

Extinction vulnerability in marine populations

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Abstract

Human impacts on the world's oceans have been substantial, leading to concerns about the extinction of marine taxa. We have compiled 133 local, regional and global extinctions of marine populations. There is typically a 53-year lag between the last sighting of an organism and the reported date of the extinction at whatever scale this has occurred. Most disappearances (80%) were detected using indirect historical comparative methods, which suggests that marine extinctions may have been underestimated because of low-detection power. Exploitation caused most marine losses at various scales (55%), followed closely by habitat loss (37%), while the remainder were linked to invasive species, climate change, pollution and disease. Several perceptions concerning the vulnerability of marine organisms appear to be too general and insufficiently conservative. Marine species cannot be considered less vulnerable on the basis of biological attributes such as high fecundity or large-scale dispersal characteristics. For commercially exploited species, it is often argued that economic extinction of exploited populations will occur before biological extinction, but this is not the case for non-target species caught in multispecies fisheries or species with high commercial value, especially if this value increases as species become rare. The perceived high potential for recovery, high variability and low extinction vulnerability of fish populations have been invoked to avoid listing commercial species of fishes under international threat criteria. However, we need to learn more about recovery, which may be hampered by negative population growth at small population sizes (Allee effect or depensation) or ecosystem shifts, as well as about spatial dynamics and connectivity of subpopulations before we can truly understand the nature of responses to severe depletions. The evidence suggests that fish populations do not fluctuate more than those of mammals, birds and butterflies, and that fishes may exhibit vulnerability similar to mammals, birds and butterflies. There is an urgent need for improved methods of detecting marine extinctions at various spatial scales, and for predicting the vulnerability of species.

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Introduction

Current evidence suggests that few marine organisms have become globally extinct in the past 300 years. Indeed, there is unequivocal documentary evidence for the extinction of only three mammals, five birds and four gastropods, while another 18 low-taxonomic level taxa could be considered extinct if their status as valid distinct species can be confirmed (Carlton *et al.* 1999). There are currently no known global marine fish extinctions, which is perhaps surprising given the long history and large

scale of fisheries exploitation (Jackson *et al.* 2001; Pauly *et al.* 2002). Indeed, more than half of the world's human population lives within the coastal zone and depends on fish for their bulk protein intake. This proportion could reach 75% by the year 2020 (Anonymous 1998; Kent 1998; Roberts and Hawkins 1999).

Recently, there has been vigorous debate about the possibility that some commercially exploited species of fish could be under threat of extinction (Mace and Hudson 1999; Musick 1999; Powles *et al.* 2000; Reynolds *et al.* 2002a). This debate was triggered by

the listing, in 1996, of species such as Atlantic cod (*Gadus morhua*, Gadidae), North Sea haddock (*Melanogrammus aeglefinus*, Gadidae) and southern bluefin tuna (*Thunnus maccoyii*, Scombridae) as vulnerable or critically endangered in the World Conservation Union's *Red List of Threatened Animals* (IUCN 1996). These species were listed because of severe declines caused by fisheries. While no one denies that strong declines have occurred, many have questioned whether declines of highly fecund, widespread and commercially important fish species that are under management really constitute the same threat of extinction as declines in other taxa such as birds and mammals. Resolution of this issue has been hindered by the considerable difficulties in determining the status of many marine organisms, and of detecting local, regional or global extinctions.

This paper aims to examine the number and pattern of extinctions of marine populations. We focus primarily on fish species, but also bring in relevant examples from other taxa. Some authors use the term 'extirpation' to refer to what we are calling an extinction that is restricted to local or regional scales. However, the dictionary definitions that we have seen invariably define 'extirpation' with connotations of deliberate eradication, and they do not convey either the idea of limited geographical extent or any uncertainty of the finality of the disappearance. We have, therefore, opted to use the term, extinction, with the qualification of its scale, ranging from global loss of all individuals (within a reasonable doubt) to regional or local losses of groups of individuals, including population segments or entire populations or stocks. The definition of the spatial scale of extinction follows that described by Carlton *et al.* (1999), and we have summarized these definitions in Table 1. We have included local and regional extinctions because they are the warning signs of conservation or management problems and are the first steps toward global extinction (Pitcher 2001).

We begin by outlining the known causes of extinctions and consider whether the detection of marine extinctions is delayed by examining a compilation of known disappearances. We hope our provisional list will encourage people to bring cases that we have overlooked to wider attention. We then examine the basis of commonly held perceptions that marine organisms are more extinction-proof than terrestrial taxa. This is followed by an examination of whether declines to extinction can be detected as they occur and possible methods for improving

detection. We conclude that extinctions at various scales and threats are likely to have been underestimated in marine organisms.

The causes of extinction

We have compiled a dataset of 133 populations and species that have become extinct locally, regionally, or globally (Table 1). This dataset is far from definitive because of the problems of recognizing and detecting extinctions that are discussed later, and therefore, can only be viewed as a preliminary indication of the relative importance of various threats.

Most marine extinctions (at all scales) were attributable to a single probable threat (80%), and the key threats, using World Conservation Union categories (Hilton-Taylor 2000), were exploitation (55%), and habitat loss/degradation (37%). Other threats were comparatively minor; 2% of extinctions were attributable to invasive species and 6% were due to other factors including climate change, pollution and disease (Table 1). In contrast, for birds, mammals and plants, habitat loss is the main cause of threat (87% of threatened species), followed by hunting and collecting (21%), invasions of alien species (18%) combined with intrinsic factors such as inbreeding and poor dispersal, recruitment and juvenile survival (14%) (Hilton-Taylor 2000).

Exploitation

Numerous marine species have undergone substantial declines due to exploitation (Sadovy 2001; Reynolds *et al.* 2002a). Globally extinct species include mammals such as Steller's sea cow and the Caribbean monk seal (see Table 1 for details and scientific names). Local and regional extinctions resulting from over-exploitation include the sea otter, northern elephant seal, dugong, barndoor skate, common skate, long-nose skate, white skate, angel shark, small-spotted catshark, smoothhound, thornback ray, stingray, bramble shark, and smalltooth sawfish (Table 1). Fishing has also caused regional and local losses of bony fishes (teleosts) and molluscs, such as the Icelandic spring-spawning herring population (Beverton 1990, 1992), and white abalone from NE Pacific shores (Table 1).

Local and regional extinctions are not restricted to western-style heavily mechanized fisheries. There have been local-scale extinctions in subsistence and artisanal fisheries, such as the rainbow parrotfish (*Scarus guacamaia*, Scaridae) from parts of

Table 1 Extinctions of marine populations and species including spatial scale, probable cause, correlate of extinction, detection method, date of last sighting, date extinction was reported and the calculated reporting delay.

Names (Family, latin binomial, common)	Geographical location ¹	Extinction scale ²	Extinction cause ³	Extinction correlate ⁴	Detection method ⁵	Last sighting (year)	Reporting date (year)	Reporting delay (year)	Reference ⁶
Mammalia									
Balaenidae									
<i>Balaena mysticetus</i> Bowhead whale	E Greenland	Local	Exploitation	?	Indirect	1828	?	n/a	1
<i>Eubalaena glacialis</i> Right whale	Bay of Biscay	Local	Exploitation	Large size	Indirect	1059	1881	822	2, 3
Delphinidae									
<i>Tursiops truncatus</i> Bottlenose dolphin	Wadden Sea	Local	Habitat loss	Large size	Indirect	1937	1981	44	2, 3
<i>Tursiops truncatus</i> Bottlenose dolphin	Netherlands	Local	Habitat loss	Large size	Indirect	1965	1981	16	2, 3
Dugongidae									
<i>Dugong dugon</i> Dugong	China	Local	Exploitation	Large size	Direct	2000	2000	0	4
<i>Hydrodamalis gigas</i> Steller's sea cow	NW Pacific	Global	Exploitation	Large size	Direct	1768	1768	0	5, 6
Eschrichtiidae									
<i>Eschrichtius robustus</i> Gray whale	Wadden Sea	Local	Exploitation	Large size	Indirect	1640	1970	330	2, 3
Mustelidae									
<i>Enhydra lutris</i> Sea otter	NE Pacific	Regional	Exploitation	?	Direct	1800	1981	181	5, 7
<i>Mustela macrodon</i> Sea mink	NW Atlantic	Global	Exploitation	Large size	Direct	1880	1880	0	5, 8
Phocidae									
<i>Halichoerus grypus</i> Grey seal	Wadden Sea	Local	Exploitation, habitat loss	Large size	Indirect	1400	1914	514	2, 3
<i>Monachus tropicalis</i> West Indian monk seal	Gulf of Mexico, Caribbean	Global	Exploitation	?	Direct	1952	1972	20	5, 7
<i>Phoca vitulina</i> Harbour seal	Dutch Rhine- Meuse-Scheldt Delta	Local	Exploitation, habitat loss, other	?	Direct	1972	1972	0	2, 3, 9
Phocoenidae									
<i>Phocoena phocoena</i> Harbour porpoise	Bay of Biscay	Local	Exploitation	?	Indirect	1771	1998	227	10
<i>Phocoena phocoena</i> Harbour porpoise	Wadden Sea	Local	Exploitation ?	Large size	Indirect	1965	2000	35	2, 3
Aves									
Accipitridae									
<i>Haliaeetus albicilla</i> White-tailed eagle	Wadden Sea	Local	Exploitation, habitat loss	?	Indirect	200	2000	1800	2, 3
Alcidae									
<i>Alca impennis</i> Great Auk	N Atlantic	Global	Exploitation	?	Direct	1844	1844	0	5, 7, 8, 11

