharks have historically been of relatively low economic value, IUU fishing is generally seen as a potentially serious threat to chondrichthyan species richness and abundance (Clarke *et al.*, 2006). IUU fishing refers to harvesting that does not comply with national, regional or global fisheries conservation and management obligations (Agnew *et al.*, 2008; Ainsworth and Pitcher, 2005; Gewin, 2004; Sumaila *et al.*, 2006). In the context of chondrichthyans, illegal harvest principally targets species for the highly lucrative trade in fins, for example, sawfishes (*Pristis* spp.) and blue sharks (Clarke *et al.*, 2006). IUU fishing on the high seas or in distant waters from landing ports can be a highly organised, mobile and elusive activity that undermines the sustainable management efforts of fish resources under the jurisdiction of responsible countries. International cooperation is therefore essential to combat this serious problem effectively, especially considering that conservative estimates place the harvest due to IUU fishing at three times that of managed fishing quotas (Agnew *et al.*, 2008; Gewin, 2004).

As an example, IUU fishing continues to thrive in the northern region of Australia's Fishing Zone (AFZ) and is largely undertaken by traditional or small-scale Indonesian vessels (Field *et al.*, 2009). Indonesian fishermen involved in IUU fishing in this area target specific species such as shark, reef fish, sea cucumber (*Holothuria* spp.) and trochus (*Trochus* spp.) that are destined for the Asian market (Field *et al.*, 2009). Since 1974, traditional, non-motorised, Indonesian vessels have been allowed access to a defined area of the AFZ north west of Broome (Fig. 4.5) in which Australia agrees not to enforce its fisheries laws allowing traditional access; this area is known as the Memorandum of Understanding (MoU) 1974 Box (Field *et al.*, 2009). Historically, IUU fishing by Indonesian vessels occurred either in the MoU Box as a result of opportunistic fishing in other areas of the AFZ, or around the MoU Box contrary to the agreed rules. More recently, there has been a noticeable shift away from what could be termed 'traditional' fishing. Motorised vessels are being found as far east as the Torres Strait, and are largely targeting sharks for their valuable fins. This has led to marked changes in the abundance and species composition of sharks in the region (Field *et al.*, 2009) and is predicted to have ecosystem and economic consequences (Pascoe *et al.*, 2008).

3.1.5. Recreational fishing

Recreational fishing is a popular and growing activity in many parts of the world (Stevens *et al.*, 2005). Although chondrichthyans are mainly by-catch species for many recreational fishers, they are also targeted by others as game or sport fishes (Stevens *et al.*, 2005). Recreational fishing catches are typically small relative to commercial catches, although few data are available specifically for chondrichthyans due to a general absence of formal reporting requirements or dedicated surveys. The few data that do exist provide some interesting insight; however, the impact of recreational fishing on chondrichthyans is difficult to predict. In Australia and New Zealand, recreational catches are relatively low. The total commercial shark catch reported to the FAO (Food and Agriculture Organization of the United Nations, 2000) for Australia was approximately 7500 tonnes in the year 2000. At the same time, a national recreational and indigenous fishing survey estimated that the total shark catch was around 1200 tonnes (Henry and Lyle, 2003), representing approximately 16% of the annual commercial catch, although about 81% was reported as ‘released alive’. This is slightly more than the proportional catch reported for recreational fishers in New Zealand targeting rig (*Mustelus lenticulatus*), spiny dogfish and elephant fish (*Callorhinchus milli*) (Fig. 4.5), where recreational fishers caught between 6% and 8% of the total reported commercial shark catch (Francis, 1998). The largest recreational catch for sharks on the east coast of the USA and in the Gulf of Mexico is estimated at around 35,000 tonnes per year, of which approximately 30% were reported killed (Musick *et al.*, 1993). Recently, catches have been revised to 11.1 million individual sharks from all species caught by recreational fishers, and 0.448 million of these were harvested (Marine Recreational Fisheries Statistics Survey, 2001). More specifically, catches of large coastal sharks (e.g. great white, sandbar, blacktip, mako sharks) in the region are thought to be greater than that taken by the commercial fishery (Cortés *et al.*, 2002), such that the two mortality sources together are hypothesised to be the primary drivers of the decline in blacktip (*C. limbatus*) and sandbar sharks (*C. plumbeus*) (Baum and Myers, 2004; Cortés *et al.*, 2002; Musick *et al.*, 1993; Shepherd and Myers, 2005) (Fig. 4.5).

Other types of recreational fishing can also reduce chondrichthyan species abundance. For example, the recreational spearfishing of grey nurse sharks *(Carcharias taurus*) during the 1960s and 1970s on the east coast of Australia (Fig. 4.5) contributed to a large decline in population size, leading to legislation for protection in 1984 (Pollard, 1996). Today, this species is fully protected throughout Australia, although concerns regarding their future still remain (Environment Australia, 2002; Otway and Burke, 2004; Otway *et al.*, 2004).

Another concern is that recreational fishing usually takes place in inshore waters, close to coasts and in bays, estuaries and rivers. These areas have been identified as important habitats for many chondrichthyans, especially for breeding, pupping or nursery areas (Stevens *et al.*, 2000, 2005). Recreational fishing often affects juveniles more than adults. Indeed, recreational fishers in Tasmania (Fig. 4.5) were responsible for declines in gummy and school sharks in the 1960s and 1970s by gillnetting in nursery areas (Williams and Schaap, 1992). In recent years, however, growing emphasis on catch and live release is hoped to reduce the negative impacts of recreational fishing on many shark species, while also providing important scientific information for effective species management (Stevens *et al.*, 2000).

3.2. Beach meshing

Shark attacks worldwide are rare (Stevens *et al.*, 2005). However, at beaches where attacks were historically common, authorities in Australia and South Africa continue to protect swimmers by setting dedicated shark nets and drum-lines (Burgess and Simpfendorfer, 2005). In response to a number of unprovoked shark attacks in Sydney Harbour, beach meshing programmes started in New South Wales, Australia in 1937 using 50–60 cm gillnets. This success led to similar programmes in South Africa in 1952, Hawaii in 1959, Queensland in 1962, New Zealand in 1969 and Hong Kong in 1995 (Burgess and Simpfendorfer, 2005).

These programmes have generally been successful in reducing incidences of shark attacks on human swimmers, although this has come at a cost. In Australia and South Africa, around 1500 and 1200 sharks, respectively, are caught each year. In general, catch rates in these programmes show a rapid initial decline, after which they become stable, although there is considerable variation among species and locations (Reid and Krogh, 1992; Simpfendorfer, 1992). It is also thought that beach meshing has the greatest negative impact when deployed along coastlines rather than around single beaches, increasing the overall probability of capture while also serving to fragment habitat and disrupt migratory behaviour. Total catches are relatively small compared to fishery catches, but beach meshing is an important mortality source for small endemic populations. In Australia, a decline in grey nurse sharks is evident from beach meshing figures: in New South Wales grey nurse sharks mesh catches declined from 19 individuals per month in 1937 (Coppleson, 1962), to 0.29 individuals per month between 1972 and 1990 (Krogh, 1994). Beach meshing and spear-fishing were considered the main cultprits (Otway *et al.*, 2004). Beach meshing also kills many harmless chondrichthyans; for example, the Queensland (Australia) beach-meshing programme caught 13,765 rays between 1962 and 1988, and in New South Wales, 2074 rays were caught between 1972 and 1990 (Krogh and Reid, 1996).

3.3. Habitat loss

Chondrichthyans have evolved to fill many niches across a broad range of habitats (Compagno, 1990) and it is unlikely that they will be able to adapt quickly to human-induced changes in their environments (Cortés, 2002; García *et al.*, 2008). Therefore, species with highly specialised life histories (e.g. ontogenetic spatial and cephalopod diet specialisation by *Hemigaleus australiensis*; Taylor and Bennett, 2008) and limited spatial or environmental ranges are predicted to be more at risk from habitat change. Habitat degradation and loss alter the dynamics, distribution and possibly behaviour of its inhabitants. This includes both reduction in spatial extent of habitat (habitat loss) and the composition and interactions of the biological communities that rely on them (habitat degradation).

Habitat requirements can vary considerably over the different stages of the life cycle of species, so habitat loss and degradation can operate insidiously to reduce aspects of performance in terms of reproduction, dispersal or foraging ecology (Martinez *et al.*, 2007; McMichael, 2001; Musick *et al.*, 2000a). Most chondrichthyan species use some type of specific habitat for breeding, shelter or feeding that can encompass everything from freshwater rivers and lakes, shallow estuaries and coastal bays, to coral reefs, kelp forests and the deep sea (Stevens *et al.*, 2005). A number of species require shallow coastal areas as nurseries protected from large predators and inclement environmental conditions. Juveniles can remain in these areas during their early development to maximise survival. As such, the loss of estuarine and coastal nursery habitats from the destruction of mangrove forests, aquaculture and other coastal developments can compromise the recruitment in some species. The continuing loss of these important habitats could exacerbate the extinction risk of associated species in addition to direct threats of over-harvest (Kinney and Simpfendorfer, 2009).

The effects of fishing itself can be far more wide-reaching than just removal of individuals. Destructive fishing practices such as trawling and dynamite fishing change habitat structures by reducing substratum complexity and diversity. Some of these effects can be most detrimental for deepwater species that tend to be adapted to relatively stable environments. Unfortunately, dedicated research examining effects of habitat loss and degradation on shark populations has generally been lacking, with current predictions based largely on the expectation of chondrichthyans' roles in ecosystem function (see Section 5).

3.4. Pollution and non-indigenous species

Water pollution is a major problem that affects almost all freshwater and marine environment habitats and ecosystems, and it can directly affect chondrichthyans through changes in water quality and habitat degradation.

There are four main types of pollutants: (1) those that affect the physical properties of the environment, (2) those that cause eutrophication, (3) poisons and (4) pathogens that can affect the health of an individual or influence community or ecosystem structure. Pollutants can even have multiple effects, such as sewage effluent containing harmful toxins that cause eutrophication leading to dissolved oxygen depletion (Pastorok and Bilyard, 1985).

Pollutants that alter the physical properties of water and cause eutrophication have greater effects on the ecosystems on which chondrichthyans rely, than on individuals directly. This is because sharks and rays are generally highly mobile animals that can remove themselves from harmful situations if required. However, endemic species or populations restricted to small regions might be at greater risk to broad-scale pollution events. Certain life stages can also be more sensitive to the effects of pollution than others, especially embryos or juveniles with higher metabolic rates than adults. Chondrichthyans can bio-accumulate heavy metals such as mercury (Lyle, 1984; Walker, 1976, 1988; Watling *et al.*, 1982), especially coastal species that live in shallow turbid environments where freshwater outflow meets marine waters (e.g. Fairey *et al.*, 1997). Bio-accumulation of other pollutants can occur also, such as organic chemical compounds (Davis *et al.*, 2002; Fisk *et al.*, 2002; Gelsleichter *et al.*, 2005; Storelli and Marcotrigiano, 2001; Storelli *et al.*, 2005). These metals and organic compounds can have adverse effects on reproductive, immune, endocrine and nervous systems (Betka and Callard, 1999; Clarkson, 1994; Gelsleichter *et al.*, 2005; Koller, 1979; Scheuhammer, 1991). In male sharks, heavy metals such as cadmium (a known spermatotoxicant) have been observed in high concentrations in some species (Betka and Callard, 1999). In female bonnethead sharks (*Sphyrna tiburo*), exposure to organic compounds such as PCBs can reduce fertility through disruption of the endocrine system (Gelsleichter *et al.*, 2005). Although many chondrichthyans have been exposed to bio-accumulating pollutants, their effects are still relatively unexplored.

Other sources of pollution include oil spills and leaks that can contaminate tissues when ingested (Anonymous, 1993), flotsam and jetsam that can compromise digestion or entrap individuals (Sazima *et al.*, 2002), and ghost netting (Stevens *et al.*, 2005). Other types of environmental pollution include increased thermal outflows and discharges, and disruption of natural electro-magnetic fields by generation of artificial fields around undersea cables that can alter chondrichthyan behaviour because of their reliance on electro-magnetic sensory perception for foraging (Filer *et al.*, 2008; Hoisington and Lowe, 2005; Walker, 2001).

A final primary source of marine pollution to consider is from ships' ballast water from large commercial vessels that travel worldwide, and can transport non-indigenous marine species to new habitats (Drake *et al.*, 2007; Elliott, 2003; Ruiz *et al.*, 2000). There is little direct evidence that non-indigenous species threaten chondrichthyans; however, increasing invasions might erode the integrity of natural ecosystems upon which chondrichthyans rely.

4. CHONDRICHTHYAN EXTINCTION RISK

Given acceleration in species loss globally due mainly to human-mediated changes to the biosphere, there has been a growing interest in identifying and ranking the species characteristics and environmental contexts that could predict the proneness of species to extinction (Dulvy *et al.*, 2003; McKinney, 1997; Pimm *et al.*, 2006; Purvis *et al.*, 2000a; Sodhi *et al.*, 2008a,b). A capacity to predict species' responses to threats based on intrinsic ecological, life history or environmental traits is important to improve management efficiency and prioritise efforts to recover threatened taxa (Pimm *et al.*, 2006; Sodhi *et al.*, 2008b). For example, predictors of the predisposition of species to extinction could be used for selecting potentially sensitive taxa to monitor for early detection of population decline, enabling decision makers to choose how best to allocate finite conservation and management resources (Duncan and Young, 2000).

