

The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems

J. D. Stevens, R. Bonfil, N. K. Dulvy, and
P. A. Walker



Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. – ICES Journal of Marine Science, 57: 476–494.

The impact of fishing on chondrichthyan stocks around the world is currently the focus of considerable international concern. Most chondrichthyan populations are of low productivity relative to teleost fishes, a consequence of their different life-history strategies. This is reflected in the poor record of sustainability of target shark fisheries. Most sharks and some batoids are predators at, or near, the top of marine food webs. The effects of fishing are examined at the single-species level and through trophic interactions. We summarize the status of chondrichthyan fisheries from around the world. Some 50% of the estimated global catch of chondrichthyans is taken as by-catch, does not appear in official fishery statistics, and is almost totally unmanaged. When taken as by-catch, they are often subjected to high fishing mortality directed at teleost target species. Consequently, some skates, sawfish, and deep-water dogfish have been virtually extirpated from large regions. Some chondrichthyans are more resilient to fishing and we examine predictions on the vulnerability of different species based on their life-history and population parameters. At the species level, fishing may alter size structure and population parameters in response to changes in species abundance. We review the evidence for such density-dependent change. Fishing can affect trophic interactions and we examine cases of apparent species replacement and shifts in community composition. Sharks and rays learn to associate trawlers with food and feeding on discards may increase their populations. Using ECOSIM, we make some predictions about the long-term response of ecosystems to fishing on sharks. Three different environments are analysed: a tropical shelf ecosystem in Venezuela, a Hawaiian coral reef ecosystem, and a North Pacific oceanic ecosystem.

© 2000 International Council for the Exploration of the Sea

Key words: community structure, ECOSIM, ecosystem, elasmobranchs, extinction, fishing effects, mass-balance model, population impacts, species replacement, species vulnerability, trophic interactions.

J. D. Stevens: CSIRO Marine Research, GPO Box 1538, Hobart, Tasmania 7001, Australia. Tel: +61 3 6232 5353; fax: +61 3 6232 5000; e-mail: john.stevens@marine.csiro.au. R. Bonfil: Instituto Nacional de la Pesca, Pitagoras 1320 Mexico, DF 03310 Mexico. Current address: Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, BC V6T 1Z4 Canada. N. K. Dulvy: Marine Sciences and Coastal Management, University of Newcastle-upon-Tyne, Newcastle-upon-Tyne, NE1 7RU, UK. P. A. Walker: National Institute for Coastal and Marine Management (RIKZ), Postbus 207, 9750 AE Haren, The Netherlands.

Introduction

Concerns over the impact of fishing on shark and ray populations around the world are currently being raised at an international level through a number of fora. The Species Survival Commission of IUCN has formed a Shark Specialist Group (SSG), which is preparing a global Action Plan for the conservation and management of sharks. The parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) took unprecedented action in

1994 by mandating a review of the status and trade in sharks, a group of animals not currently listed on the CITES Appendices. As part of this process, the United Nations Food and Agriculture Organization (FAO) formed a Technical Working Group (TWG) on sharks.

Why have these concerns about chondrichthyans been raised? Several factors are involved. Sharks and rays appear to be particularly vulnerable to over-exploitation because of their K-selected life-history strategy (characterized by slow growth, late attainment of sexual maturity, long life spans, low fecundity, and natural

mortality, and a close relationship between the number of young produced and the size of the breeding biomass). Teleost populations typically show considerable short-term variability in recruitment mainly due to environmental factors affecting their eggs and larvae. Their high fecundity–high mortality strategy provides them with a greater capacity for density-dependent change than is the case for chondrichthyans. Once overfished, many shark populations would take several decades to recover. The poor record of sustainability of target shark fisheries is cited as evidence of their vulnerability, but is also magnified by the fact that few countries have any form of management for these resources. Poor baseline data on species identification and landings have been collected because sharks have historically been of low economic value in most countries, and lack of data is fundamental to the concerns. As research priorities are usually linked to the economic value of the fisheries, relatively little research has been carried out on this group. More recently, certain shark parts (notably fins) have increased dramatically in value. As the bodies are often discarded after the fins have been removed, and because many of the landings are by-catch from fisheries targeting other species, or are in countries without adequate fisheries information-gathering systems, much of the catch goes unrecorded. Compounding the problem is the oceanic and highly migratory nature of many species, placing them outside the responsibility of individual countries and outside the mandate of international bodies, which were mostly set up for management of tunas. These factors have contributed to a situation where the reported chondrichthyan catch is only about half of the estimated global catch (Bonfil, 1994).

Holden (1973) asked the question of whether long-term sustainable fisheries for elasmobranchs were possible. His answer was yes, providing exploitation proceeded slowly and providing the species was relatively fecund and had sufficient capacity for density-dependent change. T. I. Walker (1998) pointed out that some species of sharks can be harvested sustainably and suggested that these fisheries have some advantages because they can produce relatively stable yields which are less prone to interannual environmental effects than those for most teleost stocks.

Most sharks are predators at, or near, the top of marine food chains. How does their removal affect the structure and function of marine ecosystems? The direct effects of fishing through the capture of individual species can result in changes in abundance, size structure, life-history parameters (density-dependent change), and, at the extreme, could lead to extinction. The indirect effects involve trophic interactions at the community level through selective removal of predator or prey species, removal of competitors, species replacement, and enhancement of food supply through discards.

We summarize the direct effects of fishing on chondrichthyans by reviewing global information on the responses of shark and ray populations to fisheries. We then examine this information with respect to predictions on the vulnerability of different species to fishing, based on life-history and population parameters. We review what little is known about trophic interactions, and finally we carry out some simple modelling of three selected ecosystems to examine the effects of chondrichthyan removal.

Direct effects

Abundance

A decrease in abundance, particularly of the larger size classes, is a common feature of exploited fish populations (Russ, 1991). There is ample historic evidence of major declines in chondrichthyan populations from fisheries around the world.

Global reported landings of chondrichthyan fishes have been increasing steadily since 1984 and currently stand at about 760 000 t (Fig. 1a). However, the total catch is probably nearer to 1.5 million tonnes, due to a large unreported by-catch (Bonfil, 1994). Reported landings for the major oceans are shown in Fig. 1b. There have been a number of recent reviews (Compagno, 1990; Bonfil, 1994; Rose, 1996) and T. I. Walker (1998) gives an excellent overview. Reported landings for the top 10 countries are shown in Figs 2a–c. At 100 000 t in 1996, Indonesia reported the world's highest landings, sharks comprising about 66% of this total. Unfortunately, little species-specific or fishery-specific data are available from areas with the highest catches, and virtually nothing is known about the status of individual stocks. However, large annual, or rapidly increasing, landings in recent times are a cause for concern. Of the top 10 countries, some have artisanal, multispecies, and multi-gear fisheries, while Japan and Taiwan have high-seas fleets. Of these countries, only the USA manages its chondrichthyan resources. The main groups taken are carcharhinids, sphyrnids, and batoids. Other countries where substantial declines in landings were apparent, or which made mention of overfished resources in their reports to CITES, were Brazil, Venezuela, Peru, Maldives, Malta, and the Azores.

During the 1940s, several target shark fisheries developed in response to the market for vitamin A from livers; more recently, fisheries have targeted chondrichthyans for their meat, fins, livers, and other products (Table 1). The literature contains many references to the apparent “boom and bust” pattern of these fisheries during the 1940–1970 period (Holden, 1974; Anderson, 1990; Compagno, 1990). Frequently cited examples are the Californian fishery for soupfin (*Galeorhinus galeus*), the Norwegian fishery for

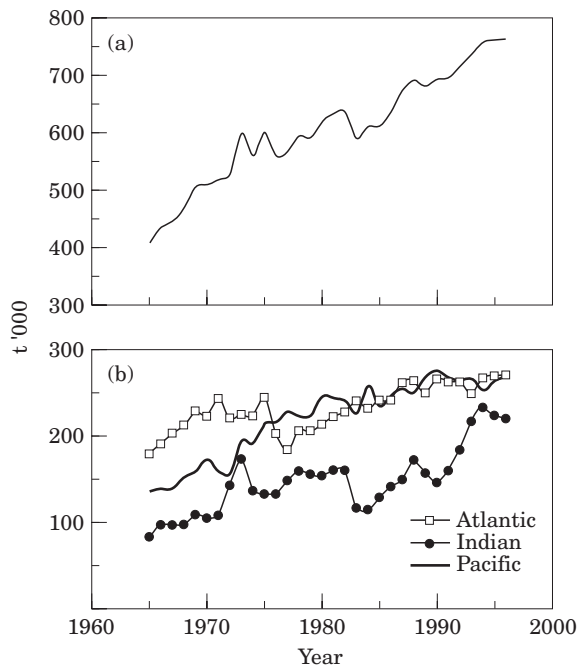


Figure 1. Landings of chondrichthyans, 1965–1996: (a) total and (b) for the Atlantic (including the Mediterranean), Pacific, and Indian Ocean separately (data from Compagno, 1990, and FAO Yearbooks of Fishery Statistics).

porbeagle (*Lamna nasus*), and several fisheries for basking shark (*Cetorhinus maximus*) and spiny dogfish (*Squalus acanthias*) (Table 1). In most instances, economic and marketing factors were involved in the collapse and it is difficult to disentangle these from biological factors. For basking shark, which has a widespread distribution, local depletion is a more likely explanation. Where the species has a more restricted range and where the fishery was intensive and expanded rapidly, as for Californian soupfin, stock collapse is more plausible.

Chondrichthyans are a common but unspecified by-catch in many fisheries, particularly those using demersal trawls, long-lines, or gillnets (Table 2). In most countries, there are virtually no regulations over the amount taken. Where there is some form of management and information on species biology, regulations in target fisheries would presumably aim to balance total mortality and production. However, in by-catch fisheries where species may be lumped into categories such as “skates and rays”, total mortality on the target species may be well above replacement mortality (at which population growth is zero) for individual chondrichthyan species. Particular areas of concern highlighted by the IUCN SSG and the FAO TWG on sharks are the catches of batoids and deep-water squalids in demersal trawls, and pelagic sharks in high seas and coastal long-lining.

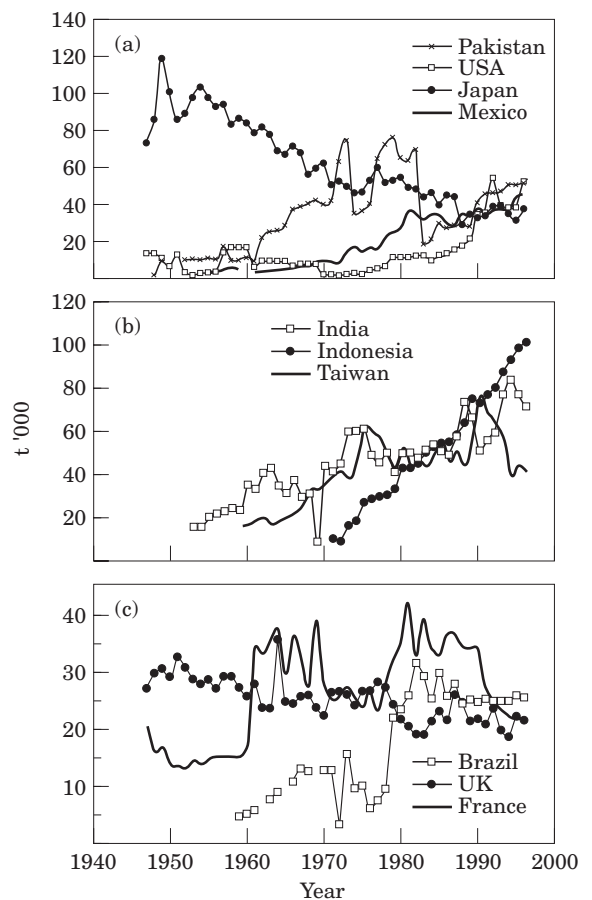


Figure 2. Landings for the top 10 chondrichthyan fishing countries: (a) Pakistan, USA, Mexico, and Japan, (b) Indonesia, Taiwan, and India, (c) France, Brazil, and UK (data from Bonfil, 1994, and FAO Yearbooks of Fishery Statistics).