Anatidae										
<i>Camptorhynchus labradorius</i>	Labrador duck	NW Atlantic	Global	Exploitation	?	Direct	1875	1985	110	5, 8, 11
<i>Mergus australis</i>	Auckland Islands merganser	SW Pacific	Global	Exploitation, invasion	?	Direct	1902	1987	85	5, 11
<i>Somateria mollissima</i>	Eider duck	Wadden Sea	Local	Exploitation	?	Indirect	?	1991	n/a	2, 3
Haematopodidae										
<i>Haematopus meadewaldoni</i>	Canary Islands oystercatcher	NE Atlantic	Global	Invasion	Small range	Direct	1913	1982	69	5
Laridae										
<i>Hydroprogne caspia</i>	Caspian tern	S North Sea	Local	?	?	Indirect	1928	2000	72	2, 3
<i>Larus canus</i>	Common gull	Wadden Sea	Local	Exploitation	?	Indirect	1850	2000	150	2, 3
<i>Larus fuscus</i>	Lesser black-backed gull	Wadden Sea	Local	Exploitation	?	Indirect	1850	2000	150	2, 3
<i>Sterna dougallii</i>	Roseate tern	German Wadden Sea	Local	?	?	Indirect	1900	2000	100	2
Pelecanidae										
<i>Pelecanus crispus</i>	Dalmatian pelican	Wadden Sea	Local	Exploitation, habitat loss	?	Indirect	200	2000	1800	2, 3
Phalacrocoracidae										
<i>Phalacrocorax perspicillatus</i>	Pallas's cormorant	NW Pacific	Global	Exploitation	Large size, specialist	Direct	1850	1882	32	5
Pisces										
Acipenseridae										
<i>Acipenser sturio</i>	European sturgeon	Adriatic Sea	Local	Exploitation	Large size, specialist	Indirect	1948	2001	53	12
<i>Acipenser sturio</i>	European sturgeon	SE North Sea	Local	Exploitation, habitat loss	Large size, specialist	Indirect	1955	2000	45	2, 3
<i>Acipenser oxyrinchus oxyrinchus</i>	Atlantic sturgeon	Connecticut, St. Marys & St. Johns Rivers, USA	Local	Exploitation, habitat loss	Large size, specialist	Indirect	?	?	n/a	13, 14
Antennariidae										
<i>Antennarius pauciradiatus</i>	Dwarf frogfish	Bermuda	Local	Habitat loss	Specialist	Indirect	1930	1999	69	15
Apogonidae										
<i>Apogon affinis</i>	Bigtooth cardinalfish	Bermuda	Local	Habitat loss	Specialist	Indirect	1931	1999	68	15
<i>Apogon robinsi</i>	Roughlip cardinalfish	Bermuda	Local	Habitat loss ?	Specialist	Indirect	1876	1999	123	15
<i>Phaeoptyx conklini</i>	Freckled cardinalfish	Bermuda	Local	Habitat loss ?	Specialist	Indirect	1919	1999	80	15
Clupeidae										
<i>Alosa alosa</i>	Allis shad	North Sea	Local	Exploitation, habitat loss, other	Specialist	Indirect	?	2000	n/a	2, 3
<i>Clupea harengus</i>	Herring (Zuiderzee race)	Wadden Sea	Local	Habitat loss	Specialist	Indirect	1937	2000	63	2, 3
<i>Clupea harengus</i>	Icelandic spring-spawning population	Iceland	Local	Exploitation	Small range	Direct	1972	1990	18	16

Table 1 continued

Names (Family, latin binomial, common)	Geographical location ¹	Extinction scale ²	Extinction cause ³	Extinction correlate ⁴	Detection method ⁵	Last sighting (year)	Reporting date (year)	Reporting delay (year)	Reference ⁶
Dactyloscopidae									
<i>Gillellus greyae</i> Arrow stargazer	Bermuda	Local	Habitat loss ?	Specialist	Indirect	1908	1999	91	15
Gasterosteidae									
<i>Spinachia spinachia</i> Fifteen-spined stickleback	Wadden Sea	Local	Habitat loss	Specialist	Indirect	1932	1987	55	2, 3
Gobiidae									
<i>Ctenogobius boleosoma</i> Darter goby	Bermuda	Local	Habitat loss ?	?	Indirect	1903	1999	96	15
Labridae									
<i>Anampses viridis</i> Green wrasse	Mauritius	Global	Other ?	Specialist	Indirect	1839	1972	133	17
Labrisomidae									
<i>Paraclinus nigripinnis</i> Blackfin blenny	Bermuda	Local	Habitat loss ?	?	Indirect	1906	1999	93	15
Monacanthidae									
<i>Oxymonacanthus longirostris</i> Harlequin leatherjacket	Okinawa, Japan	Local	Habitat loss	Specialist	Direct	1998	2001	3	18
Muraenidae									
<i>Enchelycore anatina</i> Fangtooth moray	Bermuda	Local	Habitat loss ?	?	Indirect	1872	1999	127	15
Ostraciidae									
<i>Lactophrys trigonus</i> Buffalo trunkfish	Bermuda	Local	Exploitation, habitat loss	?	Indirect	1930	1999	69	15
Pomacentridae									
<i>Azurina eupalama</i> Galapagos damsel	Galapagos I.	Global	Habitat loss	?	Direct	1982	1991	9	19, 20
Prototrociidae									
<i>Prototoctes oxyrhynchus</i> New Zealand grayling	New Zealand	Global	Exploitation, invasion	Specialist	Direct	1923	1974	51	21, 22
Salmonidae									
<i>Coregonus oxyrinchus</i> Whitefish	North Sea	Local	Habitat loss	Specialist	Indirect	?	2000	n/a	2, 3
<i>Salmo salar</i> Atlantic salmon	SE North Sea rivers	Local	Habitat loss, other	Specialist	Indirect	1950	2000	50	2, 3
<i>Salmo salar</i> Atlantic salmon	NW Atlantic	Local	Exploitation, habitat loss	Specialist	?	?	?	?	14
Scaridae									
<i>Bolbometopon muricatum</i> Bumphead parrotfish	Lau islands, Fiji	Local	Exploitation	Large size	Direct	1999	2000	1	23
<i>Nicholsina usta</i> Emerald parrotfish	Bermuda	Local	Habitat loss	?	Indirect	1929	1999	70	15
Sciaenidae									
<i>Argyrosomus regius</i> Meagre	Wadden Sea	Local	Exploitation	Large size	Indirect	50	2000	1950	2, 3
<i>Bahaba taipingensis</i> Chinese bahaba	S China	Regional	Exploitation	Large size, small range	Indirect	2000	2001	1	24

Scorpaenidae											
<i>Scorpaena grandicornis</i>	Plumed scorpionfish	Bermuda	Local	Habitat loss	?	Indirect	1903	1999	96	15	
Serranidae											
<i>Epinephelus marginatus</i>	Dusky grouper	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12	
Syngnathidae											
<i>Cosmocampus brachycephalus</i>	Crested pipefish	Bermuda	Local	Habitat loss	?	Indirect	1910	1999	89	15	
<i>Syngnathus typhle</i>	Deep-snouted pipefish	Wadden Sea	Local	Habitat loss	Specialist	Indirect	1932	2000	68	2, 3	
Trachinidae											
<i>Trachinus draco</i>	Greater weaver	Wadden Sea	Local	Exploitation, habitat loss	?	Indirect	?	2000	n/a	2, 3	
Chondrichthyes											
Dalatiidae											
<i>Oxynotus centrina</i>	Angular rough shark	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12	
<i>Oxynotus centrina</i>	Angular rough shark	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1992	1997	5	25	
Dasyatidae											
<i>Dasyatis pastinaca</i>	Stingray	Wadden Sea	Local	Exploitation	Large size	Indirect	1966	2000	34	2, 3, 26	
Echinorhinidae											
<i>Echinorhinus brucus</i>	Bramble shark	Bay of Biscay	Local	Exploitation	Large size	Indirect	1981	1998	17	10	
Heptranchidae											
<i>Heptranchias perlo</i>	Sharpnose seven gill shark	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12	
Myliobatidae											
<i>Myliobatis aquila</i>	Common eagle ray	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1976	1997	21	25	
Pristidae											
<i>Pristis pectinata</i>	Smalltooth sawfish	Bermuda	Local	Exploitation	Large size	Indirect	1931	1999	68	15	
<i>Pristis pectinata</i>	Smalltooth sawfish	W Atlantic	Regional	Exploitation	Large size	Indirect	?	2000	n/a	14, 27	
<i>Pristis perotteti</i>	Large-tooth sawfish	Gulf of California, USA	Local	Exploitation	Large size	Indirect	?	?	?	14	
Rajidae											
<i>Dipturus alba</i>	White skate	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12	
<i>Dipturus batis</i>	Common skate	Irish Sea	Local	Exploitation	Large size	Direct	1981	1981	0	28–30	
<i>Dipturus batis</i>	Common skate	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12	
<i>Dipturus batis</i>	Common skate	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1960	1997	37	25	
<i>Dipturus oxyrinchus</i>	Long-nose skate	Irish Sea	Local	Exploitation	Large size	Indirect	1880	2000	120	29	
<i>Dipturus oxyrinchus</i>	Long-nose skate	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1984	1997	13	25	
<i>Leucoraja circularis</i>	Sandy ray	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12	
<i>Leucoraja circularis</i>	Sandy ray	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1960	1997	37	25	
<i>Leucoraja mirelatus</i>	Maltese ray	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1989	1997	8	25	