Current evidence supports the notion that particular combinations of life history and ecological characteristics (organism size, dispersal capacity and native geographic range) and other reproductive, dispersal, morphological and physiological attributes can influence a species' proneness to extinction (Duncan and Young, 2000; Sodhi *et al.*, 2008b), with the strength of effect often depending on environmental context (Brook *et al.*, 2008; Pimm *et al.*, 2006; Sodhi *et al.*, 2008a). Indeed, rare species tend to have lower reproductive effort and dispersal capacity and more restricted geographic ranges than common species (Blackburn and Cassey, 2004; Kunin and Gaston, 1993, 1997; Pocock *et al.*, 2006). A population's distribution will also affect its probability of extinction, especially over longer timescales. Widespread species are generally more resilient to local environmental disturbances and ecosystem changes because entire range-wide catastrophes become progressively less likely as a distribution increases (Brook *et al.*, 2008). Fragmented populations are also more vulnerable due to the loss of connectivity between subpopulations, reducing geneflow and resilience of the population to change (Caughley and Gunn, 1996; Dulvy *et al.*, 2003; Saunders *et al.*, 1991).

Species' traits such as body size are closely correlated with other life history attributes such as a geographic extent, potential fecundity, dispersal capacity and niche breadth. Thus, the extinction risk of a species can be classified based on the suite of characteristics that permit recovery from over-harvesting or changes in the environment such as habitat loss.

Specialised life histories that suit narrow ecological niches can increase the risk of extinction by limiting the ability of the species to adapt rapidly to change. Likewise, large body size tends to correlate positively with extinction risk (Cardillo *et al.*, 2005; Johnson, 2002; Olden *et al.*, 2007), and higher reproductive rates can increase capacity to recover from depletion (Purvis *et al.*, 2000b).

4.1. Drivers of threat risk in chondrichthyans and teleosts

Marine species were once considered to have a lower risk of extinction than terrestrial taxa due to the their longer presence in the fossil record (Culotta, 1994; Norse, 1993), high relative fecundity and larger geographic ranges (Dulvy *et al.*, 2003). However, this view is now contested (McKinney, 1998). Despite recent debate on the number of marine fish that have become globally extinct (del Monte-Luna *et al.*, 2007; Dulvy *et al.*, 2003), the number is but a small fraction of the extant species. Dulvy *et al.* (2003) suggested that three species have become extinct within the human timeframe (New Zealand grayling *Prototroctes oxyrhynchus*, green wrasse *Anampses viridis*, and Galápagos damsel *Azurina eupalama*), although del Monte-Luna *et al.* (2007) confirmed the loss of *P. oxyrhynchus* and *A. viridis* and provided evidence for the debate over the believed loss of *A. eupalama*. Currently, only four species found in brackish and/or saltwater are listed on the IUCN's Red List as *Extinct*: the European sturgeon (*Huso huso*) and bastard sturgeon (*Acipenser nudiventris*) due to over-harvest, the New Zealand grayling due to the release of introduced species, and the Madagascan lampeye (*Pantanodon madagascariensis*) due to habitat loss. There are, however, many species listed as currently experiencing local and regional declines, thus rendering them vulnerable to extinction.

Of all the larger marine taxa, chondrichthyans (sharks, rays and chimaeras) are considered the most vulnerable to extinction because of their tendency toward large size, slow growth and late maturation (Cortés, 2000; García *et al.*, 2008). In fact, the number of chondrichthyan species that are listed as either locally, regionally or globally extinct equals the total number of teleost extinctions (Dulvy *et al.*, 2003), but Red-Listed chondrichthyans outnumber the total number of teleost species listed. This raises the questions: are chondrichthyans at greater risk of extinction than teleosts or perhaps other marine taxa? If so, then what are the principal life history traits that drive this difference? Do chondrichthyans simply represent a higher proportion of listed species because of their high profile for protection (Pimm *et al.*, 2006)? Despite the repetition of their apparent greater risk in the literature (e.g. Baum *et al.*, 2003; Camhi *et al.*, 1998; Cortés, 2000; Myers and Worm, 2005; Robbins *et al.*, 2006), there has been little, if any, direct qualitative or quantitative analysis of the available data to test the assertion.

With the understanding that there has not yet been a comprehensive overview and formal analysis of chondrichthyan threat risk relative to teleosts, we constructed a detailed analysis of the ecological, life history and human-relationship data relative to the IUCN's Red List categorisation for extant chondrichthyans and teleosts. This includes classes Elasmobranchii (sharks and rays), Holocephali (chimaeras), Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes) (Table 4.1). We excluded Classes Cephalaspidomorphi (lampreys) and Myxini (hagfishes) from all analyses. Our main aim was to determine the primary drivers of threat risk for each taxon and whether overall susceptibility differed between chondrichthyans and teleosts.

4.2. Global distribution of threatened chondrichthyan taxa

To examine the spatial distribution of threatened Chondrichthyan species from marine and estuarine habitats in the IUCN Red List, we examined all populations listed as critically endangered, endangered and vulnerable (International Union for the Conservation of Nature and Natural Resources, 2008) using the websites www.iucnredlist.org and www.fishbase.org. From these, we plotted the approximate centroid of each threatened population's distribution in latitude and longitude coordinates (0.5° precision). These data provide a map of the relative global distribution of threatened chondrichthyan populations from least (vulnerable) to most (critically endangered) threatened (Figs. 4.6 and 4.7). Generally, the central

Table 4.1 Summary of chondrichthyan [including Classes Elasmobranchii (sharks and rays) and Holocephali (chimaeras)] and teleost [including Classes Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes)] species' taxonomic sample distribution

Class	Orders	Families	Genera	Species (marine)	Analysed *n*
Chondrichthyans					
Elasmobranchii	11	44	175	961 (937)	216–218
Holocephali	1	3	6	37 (37)	3–9
Total	12	47	181	998 (974)	219–227
Teleosts					
Actinopterygii	45	468	4592	27,388 (15,397)	141–385
Sarcopterygii	3	4	4	11 (2)	1
Total	48	472	4596	27,399 (15,399)	142–386
Totals	60	519	4777	28,397 (16,373)	367–612

Total number of species is presented for all milieus and marine only. The final number of species analysed depended on the particular set of attributes included in the model sets (see Tables 4.3 and 4.4), so sample size ranges are shown.

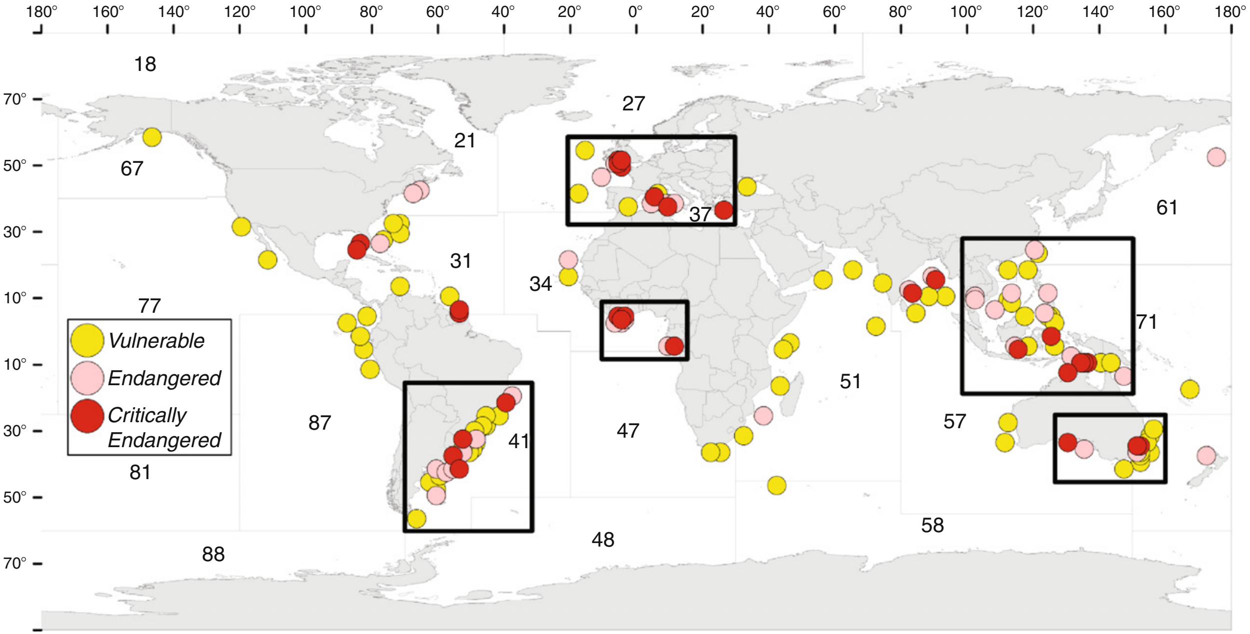

Figure 4.6 Global distribution of IUCN Red-Listed threatened chondrichthyan species. Each dot represents the approximate centroid coordinate (0.5° precision determined from cross-referencing data from www.iucnredlist.org and www.fishbase.org) for sub-populations of 115 separate chondrichthyan species listed as vulnerable (light grey), endangered (mid-tone grey) or critically endangered (dark grey) according to the IUCN Red List (www.iucnredlist.org).

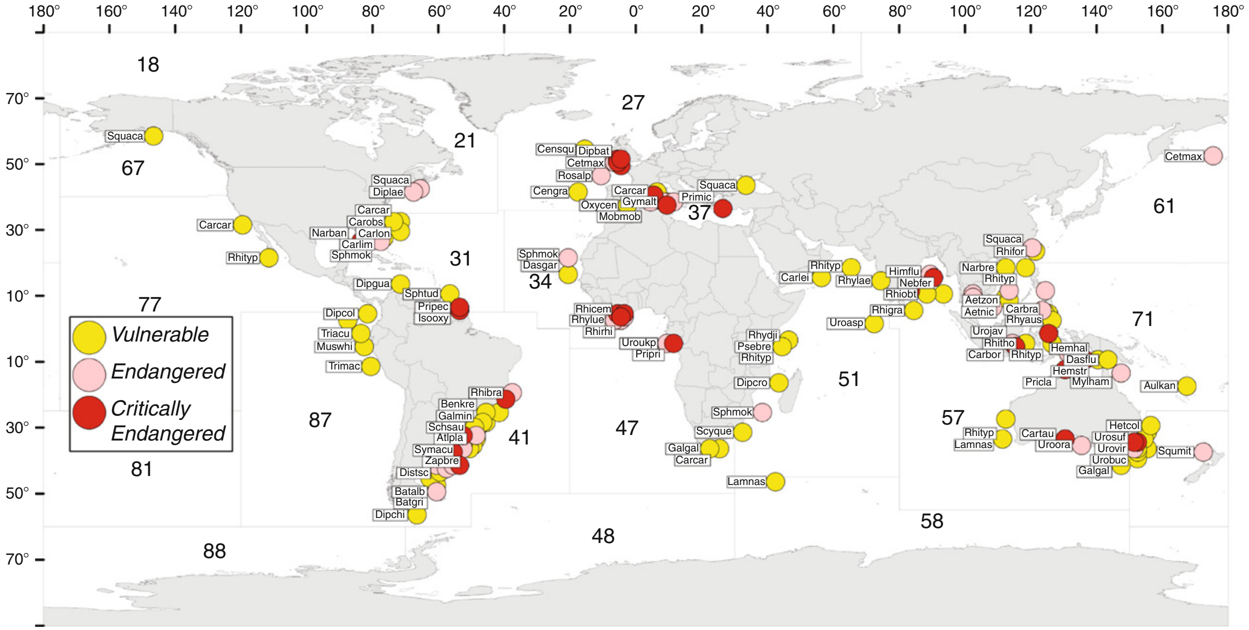

Figure 4.7 Global distribution of IUCN Red-Listed threatened chondrichthyan species (see Fig. 4.6 for details) with species labels: aetfla, *Aetobatus flagellum*; aetmac, *Aetomylaeus maculatus*; aetnic, *Aetomylaeus nichofii*; aetves, *Aetomylaeus vespertilio*; aetzon, *Aetoplatea zonura*; anocus, *Anoxypristis cuspidata*; atlcas, *Atlantoraja castelnaui*; atlcyc, *Atlantoraja cyclophora*; atlpla, *Atlantoraja platana*; aulkan, *Aulohalaelurus kanakorum*; batalb, *Bathyraja albomaculata*; batgri, *Bathyraja griseocauda*; benkre, *Benthobatis kreffti*; carbor, *Carcharhinus borneensis*; carbra, *Carcharhinus brachyurus*; carcar, *Carcharodon carcharias**; carhem, *Carcharhinus hemiodon*; carlei, *Carcharhinus leiodon*; carlim, *Carcharhinus limbatus*; carlon, *Carcharhinus longimanus*; carobs, *Carcharhinus obscurus*; carsig, *Carcharhinus signatus*; cartau, *Carcharias taurus*; cengra, *Centrophorus granulosus*; cenhar, *Centrophorus harrissoni*; censqu, *Centrophorus squamosus*; cetmax, *Cetorhinus maximus*; dasflu, *Dasyatis fluviorum*; dasgar, *Dasyatis garouaensis*; daslao, *Dasyatis laosensis*; dipbat, *Dipturus batis*; dipchi, *Dipturus chilensis*; dipcol, *Diplobatis colombiensis*; dipcro, *Dipturus*.

distribution of threatened sharks covered much of the coastal regions in eastern North America, north-western and south-eastern South America, western Africa, Europe (including the Mediterranean), Indian Ocean, south and south-eastern Asia, and eastern Australia (Figs. 4.5 and 4.6). Obvious clusters of threatened species were found in five regions: (1) south-eastern South America along the coasts of southern Brazil, Uruguay and Argentina; (2) western Europe and the Mediterranean; (3) western Africa; (4) South China Sea and Southeast Asia and (5) south-eastern Australia. The highest concentration of critically endangered species was in western Europe, western Africa and Southeast Asia (Figs. 4.5 and 4.6).