Over the last 20 years, a serious decline has been documented for a number of ray species. The common skate (*Dipturus batis*) has been “brought to the brink of extinction” by trawling in the Irish Sea (Brander, 1981) and the barndoor skate (*D. laevis*) could become the first well-documented example of extinction in a marine fish species if current trends continue (Casey and Myers, 1998). Sawfishes (family Pristidae) may be one of the most threatened groups, although quantitative catch data are mostly lacking. They are mainly demersal in shallow coastal, estuarine, and freshwater habitats and are particularly vulnerable to all types of gear. Little is known about the biology of deep-water squalid sharks. However, the low productivity of many deep-water fish in general and the apparent sensitivity of deep-water squalids to fishing (Wilson and Seki, 1994; Graham et al., 1997) suggest that they may be even more vulnerable than the spiny dogfish, their highly unproductive relative from shelf waters.

Table 1. Summary of target fisheries for chondrichthyans.

Species stock	Period	Max. catch (t)	Year	Status	Management (year)	Reference
<i>Galeorhinus galeus</i>						
California	1930–1950	4185	(1939)	Apparent collapse	No	Ripley, 1946
Australia	1930–pres.	3158	(1969)	84% decline in mature biomass	Yes (1988)	Olsen, 1959; Punt & Walker, 1998
New Zealand	1930–pres.	5600	(1984)	Concerns over sustainability	Yes (1986)	Francis, 1998
<i>Lamna nasus</i>						
NE Atlantic	1947–pres.	6000	(1947)	Depleted	Some	Bonfil, 1994; Hurley, 1998
NW Atlantic	1961–pres.	8060	(1964)	Apparent collapse	Some	Bonfil, 1994; Hurley, 1998
<i>Cetorhinus maximus</i>						
Ireland	1946–1975	1808	(1952) ¹	Major catch decline	No	Kunzlic, 1988
NE Atlantic	1946–1986	4266	(1960) ¹	Catch decline	Some	Kunzlic, 1988
<i>Squalus acanthias</i>						
NE Pacific	1870–pres.	53 483	(1944)	Recovered, after 75% decline in marketable biomass	Yes (1978)	Ketchen, 1986
NW Atlantic	1960–pres.	25 620	(1974)	Recent stock decline	No	Rago <i>et al.</i> , 1998
NE Atlantic	1963–pres.	43 911	(1987)	Recent catch and size decline	Some	Ketchen, 1986; Fahy & Gleeson, 1990
<i>Alopias vulpinus</i>						
Westcoast USA	1978–pres.	1087	(1982)	Decline in catch and size	Yes (1985)	Holts, 1988
<i>Squatina californica</i>						
California	1976–1994	590	(1985)	Decline in catch and size	Yes	Holts, 1988
Multispecies shark stock						
E coast USA	1980–pres.	7700	(1989)	Many species overfished	Yes (1993)	Musick <i>et al.</i> , 1993
<i>Mustelus antarcticus</i>						
S Australia	1930–pres.	3450	(1993)	Sustainable catches	Yes (1988)	Walker, 1997
<i>Mustelus lenticulatus</i>						
New Zealand	1930–pres.	3800	(1983)	Rebuilding (overfished in 1980s)	Yes (1986)	Francis, 1998
<i>Furgaleus macki</i>						
S Australia	1976–pres.	611	(1981)	77% decline in biomass	Yes (1988)	Simpfendorfer & Donohue, 1998
<i>Callorhynchus milii</i>						
New Zealand	1936–pres.	1200	(1971)	Rebuilding (overfished in 1980s)	Yes (1986)	Francis, 1998

¹Catch in numbers.

Pelagic sharks represent a large by-catch of global high-seas long-line fisheries targeting tuna and billfish, and are retained primarily for their highly valued fins. There are currently few regulations for reporting their by-catch in the oceanic zone, which comprises mainly blue *Prionace glauca*, oceanic whitetip (*Carcharhinus longimanus*), and silky shark (*Carcharhinus falciformis*). Stevens (2000) estimated that 136 600 t, between 45 700 and 233 000 t, and 104 600 t of these three species, respectively, were caught by these fisheries in the Pacific in 1994. Nakano and Watanabe (1992) estimate that the high-seas fisheries of the North Pacific caught 5 million (about 150 000 t) blue shark during 1988 and Bonfil (1994) estimated that 6.2–6.5 million of this species are taken annually around the world. Blue shark, in

particular, may be a key species in the oceanic pelagic ecosystem.

Long-established shark-control programmes by means of beach meshing exist off New South Wales (since 1937) and Queensland (1962), Australia, and off Dunedin (1969), New Zealand, and KwaZulu-Natal (Durban, 1952), South Africa. In general, catch rates in these programmes show a rapid initial decline, after which they become stable, although there are variations between species and locations (Reid and Krogh, 1992; Simpfendorfer, 1992). It has been hypothesized that this pattern is caused by fishing down a resident community, followed by a relatively constant harvest of immigrants. Alternatively, the sharks may learn to avoid the nets that are often placed in much the same location (Dudley and

Table 2. Summary of fisheries in which chondrichthyans are taken as a by-catch.

Species	Period	Reported trends	Reference
Multispecies			
NW Mediterranean	1957–1995	Declines in comm. catch, number of spp. halved (first on shelf, followed by slope)	Aldebert, 1997
S North Sea	1950–1990	Decline in by-catch of 8 spp.	De Vooy & van der Meer, 1998
S Bay of Biscay	1727–pres.	Disappearance of large demersal spp.	Quéro & Cendrero, 1996
Gulf of Thailand	1963–72	Decline in rhinobatids/rays, to a lesser extent in sharks	Pauly, 1979
Andaman Sea	1966–71	Decline in rays and sharks	Pauly, 1979
<i>Dipturus batis</i>			
Irish Sea	1902–pres.	Population close to extinction	Brander, 1981
NW North Sea	1930–pres.	Common 50 years ago, now rare	Walker & Hislop, 1998
<i>Dipturus laevis</i>			
NW Atlantic	1954–pres.	Common 45 years ago; none caught in last 20 years	Casey & Myers, 1998
<i>Raja alba</i> and <i>Dipturus oxyrinchus</i>			
Irish Sea		Close to local extinction	Dulvey <i>et al.</i> , 2000
<i>Centrophorus</i> spp.			
Australia	1976–1997	Survey catch rates declined (from 126 to 0.4 kg h)	Graham <i>et al.</i> , 1997
Pristidae			
Fresh water		Major declines in range or abundance; some populations may be close to extinction	Compagno and Cook, 1995

Cliff, 1993). There is some evidence that the impacts are relatively local, at least for some species (Holden, 1977; Dudley and Cliff, 1993; T. I. Walker, 1998).

The recreational catch is often ignored when reviewing impacts due to fishing, which may be partly due to the difficulties in obtaining meaningful estimates. Hook and line catch by anglers is often small compared to commercial catches. For instance, catches of rig (*Mustelus lenticulatus*), spiny dogfish, and elephant fish (*Callorhynchus milii*) by anglers in New Zealand varied between 6% and 8% of their total landings (Francis, 1998). However, in the USA, which has the largest recreational fisheries, landings of large sharks from the Atlantic coast and Gulf of Mexico were estimated at 8000 t per year between 1970 and 1986 (Anderson, 1990). Data for 1996 suggest that some 5.4 million chondrichthyans were caught by anglers in these waters, of which about 445 000 were retained (Camhi, 1998). While the impact of these catches in isolation is not known, in combination with commercial landings they are likely to have contributed to stock depletion in the area (Musick *et al.*, 1993).

Recreational fishers also use other gear. Williams and Schaap (1992) documented the likely impact of gillnets in causing significant mortality on juvenile gummy shark (*Mustelus antarcticus*) and soupfin in two Tasmanian shark nursery areas. During the 1960s and 1970s, large numbers of grey nurse sharks (*Carcharias taurus*) were shot by spearfishers off the coast of New South Wales, which contributed to a dramatic decline in numbers and led to legislation for protection in 1984 (Pollard, 1996).

Size and age structure

Shifts in length compositions to smaller sizes have been attributed to exploitation for a number of species (Anderson, 1985; Walker and Heessen, 1996; Rago *et al.*, 1998). Changes in the size structure may also be due to the size-selective properties of the gear used. They may have significant implications for the reproductive output. Fecundity tends to increase with body size so that populations with a higher proportion of larger fish have a greater reproductive potential. For instance, litter size in gummy shark increases with maternal size (Walker *et al.*, 1998) and mesh size in the gillnet fishery for this species in southern Australia has been adjusted as a management measure to allow a greater escapement of larger females and to protect the breeding stock.

Walker *et al.* (1998) have shown that length-selective fishing mortality in gummy shark has caused an apparent change in growth rate over time. The gillnets used have the effect of culling a higher proportion of faster-growing sharks among the younger age classes and a higher proportion of slower-growing sharks among the older ones. This process affects the size and age structure of the population in complex ways. Jennings and Kaiser (1998) note that fishing acts as a selective force and life-history traits such as growth that are at least partly inheritable may be expected to evolve under sustained exploitation.

Changes in population parameters

Continued fishing may affect specific population parameters in response to changes in species abundance. While there has been considerable discussion in the literature on chondrichthyans on possible mechanisms for density-dependent change, there is little empirical evidence. For spiny dogfish, [Holden \(1973\)](#) suggested that compensatory mechanisms most likely acted through changes in fecundity. This is partially supported by the observations of [Gauld \(1979\)](#), who showed an increase in the number of ova produced per female, but he did not have the data to show an increase in the number of embryos. [Wood et al. \(1979\)](#) considered that changes in fecundity would provide insufficient compensatory change in this species, and instead favoured a reduction in natural mortality. [Fahy \(1989\)](#) considered it more likely that recovery of some spiny dogfish stocks was due to immigration and re-colonization from less depleted areas, rather than through changes in fecundity, natural mortality, or growth rate. Additional evidence from other chondrichthyans raises doubts as to whether an increase in fecundity could provide sufficient compensatory change by itself. [Brander \(1981\)](#) and [Walker and Hislop \(1998\)](#) demonstrated that changes in fecundity have a relatively small effect on the mortality at which the Irish Sea stock of the common skate and North Sea populations of rajids collapse. Rather, it is the net recruitment rate that is important, and juvenile survival appears to be the key factor. [Walker \(1992\)](#) found no evidence for a change in fecundity of gummy shark as a result of exploitation. [Bonfil \(1996\)](#) used a simulation approach through an age-structured model to evaluate the potential effectiveness of various mechanisms. The model was more sensitive to variations in mortality and age of first maturity than to variations in fecundity. Even unreasonably large increases in fecundity only provided effective compensatory change under very low fishing mortalities. These results supported the conclusions of [Brander \(1981\)](#) that increased survival of juveniles provides greater resilience to fishing pressure than increased fecundity. In reality, species may show a combination of different compensatory changes.