Table 1 continued

Names (Family, latin binomial, common)	Geographical location ¹	Extinction scale ²	Extinction cause ³	Extinction correlate ⁴	Detection method ⁵	Last sighting (year)	Reporting date (year)	Reporting delay (year)	Reference ⁶
<i>Leucoraja naevis</i> Cuckoo ray	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1989	1997	8	25
<i>Raja clavata</i> Thornback ray	Wadden Sea	Local	Exploitation	Large size	Indirect	1960	2000	40	2, 3, 31
<i>Raja microocellata</i> Small-eyed ray	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1960	1997	37	25
<i>Rostroraja alba</i> White skate	Irish Sea and English channel	Local	Exploitation	Large size	Indirect	1880	n/a	n/a	29, 30
Scyliorhinidae									
<i>Scyliorhinus canicula</i> Small-spotted catshark or lesser spotted dogfish	Wadden Sea	Local	Exploitation ?	Large size	Indirect	1955	2000	45	2, 3
<i>Scyliorhinus stellarus</i> Nurse hound	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1987	1997	10	25
Squatinae									
<i>Squatina squatina</i> Angel shark	Bay of Biscay	Local	Exploitation	Large size	Direct	?	?	n/a	10
<i>Squatina squatina</i> Angel shark	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12
<i>Squatina squatina</i> Angel shark	Irish Sea/English Channel	Local	Exploitation	Large size	Indirect	1998	2000	2	30
Triakidae									
<i>Galeorhinus galeus</i> Tope or soupfin shark	Adriatic Sea	Local	Exploitation	Large size	Indirect	1948	2001	53	12
<i>Galeorhinus galeus</i> Tope or soupfin shark	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1984	1997	13	25
<i>Mustelus asterias</i> Starry smoothhound	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1970	1997	27	25
<i>Mustelus mustelus</i> Smoothhound	Gulf of Lions, Mediterranean Sea	Local	Exploitation	Large size	Indirect	1989	1997	8	25
<i>Mustelus mustelus</i> Smoothhound	Wadden Sea	Local	Exploitation ?	Large size	Indirect	1991	1991	0	2, 3
Echinodermata									
Diadematidae									
<i>Diadema antillarum</i> Long-spined urchin	Caribbean	Regional	Other	?	Direct	1983	1983	0	32
Echinidae									
<i>Paracentrotus lividus</i> Purple sea urchin	Lough Hyne, Ireland	Local	Other, exploitation?	?	Direct	2000	2002	2	33
Toxopneustidae									
<i>Triploneustes gratilla</i> Short-spined sea urchin	Bolinao, Philippines	Local	Exploitation	?	?	1995	1995	0	34
Mollusca									

Acmaeidae										
<i>Collisella' edmitchelli</i> Rocky shore limpet	NE Pacific	Global	Habitat loss	Specialist	Indirect	1861	1984	123	5, 35	
Buccinidae										
<i>Buccinum undatum</i> Whelk	Wadden Sea	Local	Exploitation, habitat loss	?	Indirect	?	2000	n/a	2, 3	
Cerithiidae										
<i>Cerithidea californica</i> Mudsnail	S California	Local	Exploitation, invasion	Specialist	Indirect	1960	1975	15	5	
<i>Cerithidea fuscata</i> Horn snail	NE Pacific	Global	Exploitation	Specialist	Indirect	1935	1992	57	5, 35	
Corambidae										
<i>Corambe obscura</i> Obscure corambe	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3	
Dolabriferidae										
<i>Phyllaplysia smaragda</i> Emerald leafslug	Indian river lagoon, Florida	Local ?	Habitat loss	Specialist	Indirect	1981	1994	13	5, 35–37	
Haliotidae										
<i>Haliotis sorenseni</i> White abalone	NE Pacific	Global	Exploitation	?	Direct	?	?	n/a	38–40	
Hermaeidae										
<i>Stiliger vossi</i>	Biscayne Bay, Florida	Local	?	?	Indirect	1960	1994	34	36, 37	
Lacunidae										
<i>Lacuna vincta</i> Northern lacuna	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3	
Littorinidae										
<i>Littoraria flammea</i> Periwinkle	China	Global	Habitat loss	Specialist	Indirect	1840	1992	152	5, 35	
Lottidae										
<i>Lottia alveus alveus</i> Atlantic eelgrass limpet	NW Atlantic	Global	Habitat loss	Specialist	Indirect	1929	1992	63	8, 35, 41	
Mytilidae										
<i>Mytilus trossulus</i> Foolish mussel	S California	Local	Invasion	Specialist	Indirect	?	?	n/a	5	
Ostreidae										
<i>Crassostrea virginica</i> Eastern oyster	Chesapeake Bay, USA	Local	Exploitation, habitat loss	?	Indirect	1878	1988	110	42	
<i>Ostrea edulis</i> Edible oyster	Wadden Sea	Local	Exploitation, habitat loss	?	Indirect	?	2000	n/a	2, 3	
Rissoidae										
<i>Onoba [Cingula] semicostata aculeus</i>	Wadden Sea	Local	?	?	Indirect	?	2000	n/a	2, 3	
<i>Rissoa membranacea</i>	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3	
Tridacnidae										
<i>Hippopus hippopus</i> Giant clam	Guam, Fiji & Tonga	Local	Exploitation	Large size	Indirect	?	1988	n/a	43, 44	
<i>Tridacna gigas</i> Giant clam	Carolines and Fiji (Lau islands)	Local	Exploitation	Large size, small range	Indirect	?	1988	n/a	43, 44	
Arthropoda										
Mysidae										
<i>Acanthomysis longicornis</i>	Gulf of Naples, Mediterranean Sea	Local	Other	?	Indirect	1929	2001	72	45	

Table 1 continued

Names (Family, latin binomial, common)	Geographical location ¹	Extinction scale ²	Extinction cause ³	Extinction correlate ⁴	Detection method ⁵	Last sighting (year)	Reporting date (year)	Reporting delay (year)	Reference ⁶
<i>Mysidopsis angusta</i>	Gulf of Naples, Mediterranean Sea	Local	Other	?	Indirect	1929	2001	72	45
Nephropidae									
<i>Homarus gammarus</i> Lobster	Wadden Sea	Local	Exploitation, habitat loss	Large size	Indirect	?	2000	n/a	2, 3
Upogebiidae									
<i>Upogebia bermudensis</i> mud shrimp	Bermuda	Local	Habitat loss	Specialist	Indirect	1902	1999	97	15
Xanthidae									
<i>Rhithropanopeus harrisi</i> Harris mud crab	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Annelida									
Ampharetidae									
<i>Alkmaria romijni</i>	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Sabellariidae									
<i>Sabellaria spinulosa</i>	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Coelenterata									
Edwardssidae									
<i>Edwardsia ivella</i> anemone	Sussex, UK	Global	Habitat loss	Small range	Direct	1983	1992	9	5
Milleporidae									
<i>Millepora boschmai</i> Fire coral	E Pacific	Global	Other	Small range	Direct	1998	1998	0	46
Siderastreidae									
<i>Siderastrea glynni</i>	E Pacific	Global	Other	Small range	Direct	1998	2001	3	46
Algae									
Ceramiaceae									
<i>Antithamnion vollosum</i> Red algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
<i>Ceramium diaphanum</i> Red algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
<i>Gigartina australis</i> Turkish towel algae	Sydney Harbour, Australia	Global	Habitat loss, other	?	Indirect	1892	2001	109	47, 48
<i>Spermothamnion repens</i> Red algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Corallinaceae									
<i>Corallina officinalis</i> Red algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
<i>Jania rubens</i> Red algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Delesseriaceae									
<i>Vanvoorstia bennettiana</i> Bennett's seaweed	Sydney Harbour, Australia	Global	Habitat loss, other	Small range	Indirect	1916	1992	76	48

Spongitiaceae										
<i>Pneophyllum fragile</i>	Red algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Cladophoraceae										
<i>Cladophora dalmatica</i>	Green algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Punctariaceae										
<i>Punctaria hiemalis</i>	Brown algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Scytosiphonaceae										
<i>Colpomenia peregrina</i>	Brown algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3
Sphacelariaceae										
<i>Sphacelaria cirrosa</i>	Brown algae	Wadden Sea	Local	Habitat loss	?	Indirect	?	2000	n/a	2, 3

¹This is intended to convey the location of smaller-scale extinctions, rather than the absolute extent of the extinction. We have attempted to use the smallest inclusive description of each geographical extent of extinction.