4.3. Ecological, life history and human-relationship attributes

For each species, we compiled attributes likely to contribute to the propensity to become threatened and by proxy, extinct (Brook *et al.*, 2008; García *et al.*, 2008; Olden *et al.*, 2007; Sodhi *et al.*, 2008b; Traill *et al.*, 2007). These included information on size, fecundity, mode of fertilisation, longevity, age at maturity, geographic range, growth rates, natural mortality, migratory behaviour, habitat, general temperature regime, salinity preference,

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crosnieri; **dipgua, *Diplobatis guamachensis*; diplae, *Dipturus laevis*; dipmen, *Dipturus mennii*; distsc, *Discopyge tschudii*; galgal, *Galeorhinus galeus*; galmin, *Galeus mincaronei*; glygan, *Glyphis gangeticus*; glygly, *Glyphis glyphis*; gurdor, *Gurgesiella dorsalifera*; gymalt, *Gymnura altavela*; hemhal, *Hemiscyllium hallstromi*; hemleu, *Hemitriakis leucoperiptera*; hemstr, *Hemiscyllium strahani*; hetcol, *Heteroscyllium colcloughi*; himcha, *Himantura chaophraya*; himflu, *Himantura fluviatilis*; himoxy, *Himantura oxyrhyncha*; himsig, *Himantura signifer*; isooxy, *Isogomphodon oxyrhynchus*; isupau, *Isurus paucus*; lamnas, *Lamna nasus*; leumel, *Leucoraja melitensis*; mobmob, *Mobula mobular*; musfas, *Mustelus fasciatus*; mussch, *Mustelus schmitti*; muswhi, *Mustelus whitneyi*; mylham, *Myliobatis hamlyni*; narban, *Narcine bancroftii*; narbre, *Narcine brevilabiata*; nebfer, *Nebrius ferrugineus*; negacu, *Negaprion acutidens*; odofer, *Odontaspis ferox*; oxycen, *Oxynotus centrina*; pricla, *Pristis clavata*; primic, *Pristis microdon*; pripec, *Pristis pectinata*; priper, *Pristis perotteti*; pripri, *Pristis pristis*; prizij, *Pristis zijsron*; psebre, *Pseudoginglymostoma brevicaudatum*; rhianc, *Rhina ancylostoma*; rhibra, *Rhinoptera brasiliensis*; rhicem, *Rhinobatos cemiculus*; rhifor, *Rhinobatos formosensis*; rhigra, *Rhinobatos granulatus*; rhihor, *Rhinobatos horkelii*; rhijav, *Rhinoptera javanica*; rhiobt, *Rhinobatos obtusus*; rhirhi, *Rhinobatos rhinobatos*; rhitho, *Rhinobatos thouin*; rhityp, *Rhincodon typus**; rhyaus, *Rhynchobatus australiae*; rhydji, *Rhynchobatus djiddensis*; rhylae, *Rhynchobatus laevis*; rhylue, *Rhynchobatus luebberti*; rosalb, *Rostroraja alba*; schsau, *Schroederichthys saurisqualus*; scyque, *Scylliogaleus quecketti*; sphmok, *Sphyrna mokarran*; sphtud, *Sphyrna tudes*; squaca, *Squalus acanthias*; squacu, *Squatina aculeata*; squarg, *Squatina argentina*; squgug, *Squatina guggenheim*; squmit, *Squalus mitsukurii*; squocc, *Squatina occulta*; squocu, *Squatina oculata*; squsqu, *Squatina squatina*; stefas, *Stegostoma fasciatum*; symacu, *Sympterygia acuta*; taemey, *Taeniura meyeni*; triacu, *Triakis acutipinna*; trimac, *Triakis maculata*; uroasp, *Urogymnus asperrimus*; urobuc, *Urolophus bucculentus*; urojav, *Urolophus javanicus*; uroora, *Urolophus orarius*; urosuf, *Urolophus sufflavus*; uroukp, *Urogymnus ukpam*; urovir, *Urolophus viridis*; zapbre, *Zapteryx brevirostris*; *, global distribution.**

commercial importance, whether the species was a target of recreational fishing, and if it was considered dangerous to humans (Table 4.2). Life history and environmental data for 28,505 species of marine and estuarine fish were extracted from FishBase (Froese and Pauly, 2004). Where there were data available for multiple populations per species, they were grouped by species, with mean, minimum and maximum values calculated for each parameter. Species with aquaculture populations were excluded from the data set. Complete data were missing for most species, so we examined only the most complete data to maximise the number of species considered in the analyses. The final data set for analysis included the following terms:

Length (*LNG*). Extinction risk in many taxa has been linked to organism size (Brook *et al.*, 2008; Cardillo *et al.*, 2005; Johnson, 2002; Olden *et al.*, 2007; Purvis *et al.*, 2000b; Raup, 1994; Sodhi *et al.*, 2008a). Most length measurements were either 'standard' or 'total length', but we could not standardise length measurements due to a lack of data on species-specific relationships.

Range (*RGE*). Range extent is an important indicator of the propensity of a species to become threatened (Brook *et al.*, 2008; Croci *et al.*, 2007; Oborny *et al.*, 2005; Pimm *et al.*, 2006). This is because widespread species tend to have a higher capacity to tolerate new environments given that they have already encountered a variety of climatic and habitat conditions in their evolutionary history and acquired relatively high phenotypic plasticity (Croci *et al.*, 2007). FishBase provides information on the number of FAO Fisheries Areas occupied by a particular species. We initially considered the variable as an ordinal integer, but due to high skewnesss, we re-classified the variable into a three-level factor ([1] 1 FAO area, [2] 2 FAO areas, and [3] >2 FAO areas).

Habitat (*HBT*). The type of habitat occupied by a species can influence its distribution given the variation in abiotic factors that dictate habitat distributions (García *et al.*, 2008). Species were categorised into one of three habitat classes: [1] demersal (including bathydemersal and demersal), [2] pelagic (including bathypelagic, benthopelagic and pelagic), or [3] reef-associated (around reefs from 0 to 200 m; Froese and Pauly, 2004).

Environmental temperature class (ETP). As a measure of latitudinal and bathymetric variation in the probability of being classed as threatened (Worm *et al.*, 2005), we also included a three-level factor describing the principal temperature environment occupied by each species. These included [1] tropical (including subtropical and tropical), [2] temperate (including high-latitude or strictly temperate species) or [3] deep-water (see also García *et al.*, 2008).

Commercial fisheries interest (CMI). We hypothesised that species would be, on average, more likely to be classed as 'threatened' if targeted by fisheries (Pauly *et al.*, 1998; Roberts, 2003; Roberts and Hawkins, 1999). We therefore classified each species with respect to its primary interest to fisheries: [1] of commercial interest, [2] of primarily artisanal interest

Table 4.2 Summary of marine fish (*chond*, chondrichthyan; *teleo*, teleost) species' threat status (threatened, critically endangered, endangered or vulnerable; not threatened, least concern, lower risk, or near threatened) and ecological, life history and human-relationship attributes with a list of the species frequency (available data) for the different category levels

Parameter abbreviation	Description	Levels	*n* Marine species with data (%)	
			Chond	*Teleo*
TH08	Threatened (IUCN, 2008)	[0] No	246 (70)	212 (59)
		[1] Yes	108 (30)	145 (41)
LNG	Length	Continuous (cm)	754	12,408
HBT	Habitat	[1] Demersal	756 (78)	7729 (50)
		[2] Pelagic	111 (11)	3535 (23)
		[3] Reef-associated	107 (11)	4135 (27)
ETP	Environmental temperature	[1] Deep water	374 (38)	3263 (21)
		[2] Temperate	84 (9)	1936 (13)
		[3] Tropical	516 (53)	10,198 (66)
RGE	Range (FAO areas)	[1] 1	395 (41)	6798 (44)
		[2] 2	279 (29)	3830 (25)
		[3] > 2	299 (30)	4751 (31)
CMI	Commercial fishing	[1] Artisanal	213 (41)	1569 (32)
		[2] Commercial	128 (25)	1661 (34)
		[3] No fishing interest	175 (34)	1636 (34)
GME	Game fished?	[0] No	869 (89)	14,590 (95)
		[1] Yes	105 (11)	809 (5)
DGR	Dangerous?	[0] No	799 (82)	14,755 (96)
		[1] Yes	175 (18)	619 (4)
WT	Max. weight	Continuous (g)	107	980
LGV	Longevity	Continuous (years)	33	510
FEC	Max. fecundity	Continuous (eggs/female)	153	395

(*continued*)

Table 4.2 (*continued*)

Parameter abbreviation	Description	Levels	*n* Marine species with data (%)	
			Chond	*Teleo*
MTL	Length maturity	Length at min fecundity (cm)	3	150
MTA	Age maturity	Female minimum age at maturity	38	165
LVB	Max. asymptotic length	Max. von Bertalanffy length (L_∞)	2	94
GRT	Growth	Max. growth constant (K)	2	94
MNT	Natural mortality	Max. natural mortality rate (per year)	2	94
RMO	Reproduction mode	[1] Dioecism	855 (100)	2029 (83)
		[2] Parthenogenesis	0	2 (0.8)
		[3] Protandry	0	56 (2)
		[4] Protogyny	0	312 (13)
		[5] Hermaphroditism	0	42 (2)
FTM	Fertilisation method	[1] External	2 (0.2)	2007 (85)
		[2] Brood pouch	0	46 (2)
		[3] In mouth	0	6 (0.3)
		[4] Oviduct	850 (>99)	291 (12)
		[5] Other	0	4 (0.2)
MGR	Migratory behaviour	[1] Amphidromous	2 (4)	74 (4)
		[2] Anadromous	0	129 (7)
		[3] Catadromous	0	59 (3)
		[4] Limnodromous	0	3 (0.2)
		[5] Non-migratory	0	1111 (60)
		[6] Oceanodromous	45 (96)	447 (24)
		[7] Potamodromous	0	22 (1)

Parameters in boldface were included in the threat risk analysis (see Tables 4.3 and 4.4).

(including subsistence and minor commercial interest) or [3] no major interest. We hypothesised that species of commercial interest would have a higher threat risk than other categories.

Game fish (*GME*). Much like the justification for the impact of fisheries interest in a species, we had sufficient information to include whether a species was a targeted game fish. We hypothesised that game fishing would increase the threat risk of a species (Robbins *et al*., 2006).

Dangerous (*DGR*). The perceived or real threat of danger to humans is thought to have been responsible for the depletion of many local populations of sharks prior to the recognition of this taxon's plight (Burgess and Simpfendorfer, 2005). We therefore classed each species as [1] dangerous (including high predation risk, toxic, venomous) or [0] harmless.

4.4. Threat risk analysis

To determine the relationships between the ecological, life history and human-relationship traits and the threat risk of the compiled species, we fitted generalised linear mixed-effect models (GLMM) to the data using the lmer function implemented in the *R* Package V2.5 (R Development Core Team, 2009). For each GLMM, we coded species threat probability [i.e. IUCN Red-Listed (critically endangered, endangered or vulnerable) or not] as a binomial response variable and each trait as a linear predictor (fixed factors), assigning each model a binomial error distribution and a logit link function. We accounted for potential spatial bias in listing probability (i.e. some regions of the Earth might receive greater species assessment scrutiny than others) by removing all non-listed species or those listed as data deficient (International Union for the Conservation of Nature and Natural Resources, 2008) (cf. Olden *et al*., 2007). We also removed all species coded as extinct/extinct in the wild or those listed because of range restrictions (i.e. listed under Criteria B, D2 or both). This latter category was removed to avoid circularity in assessing correlates of threat risk among taxa (e.g. Bradshaw *et al*., 2008; Sodhi *et al*., 2008a).

Species are phylogenetic units with shared evolutionary histories and are not statistically independent (Felsenstein, 1985). We therefore decomposed the variance across species by coding the GLMM random-effects error structure as a hierarchical taxonomic effect (Blackburn and Duncan, 2001). We had adequate replication to use the nested random effect of Order/Family, but insufficient replication at finer taxonomic resolution. The amount of variance in threat probability captured by each model considered was assessed as the per cent deviance explained (%DE) in the binomial response, expressed relative to the deviance of a null model with no fixed effects, but retaining the hierarchical random effect (Brook *et al*., 2006).