Other documented observations of apparent density-dependent change include increased growth rates in juvenile soupfin ([Stevens and West, 1997](#)) and sandbar shark (*Carcharhinus plumbeus*) ([Sminkey and Musick, 1995](#)) following heavy fishing pressure. Based on a modelling approach, the observed increase in growth rate of thornback ray (*Raja clavata*) is expected to have led to maturation at an earlier age and larger size ([Walker, P. A., 1998](#)). Because of the positive relationship between size and fecundity, this has probably led to a higher fecundity.

Extinctions

Major population declines are of greatest significance for endemic species where there could be a real threat of extinction. Chondrichthyan biodiversity is highest in the Indo-West Pacific region. This is evident from the extreme richness of the Australian fauna with 296 species compared to 182 from Southern Africa and 130 from the eastern North Atlantic and Mediterranean. About 73% of the rays, 48% of the sharks, and slightly more than half of the chimaeras are endemic to Australia ([Last and Stevens, 1994](#)). In the Australasian region, greatest biodiversity is found in demersal habitats with the continental slopes being slightly richer in species than the adjacent shelves. Demersal slope habitats also have higher rates of endemism, except in northwestern Australia where more than 60% of the endemics are demersal shelf species ([Last and Séret, 1999](#)). The highest chondrichthyan catches occur in Indonesia, which also has high biodiversity and rates of endemism and minimal controls on fishing. This combination of factors, together with our incomplete knowledge of the catch composition, suggests a higher than average extinction risk.

[Roberts and Hawkins \(1999\)](#) addressed the issue of marine extinctions. Only one species, the barndoor skate ([Casey and Myers, 1998](#)), is known to have been driven to the verge of extinction due to large-scale fisheries operations. Three other skates are considered locally extinct: the common skate, the long-nose skate (*Dipturus oxyrinchus*), and the white skate (*Rostroraja alba*) ([Brander, 1981; Dulvy et al., 2000](#)). In view of the high endemism (possibly up to 55% of 230 known species; [McEachran, 1990](#)), skates currently represent one of the most threatened groups of all marine species. However, assessing their vulnerability is difficult due to the practice of aggregating catch statistics ([Dulvy et al., 2000](#)).

Effects on community structure

Variable resilience to fishing pressure

Among the nearly 1000 species of known chondrichthyans, there is considerable variation in life-history parameters. The resilience of a particular species to fishing pressure will depend on both its vulnerability and its productivity, including its scope for density-dependent response. [Hoenig and Gruber \(1990\)](#) suggested the possibility of ranking shark species according to their resilience based on critical aspects of their life history. They considered that natural mortality rate, age at maturity, fecundity, and, in particular, the intrinsic rate of population increase might be useful for this purpose. [Pratt and Casey \(1990\)](#) reviewed reproductive and growth parameters that might be used to indicate

vulnerability of shark species to fisheries. Smith *et al.* (1998) ranked 26 species according to their intrinsic rate of population increase, providing a relative measure of their recovery ability from exploitation (“rebound” potential). Their method incorporated density-dependence, as the intrinsic rate of population increase depended on the level of fishing mortality and the resulting decrease in population size. Productivity was strongly affected by age at maturity, and little affected by maximum age. Sharks with the highest rebound potential tended to be smaller, early maturing, relatively short-lived inshore coastal species (*Mustelus* spp., *Rhizoprionodon* spp., and *Sphyrna tiburo*). Those with the lowest recovery potential tended to be larger, slow-growing, late-maturing, and long-lived coastal species (*Carcharhinus obscurus*, *C. plumbeus*, *C. leucas*, *Sphyrna lewini*, *Negaprion* spp., and *Notorhynchus cepedianus*). The smaller spiny dogfish leopard shark (*Triakis semifasciata*) and soupfin were also in this group. The large pelagic species, such as blue shark, were generally in the mid-range of the productivity spectrum (Smith *et al.*, 1998).

Brander (1981) ranked various skate species according to the total mortality that their populations could withstand without collapsing, based on age at maturity and fecundity. Walker and Hislop (1998) produced a similar ranking using demographic models that estimated levels of total mortality below which the populations decline. The larger, late-maturing species, such as *D. batis*, tended to be the least productive among the skates examined.

Demographic parameters such as rebound potential may be the most useful for ranking species for management or conservation prioritization. However, there are significant problems in obtaining suitable data to allow consistent calculation of the different parameters required for large numbers of species (Smith *et al.*, 1998).

Alternative approaches to determining vulnerability have looked for life-history traits that are correlated with response to exploitation. Generally, a large size, small geographic range, and ecological specialization are correlated with vulnerability to extinction in animals (Brown, 1995). Evidence supporting a body size–vulnerability relationship in marine fish is fairly convincing for tropical and temperate teleosts (Jennings *et al.*, 1998, 1999a), but is only suggestive for elasmobranchs. In comparison to the amount and quality of data required by demographic models, the maximum size of each species may be easily obtained from the literature. In skates, body size appears to be a good predictor of vulnerability to exploitation (Walker and Hislop, 1998; Dulvy *et al.*, 2000), possibly because they exhibit conservative morphology and life-history variation compared to other chondrichthyans (McEachran and Dunn, 1998). Most life-history trait variation, including growth, age at maturity, offspring size, and fecundity, is correlated with body size (Holden, 1973; Brander, 1981;

Table 3. Abundance trends (D: decreasing; I: increasing) in north-west (NW) and north-east (NE) Atlantic skates ranked by maximum total length (TL in cm; data from Casey and Myers, 1998; Walker and Hislop, 1998; Dulvy *et al.*, 2000; NEFSC, 2000).

Species	TL (cm)	Trend	Region
<i>Dipturus batis</i>	250	D	NE
<i>Rostroraja alba</i>	200	D	NE
<i>Dipturus laevis</i>	152	D	NW
<i>Dipturus oxyrinchus</i>	150	D	NE
<i>Raja brachyura</i>	120	D	NE
<i>Amblyraja radiata</i>	111	D	NE
<i>Leucoraja ocellata</i>	100	I	NW
<i>Amblyraja radiata</i>	100	I	NW
<i>Raja eglanteria</i>	94	I	NW
<i>Raja clavata</i>	90	D	NE
<i>Raja microocellata</i>	80	I	NE
<i>Leucoraja naevus</i>	70	I	NE
<i>Malacoraja senta</i>	61	D	NW
<i>Rajella fyllae</i>	55	D	NE
<i>Leucoraja erinacea</i>	53	I	NW

Casey and Myers, 1998). As a result, body size is correlated to demography (Walker and Hislop, 1998; Dulvey *et al.*, 2000). In the North Sea, the four largest species have undergone declines, while the two smallest species have increased in abundance (Walker and Heessen, 1996; Rijnsdorp *et al.*, 1997; Walker and Hislop, 1998). In the Irish Sea, there is evidence for localized extirpation of the three largest species over the past century. Of the remaining five species, the two largest ones are declining in abundance, whereas the two smallest species have increased in abundance (Brander, 1981; Dulvy *et al.*, 2000). However, such a pattern is less clear for western Atlantic skates. Although the largest species, the barndoor skate, has been nearly extirpated in the northern part of its range and is at very low abundance in the southerly part of its range (Casey and Myers, 1998), the next largest species, the winter skate (*Leucoraja ocellata*), is increasing in abundance and some smaller skates are decreasing in abundance (Table 3).

In Pacific sharks, there is no correlation between body size and Smith *et al.*'s (1998) rebound potential (Table 4). This lack of correlation could be due either to their diverse life histories or to problems with demographic parameter estimates. While the detection of species that are potentially vulnerable to exploitation is in its infancy, refinements of the approaches may well lead to useful tools for *a priori* assessment of vulnerability.

Changes in species composition and diversity

Large-scale exploitation has led to changes in fish community structure. Fishers tend to remove the largest

Table 4. Statistics (d.f.=1, 18) of the relationships between rebound potentials and life-history traits of Pacific sharks, recalculated from Smith *et al.* (1988) using phylogenetic contrasts. Species are not statistically independent because closely related taxa share many features of morphology, life histories, and ecology by descent from a common ancestor. A “contrast” is a difference in the trait of interest between two related taxa. Since the differences between close relatives have evolved since they last shared a common ancestor, they are evolutionarily independent (Felsenstein, 1985). The phylogenies described in Dulvy and Reynolds (1997) were used and traits were \log_{10} transformed for analysis.

Dependent trait	F	P-value
Body size	3.1	0.095
Age at maturity	3148	<0.0001
Fecundity	1.7	0.21
Maximum age	72.5	<0.0001

species first and then work their way down the food chain catching smaller species (Pauly *et al.*, 1998). Consequently, changes in species composition of fished communities may be expected, with small, faster-growing, and earlier-maturing species predominating. Small species may also be less desirable on the market, and may therefore be subjected to lower fishing mortality (Jennings and Kaiser, 1998; Jennings *et al.*, 1999b). Within the chondrichthyans, the examples for skates discussed above reveal a broadly similar pattern. Similar patterns have also been reported in shark communities: as larger sharks were depleted smaller species proliferated (van der Elst, 1979). The general paradigm is that larger species decline while smaller species predominate.

There have also been declines in diversity associated with increasing fishing pressures, particularly in large predatory taxa (Jennings and Kaiser, 1998). Chondrichthyans tend to be high in the food web (Cortes, 1999) and, due to their greater vulnerability (relative to teleosts), are likely to be the first to decline from fishing. Rogers *et al.* (1999) suggested that fishing, through the differential vulnerability of elasmobranchs relative to teleosts, is responsible for major variations in fish diversity in the North-east Atlantic.

Indirect effects

Trophic interactions

Since most chondrichthyans are predators at or near the top of marine food webs, the obvious question to ask is what happens to their prey species when these predators are removed? Conversely, when huge quantities of prey species are caught in large-scale fisheries, what are the effects on the predators? There are diverging views on what is likely to happen. Beddington (1984) suggests that on the basis of ecological theory the removal of a

top predator may be expected to have “knock-on” effects in the remaining community. These effects may involve changes in species composition in the prey community or maybe increases in the preferred prey of the predator. He notes that effects may be particularly pronounced in complex communities.