²Scale of extinction was categorised following Carlton *et al.* (1999) whereby local = the disappearance of a population from a small area of habitat e.g. mollusc extinctions from Californian shorelines or skate disappearances from the Irish Sea, regional = the disappearance from a substantial part of an ocean basin or former range, e.g. sea otter from the NE Pacific coastline and global = complete extinction, within reasonable doubt. These species where isolated individuals may be still be present but where breeding is doubtful can be considered functionally extinct (Carlton *et al.* 1999), e.g. Irish Sea common skate or the white abalone. While species and populations may have gone extinct from a number of locations we only list the best-documented disappearances. Note that the Wadden Sea Gulls and the Sea Otter are now recovering.

³Extinction causes are categorised according to World Conservation Union Red List (Hilton-Taylor 2000), where 'habitat loss' includes habitat degradation and 'other' includes pollution, global warming, disease.

⁴'Large size' broadly categorises species with slow life histories and low productivity, 'small range' refers to geographical range size and includes species endemic to small geographic ranges, 'specialist' includes habitat specificity, diadromy/catadromy and flightlessness, and also includes the categories defined as 'intrinsic' by World Conservation Union; low dispersal, parental care, and low competitive ability (when faced by alien invasive).

⁵Direct detection methods include monitoring or ecological censusing and historical methods include archaeological, sub-fossil or historical species list comparisons.

⁶1. Allen and Keay (2001), 2. Wolff (2000), 3. Wolff (2000), 4. Morton (2001), 5. Carlton *et al.* (1999), 6. Jackson *et al.* (2001), 7. Day (1989), 8. COSEWIC (2002), 9. Reijnders (1985), 10. Quero (1998), 11. Halliday (1978), 12. Jukic-Peladic *et al.* (2001), 13. Colligan *et al.* (1998), 14. Musick *et al.* (2000), 15. Smith-Vaniz *et al.* (1999), 16. Beverton (1990), 17. Hawkins *et al.* (2000), 18. Kokita and Nakazono (2001), 19. Jennings *et al.* (1994), 20. Roberts and Hawkins (1999), 21. Balouet (1990), 22. McDowell (1996), 23. Dulvy and Polunin (unpublished data), 24. Sadovy and Cheung (2002), 25. Aldebert (1997), 26. Walker (1995), 27. Anonymous (2000), 28. Brander (1981), 29. Dulvy *et al.* (2000), 30. Rogers and Ellis (2000), 31. Walker and Hislop (1998), 32. Lessios (1988), 33. Barnes *et al.* (2002), 34. Talaue-McManus and Kesner (1995), 35. Carlton (1993), 36. Clark and Rosenzweig (1994), 37. Clark (1994), 38. Tegner *et al.* (1996), 39. Davis *et al.* (1998), 40. Karpov *et al.* (2000), 41. Carlton *et al.* (1991), 42. McCormick-Ray (1998), 43. Lewis *et al.* (1988), 44. Paulay (1996), 45. Wittmann (2001), 46. Fenner (2001), 47. Millar and Kraft (1993) and 48. Millar (2001).

the Caribbean, the bumphead parrotfish from some Pacific islands, the Napoleon wrasse (*Chelinus undulatus*, Labridae) from parts of Fiji and Hong Kong and giant clams from the Fiji, Guam, Tonga and Caroline Islands (Table 1).

Many species are taken as by-catch when fishing for more valuable and abundant species, but primary target species such as tropical groupers (Serranidae), Napoleon wrasse (Donaldson and Sadovy 2001), giant clams, white abalone, totoaba (*Totoaba totoaba*, Sciaenidae) and Chinese bahaba (*Bahaba taipingensis*, Sciaenidae) have also been fished out on small spatial scales (local to regional). The goliath, Nassau, Warsaw and potato groupers and the speckled hind (*Epinephelus itajara*, *E. striatus*, *E. nigritus*, *E. tukula*, *E. drummondhayi*, Serranidae) have been severely depleted in parts of their range (Huntsman *et al.* 1999; Sadovy and Eklund 1999).

Habitat loss

The effects of habitat loss are difficult to separate from other impacts, such as exploitation, but at least 14 extinctions at various scales have resulted from habitat loss combined with other threats (Table 1). Natural impacts known to cause habitat loss include earthquakes, storms, hurricanes, freshwater input and diseases (Edmunds and Carpenter 2001). Human-induced habitat loss has been caused by coastal reclamation and development with associated pollution, leading to changes in water clarity, sediment loading and added nutrient inputs (Short and Wyllie-Echeverria 1996). However, the distinction between natural and human impacts is now blurred by the rise in anthropogenic effects on the frequency and intensity of impacts that were previously considered natural, such as hurricanes (Harvell *et al.* 1999; Ruiz *et al.* 2000b; Walsh and Ryan 2000; Goldenberg *et al.* 2001; McCarty 2001). Climate change, which is at least partly human-induced, is predicted to increase the frequency of both El Niño and La Niña events. In the Atlantic Ocean, there is a reduced chance (28%) of hurricane strikes during El Niño phases, while during La Niña phases there is a 66% increase in the probability of hurricane strikes (Bove *et al.* 1998).

Mangroves stabilize sediments and provide important juvenile habitat for a number of reef and lagoon fishes and crustaceans. Mangroves are cleared to support wood chip industries, shrimp aquaculture and for a host of artisanal uses, such as grazing fodder, medicine and building material (Semesi 1991;

Ong 1995; Dierberg and Kiattisimkul 1996). The global rate of mangrove habitat loss is at least 1% per year, but local losses can be higher: examples include about 18% in Mexico over 16 years and 16–32% in Thailand between 1979 and 1993 (Dierberg and Kiattisimkul 1996; Kovacs *et al.* 2001). While loss of mangroves has clearly affected local populations of plants and animals, it is not known whether there have been associated global extinctions.

Declines and extinctions can be associated with the loss of habitat essential for the completion of critical parts of the life cycle, such as migration bottlenecks or spawning and nursery habitat (McDowall 1992). The inner Bay of Fundy Atlantic salmon (*Salmo salar*, Salmonidae) population and the Interior Fraser River Coho salmon (*Oncorhynchus kisutch*, Salmonidae) population are listed as 'endangered' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This committee defines 'endangered' to mean that these populations face imminent extinction. Atlantic salmon are locally extinct from 14 other Canadian rivers, in addition to the Bay of Fundy catchment (Musick *et al.* 2000). In USA, the Atlantic salmon was historically native to nearly every major coastal river north of the Hudson River, New York. Almost all US populations of the Atlantic salmon have been lost apart from remnant populations in eight rivers in Maine (Musick *et al.* 2000). Sturgeon and Pacific salmon declines are reviewed elsewhere and are beyond the scope of this review, so we have only summarised the key information here (e.g. Allendorf *et al.* 1997; Billard and Lecointre 2001). Pacific salmon stocks have disappeared because of terrestrial degradation, acid rain, dams, pollution, loss of water from streams, over-exploitation, inappropriate management and climate change (Lichatowich *et al.* 1999; Beamish *et al.* 2000; Bradford and Irvine 2000). Sturgeons also have specialized habitat requirements and low population growth rates, and are consequently particularly susceptible to habitat loss and exploitation. Currently, 27 out of 29 species are listed as endangered under World Conservation Union *Red List* criteria (Boreman 1997; Jonsson *et al.* 1999; Billard and Lecointre 2001).

Habitat loss and degradation may also be caused by fishing, particularly by bottom trawling, which is estimated to cover half of the global continental shelf area (Dayton *et al.* 1995; Watling and Norse 1998). This trawled area is estimated to be 150-fold greater than the land area clear felled by forestry each year (Watling and Norse 1998). Benthic fishing gears such as trawls and mollusc dredges have altered benthic

species composition, structural complexity, trophic structure, size structure and productivity of benthic communities (Jennings and Kaiser 1998; Watling and Norse 1998; Hall 1999; Turner *et al.* 1999; Collie *et al.* 2000; Kaiser and de Groot 2000; Jennings *et al.* 2001a,c; Dulvy *et al.* 2002). Fishing activities are very patchy on a small scale; areas can be fished up to eight times a year in the North Sea or 25–141 times a year in the Clyde estuary (Rijnsdorp *et al.* 1998; S. J. Marrs pers. comm.). While trawling and dredging have clear local impacts on benthic habitats and populations, it is difficult to know whether this has resulted in larger scale extinctions.