We constructed the model sets to reflect particular *a priori* hypotheses to identify the most important drivers of threat risk in the IUCN-listed species

Table 4.3 Generalised linear mixed-effect models used to examine the correlation between fish threat status (either for chondrichthyan or teleost species groups separately) and a set of ecological, life history and human-relationship attributes

Model No.	Term combinations	Analytical theme
(A) Phase 1 (P1): Ecology and life history		
1	~LNG	Allometry (body size)
2	~RGE	Range
3	~LNG + RGE	Allometry + range
4	~LNG + RGE + HBT	Allometry + range + habitat
5	~LNG + RGE + ETP	Allometry + range + temperature
6	~ LNG + RGE + HBT + ETP	Saturated
7	~1	Null (intercept)
(B) Phase 2: Human relationship		
1	~ [P1 + · · ·]	Supported Phase 1 terms
2	~ [P1 + · · ·] + CMI	+Commercial fishing interest
3	~ [P1 + · · ·] + GME	+Game fishing
4	~ [P1 + · · ·] + CMI + GME	+General fishing interest
5	~ [P1 + · · ·] + DGR	+Danger to humans
6	~ [P1 + · · ·] + CMI + GME + DGR	Saturated
7	~1	Null (intercept)

Model combinations, derived a priori, represent particular analytical 'themes' grouping related traits. Terms include LNG, length; RGE, geographic range; HBT, habitat; ETP, environmental temperature class; CMI, commercial fishing interest; GME, game-fished; DGR, dangerous to humans (see also Table 4.2).

collated (Tables 4.3 and 4.4). We first split the modelling approach into two phases to examine different aspects of the relationships: (1) Phase 1 examined the relationship between threat risk (species coded as threatened or not threatened) and the four ecological and life history traits length, range, habitat and environmental temperature. Threatened species were those classed as critically endangered, endangered or vulnerable, with near threatened and least concern taken as not threatened. We also considered a second set of models where near threatened species were removed from the not threatened group; results were similar although there was a moderate increase in the % deviance explained and model ranking (results not shown). No interactions were considered in this phase. Combinations of these traits were constructed to produce seven models (Table 4.3A); (2) Phase 2 examined the influence between the threat response variable and the three human-relationship variables commercial fisheries interest, game-fished and dangerous, but also included the principal ecological and life history traits identified in Phase 1 (see Table 4.3B and Section 4.2). We applied the same two-phase approach to all chondrichthyan and teleost species

Table 4.4 Generalised linear mixed-effect models used to examine the correlation between fish threat status (for chondrichthyan and teleost species combined) and a set of ecological, life history and human-relationship attributes

Model No.	Term combinations	Analytical theme
(A) Phase 1: Ecology and life history		
1	∼LNG	Allometry
2	∼LNG + GRP	Allometry + group
3	∼LNG + GRP + (LNG × GRP)	Allometry + group interaction
4	∼RGE	Range
5	∼RGE + GRP	Range + group
6	∼RGE + GRP + (RGE × GRP)	Range + group interaction
7	∼LNG + RGE + GRP	Allometry + range + group
8	∼LNG + RGE + HBT + GRP	Allometry + range + habitat + group
9	∼LNG + RGE + ETP+ GRP	Allometry + range + temperature+ group
10	∼LNG + RGE + HBT + ETP + GRP + LNG + RGE + HBT + ETP + GRP	Saturated
11	∼1	Null (intercept)
(B) Phase 2: Human relationship		
1	∼ [P1 + · · ·]	Supported Phase 1 terms
2	∼ [P1 + · · ·] + CMI	+Commercial fishing interest
3	∼ [P1 + · · ·] + GME	+Game fishing
4	∼ [P1 + · · ·] + CMI + GME	+General fishing interest
5	∼ [P1 + · · ·] + DGR	+Danger to humans
6	∼ [P1 + · · ·] + CMI + GME + DGR	Saturated
7	∼1	Null (intercept)

Model combinations, derived *a priori*, represent particular analytical 'themes' grouping related traits. Terms include LNG, length; GRP, taxonomic grouping (chondrichthyan or teleost); RGE, geographic range; HBT, habitat; ETP, environmental temperature class; CMI, commercial fishing interest; GME, game-fished; DGR, dangerous to humans (see also Table 4.3).

separately, and then added the fixed term *Group* to test for different threat risks between the two taxonomic groups explicitly. We also considered the Group × length interaction (Table 4.4) to examine whether the relationship between *length* and threat risk differs between groups. We only considered species that were restricted to the marine environment.

We used an index of Kullback–Leibler (K–L) information loss, Akaike's Information Criterion corrected for small sample sizes ($\mathrm{AIC_c}$), to assign relative strengths of evidence to the different competing models (Burnham and Anderson, 2002) as well as the dimension-consistent Bayesian information criterion (BIC), an approximation of the Bayes factor given no informative prior information on relative model support (Burnham and Anderson, 2002). These indices of model parsimony identify the relative evidence of model(s) from a set of candidate models. The relative likelihoods of candidate models were calculated using AIC_c and BIC weights (Burnham and Anderson, 2002), with the weight ($w\text{AIC}_c$ and wBIC) of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set. However, the K–L prior used to justify AIC_c weighting can favour more complex models when sample sizes are large (Burnham and Anderson, 2004; Link and Barker, 2006). We therefore considered both weightings for determining the contribution of the most important major correlates of extinction risk and to identify any weak tapering effects (Burnham and Anderson, 2004; Link and Barker, 2006).

4.5. Modelling results

We compiled data for a total of 28,397 fish species (998 chondrichthyans; 27,399 teleosts); however, specific ecological, life history and human-relationship data were missing for most species (see Table 4.1). Of the species in the database, 525 (52%) chondrichthyan and only 2,272 (8%) teleost species were Red-Listed (see also Table 4.1), so subsequent threat-risk analyses were limited in sample size (Tables 4.5–4.7). Of the listed species, 518 were classed as data deficient (175 chondrichthyans; 343 teleosts). Excluded from the analyses were the 99 species that were classed as extinct/extinct in the wild (all teleosts).

The distribution of species among the IUCN categories revealed a generally higher threat risk for teleosts than sharks (Fig. 4.8). Ordering the categories from least concern through to extinct/extinct in the wild (i.e. from lowest to highest risk categories) shows a biased distribution for the proportion of teleost species in the higher-risk categories (i.e. to the right of Fig. 4.8) compared to chondrichthyans, but a similar proportion of least concern species in both taxonomic groups. Of the IUCN Red-Listed species, there is a higher proportion of data-deficient species among the chondrichthyans (Fig. 4.8).

The principal correlates of threat risk in the Red-Listed species generally support what is known for many other taxa, but the drivers of risk differed between chondrichthyans and teleosts. Our exploration first revealed that marine species for which there was information available on threat risk, there was only evidence for weak correlation (Spearman's ρ) among attributes considered. The maximum $|\rho|$ was 0.445 between *length* and *range* for listed chondrichthyans, and 0.500 between *game fish* and *habitat* for listed teleosts. We are thus confident that the results of our GLMMs were not

Table 4.5 Correlates of marine chondrichthyan threat risk

Model	*k*	*LL*	ΔBIC	*w*BIC	ΔAIC_c	*w*AIC_c	% DE
(A) Phase 1							
~LNG	4	−112.228	0.000	0.860	0.000	0.614	3.9
~LNG+RGE	6	−111.400	9.094	0.009	2.556	0.171	4.6
~LNG+RGE +ETP	8	−110.124	17.292	<0.001	4.297	0.072	5.7
~LNG+RGE +HBT	8	−110.126	17.296	<0.001	4.301	0.072	5.7
~LNG+RGE +HBT+ETP	10	−108.306	24.407	<0.001	5.039	0.049	7.3
(B) Phase 2							
~LNG+RGE	6	−119.625	2.182	0.238	0.000	0.387	5.5
~LNG+RGE +DGR	7	−118.866	6.067	0.034	0.615	0.284	6.1
~LNG+RGE +GME	7	−119.474	7.283	0.019	1.831	0.155	5.7
~LNG+RGE +CMI	8	−118.828	11.394	0.002	2.692	0.101	6.2
~LNG+RGE +CMI+GME	9	−118.742	16.624	<0.001	4.692	0.037	6.2

The five most parsimonious generalised linear mixed-effect models investigating (A) Phase 1: ecological and life history correlates and (B) Phase 2: human-relationship attributes, after accounting for the effects of length and range (n = 216 species). Models include nested (hierarchical) taxonomic (order/family) random intercepts. Models are ranked according to the small-sample Akaike's Information Criterion (AIC_c). Terms shown are LNG = length, RGE = range, HBT = habitat, ETP = environmental temperature, CMI = commercial fisheries interest, GME = status as game fish, DGR = danger to humans. Also shown are number of parameters (k), maximum log-likelihood (*LL*), difference in the Bayesian Information Criterion (BIC) and AIC_c for each model from the most parsimonious model (ΔBIC, ΔAIC_c), model weight (*w*BIC, *w*AIC_c), and per cent deviance explained (%DE) in the response variable (threat probability) by the model under consideration.

unduly biased. For chondrichthyans, threat risk was correlated principally with body *length* (larger species are more threatened), accounting for 0.61 of the AIC_c weight in the Phase 1 analysis; however, this attribute accounted for only 3.9% of the deviance explained (%DE) after taking taxonomy (phylogeny) into account (Table 4.5A). There was also weak support for a small effect of *range* on threat risk (decreasing threat with increasing range; Table 4.5A; Fig. 4.9A), so we included these two terms into the Phase 2 model set as 'control' variables. Although there was some *w*AIC_c support for the models including *environmental temperature* and *habitat* (Table 4.5 A and B), model predictions appeared to support the idea that reef-associated and deep-water chondrichthyans had lower threat risk (Fig. 4.9A). The Phase 2 analysis for chondrichthyans examining whether human-relationship attributes further influenced threat risk revealed that the term *dangerous*

Table 4.6 Correlates of marine teleost threat risk

Model	*k*	*LL*	ΔBIC	*w*BIC	ΔAIC$_c$	*w*AIC$_c$	% DE
(A) Phase 1							
~LNG+RGE +ETP	8	−96.069	6.099	0.033	0.000	0.357	14.0
~LNG+RGE	6	−98.449	0.000	0.692	0.482	0.280	11.9
~LNG+RGE +HBT	8	−96.483	6.928	0.022	0.829	0.236	13.6
~LNG+RGE +HBT+ETP	10	−94.953	14.727	<0.001	2.125	0.123	15.0
~LNG	4	−104.907	2.057	0.247	9.197	0.004	6.1
(B) Phase 2							
~LNG+RGE +ETP+HBT	10	−94.953	4.471	0.095	0.000	0.447	15.0
~LNG+RGE +ETP+HBT +GME	11	−94.690	9.374	0.008	1.682	0.193	15.2
~LNG+RGE +ETP+HBT +DGR	11	−94.916	9.825	0.007	2.134	0.154	15.0
~LNG+RGE +ETP+HBT +CMI	12	−94.059	13.540	0.001	2.648	0.119	15.8
~LNG+RGE +ETP+HBT +CMI+GME	13	−93.491	17.927	<0.001	3.856	0.065	16.3

The five most parsimonious generalised linear mixed-effect models investigating (A) Phase 1: ecological and life history correlates and (B) Phase 2: human-realationship attributes, after accounting for the effects of length and range ($n = 228$ species). Models include nested (hierarchical) taxonomic (order/family) random intercepts. Models are ranked according to the small-sample Akaike's information criterion (AIC$_c$). Terms shown are LNG = length, RGE = range, HBT = habitat, ETP = environmental temperature, CMI = commercial fisheries interest, GME = status as game fish, DGR = danger to humans. Also shown are number of parameters (*k*), maximum log-likelihood (*LL*), difference in the Bayesian Information Criterion (BIC) and AIC$_c$ for each model from the most parsimonious model (ΔBIC, ΔAIC$_c$), model weight (*w*BIC, *w*AIC$_c$), and per cent deviance explained (%DE) in the response variable (threat probability) by the model under consideration.

(whether a species was considered potentially harmful to humans) had some support (Table 4.5B; Fig. 4.10C)—contrary to expectation, potentially harmful sharks had a lower threat risk than harmless species (Fig. 4.10C).