Predator removal

In their review of the effects of fishing on marine ecosystems, Jennings and Kaiser (1998) consider that the best evidence for “top down” control in aquatic ecosystems comes from studies in lakes. Species diversity tends to be lower and life-history traits more conservative in lake ecosystems, with a few key species dominating trophic groups. Most marine ecosystems are far more diverse with complex inter-relationships between species. As a consequence, predator–prey interactions are less tightly coupled due to factors such as prey switching, ontogenetic changes in diet, and cannibalism. Consequently, possible effects following declines in predator abundance in marine ecosystems are usually weak (Jennings and Kaiser, 1998). This is significant because it has often been suggested that removal of predators would allow fishers to catch more of their prey. As noted by Larkin (1979), “don’t expect big changes for a predator that loses a species of prey . . . or for that matter for . . . the prey that loses a predator. Don’t expect long-term benefits to prey from predator control”. In the North-east Pacific, the widespread belief that intense predation by spiny dogfish significantly affected the abundance of commercially more valuable species in part led to a subsidised “pest control” programme. In particular, this shark was thought to inflict high mortality on salmon and herring stocks. Evidence for significant predation on salmon is weak. While a questionable study concluded that in British Columbia waters 230 000 t of herring were consumed per year, Ketchen (1986) considered that an annual figure over 80 000 t was unlikely, as was the possibility that dogfish significantly affected the supply of herring to fishers. He also noted that there was nothing to suggest that herring were more abundant during the 1940s and early 1950s when abundance of spiny dogfish was low.

In the North-west Atlantic, the biomass of spiny dogfish increased in the 1970s and 1980s as the stocks of more valuable teleosts were reduced. Overholtz *et al.* (1991) estimated that dogfish consumed about 250 000 t of sandeel, mackerel, herring, and silver hake annually. This was about 53% of the total consumption by the three major categories of predators (piscivorous fish, marine mammals, and seabirds). Consumption of harvested species by predators was about twice the amount taken by the commercial fishery. Such a high predation on valuable species fuelled discussion of possible adaptive management measures aimed at

Table 5. Percentage species composition of demersal fish on Georges Bank before (1963) and after (1986) heavy exploitation and in the North Sea (data from Sherman *et al.*, 1990).

Area	Years	Gadoids	Dogfish	Flounders	Skates	Others
Georges Bank	1963	55	2	12	22	9
	1986	11	41	3	33	12
North Sea	1977–1985	65	2	16	2	15

controlling the numbers of dogfish (Rothschild, 1991; Sherman, 1991; Overholtz *et al.*, 1991). Sherman (1991) noted that spiny dogfish in the North Sea, where they are regularly fished, as are the skates, represent only 2% of the fish biomass (Table 5), and consequently their predation impact on more valuable species is small.

In Natal, South Africa, anglers claimed that the species composition of their catches had changed, largely as a result of increased catches of small sharks. Van der Elst (1979) examined angling records and showed a general decline in teleost catches from 1956 to 1976, while shark catches increased, particularly from 1973 to 1976. While the mean weight of teleosts showed no significant trend, the mean weight of sharks decreased due to higher catch rates of *Rhizoprionodon acutus* since 1973 and juvenile *C. obscurus* since 1968. Based on limited, qualitative literature data, together with feeding observations in captivity, van der Elst (1979) suggested that many species of large sharks fed preferentially on small sharks. Because the abundance of large sharks had been reduced due to the pest control programme introduced in Durban in 1952 and in Natal in the early 1960s, van der Elst (1979) hypothesized that the abundance of small sharks had increased due to reduced predation by larger sharks. However, Dudley and Cliff (1993) pointed out that small sharks were not nearly as important in the diet of large sharks as had been suggested and that the angling catch of teleosts had started to decline some 6 years prior to the introduction of shark nets in Natal. They concluded that van der Elst's (1979) claims were exaggerated. In a later paper, van der Elst (1989) suggested that beach meshing may only have been partly responsible for the change and that the decline in teleosts through angling may have led to replacement by small sharks through reduced food competition. He also noted an increase in the chondrichthyan component of recreational catches in the Eastern and Western Cape waters, where there is no shark netting.

Wallett (1983) cites an example from Tasmania, where a shark fishery was set up next to a crayfish factory. After 2 years, catches of both sharks and crayfish had declined and both the fishing company and the factory had to close. It was discovered that large numbers of octopus infested the coastal waters. The conclusion was that the removal of sharks had reduced predation on

octopus, which subsequently depleted the crayfish. However, no references were given for this account and we suspect it is purely anecdotal.

Predator–prey linkages are likely to be more direct at the very top of the food chain and the interactions between white sharks (*Carcharodon carcharias*) and pinnipeds might provide opportunities for studying the dynamics of predator or prey removal. Juvenile white sharks feed mainly on fish, but above some 3 m total length their diet consists primarily of marine mammals. Unfortunately, exploitation by man and subsequent protective legislation for certain shark and pinniped populations complicates the situation. There has been a general increase in the incidence of shark-bitten pinnipeds off the Californian coast since the mid-1970s (Long *et al.*, 1996). Lower numbers (and presumably lower mortality) before this time have been related to mortality of juvenile white sharks in gillnets, which were commonly used before they were banned in the early 1980s. The increase in records of shark-bitten pinnipeds appears to be correlated with increases in both prey and predators (Long *et al.*, 1996).

Prey removal

There is little evidence, aside from anecdotal reports, of the impacts of prey removal on chondrichthyan populations. In the Gulf of Thailand, Pauly (1979) initially reported major declines in catch rates of small demersal fish species such as leiognathids. He hypothesized that the virgin stock was already fully exploited by its natural predators and that the large commercial catch had caused a stock collapse, followed by a collapse of its predators stocks, including sharks. However, a subsequent re-analysis of the data (Pauly, 1988) showed no more than a moderate decline in the leiognathids.

Jennings and Kaiser (1998) note that the reductions in population size of marine mammals, tunas, and sharks will have reduced the number of these animals that die from natural causes and sink to the sea floor. They cite a study by Smith (1985) in the Santa Catalina basin, which suggests that some 11% of the respiratory requirements of the benthic community are met by nekton carcasses reaching the sea floor. Similar to effects of discards on scavengers, Jennings and Kaiser (1998)

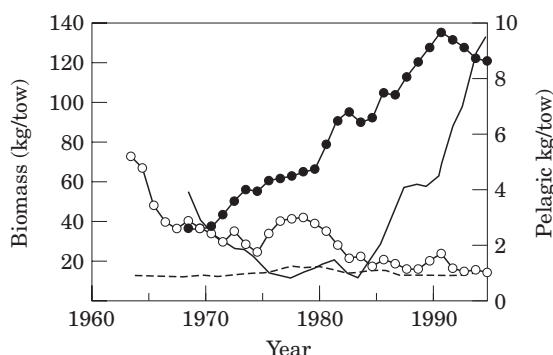


Figure 3. Changes in biomass of four species groups in the Georges Bank region, NW Atlantic (solid circles: elasmobranchs; open circles: groundfish; solid line: pelagics; dashed line: others; reproduced from Sinclair and Murawski, 1997).

suggest that a reduction in carcasses may have an effect on benthic communities in the deep ocean.

Species replacement: competitive release

The biomass of fish in both unexploited and exploited ecosystems has been shown to be relatively stable over time. Exploitation tends to remove larger species and larger individuals from ecosystems. Consequently, the abundance of smaller individuals and species has increased, although single species or species groups often show large variations over time (Pope *et al.*, 1988; Murawski and Idoine, 1992; Duplisea *et al.*, 1997).

Species replacement over a period of about a decade has been reported on Georges Bank (Murawski and Idoine, 1992), while in other areas such a pattern is either not evident (North Sea; Pope *et al.*, 1988) or not consistent over several years (Scotian Shelf; Duplisea *et al.*, 1997).

Demersal fish resources on Georges Bank have been subjected to heavy fishing pressure, resulting in large changes in species biomass and apparent changes in species composition, based on survey data (Table 5; Fig. 3). The decrease in marketable species was confirmed by commercial catch data. Coincident with this decline, the catch rate of chondrichthyans (mainly skates and spiny dogfish) in the survey increased steadily (Fig. 3). Interpretation of these trends is complicated by the fact that fishing intensity for various species underwent large changes over the period. For instance, these involved the expansion of foreign fleets fishing the area, followed by the declaration of an Exclusive Economic Zone after which fishing was reserved for the national US fleet. However, Murawski and Idoine (1992) suggest that the elasmobranchs may have increased in abundance to exploit available food resources because of the high dietary overlap between gadoids and dogfish and flounders and skate (Grosslein *et al.*, 1980).

However, there is no evidence that either food or space is a limiting resource in the area (Fogarty and Murawski, 1998). Increased growth rates and earlier maturation are now evident in some gadoids, which suggests that food is not limiting. This suggests that interspecific competition has only operated in one direction, otherwise the increased elasmobranch population would be expected to limit density-dependent effects in the gadoids (Fogarty and Murawski, 1998). Because there is no evidence of predation by gadoids on juvenile elasmobranchs, the increase in the latter cannot be attributed to reduced predation pressure (Langton and Bowman, 1980; Fogarty and Murawski, 1998).

Alternatively, the interaction may be two-way but depend on the relative densities: when teleosts are at high density, in ecosystem terms they may be competitively dominant over elasmobranchs owing to their numerical abundance and *vice versa*. The shift in community would then result from a combination of food availability, competitive ability, and relative density of the competitors.

In reviewing the case, Jennings and Kaiser (1998) suggest that evidence for significant food web interactions between gadoids and elasmobranchs is weak and that the observed changes are largely due to the continued overfishing of the former and lack of fishing pressure on the latter. In recent years, with declining availability of the traditional teleost species, fishers have been targeting spiny dogfish with the result that there is now serious concern over the status of the stocks (Rago *et al.*, 1998).

Dulvy *et al.* (2000) suggest that the removal of larger skates may have led to an increase in smaller skates through increased food availability. Skates tend to be generalist bottom feeders and there is considerable dietary overlap between species. This competitive release has also been suggested as the reason for the increase in *A. radiata* in the North Sea (Walker and Heessen, 1996).

Jennings and Kaiser (1998) conclude that intraspecific competition and predation has rarely been shown to control cycles in fish populations and that there is little convincing evidence to suggest that fishing has caused compensatory replacement of one fish stock for another. Daan (1980) also concluded that clear cases of species replacement due to fishing were hard to find.

Effects of discards

Discards from fisheries affect the amount of food available to scavengers and thus may be expected to have an effect on certain components of the ecosystem. Although some studies conclude that Australian prawn trawling had few significant, long-term impacts (Kennelly, 1995), about 95% of the by-catch in the Northern Prawn fishery is discarded, and most of it is dead (Wassenberg and

Hill, 1989; Hill and Wassenberg, 1990). About half of the discards float and are scavenged by birds, dolphins, and sharks. The other half sinks and is preyed upon by sharks in mid-water and teleosts, sharks, and crustaceans on the bottom. Sharks and dolphins were the most common scavengers of floating discards at night, while birds scavenged only during the day. In a nearby area that had not been trawled for 8 years, no dolphins and fewer birds were seen, but there were more sharks (Hill and Wassenberg, 1990). Many scavengers learn to associate trawlers with food and their populations may benefit from feeding on discards (Blaber and Wassenberg, 1989; Hill and Wassenberg, 1990). Comparing survey results before and after 20 years of prawn trawling, Harris and Poiner (1991) noted a slight increase in abundance of carcharhinid sharks. They suggested that the disposal of by-catch might be an important factor in explaining this increase, although they noted that cessation of foreign gillnetting in the area may also have contributed. Also P. A. Walker (1998) suggests that the scavenging feeding behaviour of *A. radiata* may have contributed to its increase in the North Sea.