Fish abundance and diversity on coral reefs are clearly linked to habitat types, such as the abundance of hard corals, substrate topography and interstitial spaces (e.g. Friedlander and Parrish 1998). Hurricanes, blast fishing and coral mining reduce hard coral habitat and blast fishing particularly could lead to extinctions over small areas (e.g. Guard and Masai-ganah 1997). While coral removal is associated with reduced abundance and diversity of reef fishes (Dawson Shepherd *et al.* 1992; Dulvy *et al.* 1995), there is no evidence that hurricanes, coral mining or blast fishing have actually caused extinctions except on very small scales. One of the best documented cases of local extinction due to habitat loss is the demise of 10–14 shallow water reef and lagoon fishes due to the dredging of Castle Harbour, Bermuda (Smith-Vanis *et al.* 1999). Approximately one-fifth of the natural harbour area was lost to dredging and landfill for the construction of Kindley Air Force Base between 1941 and 1944. Castle Harbour previously supported luxuriant coral reefs and very clear water. Following construction, most corals disappeared (over an unknown time scale) due to extensive siltation and turbidity (Smith-Vanis *et al.* 1999). Another example of local extinction through habitat loss is the disappearance of a 44.6-km² population of oysters in Tangier Sound, Chesapeake Bay, which is attributed to the mechanical impact of fishing gears (McCormick-Ray 1998; Jackson *et al.* 2001). The exploitation of ecosystem engineers also has indirect impacts on benthic habitats, potentially resulting in extinctions. Deepwater groupers (e.g. *Epinephelus morio*, Serranidae) and tilefishes (e.g. *Lopholatilus chamaeleoticeps*, Malacanthidae) form excavations and burrows that create shelter for fishes and invertebrates in otherwise structurally barren soft substrates (Coleman and Williams 2002).

The importance of habitat for fish productivity is recognized in US Law under the (1996) amendments

to the Magnuson–Stevens Fishery Conservation and Management Act (Kurland 1998). This act defines essential fish habitat as those waters and substrate necessary for spawning, breeding, feeding, or growth to maturity (Rosenburg *et al.* 2000).

Invasive species

Documentation of marine invasions and their impacts has lagged behind terrestrial studies, but a recent review suggests that the North American coastline alone may be host to 298 foreign species, most of which arrived in the ballast tanks of ships (Ruiz *et al.* 2000b; Wonham *et al.* 2000). In Hawaii, there have been 101 known marine invasions since the beginning of the last century (Coles *et al.* 1999). Most were crustaceans and molluscs, but the taxonomic range of invaders spans dinoflagellates to fishes (Ruiz *et al.* 2000a). Forty species have been introduced to the Wadden Sea, yet none are believed to have caused any of the 42 extinctions documented there in the past 2000 years (Wolff 2000a). In contrast, small-scale impact experiments suggest that while invading species can potentially cause extinctions, these losses may be difficult to detect (Grosholz 2001). In California, the introduced Japanese mud snail (*Batillaria attramentaria*, Potamididae) is a more efficient forager than the native snail (*Cerithidea californica*, Cerithiidae), and it is predicted by demographic models to eventually replace the native species (Byers 2000). Molecular analyses of museum specimens suggest that alien mussels (*Mytilus galloprovincialis*, Mytilidae) had already displaced the native mussel (*M. trossulus*) in southern California, some time in the last century (Geller 1999). The studies reviewed above (see also Carlton 1999) suggest that alien species may be a less important cause of extinctions in the marine environment than in terrestrial or freshwater systems. This is a tenuous conclusion, and the impacts of marine invasions deserve much more attention than they have received to date.

Other threats

Climate change

There is concern that climatic change, particularly as manifested by increased frequency and severity of El Niño Southern Oscillation (ENSO) events, may lead to habitat loss and marine extinctions (Scavia *et al.* 2002). In the tropics ENSO events are associated with elevated water temperature and unusually calm con-

ditions. Such conditions have been associated with coral bleaching, where coral hosts lose their symbiotic single-celled algae and may subsequently die (Glynn 1996). Prior to 1979 coral bleaching events were localized with presumed local causes. Since then bleaching events have been observed across ocean basins, each coinciding with an El Niño period (Glynn 1996; Hoegh-Gulburg 1999; Stone *et al.* 1999). During an El Niño event, there is a shift of equatorial warm water from the western to the eastern Pacific Ocean, displacing the cold tongue of water normally found there. During a La Niña event the warm water pool remains in the western equatorial Pacific, but the easterly cold tongue is 3 °C cooler than normal (http://www.pmel.noaa.gov/tao/el_nino/el_nino_story.html, last accessed 22/08/2002). Pacific Ocean temperature changes affect other oceans, and sea temperatures are tightly coupled to regional atmospheric conditions and wind patterns (McGowan *et al.* 1998; Barsugli *et al.* 1999). Sea surface temperatures 1 °C greater than the maximum summer monthly average for a number of weeks are known to cause mass coral mortality (Goreau and Hayes 1994; Cumming *et al.* 2002; Toscano *et al.* 2002). The recent 1998–1999 event flipped from a strong El Niño to a strong La Niña event, raising temperatures in some tropical areas to the highest values recorded in 150 years, and possibly longer (Wilkinson 2000). The unprecedented severity of this event is indicated by the death of ancient corals up to 700 years old (Hoegh-Gulburg 1999; Souter and Linden 2000). This climatic event was associated with widespread coral bleaching and the global loss of 4% of coral reefs since 1998. This is in addition to the loss of 11% of coral reefs in the decade prior to this event (Wilkinson 2000). Locally, coral mortality was higher, with 75–90% of coral colonies killed in shallow waters <15 m (Souter and Linden 2000). High temperatures and bleaching often extend down to the depth limit of shallow coral communities (approximately 50 m) (Souter and Linden 2000). Two species of coral are thought to have possibly become globally extinct due to bleaching (*Siderastrea glynni* and *Millepora boschmai*, Table 1). Both have small geographic ranges in the Eastern Pacific, directly in the path of ENSO events (Glynn and de Weerd 1991; Fenner 2001).

The large scale of bleaching in the last decade and subsequent loss of reefs might reasonably be predicted to cause the local or regional extinction of coral-associated species. Two obligate coral-feeding fish species have disappeared from aquarium trade

catches in the Maldives and may be gone from this area (Table 1, M. Saleem, pers. comm.). One of these species, the harlequin leatherjacket (*Oxymonacanthus longirostris*, Monacanthidae), has also disappeared from small study sites in Southern Japan (Kokita and Nakazono 2001). A previously common planktivorous, coral-associated Galápagos damselfish (*Azurina eupalama*, Pomacentridae) has not been seen since the 1982–3 ENSO bleaching event despite concerted searches (Table 1, G. Edgar and S. Jennings, pers. comm.). There are also concerns over the status of a number of coral-associated fishes that appear to have disappeared from some sites in the Western Pacific (T. J. Donaldson, pers. comm.).

It is forecast that ENSO-linked coral bleaching will become annual events in SE Asia and the Caribbean by the year 2020 and in the Great Barrier Reef, Australia somewhere between 2040 and 2070, depending on latitude (Hoegh-Gulburg 1999). Given these forecasts, we expect significant decreases in global coral cover, though the scale of loss of corals and reef-associated species cannot yet be predicted with any certainty (Carlton 1993).

Pollution

Pollution disrupts reproductive physiology, mating systems, and life histories of organisms and probably combines with other extinction-causing factors to reduce population persistence (Kime 1995; Jones and Reynolds 1997). Pollution has been implicated in one of the best-documented global extinctions: Bennett's seaweed (*Vanvoorstia bennettiana*, Delesseriaceae) (Millar 2002). This red alga was found around Sydney Harbour in the 1850s, and it was presumably common, since large quantities of it were discovered by dredging crudely from a small boat. However, the last known collection of this species was in 1886; subsequent exhaustive searches have failed to find it. This narrowly distributed plant had a fine reticulate thallus and may have been choked by the fine sediment discharged by storm drains into Sydney Harbour (Millar 2002). Pollution may also have caused the disappearance of another Australian red alga (*Gigartina australis*, Gigartinaceae) (Millar 2002). The eutrophication of the Indian River lagoon, FL, USA due to changes in upland drainage appears to have caused the local extinction of the emerald leafslug (*Phylla-physia smargada*, Dolabriferidae) and the decline of 70% of opisthobranch mollusc species in the area (Clark 1995). However, Carlton *et al.* (1999) suggest that the emerald leafslug may have specialized on the epiphytic algae growing on the basal stems of

seagrass and that its disappearance may be linked to disease-induced habitat loss, in turn possibly linked to the depletion of large herbivorous vertebrates (Jackson *et al.* 2001). Pollution, combined with habitat loss and over-exploitation, has caused the extinction of Allis shad and Atlantic salmon from the Wadden Sea (Table 1, for details) (Wolff 2000a,b). Major oil spills and chronic pollution have caused local losses of 11 hard coral species from an assemblage of 42 species; by comparison only three species disappeared from a control reef over the same 4-year time span (Loya 1976). While oil spills cause population declines and species redistribution, we are not aware that they have caused global extinctions (Paine *et al.* 1996; Peterson 2001).