For marine teleosts, *length* again was positively related to threat risk but accounted for only 6.1% of the deviance in the response (Table 4.6A). The addition of *range* improved model fit, raising %DE to 11.9% (Table 4.6A). *Environmental temperature* and *habitat* also received high support (Table 4.6A),

Table 4.7 Correlates of marine chondrichthyan and teleost threat risk

Model	k	LL	ΔBIC	wBIC	ΔAIC_c	$wAIC_c$	% DE
(A) Phase 1							
~LNG+RGE +ETP+GRP	9	−210.160	8.870	0.005	0.000	0.456	8.4
~LNG+RGE +GRP	7	−212.349	1.056	0.246	0.219	0.409	7.4
~LNG+RGE +HBT+ETP +GRP	11	−210.000	20.740	<0.001	3.875	0.066	8.5
~LNG+RGE +HBT+GRP	9	−212.336	13.223	0.001	4.352	0.052	7.5
~LNG+GRP	5	−217.917	0.000	0.417	7.235	0.012	5.0
(B) Phase 2							
~LNG+RGE +ETP+GRP	9	−210.160	0.000	0.654	0.000	0.378	8.4
~LNG+RGE +ETP+GRP +GME	10	−209.509	4.793	0.060	0.791	0.254	8.7
~LNG+RGE +ETP+GRP +DGR	10	−209.968	5.711	0.038	1.709	0.161	8.5
~LNG+RGE +ETP+GRP +CMI	11	−209.352	10.574	0.003	2.579	0.104	8.8
~LNG+RGE +ETP+GRP +CMI+GME	12	−209.624	5.132	0.059	2.209	0.117	9.1

The five most parsimonious generalised linear mixed-effect models investigating (A) Phase 1: ecological and life history correlates and (B) Phase 2: human-relationship attributes, after accounting for the effects of length and range (n = 444 species). Models include nested (hierarchical) taxonomic (order/family) random intercepts. Models are ranked according to the small-sample Akaike's information criterion (AIC_c). Terms shown are GRP = taxonomic group chondrichthyan or teleost), LNG = length, RGE = range, HBT = habitat, ETP = environmental temperature, CMI = commercial fisheries interest, GME = status as game fish, DGR = danger to humans. Also shown are number of parameters (k), maximum log-likelihood (LL), difference in the Bayesian Information Critertion (BIC) and AIC_c for each model from the most parsimonious model (ΔBIC, ΔAIC_c), model weight (wBIC, $wAIC_c$), and per cent deviance explained (%DE) in the response variable (threat probability) by the model under consideration.

with lower risk predicted for pelagic and higher risk for deepwater species (Fig. 4.9B and C). Including length, range, habitat and environmental temperature in the Phase 2 models, teleosts demonstrated little response to any of the human-relationship attributes considered (Table 4.6B; Fig. 4.10). Combining the two taxonomic groups (marine species only) and setting the *Group*

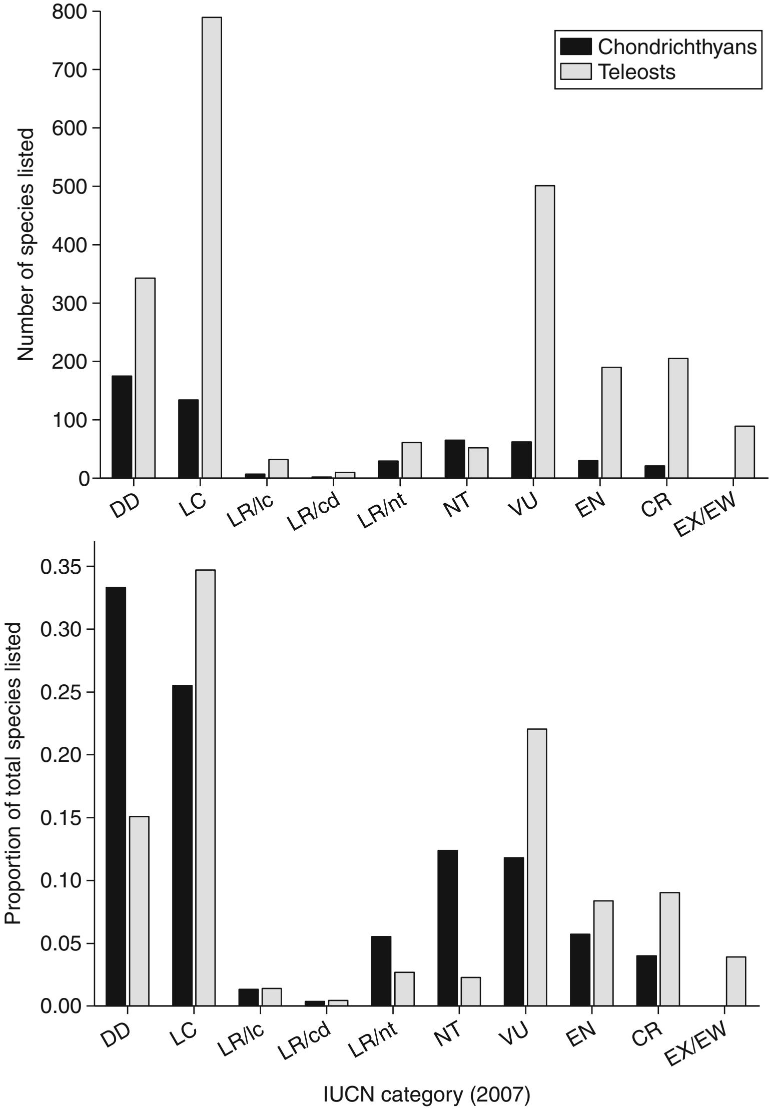

Figure 4.8 Frequency distribution (top panel: number of species; bottom panel: proportion of species listed per taxonomic group) of chondrichthyans (Classes Elasmobranchii and Holocephalii) and teleosts (Classes Actinopterygii and Sarcopterygii) in the 2008 World Conservation Union's (IUCN) Red List (www.iucnredlist.org). Categories are ordered left to right from least threatened to most threatened. DD, data deficient; LC, least concern; LR/lc, lower risk/least concern; LR/cd, lower risk/conservation dependent; LR/nt, lower risk/near threatened; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; EX/EW, extinct/extinct in the wild.

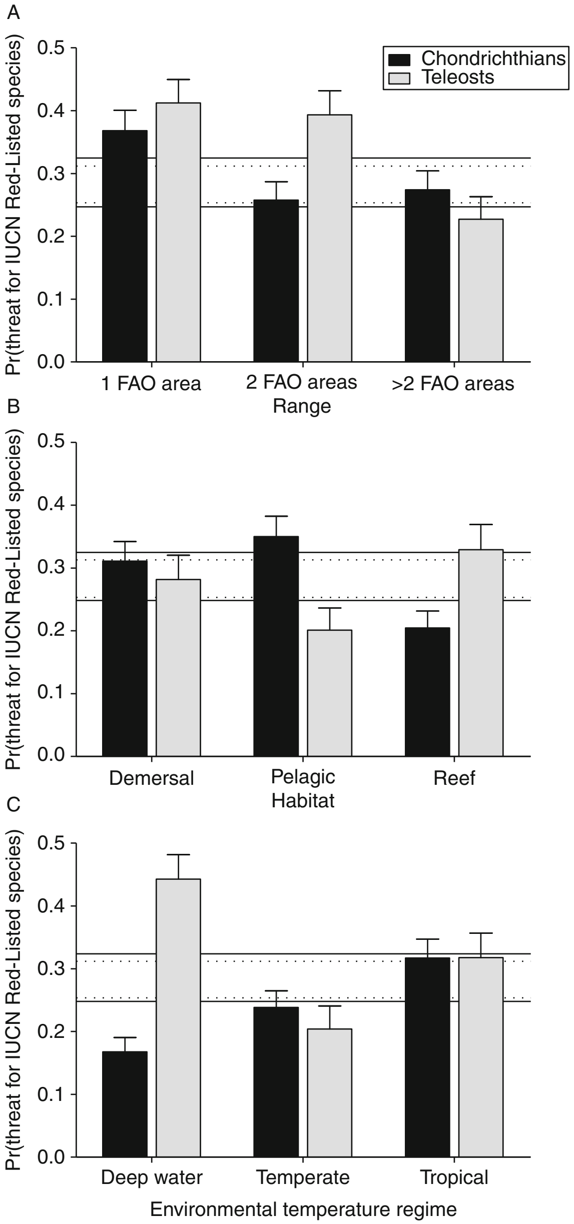

Figure 4.9 Phase 1 predicted threat risk of IUCN Red-Listed marine chondrichthyan (Classes Elasmobranchii and Holocephalii) and teleost (Classes Actinopterygii and Sarcopterygii) based on generalised linear mixed-effect models that account for phylogenetic relatedness among species (nested random effect = order/family). Risks are predicted as a probability between 0 and 1 relative to the different levels of the three

term as a fixed effect revealed important support for taxonomic group even after accounting for *length* (Table 4.7A). This demonstrates that teleosts have a generally higher threat risk than chondrichthyans *even after accounting for size differences*, although the effect is weak (Table 4.7B).

4.6. Relative threat risk of chondrichthyans and teleosts

Our quantitative threat risk analysis revealed some important insights into the relative threat risk of the major marine fish taxa, some of which can appear somewhat counter-intuitive. Of particular importance was the finding that listed teleosts are in general placed more frequently into the higher-risk categories of the IUCN Red List relative to chondrichthyans. However, this is not because the relatively few listed teleosts just happen to be larger-species. Indeed, Red-Listed teleosts were in fact smaller on average than the distribution of all teleosts for which length data were available (Fig. 4.11).

The relatively higher threat risk of teleosts compared to chondrichthyans could be misleading, however, if not properly contextualised. Of foremost importance is that only a small proportion of all marine teleosts have been described adequately for a reliable Red Listing (~8%), whereas >52% of all known chondrichthyan species have been Red Listed, although many admittedly are placed within the data-deficient category. Therefore, extrapolating true threat risk to the entire marine teleost taxon from the small data set described here is potentially unreliable. Another possible bias is that because of their generally larger size, their stigma in the public eye, and the recent attention brought to the conservation literature regarding their apparently high threat risk, there might be a tendency to list chondrichthyan species at least within the lower threat-risk categories following the precautionary principle.

We also found reasonable evidence that disparities in relative threat risk between the two groups did not arise solely from the different size distributions; sharks are approximately one order of magnitude larger on average

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ecological and life history trait factors considered: *range* (number of FAO Fishing Areas – www.fao.org), *habitat* and *environmental temperature regime*. See text for full details. The observed threat probability 95% confidence intervals (chondrichthyans: dotted horizontal lines; teleosts: solid horizontal lines) were determined by a 10,000-iteration bootstrap of the probabilities predicted by the saturated model over 216 (chondrichthyan) and 228 (teleost) species. Changes to extinction probability relative to each term level were calculated by adjusting the original dataset so that all species were given the same value for that level (each level value in turn), keeping all other terms in the model as in the original dataset. Error bars represent the 10,000 iteration-bootstrapped upper 95% confidence limits.

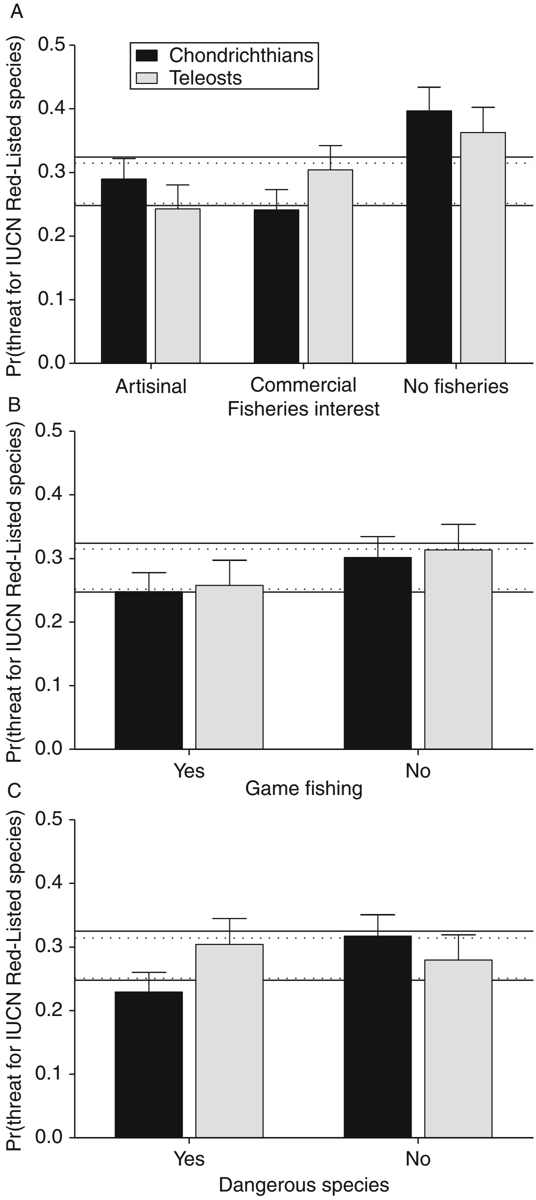

Figure 4.10 Phase 2 predicted threat risk of IUCN Red-Listed marine chondrichthyan (Classes Elasmobranchii and Holocephalii) and teleost (Classes Actinopterygii and Sarcopterygii) based on generalised linear mixed-effect models that account for phylogenetic relatedness among species (nested random effect = order/family). Risks are predicted as a probability between 0 and 1 relative to the different levels of the three human-relationship factors considered: fisheries interest, whether a species was

than teleosts (Fig. 4.11). Indeed, even after accounting for the positive influence of size (length) on threat risk, teleosts were still more likely than chondrichthyans to be classified as threatened. However, we found no evidence for an interaction between *Group* and the allometry of threat risk, suggesting that the reason for an average higher susceptibility ranking among the teleosts is due to inherently different extinction proneness between the two groups. While sharks might not have necessarily experienced the same magnitude of deterministic decline as Red-Listed teleosts (the declining population paradigm), their larger size and lower fecundity (the latter not included in the analysis) could indeed predispose the taxon to a higher risk of extinction overall (the small population paradigm) (Brook *et al.*, 2006, 2008; Caughley, 1994; Traill *et al.*, 2007).