Inferred impacts from trophic interaction models

The snapshot analysis provided by the ECOPATH model (Polovina, 1984; Chistensen and Pauly, 1993) has become a popular approach for modelling ecosystems. It is based on a mass-balance defined by trophic interactions, using data on mortality, abundance, and diet composition for each group/species included in the model. Walters *et al.* (1997) have overcome its constraint of being static by building a dynamic model, ECOSIM, that predicts changes in biomasses, yields, and consumption for each group through time.

We selected three previously published ECOPATH models, which include sharks as separate components of the ecosystem. To compare a broad range of ecosystems within the constraints of an exploratory analysis, cases were chosen from different latitudes and regimes: (1) the NE Venezuelan shelf ecosystem (Mendoza, 1993) that includes small sharks (mainly *Mustelus canis*); (2) the unexploited Hawaiian coral reef of the French Frigate Shoals (Polovina, 1984) that includes tiger sharks (*Galeocerdo cuvier*) and reef sharks *Carcharhinus* spp. as separate components; and (3) the Alaska Gyre oceanic ecosystem (Pauly *et al.*, 1996) that includes a group representing mainly salmon sharks (*Lamna ditropis*) and blue sharks. Table 6 provides the diet composition of sharks as used in each of these three models (for more details see the original papers).

For each ecosystem, ECOSIM was set to simulate changes in the biomass of all groups in response to a

Table 6. Diet composition for shark groups (expressed as a proportion of the total) considered in ECOSIM models for three ecosystems: A. NE Venezuela Shelf (based on Mendoza, 1993), B. Alaska Gyre (based on Christensen and Pauly, 1996, with modifications by Karim, University of Washington), and C. French Frigate Shoals coral reef (based on Polovina, 1984).

Prey	Shark component	
A. NE Venezuela Shelf		
	"Small sharks"	
Small sharks	0.03	
Scombrids/barracuda	0.03	
Snappers/groupers	0.05	
Carangids	0.15	
Other demersal	0.06	
Catfish	0.02	
Grunts	0.02	
Croakers	0.07	
Small pelagics	0.25	
Heterotrophic benthos	0.32	
B. Alaska Gyre		
	"Sharks"	
Pink salmon	0.04	
Sockeye salmon	0.04	
Chum salmon	0.04	
Coho salmon	0.04	
Steelhead	0.04	
Mesopelagic fish	0.20	
Small Pelagics	0.39	
Sharks	0.00	
Large fish	0.20	
Pinnipeds	0.01	
C. French Frigate shoals		
	"Tiger sharks"	"Reef sharks"
Tiger sharks	0.01	—
Birds	0.30	—
Monk seals	0.08	—
Reef sharks	0.03	—
Turtles	0.01	—
Small pelagics	0.08	0.05
Jacks	0.05	—
Reef fishes	0.28	0.90
Lobster/crabs	0.14	0.05
Tuna	0.02	—

rapid depletion of sharks owing to heavy fishing by changing the fishing mortality parameters built into the model. All simulations were run for 100 years to detect possible long-term effects in the ecosystem.

Trial runs

Initial runs were performed with the Venezuelan model under three different options of the "flow control" parameter of ECOSIM: "bottom-up", "top-down", and "mixed" control (the appropriate parameter set at an intermediate value between the two extremes). The results show that "top-down" control leads to widely fluctuating and unstable ecosystem responses as compared with the outcomes from "bottom-up" control (Fig. 4). The mixed control scenario results in a much more stable behaviour of the biomass dynamics

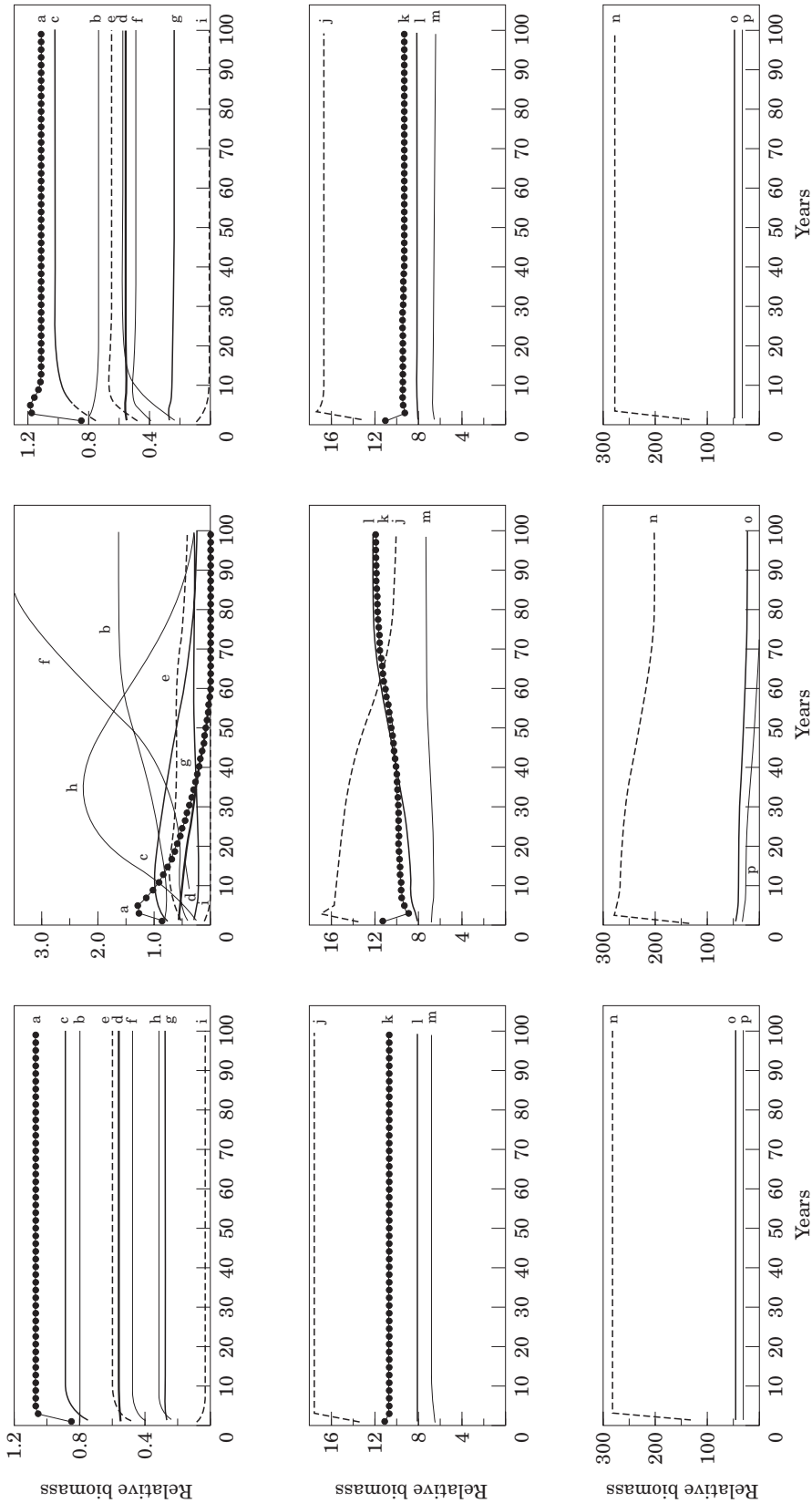


Figure 4. Biomass dynamics of the 16 trophic groups considered in the NE Venezuela Shelf ECOSIM model after overfishing of "small sharks" for three types of control (left panels: "bottom-up"; center panels: "top-down"; right panels: "bottom-up"); right panels: mixed; a: other demersal fish; b: mackerel; c: snappers and groupers; d: scombrids and barracuda; e: grunts; f: catfish; g: squid; h: croakers; i: small sharks; j: heterotrophic benthos; k: zooplankton; l: carangids; m: detritus; n: phytoplankton; o: small pelagics; p: small pelagics. Biomasses are given in relative units, which correspond to multipliers of the original values ($t \text{ km}^{-2}$) in the ECOPATH model.

for all groups than the “top-down” scenario, but the responses were stronger than those for the “bottom-up” scenario.

Walters *et al.* (1997) noticed similar behaviour in a wide range of ecosystem models analysed with ECOSIM when strong “top-down” control was assumed. Typically, in models containing a large number of functional groups, the long-term dynamics reveal continuing changes as interactions propagate through the food web. The authors argue that limited or non-existent practical experience with long-term ecosystem dynamics precludes making decisions over whether such violent community behaviours are credible or not. However, they think that strong “top-down” control should not be very common on evolutionary grounds.

On this basis, and considering the modest aims of our analysis, we chose to assume a mixed (intermediate) flow control for the remainder of the simulations.

Responses to shark depletion

The predictions of the Venezuelan shelf ecosystem model under a mixed control assumption show that shark depletion could lead to strong and unforeseen changes in the abundances of many species (Fig. 4). According to the model, these changes would be permanent as long as shark populations remain depressed. Surprisingly, not all species whose abundances increased greatly are major prey of sharks. In fact, the species undergoing the greatest relative increases in abundance (croakers, snappers/groupers, grunts, catfish, and other demersals) are all minor components in the diet of the small triakid sharks, suggesting that shark depletion propagates through the food web in a complex way. Some changes are virtually demographic explosions of up to two and a half times the original biomass (i.e. croakers). Conversely, two of the major prey items of the sharks did not increase much in abundance; they even decreased (carangids and small pelagics). Squid and benthic producers, two groups not part of the diet, suffered abundance decreases of about 10% and 15%, respectively. Clearly, the outcomes are not as predictable as one might expect.

The Alaska Gyre ecosystem responded with fairly unstable biomass dynamics and large changes in abundance (Fig. 5). Again, the dynamics shown contain some unexpected results, suggesting that the depletion of a large predator may have serious and unforeseen consequences in the ecosystem. A characteristic feature in the response of many species was a rapid increase in biomass followed by a slow and sustained decline after a peak reached some 15–20 years from the onset of the increased fishing mortality on sharks. Towards the end of the 100-years’ simulation, most of these species returned to biomass levels similar to the baseline levels,

although a few showed further decreases to even lower levels. These latter were mostly unimportant prey for sharks (all salmonid species). An exception was the “large fish” group, which, while being important in the diet (20%; Table 7), ended up at about 50% of their original biomass after booming initially.

Overall, the largest variations in biomass occurred in pinnipeds (quadrupled), large fish (halved), carnivorous zooplankton (halved), and chum salmon (doubled), but only the change in pinnipeds seemed to be permanent, at least within the time frame chosen. Interestingly, two of the most important prey, mesopelagic and small pelagic fishes, showed relatively small, initial increases in biomass and remained stable afterwards. Carnivorous zooplankton showed a biomass change that is a mirror image of the salmonids’ response: a large initial decrease was followed by a slow but sustained recovery.

The Hawaiian coral reef model offered the attractive feature that two different groups of sharks were represented, which allowed a combination of simulations (Fig. 6): removing only the tiger sharks; removing only the reef sharks; and finally (and perhaps more realistically) removing both groups together. For ease of comparison, only the nine most representative groups are shown.