Disease

The incidence of novel marine diseases and frequency of outbreaks is increasing due to climate change and anthropogenic impacts (Harvell *et al.* 1999, 2002; Ruiz *et al.* 2000b). One of the best examples of the effect that disease can have on populations is the 1983 mass mortality of the keystone sea urchin (*Diadema antillarum*, Diadematidae) resulting in a regional reduction of urchin abundances by approximately 93–99.99% (Lessios 1988).

Diseases are associated with the apparent loss of seagrass habitat and subsequent local extinctions in the Western Atlantic and the Wadden Sea in the Eastern Atlantic. In Florida Bay, approximately 4000 ha of seagrass beds were lost to disease and a further 23 000 ha degraded. The steep decline of a seagrass (*Zostera marina*, Zosteraceae) in the 1930s caused the first documented contemporary global extinction of a marine mollusc – the Atlantic eelgrass limpet (*Lottia alveus alveus*, Lottidae) (Carlton *et al.* 1991). This limpet fed solely on the surface cells of this one seagrass. A disease-induced die-off of seagrass habitat in the Dutch Wadden Sea in the 1930s also led to the local disappearance of the 15-spined stickleback (*Spinachia spinachia*, Gasterosteidae) and of the deep-snouted pipefish (*Syngnathus typhle*, Syngnathidae) (Wolff 2000b). Recent outbreaks of white- and black-band diseases have caused the unprecedented loss of large branching corals (*Acropora palmata* and *A. cervicornis*, Acroporidae) in the Caribbean (Jackson *et al.* 2001). An examination of the subfossil record on Western Caribbean reefs indicates that these corals have dominated reef community structure for the past 3800 years (Aronson *et al.* 1998, 2002; Greenstein *et al.* 1998). Recent declines in sea fans (*Gorgonia* spp., Gorgoniidae) were attributed to a fungal patho-

gen (*Aspergillus sydowii*, Trichocomaceae) (Geiser *et al.* 1998). It is argued that this pathogen is associated with African dust, derived from the drying out of Lake Chad and other Saharan areas, and transported across the Atlantic. Fungal spores collected from the transported dust clouds were demonstrated by experiment to invoke pathogenic activity (Shinn *et al.* 2000). Such coral reef diseases prevalent in the Caribbean have not had the same impact on Indo-Pacific reefs.

Why are disease outbreaks evidently on the increase in a range of hosts, particularly in the Caribbean? One hypothesis is that the removal of large-bodied species and ecosystem engineers results in an ecosystem dominated by microbial loops, that is more vulnerable to disease (Jackson 2001; Jackson *et al.* 2001). Specifically, the suggestion is that historically abundant turtles and manatees would have cropped the seagrass off near the base. Following a steep decline in turtle populations seagrass blades may have grown longer due to the reduction in herbivory. Since blade tips provide habitat for epiphytes such as algae, fungi and other microorganisms, infection can now begin in the older parts of leaves that would previously have been grazed away (Jackson *et al.* 2001).

Estimating extinction rates

It is virtually impossible to estimate how many marine extinctions at any scale might already have happened, due to problems with detections and with understanding the biological basis of vulnerability. While some progress has been made toward understanding vulnerability (Jennings *et al.* 1998, 1999b; Dulvy *et al.* 2000; Hawkins *et al.* 2000; Reynolds *et al.* 2001) we concur with previous arguments that detectability deserves far more attention than it has received in the past (McKinney 1999; Hawkins *et al.* 2000). The undersampling of poorly studied groups may underestimate extinctions because researchers tend to discover and study common species (McKinney 1999).

Delayed reporting of marine extinctions

The degree to which the reporting of marine extinctions is delayed can be estimated from the difference between the date the organism was last seen and the date on which its absence was reported. Our database of known losses on all scales (Table 1) indicates that since 1000 AD the reporting of extinctions has lagged

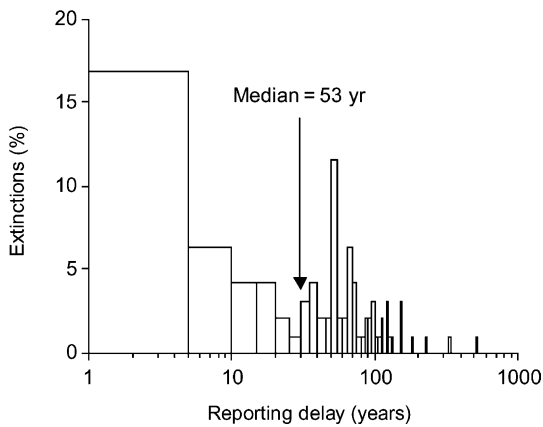


Figure 1 Frequency distribution of reporting delays of marine extinctions. Reporting delay is the time elapsed from the last sighting until the reported date of extinction ($n = 98$).

behind the last sighting date by a median of 53 years (Fig. 1; Wilcoxon signed rank $Z = -8.1$, $P < 0.001$, $n = 98$). Since the 1900s, the median reporting delay was 44 years ($n = 75$). Delayed reporting is not surprising considering that since 1900 80% of extinctions were detected using indirect historical comparative methods, such as comparing a historical trawl survey or fauna list with a comparable recent survey (e.g. Aldebert 1997; Rogers and Ellis 2000; Wolff 2000b; Jukic-Peladic *et al.* 2001). Only 18% of extinctions were detected using methods that could detect extinctions as they happen, e.g. time series of census data (Kokita and Nakazono 2001; Barnes *et al.* 2002).

An indication of improved detection ability over time is gained by examining the relationship between the date of last sighting and the reporting delay. The null expectation is a triangular distribution bounded by an upper slope of -1 (Fig. 2a). The reporting delay for most extinctions is close to the maximum possible. However, in recent years reporting delays have been smaller, as indicated by the increasing proportional distances of each point in Fig. 2(a) below the upper boundary line. These distances are expressed as percentages of the total reductions possible against time in Fig. 2(b). This confirms that reporting delay has declined significantly over the 20th century ($F_{1,56} = 64.8$, $P < 0.0001$, $R^2 = 0.46$). This improved detection of marine extinctions is supported by the increase in the number of extinctions detected each decade since the 1970s (Fig. 2c).

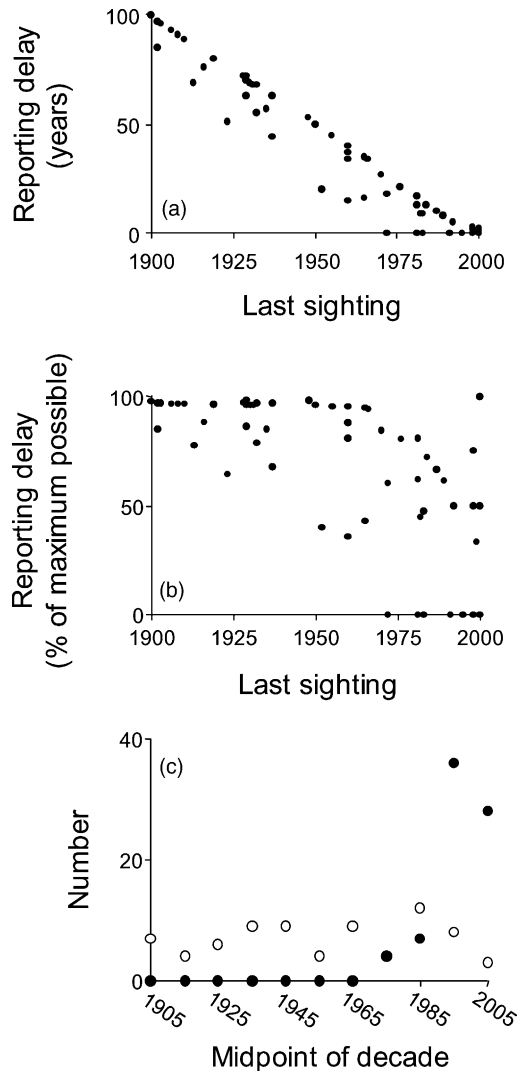


Figure 2 (a) Reporting delays of marine extinctions for reporting dates between 1900 and 2001. The null expectation is a triangular distribution bounded by an upper slope of -1 . (b) The percent reduction in reporting delays as a function of the date of last sighting ($\log_{10}[y] = -27.3 + 0.0145x$). Percent reduction in reporting delay was calculated as the vertical distance of each point below the upper boundary expressed as a percentage. (c) Numbers of last sightings (\circ) and reported extinctions (\bullet) since 1900. Note the increase in the number of extinctions detected from 1965 onwards.