Another important consideration is that total chondrichthyan species richness is considerably lower than for teleosts. Indeed, there are nearly 30 times more teleost species listed in FishBase than chondrichthyans (Table 4.1). This implies that the relative effect of extinction on total chondrichthyan species diversity is considerably higher than the loss of a single species on teleost diversity. This alone could be argued as sufficient justification to consider chondrichthyans as a special case for marine fishes, although it does not negate the obvious conclusion that there are insufficient data for teleosts to make strong inference regarding the true threat risk of that taxon.

5. IMPLICATIONS OF CHONDRICHTHYAN SPECIES LOSS ON ECOSYSTEM STRUCTURE, FUNCTION AND STABILITY

5.1. Ecosystem roles of predators

The loss of a single species is an evolutionary tragedy in its own right; however, when species loss triggers the degradation of entire biological communities, the importance of their conservation increases. There is now a rich body of evidence and theory demonstrating how predators of all major trophic levels influence the ecosystems in which they live (Baum and

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game-fished and whether a species was considered dangerous to humans. See text for full details. The observed threat probability 95% confidence intervals (chondrichthyans: dotted horizontal lines; teleosts: solid horizontal lines) were determined by a 10,000-iteration bootstrap of the probabilities predicted by the saturated model over 216 (chondrichthyan) and 228 (teleost) species. Changes to extinction probability relative to each term level were calculated by adjusting the original dataset so that all species were given the same value for that level (each level value in turn), keeping all other terms in the model as in the original dataset. Error bars represent the 10,000 iteration-bootstrapped upper 95% confidence limits.

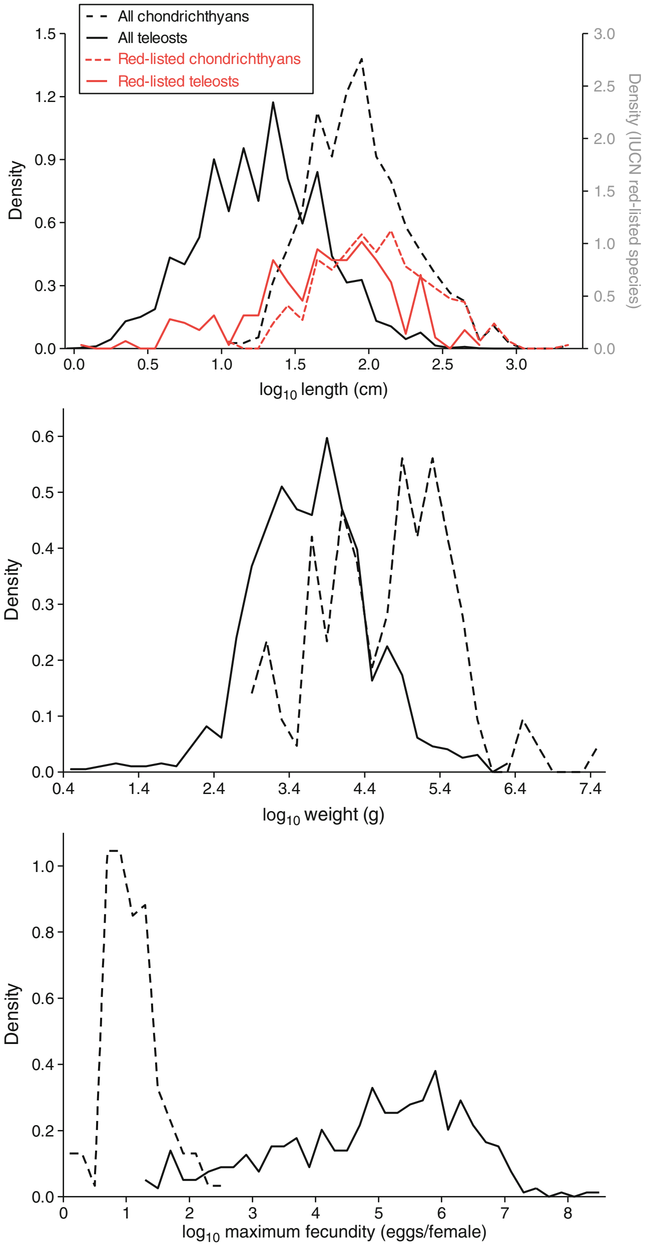

Figure 4.11 Distribution of life history traits between chondrichthyans (Classes Elasmobranchii and Holocephalii) and teleosts (Classes Actinopterygii and Sarcopterygii). Top panel: density distribution of $\log_{10}$-transformed body length (cm), showing all species and only the IUCN Red-Listed species for each taxon used in the threat-risk analyses. Middle panel: density distribution of $\log_{10}$-transformed body weight (g). Bottom panel: density distribution of $\log_{10}$-transformed fecundity (eggs/female).

Worm, 2009). Most pertinent is the suite of processes known as *trophic cascades* which are defined as ‘reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population, community or trophic level across more than one link in a food web’ (Pace *et al.*, 1999). This concept has been further simplified into two discrete categories known popularly as ‘top-down’ or ‘bottom-up’ control. Top-down control is a trophic cascade where lower food-web component species are regulated by an upper-level predator, whereas, in contrast, ‘bottom-up’ control is the regulation of food-web components by primary producers or the input of limiting resources into a system (Pace *et al.*, 1999). Although a system can demonstrate a predominant type of trophic cascade, many ecosystems demonstrate elements of both bottom-up and top-down control (Pace *et al.*, 1999).

There are many examples of terrestrial trophic cascades, although most of the empirical evidence and theory has been garnered from lakes, streams and intertidal zones (Pace *et al.*, 1999). Examples range from killer whales regulating kelp forest growth via predation on otters and the subsequent increase in herbivorous sea urchins (see more detail in Section 5.2), to mosquitoes affecting protozoan abundance that changes bacteria composition in pitcher plants (see Pace *et al.*, 1999 for a review). The main way in which predators tend to propagate indirect effects down trophic webs is by directly altering the numerical abundance of herbivores, but predators can also modify herbivore foraging behaviour in response to variation in perceived predation risk (Schmitz *et al.*, 2004). Indeed, there is evidence that shifting predation risk in the presence of different predator types affects plant community composition, leading to changes in net primary production and nutrient cycling (Schmitz, 2003, 2008; Schmitz *et al.*, 2004).

The loss of predators in many ecosystems reduces species richness, leading to reduced community stability, lower productivity and nutrient cycling (Duffy, 2006; Schmitz, 2008; Schmitz *et al.*, 2000; Stachowicz *et al.*, 2007; Worm *et al.*, 2006) (Fig. 4.12). This in turn reduces ecosystem resilience to stochastic perturbations that operate independently of community structure or species abundance (such as severe El Niño events, intense storms and tsunamis) (Hughes *et al.*, 2005). Such changes in community structure are thought to arise through direct reduction in predator abundance that leads to cascading trophic imbalances and re-equilibration to new stable states (see Scheffer *et al.*, 2001). These situations of ‘predator release’ of prey usually change the foraging capacity (such as increased herbivore or meso-predator survival rates) and alter foraging behaviour (O’Connor and Bruno, 2007). The subsequent decline in plant biomass through increased grazing pressure depends on the strength and number of linkages in a particular food web (Halaj and Wise, 2001; Polis and Strong, 1996). Therefore, the strength of top-down effects of predator reduction and loss will vary between ecosystems with the complexity of food webs, and

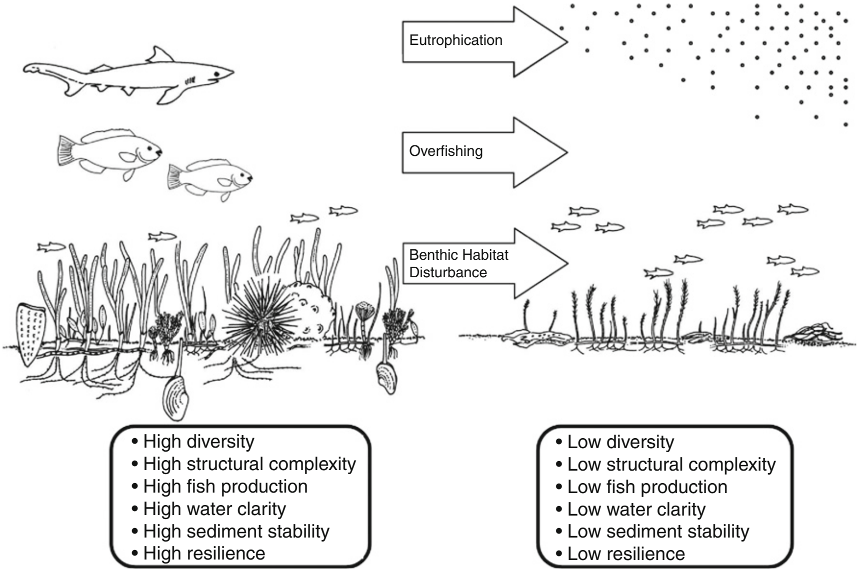

Figure 4.12 An example of how predator removal and other human-mediated changes to marine ecosystems reduce species richness, habitat structure and ecosystem function. Here, over-fishing of higher fish predators, eutrophication and benthic habitat disturbance all lead to a depauperate biological community in this seagrass ecosystem (reproduced with permission from Duffy, 2006).

compensation can occur where changes in the upper trophic levels do not necessarily impact lower levels (Pace *et al.*, 1999). Furthermore, ecosystem changes can arise from the different functions of a predator species where there is niche partitioning of age and life-cycle stages (Bolnick *et al.*, 2003; Field *et al.*, 2005; Pace *et al.*, 1999; Polis, 1984; Schmitz *et al.*, 2004; Taylor and Bennett, 2008).

5.2. Predator loss in the marine realm

Worldwide, there is much concern regarding changes seen in marine environments through observed shifts in ecosystem composition and the subsequent loss of resources and ecosystem services (Hughes *et al.*, 2005; Shurin *et al.*, 2002; Worm *et al.*, 2006). Although the effects of marine predator loss in marine systems is difficult to quantify given the clandestine lifestyle of many large predators (Bradshaw, 2007), there is growing empirical evidence describing the role of predatory species in modulating trophic cascades and top-down control across a range of marine ecosystems (Bascompte *et al.*, 2005; Bruno and O'Connor, 2005; Byrnes *et al.*, 2006; Duffy, 2006; Dulvy *et al.*, 2004b; Frank *et al.*, 2005, 2007; Hughes *et al.*, 2005, 2007; Jennings and Kaiser, 1998; O'Connor and Bruno, 2007; Österblom *et al.*, 2006). However, the true function of large marine predators and the potential implications of their loss is still not clearly understood for most ecosystems (Bruno and O'Connor, 2005).

A good example of a marine trophic cascade is the top-down control of kelp (*Macrocystis* spp.) forests by sea otters (*Enhydra lutris*) and other predators (Byrnes *et al.*, 2006; Estes *et al.*, 1998). In western Alaska, sea otter populations transformed nearshore reefs from two- to three-trophic level systems by limiting the distribution and abundance of herbivorous sea urchins, thereby promoting kelp forest development (Estes *et al.*, 1998). Many otter populations are now in abrupt decline over large areas due to increased killer whale predation. This has reduced predation rates by otters on sea urchins, leading to higher urchin densities and greater deforestation of kelp beds. Other predators influence these trophic cascades in kelp forests where otters are absent. Byrnes *et al.* (2006) showed that crabs (*Cancer productus* and *Cancer magister*) and starfish (*Pycnopodia helianthoides*) play a large role in maintaining kelp forest biomass by regulating herbivore numbers including the snails *Tegula brunnea* and *Tegula funebralis*, urchins *Strongylocentrotus purpuratus* and *Strongylocentrotus franciscanus*, and a crab *Pugettia producta*. Although no evidence for direct links between predator and prey densities was found, changes in kelp mass were related to changes in herbivore foraging behaviour with relative predation risks. Similar effects have been seen in seagrass communities (Byrnes *et al.*, 2006; Duffy, 2006). Predator-induced changes have also been described for other coastal ecosystems where carnivorous fishes (such as blennies *Hypleurochilus geminatus* and *Hypsoblennius hentzi*, killifish *Fundulus heteroclitus* and pinfish *Lagodon rhomboides*) have regulated numbers of herbivores that control algal diversity and biomass (Bruno and O'Connor, 2005; O'Connor and Bruno, 2007).

Another example documented in the Caribbean, Indian and western Pacific Oceans is the change of coral reef ecosystems to macroalgal-dominated communities (Dulvy *et al.*, 2004b; Hughes *et al.*, 2003, 2005, 2007; Pinnegar *et al.*, 2000; Rogers and Beets, 2001). These are often complex systems with feedback loops through mechanisms such as nutrient cycling (McClanahan, 1997) and Allee population effects (Dulvy *et al.*, 2004b).