In general, the responses to the removal of sharks were relatively stable. The removal of tiger sharks caused for some groups some of the largest changes in biomass observed in any of the analyses. Reef sharks and sea turtles increased by a factor of 9, and bottom fish and seabirds by more than factors of 3 and 2.5, respectively. Monk seals and lobster/crabs had modest increases in abundance. Many of these increases would be expected: tiger sharks prey heavily on seabirds, and are the only predator of marine turtles, monk seals, and reef sharks. The increase in reef shark abundance might also be expected because their main competitor for food had been removed. Some unexpected outcomes also occurred: a total and rapid crash in the abundance of tuna and jacks, and an increase in bottom fishes. The former two species groups represent a small component of the diet, so an increase in their numbers would have been more in line with our expectations; furthermore, bottom fishes are not part of the diet of tiger sharks. Further simulations suggested that the decreases could be explained by a trophic interaction further down the food web. Seabirds undergo a population explosion when their main predators, tiger sharks, are removed. This has a major impact on tunas and jacks, because seabirds, according to the model parameters, are their most important predators. When seabirds were culled simultaneously with the tiger sharks, tunas and jacks increased in abundance. The increase in bottom fishes is explained as a third degree effect down the food web resulting from tiger shark removal. The main predators

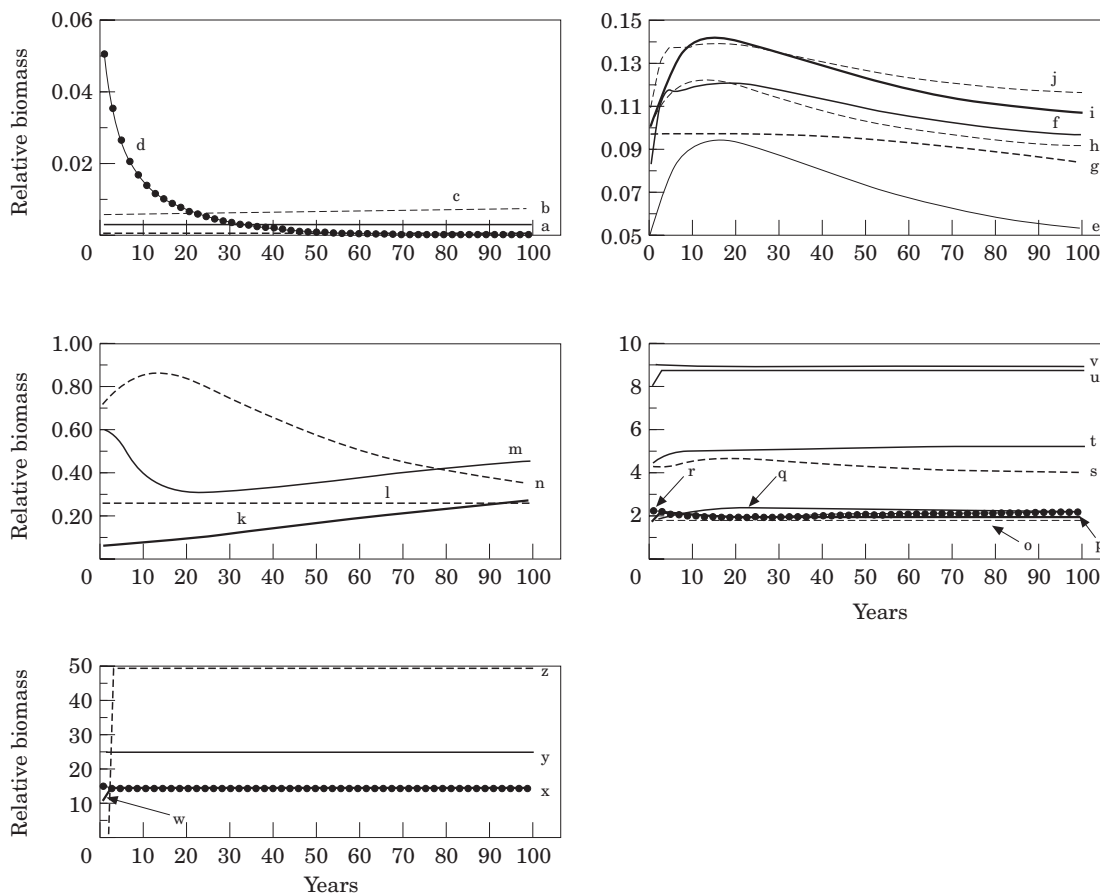


Figure 5. Biomass dynamics of the 26 trophic groups considered in the Alaska Gyre ECOSIM model after overfishing of “sharks” under mixed control (a: transient orcas; b: beaked whales; c: marine birds; d: sharks; e: chum salmon; f: pink salmon; g: toothed whales; h: coho salmon; i: steelhead; j: sockeye salmon; k: pinnipeds; l: baleen whales; m: carnivorous zooplankton; n: large fish; o: microzooplankton; p: other crustacea; q: small pelagics; r: squids; s: krill; t: mesopelagics; u: salps; v: jellies; w: bacteria; x: phytoplankton; y: small herbivorous zooplankton; z: detritus). See also Figure 4.

of bottom fishes, according to the description of this ecosystem, are the tunas. The crash in tuna populations (triggered by seabird increases after tiger shark removal) leaves the bottom fish free from predator control.

Surprisingly, the removal of reef sharks had very small effects on the biomass dynamics. There were slight increases in bottom fish and reef fish abundance, as well as slight decreases in tiger shark and tuna biomass. However, all changes were within 10% of the baseline levels. This may highlight our incomplete knowledge of the diet of reef sharks: the model considers only three groups in their diet, which comprises mainly reef fish, with small amounts of small pelagics and lobsters/crabs (Table 6). However, there is a high degree of predation within the reef fish assemblage due to a complex web of predator–prey interactions, which leaves only 19% of the production to be consumed outside the group (Polovina, 1984). In hindsight, it is not that surprising that the removal of reef sharks had only a small effect on their

main prey, because the group of reef fishes tends to be “self-regulated” in terms of the model.

Based on these results, it could only be expected that the simultaneous removal of two shark species caused very similar outcomes to the removal of only tiger sharks. The only differences were in the extent of some of the changes: notably, turtles increased by a factor of 15, and birds almost tripled.

Comparative responses across ecosystems

The most evident outcome from these analyses is that the ecosystem responses to removal of sharks are complex and fairly unpredictable. All models showed that some unimportant prey species underwent large increases in biomass after shark removal (turtles and reef sharks following tiger shark depletion in Hawaii, pinnipeds in the Alaska Gyre model, and croakers in Venezuela), while seemingly important prey groups

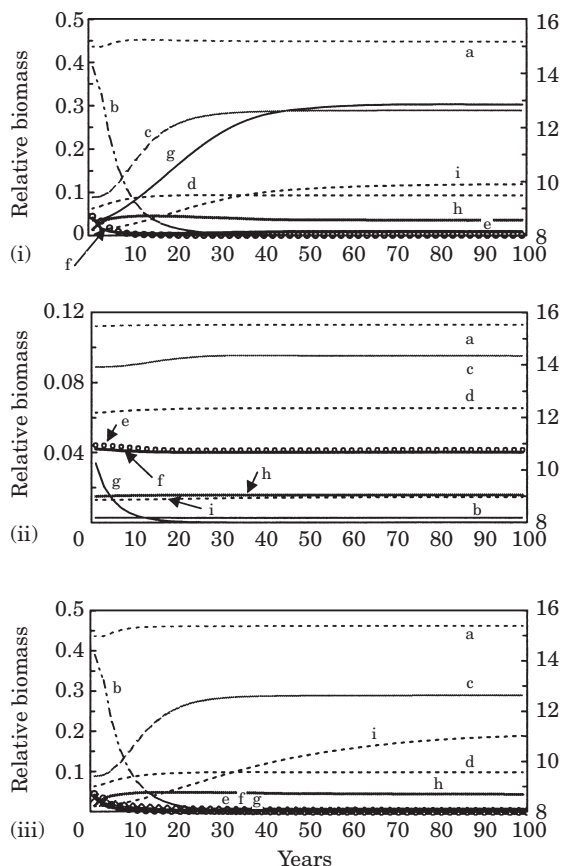


Figure 6. Biomass dynamics of nine representative trophic groups considered in the French Frigate Shoals ECOSIM model after overfishing (i) only “tiger sharks”, (ii) only “reef sharks”, (iii) both shark groups (a: reef fishes; b: jacks; c: bottom fishes; d: monk seals; e: tuna; f: tiger sharks; g: reef sharks; h: birds; i: turtles; right axis is for reef fishes and in (ii) also for jacks). See also Figure 4 (original units: g m^{-2}).

decreased in biomass. In two cases (Alaska Gyre and Venezuela Shelf), at least one group that is not a prey item of the sharks underwent a decrease in abundance, probably as a result of trophic interactions.

Within the constraints of the modelling approach used, it appears that a direct analysis of the most important prey of top predators like sharks will not offer clear insights into the ecosystem responses following their removal. The response of the reef fish in the French Frigate Shoal ecosystem suggests that the main clue to ecosystem changes lies in the role of the shark in the control of a prey group, rather than how important that prey group is in its diet. Self-regulated groups like reef fishes may show almost no response to top-predator depletion. Identifying potential self-regulated groups, as well as predator controls for each group, will allow more predictability across different ecosystems and is an important challenge for future research with ECOSIM.

The simulations of the Venezuelan shelf and the Hawaiian coral reef ecosystems appear to have at least one characteristic in common that is not shared by the Alaska Gyre ecosystem. They both had relatively stable long-term responses to the removal of sharks. Whether this stability is due to the relative simplicity of the first two models, to inherent characteristics of tropical marine ecosystems, or to fundamental differences between oceanic and coastal ecosystems is not easy to determine. However, given the experience with other ecosystems analysed with ECOSIM it seems likely that the complexity of the Alaska Gyre ecosystem plays an important role in its unstable responses (Walters *et al.*, 1997). Alternatively, a naturally occurring “top-down” control may be embedded in the Alaska Gyre ecosystem as compared to the tropical ecosystems.

Our main conclusion is that the outcomes of shark depletion across ecosystems are often difficult to foresee, but may be ecologically and economically significant, and may persist over long time periods.

Conclusions

Chondrichthyan, by nature of their K-selected life-history strategies and high position in trophic food webs, are more likely to be affected by intense fishing activity than most teleosts. The group may in fact be indicators of fishing pressure. There is sufficient evidence from the history of fisheries around the world, both targeting these fishes and taking them as by-catch, of major declines in population size. For some groups, particularly certain skate species and sawfishes, there is mounting evidence suggesting that local if not global extinction is a distinct possibility. This problem is especially acute for species with restricted distributions. The massive and uncontrolled catch of chondrichthyan in the Indo-West Pacific, coupled with the higher diversity and rates of endemism in this region, are cause for major concern. There is increasing evidence that indirect effects of fishing are affecting the composition and diversity of chondrichthyan and total fish assemblages through trophic interactions. Differential vulnerability to fishing exists among sharks and rays and large, late maturing species appear to be most vulnerable. This has caused changes in the community through competitive release, although there is little evidence for species replacement. There is good evidence that selective fishing mortality can lead to changes in growth and juvenile survival for both sharks and batoids, leading to changes in population dynamics. However, the effects of removing large numbers of these top predators on the marine ecosystem are still largely unknown. Attention needs to be focused on this poorly studied group of fishes, particularly in the ecosystem context in terms of understanding trophic interactions.