It is difficult to determine whether detection is worse or better in the sea than on land. To the best of our knowledge, a comparable analysis of terrestrial extinction detection patterns has not yet been conducted. We caution that this pattern could also be an

artefact of the spatial scale of reported disappearances. The first reported marine extinctions were broader in geographical extent compared to recently reported disappearances, that tend to be local losses, which by definition must be more common. Nonetheless, understanding smaller scales at which losses occur is critical to understanding the extinction process, for local extinctions are the first steps on the road to global extinctions (Pitcher 2001). So, while the detection of extinctions may have improved recently, the overall situation is still poor.

Perceptions about the vulnerability of marine organisms

Marine organisms are perceived to be less vulnerable to extinction than terrestrial taxa for a number of reasons. However, many of these perceptions were derived from experiences when populations were much larger than they are today, and consequently the comfort we take from them may no longer be appropriate (Roberts and Hawkins 1999; Hutchings 2001a). Here, we examine the likelihood that marine fishes and invertebrates are less vulnerable because (i) they have long fossil durations, (ii) they have high fecundity, (iii) they have large-scale dispersal, (iv) they will be saved by economic extinction before biological extinction occurs, (v) they have high capacity for recovery, and (vi) their populations are naturally highly variable.

The fossil record implies lower vulnerability in the sea than on land

It has been suggested that marine taxa might be less vulnerable to extinction than terrestrial taxa based on their higher average duration in the fossil record (McKinney 1998). In support of this hypothesis, taxa with the longest fossil record durations also appear to have a lower proportion of threatened species (McKinney 1998). The best test of this hypothesis would be to compare extinction rates between related pairs of well-studied marine and terrestrial taxa, to overcome major phylogenetic differences and sampling biases. This has not yet been done. Anecdotally, we note that some relict taxa or 'living fossils' are in trouble, such as the coelacanth (*Latimeria chalumnae*), sturgeons (Acipenseriformes) and many marine turtles (Cheloniidae). Therefore, while such elderly taxa, which are analogous to those with a long fossil record, may be specialized survivors, on a contemporary scale they may still be at risk.

Fecund species are less vulnerable

Influential thinkers of the 18th and 19th centuries, such as Jean Baptiste de Lamarck, promoted the 'paradigm of ocean inexhaustibility', which is the notion that fish stocks could never be excessively (or irreversibly) overfished, in part because of the high fecundity of fishes (Roberts and Hawkins 1999; Hutchings 2000b, 2001a). The idea that fish stocks were inexhaustible is clearly wrong but the idea that high fecundity protects species against extinctions persists in many quarters (e.g. Musick 1999; Powles *et al.* 2000), while others question this view (Roberts and Hawkins 1999; Hutchings 2000a,b, 2001a; Sadovy 2001; Reynolds *et al.* 2002a). High fecundity is expected to evolve when females have low rates of gain in offspring survival per unit of investment into each egg (Smith and Fretwell 1974; Eium and Fleming 2000). This selects for production of many small eggs. Many commercially exploited teleosts are highly fecund pelagic spawners. They often exploit rich, but temporally and spatially variable plankton. Mothers are 'bet-hedging' by buying numerous tickets in a pelagic lottery in order to maximize the probability of their offspring landing in conditions suitable for feeding or settlement (Stearns 1992; Winemiller and Rose 1993).

The question is whether such high fecundity enables rapid recovery from exploitation. Perhaps if environmental conditions are suitable, such highly fecund species might have higher rates of population growth when fishing has reduced their numbers. This can be tested by examining maximum rates of recruitment, measured as the slope at the origin of a plot of recruitment versus adult population size (Myers *et al.* 1999). Such maximum reproductive rates have proven to be fairly consistent across fish species of varying fecundities, and also similar to those of other (including terrestrial) vertebrates, with a median of 1–7 spawners produced by each spawner each year (Myers *et al.* 1999; Denney *et al.* 2002). Maximum reproductive rate, therefore, appears to be independent of fecundity across a broad phylogenetic range of organisms, confirming what life history theory has already predicted, that fecundity *per se* has little bearing on year class strength in highly fecund teleost broadcast spawners (Fig. 3).

Long-lived species typically undergo many years of low recruitment interspersed with occasional high levels of recruitment when oceanographic conditions are favourable. Given the low maximum reproductive rates of many pelagic spawning teleosts and

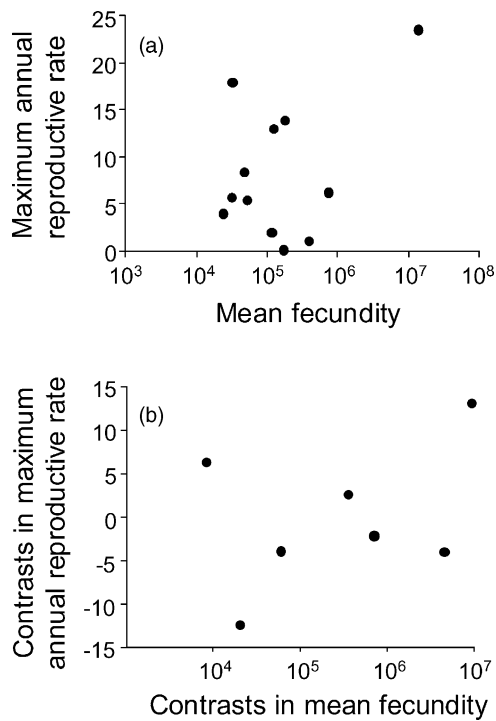


Figure 3 Relationship between mean fecundity and maximum annual reproductive rate for 12 exploited teleosts (a) cross-species analysis and (b), phylogenetically corrected analysis. The species used were: *Brevoortia patronus*, *Clupea harengus*, *Merlangius merlangus*, *Micromesistius poutassou*, *Theragra chalcogramma*, *Gadus morhua*, *Scomber scombrus*, *Anoplopoma fimbria*, *Reinhardtius hippoglossoides*, *Platichthys flesus*, *Pleuronectes platessa* and *Limanda ferruginea*. Details of methodology and data on mean fecundities and phylogeny were from Rickman *et al.* (2000), and reproductive rate data were from Myers *et al.* (1999).

the scarcity of years with suitable conditions for the production of a large cohort, the evolution of 'bet-hedging' and long life spans is predicted (Stearns 1992; Winemiller and Rose 1993; Longhurst 2002). Longevity, therefore, may be important for the persistence of highly fecund species throughout long periods of unfavourable recruitment conditions, the so-called storage effect (Mann and Mills 1979; Leaman and Beamish 1984; Warner and Chesson 1985; Beamish and McFarlane 2000; King *et al.* 2000; Hutchings 2001a; Sadovy 2001). This is reflected by the dominance of single age cohorts for extended periods in both tropical and temperate species (e.g. Hjort 1914; Russ *et al.* 1996).

For this reason, truncating the age structure of long-lived species through fishing is likely to increase extinction risk. Perhaps it is not surprising, therefore,

that it is the particularly long-lived highly fecund fishes that have undergone severe population declines and/or local extinctions. Examples include the Atlantic cod, Napoleon wrasse, the giant seabass (*Stereolepis gigas*, Polyprionidae), several species of rockfish (*Sebastes fasciatus*, *S. paucispinis*, Sebastidae), and the giant grouper (*Epinephelus lanceolatus*, Serranidae), all listed as threatened (vulnerable, endangered or critical) under World Conservation Union *Red List* criteria, while the Chinese bahaba is legally protected in China (Sadovy 2001; Sadovy and Cheung 2003). It is noteworthy that the fishes that have recovered best from exploitation also have short life spans, such as clupeids which have dominated post Second World War fisheries and the thinking of fishery researchers (Hutchings 2000a, 2001a). Unfortunately, basing the perception that fecund fishes are more capable of recovery largely on examples from only one suborder of fishes represents a phylogenetic 'house of cards' (Sadovy 2001).

The absence of any strong link between high fecundity and low vulnerability across a wide phylogenetic range of both tropical and temperate species is supported by an empirical analysis of the life history correlates of population trends of exploited NE Atlantic fishes. Populations of species that declined more than their sister species were larger, matured later, and had lower potential rates of population increase (Jennings *et al.* 1998). However, fecundity was not significantly related to the response to exploitation, suggesting that this trait was a poor predictor of vulnerability. Fecundity also appears to be a poor predictor of demography and response to exploitation in less fecund groups. Demographic models of 26 Pacific shark species were used to calculate 'rebound potential', which is the rate of population increase at a standardized density – the estimated point of maximum sustainable yield (Smith *et al.* 1999). The best predictors of rebound potential were maximum age and age at maturity, and again fecundity was a poor predictor of this measure of resilience, even when phylogenetic relationships were taken into account (Smith *et al.* 1999; Stevens *et al.* 2000).