In continental-shelf and open-ocean ecosystems, trophic cascades or changes in fish community structure (Frank *et al.*, 2005; Hughes *et al.*, 2005; Levin *et al.*, 2006; Link and Garrison, 2002; Mangel and Levin, 2005; Österblom *et al.*, 2006; Shiomoto *et al.*, 1997) can occur, although there is some debate (see Frank *et al.*, 2007; Parsons, 1992; Reid *et al.*, 2000). Trophic changes have been noted in relatively simple systems like the Barents Sea where top-down and size-selective predation by fish have influenced zooplankton composition and abundance (Reid *et al.*, 2000), and in the North Pacific for salmon predation on zooplankton altering the abundance of phytoplankton (Shiomoto *et al.*, 1997). Until recently, however, continental-shelf ecosystems were thought to be largely immune to top-down control because of their relatively wide-distribution, high species diversity and food web complexity (Steele, 1998). Currently, it is thought that these can affect elements of the trophic web or the entire ecosystem (Frank *et al.*, 2005) as a combination of top-down and bottom-up processes. This has resulted in predator replacement, increased production at lower trophic levels and/or long-term ecosystem-level change (Frank *et al.*, 2007). Furthermore, these long-term ecosystem changes might be responsible for the slow or failed recovery many previously exploited fish populations (Hutchings, 2000; Shelton *et al.*, 2005; Worm and Myers, 2003).

5.3. Ecosystem roles of chondrichthyans

Chondrichthyans are generally apex predators, so predicting the effects of their removal are complex. As with other large species of predatory fishes, not only does their removal release prey populations from a major mortality source, the reduction in predators can sometimes have unexpected second- and third-degree implications for non-prey species through trophic linkages (Baum and Worm, 2009; Schindler *et al.*, 2002; Stevens *et al.*, 2000) that can in turn affect ecosystem functions (Worm *et al.*, 2006). The role of sharks in maintaining diversity and ecosystem structure are virtually unexplored (Camhi *et al.*, 1998). Although there have been many diet studies (e.g. Bethea *et al.*, 2006; Ellis and Musick, 2007; Estrada *et al.*, 2006; Huveneers *et al.*, 2007; Polo-Silva *et al.*, 2007; Saidi *et al.*, 2007; Simpfendorfer *et al.*, 2001; Stevens and Wiley, 1986), only a few recent studies have explored the role of chondrichthyan predators in ecosystem structuring, and most have focused on species or ecosystems of economic importance (Kitchell *et al.*, 2002; Stevens *et al.*, 2000).

Ecosystem modelling using ECOPATH/ECOSIM models (Walters *et al.*, 1997) predicted the effects of top-predator removal on many ecosystems, with varying results (Kitchell *et al.*, 2002; Stevens *et al.*, 2000). Stevens *et al.* (2000) modelled these effects in three environments: a tropical shelf ecosystem in Venezuela, a Hawaiian coral reef and a North Pacific oceanic ecosystem. This comparison of a broad range of ecosystems, each dominated by a different functional group of sharks, demonstrated different outcomes when predators were reduced or removed, but predictions were imprecise. Each model showed that some relatively minor prey species for the sharks in each system underwent large increases in biomass after shark removal. For example, turtles and reef sharks following reductions of tiger sharks in Hawaii; seals in the North Pacific following the removal of salmon sharks, and croakers (e.g. *Plagioscion* spp.) in Venezuela following the removal of small triakid sharks, principally the smooth dogfish *Mustelus canis*. In contrast, some seemingly important prey groups decreased in biomass. In the North Pacific and Venezuelan systems, at least one non-shark prey group decreased in abundance, most likely as a result of complex trophic interactions. The main conclusion was that the effects of shark reductions across ecosystems are often difficult to foresee, but might be ecologically and economically important and persist over long periods of time.

Another ECOPATH/ECOSIM modelling exercise examined the potential role of sharks and longline fisheries on pelagic ecosystems in the central North Pacific. Kitchell *et al.* (2002) evaluated changes in trophic interactions for the central Pacific Ocean and showed that the removal of blue sharks produced compensatory responses favouring other shark species and billfishes, and that their removal had only modest effects on the majority of species. However, intra- and inter-specific predation on juvenile elasmobranchs produced strong, non-linear declines in shark populations. Overall, the model revealed that blue sharks in this system are not 'keystone' predators, although if more sharks are removed by longline fisheries, food webs were predicted to degrade.

One of the first studies to identify predatory release of elasmobranch mesopredators was in the Gulf of Mexico where coastal shrimp fishing caused by-catch population declines of over 95% in bonnethead sharks (*S. tiburo*), Bancroft's numbfish (*Narcine bancroftii*) and smooth butterfly ray (*Gymnura micrura*) (Shepherd and Myers, 2005). Combined with fishing reductions in other large shark species in the pelagic longline fishery (Baum *et al.*, 2003), increases in deeper water elasmobranchs such as Atlantic angel sharks (*Squatina dumeril*) and smooth dogfish (*M. canis*) were observed.

Open-ocean ecosystems have been considered more resilent to predator loss (Steele, 1998), although changes in both the size of shark catches and species composition have been described in the Pacific Ocean (Ward and Myers, 2005). Removal of individuals from larger species, for example, blue, silky and thresher sharks, black marlin (*Makaira nigricans*) and blue marlin (*Makaira indica*), caused a coincident increase in smaller species such as pelagic stingray (*Dasyatis violacea*), skipjack tuna (*Katsuwonus pelamis*) and pomfrets (Bramidae).

More recent empirical evidence has demonstrated how changes to chondrichthyan abundance and structure, mainly through harvest, have altered marine communities and caused trophic cascades. The loss of elasmobranch diversity in the coastal northwest Atlantic has had cascading effects down to even invertebrate species (Myers *et al.*, 2007). Over the last 35 years, there has been a large reported decline in 11 of the great shark species (i.e. >85% for bull, dusky, smooth and scalloped hammerhead, tiger, blacktip and sandbar sharks; Fig. 4.5) that hunt other elasmobranch mesopredators. These declines have allowed many mesopredator populations to increase and restructure the ecosystem, with the corollary that large sharks have become functionally eliminated. Higher densities of cownose ray (*Rhinoptera bonasus*) were linked to large reductions in bivalve biomass (Blaylock, 1993) such as scallops *Argopecten irradians* (Peterson *et al.*, 1996).

Indeed, the subsequent reduction and likely depletion of scallop populations can cause rays to switch to soft and hard clams (e.g. *Mya arenaria*, *Mercenaria mercenaria*) and oysters (*Crassostrea virginica*) that themselves have been reduced by harvesting and other anthropogenic impacts. Other species of mesopredators such as skates in the north-eastern Atlantic (Dulvy *et al.*, 2000) and the long-headed eagle ray (*Aetobatus flagellum*) around Japan (Yamaguchi *et al.*, 2005) might have also been released from predation by larger sharks, although these systems have not yet been examined in sufficient detail.

Of course, many chondrichthyans, especially smaller species, are not apex predators. Yet, there is some evidence that many benthic and demersal species can have important functional roles in marine systems. For the cownose ray, foraging behaviour is also destructive to shallow habitats through the uprooting of seagrasses (Smith and Merriner, 1995), thus exacerbating any cascading effects that might arise from apex predator reduction. Skates can play an important functional role in benthic systems. On the Scotian Shelf, the proportional biomass of skates is low, and therefore might not be considered important for demersal fishes (Duplisea *et al.*, 1997). However, skates have a similar ecological role to flatfishes (Pleuronectidae), and together the two groups represent the majority of the benthic fish biomass on the Scotian Shelf. These species provide an important energy-flow pathway from the benthos and at least one component of the demersal fish assemblage by eating and processing benthic invertebrates (Martell and McLelland, 1994). Therefore, changes in abundance or diversity of either of these mesopredator groups are likely to have an effect on both benthic and demersal ecosystems.

In support of evidence found in the terrestrial realm (e.g. Schmitz, 2008), the mere presence of shark predators can alter the foraging behaviour of their prey species, leading to altered ecosystem states. An example of non-lethal predator effects is the regulation of green sea turtle (*Chelonia mydas*) foraging behaviour by tiger sharks (Heithaus *et al.*, 2007). Turtles in poor body condition foraged on higher quality seagrass beds with high risk of predation by sharks, whereas turtles in good condition foraged on lower quality seagrass beds where fewer predators hunted. A reduction or removal of tiger sharks is therefore predicted to result in greater foraging pressure on high-quality seagrass beds leading to potential overgrazing (Rose *et al.*, 1999).

6. SYNTHESIS AND KNOWLEDGE GAPS

6.1. Role of fisheries in future chondrichthyan extinctions

Despite the controversies and general paucity of good data, there is no question that fishing decreases the probability of survival of individual fishes. Relying on the assumption of density compensation, sustainable and low-impact harvests are certainly possible for any exploited fish species, especially for those with rapid generation times and fast growth rates (Hilborn and Walters, 2001; Walters and Martell, 2004). It is only when populations are reduced at rates greater than any gains achieved through density compensation that large population decline becomes inevitable. Population decline itself does not necessarily result in heightened extinction risk, especially if initial population size is large. The declining population paradigm on which much of the IUCN's Red List classification is based does tend to indicate when population decline becomes cause for concern. In other words, decline can become an issue if the current population size is vastly inferior to some original baseline estimate. However, only when population sizes fall below a MVP size does the risk of extinction rise to non-negligible values (Traill *et al.*, 2007, 2009). Of course, a rare species might already have small initial population sizes, in which case the probability of dropping below MVP with fishing harvest is much higher.

Do fisheries contribute to higher extinction risk in chondrichthyans? As for all deterministic drivers of population decline, the answer is 'yes'; however, it depends entirely on the species in question, the magnitude of decline and the population's relative distance from a species-specific MVP size (Traill *et al.*, 2009). Our review has highlighted and reinforced the understanding that large species with correspondingly slower growth rates, longer generation times and later ages of maturity are more susceptible to possible extinction risks. Importantly, we have determined that although Red-Listed teleosts have a generally higher assessed threat risk than chondrichthyans, the relatively larger chondrichthyans with lower fecundity, in themselves, suggest that high harvest-rate fisheries have a potentially greater capacity to drive certain chondrichthyan populations to sub-MVP size, especially those that already exist at low densities.

There is little debate regarding the future of demand for fish products. An ever-increasing human population and greater propensity for coastal living means that chondrichthyans stand to experience some intense harvest as demand for their products continues to rise (Clarke *et al.*, 2006; Food and Agriculture Organization of the United Nations, 2005). Indeed, as coastal resources become more and more heavily harvested, it is likely to be the pelagic mixed-species fisheries that will be called upon to supply the bulk of the demand. As highlighted, these mixed-species fisheries and their associated by-catch represent some of the greatest mortality sources for rare chondrichthyans, and currently there is little to no management or monitoring of any high-seas fisheries (Mucientes *et al.*, 2009). Coupled with more advanced technological capacity (Roberts, 2002), an increasing human population also means that the quest for previously unavailable or difficult-to-access fish resources will expose more and more species to a previously unknown mortality source. In particular, deepwater fishing is growing in reach and expanse. This is potentially problematic given the predicted slower life histories of cold water, deep-dwelling species that have likely much lower intrinsic rebound potential than meso-pelagic species.

The endeavour to determine a species-specific MVP size and relate estimates of stock size to this should be one of the foremost goals of any management strategy for chondrichthyan harvest. However, ensuring that a population does not fall below MVP should only be regarded as an absolute minimum baseline, for MVP is typically estimated as the population size below which the probability of (quasi)extinction becomes unacceptable, typically greater than 1% (Shaffer, 1981; Traill *et al.*, 2007). True sustainability should therefore regard the harvest in terms of population trends rather than population size. In other words, instead of setting PVA to estimate the probability of falling below a quasi-extinction threshold, the focus should shift to setting a minimum population size above which decline becomes unlikely. If a population does, however, fall below its MVP, then continued fishing pressure might be outweighed by stochastic factors that act synergistically to increase extinction risk (Brook *et al.*, 2008).

In summary, sustainable chondrichthyan fisheries are possible, but these must strive for stability rather than attempt to maximise yield (Hilborn *et al.*, 2003). In the words of Hilborn (2007):

> It is almost universally recognized that the future of sustainable fisheries lies with much less fishing effort, lower exploitation rates, larger fish stocks, dramatic reduction in bycatch, increased concern about ecosystem impacts of exploitation, elimination of destructive fishing practices, and much more spatial management of fisheries, including a significant portion of marine ecosystems protected from exploitation.

6.2. Climate change

The current rate of global climate warming is greater now than at any time in the last 1000 years (Walther *et al.*, 2002) and has been of increasing concern and research focus in recent decades (e.g. Graham and Harrod, 2009; Hughes *et al.*, 2003; Munday *et al.*, 2008; Roberts and Hawkins, 1999; Roessig *et al.*, 2004). As a result of climate change, extinction rates over the next century are predicted to be greater than otherwise expected (e.g. Hansen *et al.*, 2006), particularly for endemic and range-restricted species (Ahonen *et al.*, 2009; Brook *et al.*, 2008; Munday *et al.*, 2008). In addition to the predicted effects associated with increases in both maximum and minimum temperatures, daily minimum temperatures are increasing more rapidly than daily maximum temperature (Vose *et al.*, 2005), with high spatial heterogeneity expected in the response of organisms, populations and ecological communities (Genner *et al.*, 2004). Chondrichthyes is therefore one taxon that could be, on average, at relatively high risk to climate change effects due to slow rates of evolution and low phenotypic plasticity that might otherwise enable quick adaptation to rapidly changing environmental conditions (Daufresne *et al.*, 2009; Harley *et al.*, 2006; Visser, 2008).