Acknowledgements

We thank Kees Zwanenburg (Bedford Institute of Oceanography, Dartmouth) for provision of mainly US collected ECNASAP data on chondrichthyans from Cape Hatteras to the Scotian Shelf, 1970–1994. Villy Christensen (ICLARM, Manila) and Tom Okey (UBC, Vancouver) provided valuable assistance with some of the data files used for the ECOSIM analysis, and Marcelo Vasconcellos (UBC) with the use of ECOSIM. We thank Nic Bax and Tony Koslow (CSIRO Marine Research, Hobart), Bob Hueter (Mote Marine Laboratory, Sarasota), Chuck Hollingworth (University of Wales, Bangor), Niels Daan (Netherlands Institute for Fisheries Research, IJmuiden), and an anonymous referee for reviewing the manuscript and for helpful comments, and Grant West (CSIRO Marine Research) for help with editing and with the figures.

References

- Aldebert, Y. 1997. Demersal resources of the Gulf of Lions (NW Mediterranean). Impact of exploitation on fish diversity. *Vie et Milieu*, 47(4): 275–284.
- Anderson, E. D. 1985. Analysis of various sources of pelagic shark catches in the Northwest and Western Central Atlantic Ocean and Gulf of Mexico with comments on catches of other large pelagics. *In Shark Catches from Selected Fisheries off the U.S. East Coast*, pp. 1–14. NOAA Technical Report NMFS, 31. 22 pp.
- Anderson, E. D. 1990. Estimates of large shark catches in the Western Atlantic and Gulf of Mexico, 1960–1986. *In Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries. Proceedings of the Second United States–Japan Workshop East–West Center, Honolulu, Hawaii, 9–14 December 1987*, pp. 443–454. Ed. by H. L. Pratt, S. H. Gruber, and T. Taniuchi. NOAA Technical Report NMFS, 90. 518 pp.
- Beddington, J. R. 1984. The response of multispecies systems to perturbations. *In Exploitation of Marine Communities*, pp. 209–225. Ed. by R. M. May. Springer-Verlag, Berlin.
- Bonfil, R. 1994. Overview of world elasmobranch fisheries. *FAO Fisheries Technical Paper*, 341. 119 pp.
- Bonfil-Sanders, R. 1996. Elasmobranch fisheries: status, assessment and management. PhD thesis, University of British Columbia, February 1996. 301 pp.
- Blaber, S. J. M., and Wassenberg, T. J. 1989. The feeding ecology of the piscivorous birds *Phalacrocorax varius*, *P. melanoleucos* and *Sterna bergii* in Moreton Bay, Australia: diet and dependence on trawler discards. *Marine Biology*, 101: 1–10.
- Brander, K. 1981. Disappearance of common skate *Raia batis* from Irish Sea. *Nature*, 290: 48–49.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, London. 269 pp.
- Camhi, M. 1998. *Sharks on the line. A State-by-State analysis of sharks and their fisheries*. National Audubon Society, New York. 157 pp.
- Casey, J. M., and Myers, R. A. 1998. Near extinction of a large, widely distributed fish. *Science*, 281: 690–691.
- Christensen, V., and Pauly, D. (eds) 1993. *Trophic Models of Aquatic Ecosystems*. ICLARM Conference Proceedings, 26. 390 pp.
- Compagno, L. J. V. 1990. Shark exploitation and conservation. *In Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries. Proceedings of the Second United States–Japan Workshop East–West Center, Honolulu, Hawaii, 9–14 December 1987*, pp. 391–414. Ed. by H. L. Pratt, S. H. Gruber, and T. Taniuchi. NOAA Technical Report NMFS, 90. 518 pp.
- Compagno, L. J. V., and Cook, S. F. 1995. The exploitation and conservation of freshwater elasmobranchs: status of taxa and prospects for the future. *In The Biology of Freshwater Elasmobranchs. A Symposium to Honor Thomas B. Thorson*, pp. 62–90. Ed. by M. I. Oettinger, and G. D. Zorzi. *Journal of Aquaculture and Aquatic Sciences*, 7. 162 pp.
- Cortes, E. 1999. Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science*, 56(5): 707–717.
- Daan, N. 1980. A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 177: 405–421.
- de Vooy, C. G. N., and van der Meer, J. 1998. Changes between 1931 and 1990 in by-catches of 27 animal species from the southern North Sea. *Journal of Sea Research*, 39: 291–298.
- Dudley, S. F. J., and Cliff, G. 1993. Some effects of shark nets in the Natal nearshore environment. *Environmental Biology of Fishes*, 36: 243–255.
- Dulvy, N. K., Metcalfe, J. D., Glanville, J., Pawson, M. G., and Reynolds, J. D. 2000. Fishery stability, local extinctions and shifts in community structure in skates. *Conservation Biology*, 14: 283–293.
- Dulvy, N. K., and Reynolds, J. D. 1997. Evolutionary transitions among egg-laying, live-bearing and maternal inputs in sharks and rays. *Proceedings of the Royal Society of London. B*, 264: 1309–1315.
- Duplisea, D. E., Kerr, S. R., and Dickie, L. M. 1997. Demersal fish biomass size spectra on the Scotian Shelf, Canada: species replacement at the shelfwide scale. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 1725–1735.
- Fahy, E. 1989. The spurdog *Squalus acanthias* (L.) fishery in south west Ireland. *Irish Fisheries Investigations Series B*, No. 32: 3–22.
- Fahy, E., and Gleeson, P. 1990. The post-peak-yield gill-net fishery for spurdog *Squalus acanthias* L in western Ireland. *Irish Fisheries Investigations Series B*, No. 35: 3–12.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist*, 125: 1–15.
- Fogarty, M. J., and Murawski, S. A. 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications*, 8(1, suppl): S6–S22.
- Francis, M. P. 1998. New Zealand shark fisheries: development, size and management. *Marine and Freshwater Research*, 49(7): 579–591.
- Gauld, J. 1979. Reproduction and fecundity of the Scottish–Norwegian stock of spurdogs, *Squalus acanthias* (L.). *ICES CM 1979/H*: 54.
- Graham, K. J., Wood, B. R., and Andrew, N. L. 1997. The 1996–97 survey of upper slope trawling grounds between Sydney and Gabo Island (and comparisons with the 1976–77 survey). *Kapala Cruise Report No. 117*, NSW Fisheries, Cronulla, NSW. 96 pp.
- Grosslein, M. D., Langton, R. W., and Sissenwine, M. P. 1980. Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank region, in relation to

- species interactions. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 177: 374–404.
- Harris, A. N., and Poiner, I. R. 1991. Changes in species composition of demersal fish fauna of southeast Gulf of Carpentaria, Australia, after 20 years of fishing. *Marine Biology*, 111: 503–519.
- Hill, B. J., and Wassenberg, T. J. 1990. Fate of discards from prawn trawlers in Torres Strait. *Australian Journal of Marine and Freshwater Research*, 41: 53–64.
- Hoening, J. M., and Gruber, S. H. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. *In Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries. Proceedings of the Second United States–Japan Workshop East–West Center, Honolulu, Hawaii, 9–14 December 1987*, pp. 1–16. Ed. by H. L. Pratt, S. H. Gruber, and T. Taniuchi. NOAA Technical Report NMFS 90. 518 pp.
- Holden, M. J. 1973. Are long-term sustainable fisheries for elasmobranchs possible? *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 164: 360–367.
- Holden, M. J. 1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In Sea Fisheries Research*, pp. 117–137. Ed. by F. R. Harden-Jones. Paul Elek, London.
- Holden, M. J. 1977. Elasmobranchs. *In Fish Population Dynamics*, pp. 187–215. Ed. by J. A. Gulland. Wiley-Interscience, London.
- Holts, D. B. 1988. Review of U.S. west coast commercial shark fisheries. *Marine Fisheries Review*, 50(1): 1–8.
- Hunter, M. L. 1996. *Fundamentals of Conservation*. Blackwell, Cambridge, MA, USA.
- Hurley, P. C. F. 1998. A review of the fishery for pelagic sharks in Atlantic Canada. *In Science and Management of Shark Fisheries. Proceedings of an International Symposium Held at the 125th Annual Meeting of the American Fisheries Society, Tampa, Florida, USA, 30 August, 1995*, pp. 107–113. Ed. by R. E. Hueter. *Fisheries Research*, 39. 228 pp.
- Jennings, S., Greenstreet, S. P. R., and Reynolds, J. D. 1999b. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, 68: 617–627.
- Jennings, S., and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. *In Advances in Marine Biology*, pp. 201–352. Ed. by J. H. S. Blaxter, A. J. Southward, and P. A. Tyler. Academic Press, London.
- Jennings, S., Reynolds, J. D., and Mills, S. C. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London, B*, 265: 333–339.
- Jennings, S., Reynolds, J. D., and Polunin, N. V. C. 1999a. Predicting the vulnerability of tropical reef fishes to exploitation: an approach based on phylogenies and life histories. *Conservation Biology*, 13: 1466–1475.
- Kennelly, S. J. 1998. Development of by-catch reducing prawn trawls and fishing practices in NSW's prawn-trawl fisheries (and incorporating an assessment of the effect of increasing mesh size in fish trawl gear). *New South Wales Fisheries Final Report Series 5*, no. 93/180.
- Ketchen, K. S. 1986. The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 88. 78 pp.
- Kunzlic, P. A. 1988. The basking shark. Department of Agriculture and Fisheries for Scotland. *Scottish Fisheries Information Pamphlet No. 14*. 21 pp.
- Langton, R. W., and Bowman, R. E. 1980. Food of fifteen Northwest Atlantic gadiform fishes. *National Oceanic and Atmospheric Administration Technical Report NMFS SSRF-740*.
- Larkin, P. A. 1979. Predator–prey relations in fishes: an overview of the theory. *In Predator–Prey Systems in Fisheries Management*, pp. 13–22. Ed. by H. Clepper. Sport Fishing Institute, Washington, D.C.. 504 pp.
- Last, P. R., and Séret, B. 1999. Comparative biogeography of the chondrichthyan faunas of the tropical South-East Indian and South-West Pacific Oceans. *In Proceedings of the 5th Indo-Pacific Fish Conference (Nouméa, 3–8 November 1997)*, pp. 293–306. Ed. by B. Séret, and J.-Y. Sire. Société Française d'Ichtyologie & Institut de Recherche pour le Développement, Paris. 866 pp.
- Last, P. R., and Stevens, J. D. 1994. *Sharks and Rays of Australia*. C.S.I.R.O., Australia. 513 pp.+84 colour plates.
- Long, D. J., Hanni, K. D., Pyle, P., Roletto, J., Jones, R. E., and Bandar, R. 1996. White shark predation on four pinniped species in central California waters: geographic and temporal patterns inferred from wounded carcasses. *In Great White Sharks. The Biology of *Carcharodon carcharias**, pp. 263–274. Ed. by A. P. Klimley, and D. G. Ainley. Academic Press, San Diego. 517 pp.
- McEachran, J. D. 1990. Diversity in rays: why are there so many species? *Chondros*, 2: 1–6.
- McEachran, J. D., and Dunn, K. A. 1998. Phylogenetic analysis of skates, a morphologically conservative clade of elasmobranchs (Chondrichthyes: Rajidae). *Copeia*, 1998(2): 271–290.
- Mendoza, J. J. 1993. A preliminary biomass budget for the northeastern Venezuela shelf ecosystem. *In Trophic Models in Aquatic Ecosystems*, pp. 285–297. Ed. by V. Christensen, and D. Pauly. ICLARM Conference Proceedings. 26.
- Murawski, S. A., and Idoine, J. S. 1992. Multispecies size composition: a conservative property of exploited fishery systems? *Journal of Northwest Atlantic Fishery Science*, 14: 79–85.
- Musick, J. A., Branstetter, S., and Colvocoresses, J. A. 1993. Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. mid-Atlantic coast. *In Conservation Biology of Elasmobranchs*, pp. 1–19. Ed. by S. Branstetter. NOAA Technical Report NMFS, 115. 99 pp.
- Nakano, H., and Watanabe, Y. 1992. Effect of high seas driftnet fisheries on blue shark stock in the North Pacific. *In Compendium of Documents Submitted to the Scientific Review of North Pacific High Seas Driftnet Fisheries*, Sidney, B.C., Canada, 11–14 June, 1991, vol. 1. 15 pp.
- NEFSC 2000. DRAFT 30th Northeast Regional Stock Assessment Workshop (30th SAW): Stock Assessment Review Committee (SARC) consensus summary of assessments. January. Northeast Fisheries Science Center, Woods Hole, MA.
- Olsen, A. M. 1959. The status of the school shark fishery in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research*, 10: 150–176.
- Overholtz, W. J., Murawski, S. A., and Foster, K. L. 1991. Impact of predatory fish, marine mammals, and seabirds on the pelagic fish ecosystem of the northeastern USA. *ICES Marine Science Symposia*, 193: 198–208.
- Pauly, D. 1979. Theory and management of tropical multispecies stocks: a review with emphasis on the southeast Asian demersal fisheries. *ICLARM Studies and Reviews*, 1: 1–35.

- Pauly, D. 1988. Fisheries research and the demersal fisheries of Southeast Asia. In *Fish Population Dynamics*, 2nd edition, pp. 329–347. Ed. by J. A. Gulland. Wiley, New York.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. *Science*, 279: 860–863.
- Pauly, D., Christensen, V., and Haggan, N. (eds) 1996. Mass-Balance Models of North-eastern Pacific Ecosystems. Fisheries Centre Research Reports, 4(1). 131 pp.
- Pollard, D. A. 1996. The biology and conservation status of the grey nurse shark (*Carcharias taurus* Rafinesque 1810) in New South Wales, Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 6: 1–20.
- Polovina, J. J. 1984. Model of a coral reef ecosystem. I. The EcoPath model and its application to French Frigate Shoals. *Coral Reefs*, 3: 1–11.
- Pope, J. G., Stokes, T. K., Murawski, S. A., and Idoine, S. I. 1988. A comparison of fish size composition in the North Sea and on Georges Bank. In *Ecodynamics, Contributions to Theoretical Ecology*, pp. 146–152. Ed. by W. Wolff, C. J. Soeder, and F. R. Drepper. Springer-Verlag, Berlin.
- Pratt, H. L., and Casey, J. G. 1990. Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*. Proceedings of the Second United States–Japan Workshop East–West Center, Honolulu, Hawaii, 9–14 December 1987, pp. 97–109. Ed. by H. L. Pratt, S. H. Gruber, and T. Taniuchi. NOAA Technical Report NMFS, 90. 518 pp.
- Punt, A. E., and Walker, T. I. 1998. Stock assessment and risk analysis for the school shark (*Galeorhinus galeus*) off southern Australia. *Marine and Freshwater Research*, 49(7): 719–731.
- Quérou, J.-C., and Cendrero, O. 1996. Incidence de la pêche sur la biodiversité ichthyologique marine: le bassin d'Arcachon et le plateau continental sud gascogne. *Cybiurn*, 20(4): 323–356.
- Rago, P. J., Sosebee, K. A., Brodziak, J. K. T., Murawski, S. A., and Anderson, E. D. 1998. Implications of recent increases in catches on the dynamics of northwest Atlantic spiny dogfish (*Squalus acanthias*). In *Science and Management of Shark Fisheries*. Proceedings of an International Symposium held at the 125th Annual Meeting of the American Fisheries Society, Tampa, Florida, USA, 30 August, 1995, pp. 165–181. Ed. by R. E. Hueter. *Fisheries Research*, 39. 228 pp.
- Reid, D. D., and Krogh, M. 1992. Assessment of catches from protective shark meshing off New South Wales beaches between 1950 and 1990. In *Sharks, Biology and Fisheries*, pp. 283–296. Ed. by J. G. Pepperell. *Australian Journal of Marine and Freshwater Research*, 43. 349 pp.
- Rijnsdorp, A. D., van Leewen, P. I., Daan, N., and Heessen, H. J. L. 1997. Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. *ICES Journal of Marine Science*, 53: 1054–1062.
- Ripley, W. E. 1946. The biology of the soupfin *Galeorhinus zygoteris* and biochemical studies of the liver. *California Fishery Bulletin*, 64: 1–96.
- Roberts, C. M., and Hawkins, J. P. 1999. Extinction risk in the sea. *Trends in Ecology and Evolution*, 14: 241–246.
- Rogers, S. I., Clarke, K. R., and Reynolds, J. D. 1999. The taxonomic distinctness of coastal bottom-dwelling fish communities of the North-east Atlantic. *Journal of Animal Ecology*, 68: 769–782.
- Rose, D. A. 1996. An overview of world trade in sharks and other cartilaginous fishes. TRAFFIC International, Cambridge, UK. 106 pp.
- Rothschild, B. J. 1991. Multispecies interactions on Georges Bank. *ICES Marine Science Symposia*, 193: 86–92.
- Russ, G. R. 1991. Coral reef fisheries: effects and yields. In *The Ecology of Fishes on Coral Reefs*, pp. 601–635. Ed. by P. F. Sale. Academic Press, San Diego.
- Sherman, K. 1991. The large marine ecosystem concept: research and management strategy for living marine resources. *Ecological Applications*, 1: 349–360.
- Sherman, K., Cohen, E. B., and Langton, R. W. 1990. The Northeast Continental Shelf: an ecosystem at risk. In *Gulf of Maine: Sustaining Our Common Heritage*. Proceedings of an International Conference Held at Portland, Maine, 10–12 December 1989, pp. 120–167. Ed. by V. Konrad, S. Ballard, R. Erb, and A. Morin. Maine State Planning Office and the Canadian–American Center of the University of Maine, Orono, Maine, USA.
- Simpfendorfer, C. 1992. Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. In *Sharks, Biology and Fisheries*, pp. 33–43. Ed. by J. G. Pepperell. *Australian Journal of Marine and Freshwater Research*, 43. 349 pp.
- Simpfendorfer, C., and Donohue, K. 1998. Keeping the fish in “fish and chips”: research and management of the Western Australian shark fishery. *Marine and Freshwater Research*, 49(7): 593–600.
- Sinclair, A. F., and Murawski, S. A. 1997. Why have ground-fish stocks declined? In *Northwest Atlantic Groundfish: Perspectives on a Fishery Collapse*, pp. 71–93. Ed. by J. Boreman, B. S. Nakashima, J. A. Wilson, and R. L. Kendall. American Fisheries Society, Bethesda, Maryland.
- Sminkey, T. R., and Musick, J. A. 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia*, 1995(4): 871–883.
- Smith, C. R. 1985. Food for the deep sea: utilization, dispersal, and flux of nekton falls at the Santa Catalina Basin floor. *Deep-Sea Research*, 32: 417–442.
- Smith, S. E., Au, D. W., and Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*, 49(7): 663–678.
- Stevens, J. D. 2000. The population status of highly migratory oceanic sharks in the Pacific Ocean. In *Proceedings of the Symposium on Managing Highly Migratory Fish of the Pacific Ocean*, 4–6th November 1996, Monterey, California, National Coalition for Marine Conservation. Savannah. (In press.)
- Stevens, J. D., and West, G. J. 1997. Investigation of school and gummy shark nursery areas in south eastern Australia. Fisheries Research and Development Corporation Project 93/061 final report July 1997, 76 pp. + appendices and figures.
- van der Elst, R. P. 1979. A proliferation of small sharks in the shore-based Natal shark fishery. *Environmental Biology of Fishes*, 4(4): 349–362.
- van der Elst, R. P. 1989. Marine recreational angling in South Africa. In *Oceans of Life off Southern Africa*, pp. 174–176. Ed. by A. I. L. Payne, and R. J. M. Crawford. Cape Town, Vlaeberg.
- Walker, P. A. 1998. Fleeting images. Dynamics of North Sea ray populations. PhD thesis. Faculteit Biologie, Universiteit van Amsterdam. 145 pp.
- Walker, P. A., and Heessen, H. J. L. 1996. Long-term changes in ray populations in the North Sea. *ICES Journal of Marine Science*, 53: 1085–1093.
- Walker, P. A., and Hislop, J. R. G. 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. *ICES Journal of Marine Science*, 55: 392–402.

- Walker, T. I. 1992. Fishery simulation model for sharks applied to the gummy shark, *Mustelus antarcticus* Gunther, from southern Australian waters. In *Sharks: Biology and Fisheries*, pp. 195–211. Ed. by J. G. Pepperell. Australian Journal of Marine and Freshwater Research, 43. 349 pp.
- Walker, T. I. 1997. Gummy shark 1996, stock assessment report, Southern Shark Fishery Assessment Group. Australian Fisheries Management Authority, Canberra. 33 pp.
- Walker, T. I. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research*, 49(7): 553–572.
- Walker, T. I., Taylor, B. L., Hudson, R. J., and Cottier, J. P. 1998. The phenomenon of apparent change of growth rate in gummy shark (*Mustelus antarcticus*) harvested off southern Australia. In *Science and Management of Shark Fisheries. Proceedings of an International Symposium Held at the 125th Annual Meeting of the American Fisheries Society, Tampa, Florida, USA, 30 August, 1995*, pp. 139–163. Ed. by R. E. Hueter. *Fisheries Research*, 39. 228 pp.
- Wallett, T. 1983. Shark attack in southern African waters and treatment of victims. C. Struik, Cape Town. 184 pp.
- Walters, C., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass balance assessments. *Reviews in Fish Biology and Fisheries*, 7(2): 139–172.
- Wassenberg, T. J., and Hill, B. J. 1989. The effect of trawling and subsequent handling on the survival rates of the by-catch of prawn trawlers in Moreton Bay, Australia. *Fisheries Research*, 7: 99–110.
- Williams, H., and Schaap, A. H. 1992. Preliminary results of a study into the incidental mortality of sharks in gill-nets in two Tasmanian shark nursery areas. In *Sharks, Biology and Fisheries*, pp. 237–250. Ed. by J. G. Pepperell. Australian Journal of Marine and Freshwater Research, 43. 349 pp.
- Wilson, C. D., and Seki, M. P. 1994. Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central North Pacific Ocean. *Fishery Bulletin*, 92: 851–864.
- Wood, C. C., Ketchen, K. S., and Beamish, R. J. 1979. Population dynamics of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada*, 36: 647–655.