Climate change will also probably influence the phenology and physiology of some species (Sims *et al.*, 2001, 2004), with the most probable response including shifts in distribution and changes in the timing of migrations. The resultant changes to top-down control by shifting densities and configuration of the large predator guild, and the corresponding bottom-up changes expected from shifting community structure in lower trophic levels and nutrient cycling pathways (Walther *et al.*, 2002) are complex and presently impossible to predict reliably. Although it is possible that climate changes might benefit some species, the rapid pace of change combined with pressure from other threats might mean that more species will respond negatively (Brook *et al.*, 2008; Daufresne *et al.*, 2009; Visser, 2008).

The direct effects of environmental change likely to affect chondrichthyans are the same that will influence all marine life, namely increases in temperature, and changes to water chemistry (Fig. 4.13). Although most species demonstrate some physiological plasticity in their tolerances to environmental conditions, many species are expected to shift their distributions to areas conducive to maintaining physiological optima, thus we might expect a shift toward higher latitudes (McMahon and Hays, 2006; Rose, 2005). Migratory fish species are already showing changes in their ranges. For example, basking shark foraging behaviour is highly correlated with thermal ocean features, and shifted distributions northward might have occurred in the recent past (Sims and Reid, 2002), and would be more likely to occur in the future as more rapid climate warming alters thermal stratification and the strength and persistence of fronts with consequent distribution changes of its plankton prey (Cotton *et al.*, 2005; Sims, 2008).

Temperature and salinity changes are also having effects on ocean circulation (Clark *et al.*, 2002). These will enhance changes to local environmental conditions and the distributional response of their biological communities (Harley *et al.*, 2006). Another direct effect might be the increasing prevalence of disease and emergence of novel pathogens with increasing temperatures (Clark *et al.*, 2002; Harvell *et al.*, 1999, 2002, 2004; Ward and Lafferty, 2004). For coastal shark and rays species, sea-level rise will alter shallow water environments, affecting especially those that have specific habitat requirements (e.g. mangroves) for breeding, pupping or feeding (Heupel *et al.*, 2007). Sea-level rise might also lead to large-scale habitat loss for some species and disrupt coastal and estuarine ecosystems. The effects of increasing frequency of extreme weather condition and intense storm events are likely to affect behavioural changes, destroy habitats and change community structure (Heupel *et al.*, 2003; Scheffer *et al.*, 2001).

Other effects of climate change that might influence bottom-up processes are ozone depletion and ocean acidification. Ozone depletion affects

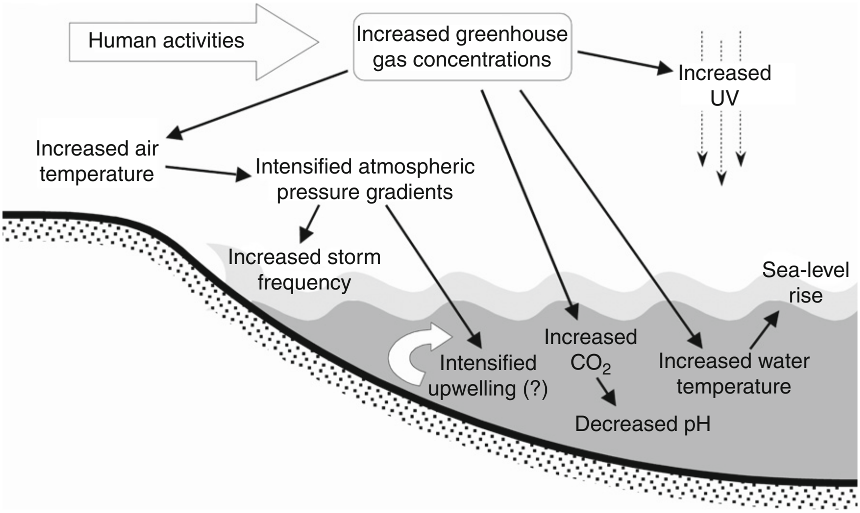

Figure 4.13 Abiotic changes to oceans predicted from climate change (reproduced with permission from Harley *et al.*, 2006). The burning of fossil fuels and deforestation increase atmospheric greenhouse gas concentrations, which lead to physical and chemical changes to ocean waters. The effect of climate change on upwelling and current processes is most uncertain.

surface phytoplankton (Zepp *et al.*, 2003) and subsequent productivity of other trophic levels. Ocean acidification has also been identified as a major threat to corals and some calciferous organisms through dissolution of their external calcium carbonate skeletons (Orr *et al.*, 2005). Although acidification to this extent will be unlikely to affect chondrichthyans directly, large potential changes are likely to alter habitat, marine community structure and prey availability for shark predators.

6.3. Extinction synergies

Recent empirical and theoretical work is beginning to identify how different factors interact synergistically to exacerbate extinction risk (Brook *et al.*, 2008). Even when systematic threats such as intensive harvest via fishing do not result in immediate extinction, a combination of secondary processes can eventually cause a species to become extinct. For example, habitat fragmentation and over-harvesting can be exacerbated by climate change. Co-extinctions represent another synergistic process which precipitates species loss more rapidly than otherwise expected. Examination of inter-specific dependencies demonstrated that many thousands of currently non-Red-Listed species could go extinct alongside their listed symbionts due to these dependencies (Koh *et al.*, 2004). Dependencies might also derive from community interactions such as the meso-predator release examples provided in Section 5 (e.g. the reduction in large predatory sharks leading to an expansion of medium-sized chondrichthyans that in turn drive a decline in scallops; Myers *et al.*, 2007). From the chondrichthyan perspective specifically, synergies among harvesting, habitat changes and climate-induced changes to marine environments are most likely to occur in the coastal realm.

6.4. Research needs

There have been great leaps in our understanding of Chondrichthyes populations since Camhi *et al.* (1998) identified a series of research needs for this taxon. Our review has expanded and updated this list by highlighting the important remaining knowledge gaps required to assess extinction risk in this taxon. We therefore offer a list of priorities for research that will enable better assessment and reduce the probability of overlooking and underestimating threats within a precautionary management and conservation framework. In order of relative importance, these are (1) estimation of minimum population sizes and the degree of life history specialisation, (2) trophic interactions and cascades, (3) expanded fisheries monitoring, (4) potential and measured effects of climate change, (5) assessing the implications of habitat loss and degradation and (6) the consequences of genetic erosion on population dynamics and resilience. Despite the recommended hierarchy, all recommendations are interlinked, as are their influences and consequences. As with most ecological research, carefully planned and orchestrated multi-disciplinary approaches can provide robust and cost-effective data.

In recent years, many chondrichthyan species have been added to the IUCN Red List. However, none of these are based on quantitative assessments of populations relative to estimated MVP size. Instead, most listings understandably rely on sparse data describing possible distribution and relative abundance changes. PVA are sorely needed for most of the species of highest concern, and these all require specific demographic and population data. However, there are limited demographic and population data available at present for most chondrichthyan species. Often surrogate demographic estimates from congeners or family members have been used in place of known information. Therefore, the highest priority for research is to obtain species-specific demographic data such as survival rates, fertility patterns and spatial range. Detailed information is also required on the degree of life history specialisation, including studies examining ontogeny, foraging niches, and intra- and inter-specific competition. These data are essential to determine whether particular life stages are relatively more vulnerable to specific threats, which can inflate estimates of extinction risk for entire populations or species.

The ecological interactions between chondrichthyans and their capacity to induce trophic cascades require much more focused study, including experimental, observational and modelling approaches. Although there have been a few ECOSIM/ECOPATH modelling studies (Kitchell *et al*., 2002; Stevens *et al*., 2000) and some quantitative analyses of time series in this regard (e.g. Myers *et al*., 2007), we currently have only a rudimentary understanding of how ecosystem changes will influence chondrichthyan extinction risk and affect the marine communities to which they belong.

With increasing demand for fisheries to provide food for a large, growing human population, we need better, more systematic and wide-coverage monitoring of chondrichthyan catch data and market trends to identify species in decline (e.g. Casey and Myers, 1998; Mucientes *et al*., 2009). Baseline data, even if they do not represent unexploited biomass, are required for the majority of harvested species. Monitoring designs must also include detailed inventories of species and sex composition and age/size structure from catches so that whole-population status can be assessed more readily. Such monitoring requires an important at-sea component to measure the magnitude of by-catch, especially in mixed-species fisheries, and the proportion of non-morbid individuals returned alive. Market surveys can also provide information to assess the relative contribution of IUU fishing on population trends (e.g. Clarke *et al*., 2006). Historical and commercial data sets must also be made freely available to the research community for effective cross-examination and interpretation (e.g. Baum *et al*., 2005; Burgess *et al*., 2005a).

There is a good understanding of the potential effects of temperature change for many individual marine species. However, the simplistic relationships between temperature and biota do not necessarily provide a good predictive platform for understanding climate change effects on future marine community structure and composition (Harley *et al*., 2006). More dedicated experimental and time series data are required to test specific hypotheses on potential range shifts, adaptation capacity and physiological tolerance envelopes for most species (Graham and Harrod, 2009). Synergies among extinction drivers require greater focus, especially for species living in environments where risks overlap (see Halpern *et al*., 2008). Chondrichthyans have evolved over many hundreds of millions of years and the taxon has persisted in spite of two mass extinction events. The genetic implications of small, bottlenecked populations must also be of primary focus in molecular studies to determine the relative contribution of potential inbreeding depression on estimates of chondrichthyan extinction risk.

7. CONCLUDING REMARKS

We are still in the fortunate situation that there are no recorded cases of chondrichthyan extinction in modern times. However, we have identified that the largest, most range-restricted and heavily harvested species might be easily pushed below their MVP sizes, which could be much larger than those estimated under stable environmental conditions.

Fishing, at all scales, represents one of the largest mortality sources for many chondrichthyan species, but there are some examples of small local fisheries that have operated without clear declines in population size of targeted species. However, mixed-species fisheries that harvest poorly measured, but presumably large quantities of chondrichthyans are of particular concern, as is IUU fishing. The lack of specific management and reporting mechanisms for the latter types means that many species might already be reduced to densities where extinction risk is unacceptably high. It is almost universally recognised now that so-called 'sustainable' fisheries will have to be the norm if they are to survive economically, and that they will have to demonstrate negligible or minimal impacts to ecosystems through careful management and stewardship (Hilborn, 2007). IUU fishing can affect shark populations and community structure, and this might be a far greater challenge to control. Recreational fishing and beach meshing can also contribute to local declines. Climate change and habitat degradation will further erode certain populations to the point where extinction risk rises appreciably.

The idea that chondrichthyans have life history characteristics that might predispose them to extinction in a rapidly changing world (e.g. relatively low reproductive potential, growth and capacity for population recovery; Pratt and Casey, 1990) is generally upheld by our results. Furthermore, because chondrichthyans tend to occupy the highest trophic levels, it is arguable that degradation of marine communities might limit the prey quality and quantity available to chondrichthyan predators, further exacerbating population reductions.

We found no strong evidence, from admittedly simple models with few parameters, that chondrichthyans are intrinsically more susceptible to extinction than other marine fishes in relation to their evolved niches and life history characteristics. However, chondrichthyans tend to be larger than many other marine fish taxa, and large body size generally correlates with slower growth and lower reproductive capacity. As such, it is the rapid *pace* of environmental change and harvesting that have the greatest potential to impede certain species from maintaining large population sizes. Any species can withstand moderate to even extreme exploitation if it does not outpace intrinsic replacement rates and adaptation potential (Brook *et al.*, 2008).

We were unable to examine all plausible correlates of threat risk due to data paucity. Many studies have examined age at maturity and growth rates in terms of vulnerability to extinction, with late-maturing and slow-growing species apparently at greater risk (Reynolds *et al.*, 2005). Therefore, a better compilation of data incorporating these and other possible correlates could reveal further subtleties in the drivers of threat risk in this taxon and other marine fishes. Another caveat is that predictors of threat risk indicate a species' sensitivity to the largely systematic (deterministic) drivers of population decline (declining population paradigm) (Cardillo, 2003; Sodhi *et al.*, 2008a), whereas actual extinction appears to correlate poorly with ecological and life history traits given that the final coup de grâce tends to result from largely stochastic processes that act independently of a species' evolutionary history (Brook *et al.*, 2006, 2008; Sodhi *et al.*, 2008b; Traill *et al.*, 2007)

There are many examples of how large predators influence communities and ecosystems via top-down (and in some cases, bottom-up) control of species occupying lower trophic levels. Thus, the removal of large predators can elicit trophic cascades and destabilise the relative abundance of smaller prey and non-prey species. However, these effects are still poorly understood, especially for large, complex trophic webs where interactions are largely unquantified. Specifically, chondrichthyans can alter prey diversity and size distributions, and their mere presence can affect the foraging behaviour of prey that alters ecosystem functions such as nutrient recycling and structural habitat complexity. Severe predator depletions can lead to permanent shifts in marine communities and alternate equilibria.

Management of shark populations must therefore take into account the rate at which drivers of decline affect specific species. Only through detailed collection of data describing demographic rates, habitat affinities, trophic linkages and geographic ranges, and how environmental stressors modify these, can extinction risk be estimated and reduced. The estimation of MVP sizes is an essential component of this endeavour and should, in our view, eventually accompany the current approaches used to manage sharks worldwide.

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