Large geographical range and wide dispersal confer resilience

Geographic range size and dispersal raise two issues relevant to extinction that deserve scrutiny (Sadovy 2001). First, marine organisms are often viewed as predominantly broadcast spawners of planktonic eggs and larvae that consequently occupy large geo-

geographic ranges with few barriers to distribution. Second, it is argued that broadcast spawning may confer high potential for the re-colonization of depleted populations (Malakoff 1997; McKinney 1997). Of course, it is worth noting at the outset that many marine fishes are not broadcast spawners, and that even pelagic broadcast spawners may have limited geographic ranges (Helfman *et al.* 1997; Reynolds *et al.* 2002b). For example, 40% of elasmobranchs are live-bearers and the egg-laying species deposit few large benthic eggs (Dulvy and Reynolds 1997). Many skate species (55%) are endemic to single zoogeographic localities (McEachran and Miyake 1990) and most species (70%) have ranges spanning less than 20 degrees of latitude, a proxy for geographic range size (Fig. 4). Even broadcast spawning species can exhibit small geographic range sizes; 24% of coral reef fishes are restricted in distribution to <800 000 km² and 9% are restricted to <50 000 km² (Hawkins *et al.* 2000).

Broadcast spawners are perceived to rain larvae down on areas far from the source. Early indications of genetic homogeneity of widely distributed broadcast spawning marine organisms had suggested few barriers to gene flow, leading to the inference that marine populations were highly interconnected (Rosenblatt and Waples 1986; Scheltema 1986a,b). Two problems have emerged with this evidence. First, these studies were based on genetic markers, such as allozymes, that often have insufficient resolution to rule out genetic differentiation and thereby reveal the possibility of low connectivity among marine populations (e.g. de Innocentis *et al.* 2001). Second, genetic homogeneity may not indicate the capacity of a species to repopulate an area because the interchange of relatively few individuals can lead to genetic homogeneity compared to the larger number

required to rescue a depleted population (e.g. Van Oppen *et al.* 1997).

Finer scale resolution afforded by the development of microsatellite and mitochondrial markers has revealed genetic differentiation in some temperate and tropical fishes over relatively small spatial scales, 100–200 km (e.g. Doherty *et al.* 1995; Rico *et al.* 1997; Lundy *et al.* 1999; Ruzzante *et al.* 2000; Planes and Fauvelot 2002). Therefore, populations may be considerably more restricted than is widely assumed.

Evidence for self-recruitment also challenges large-scale connectivity of marine populations. For example, it was estimated that up to 50% of bluehead wrasse (*Thalassoma bifasciatum*, Labridae) and 15–60% of juvenile damselfish (*Pomacentrus amboinensis*, Pomacentridae) are retained or return to natal reefs (Jones *et al.* 1999; Swearer *et al.* 1999). Local recruitment may be necessary to maintain stocks on the relatively isolated island of Bermuda, where measured pelagic larval durations were much shorter than estimated travel time to Bermuda (Schultz and Cowen 1994).

We can cast these findings into a metapopulation context to understand impacts of fishing or habitat loss on source-sink dynamics and connectivity. One possible outcome is that if a population is self-recruiting, then it will have little need for neighbouring populations to sustain it. Therefore, loss of a source neighbour will be less serious for a self-recruiting population than for a non-self-recruiting population. Conversely, if a self-recruiting population is exploited and suffers a depletion of its production of larvae, it may be less able to sustain itself than if a source population had supported it. While it is difficult to generalize the implications of the new findings on self-recruitment for extinction, the news may be good for maintaining populations when neighbours are lost, but bad for the populations that are being reduced.

A key question is how common is self-recruitment? Fish population dynamics can be divided into three categories based on intrinsic rate of population growth (r), environmental carrying capacity (K) and interannual variation in population size (σ) (Fagan *et al.* 1999, 2001). 'Persistent' species exhibit such low variability relative to their growth rates that extinction is unlikely. 'Refuge-dependent' species exhibit such high variability relative to their population growth rate that long-term persistence depends upon refugia or rescue dispersal from nearby populations. 'Carrying capacity-dependent' species exhibit low variability and low-growth rates, with larger populations better able to withstand higher levels of

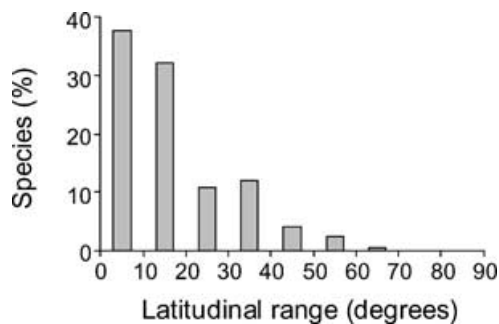


Figure 4 Frequency distribution of skate (Rajidae) latitudinal ranges. Based on data from 202 of 230 described species (Dulvy and Reynolds 2002).

variability (Fagan *et al.* 1999, 2001). An analysis by (Fagan *et al.* 2001) suggested that 21% of 91 fish populations exhibited 'carrying capacity dynamics', and 75% of fish populations exhibited extinction prone 'refuge-dependent' dynamics. These populations fluctuated so much that, in the absence of dispersal or refugia, extinction was determined to be a possibility over a 100-year time frame. For 'refuge-dependent' species, self-recruitment appears unlikely, which means that their constituent subpopulations do not exist in isolation, but act as metapopulation sources that rescue declining populations from extinction. Few fish populations could be categorized as persistent (4%), suggesting self-recruitment is either uncommon or has a relatively minor impact on persistence.

These demographic analyses need to be backed up by field studies to understand spatial connectivity of marine fish populations in relation to extinction vulnerability. For example, Western Atlantic cod and herring stocks comprise small geographically discrete subpopulations that have been serially depleted, and this may have disproportionately reduced the resilience of the entire aggregate population (Smedbol and Stephenson 2001).

Economic extinction precludes biological extinction

'It has often been assumed, usually tacitly, that extermination (of fisheries) was either impossible or unprofitable' (Clark 1972). The unprofitability argument stems from the expectation that economic extinction would be achieved before the point of biological extinction (Clark 1972, 1990; Beverton 1990, 1992). This is illustrated in Fig. 5(a), which shows the numbers of individuals caught and the value or costs of fishing for a targeted species according to population size. The costs and values are expressed as per unit effort (e.g. per day fishing, or per net set). In this simplistic model, more fish will be caught per day's fishing if the fish are more abundant, up to a limit (e.g. capacity of the boat). Assuming that the individual value per fish remains constant, a day's fishing will, therefore, provide a greater value of the total catch per day at high population sizes. The total cost of fishing per day increases less steeply with population size than does the value because capital investment will be fixed, and costs of fuel, labour, setting the nets, and so-on are largely independent of fish population size. Under this scenario, fishers are expected to reduce the fish population until the total

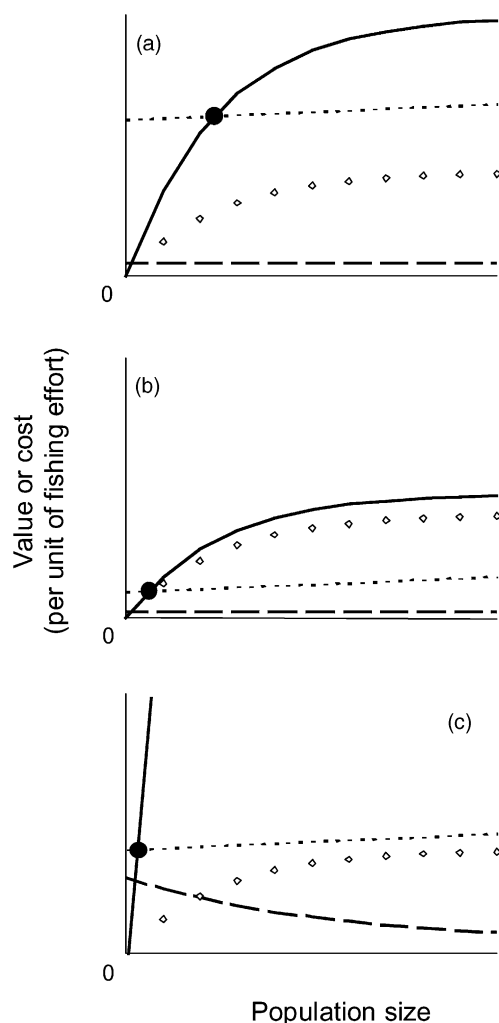


Figure 5 Total catch values (—), total catch costs (---) and number of individuals caught (◇) per unit of fishing effort as a function of population size for (a), primary target species (b), bycatch species and (c), fish with a rarity value. The point of economic extinction is (●). We assume constant per fish values (---) except for case (c) where value increases exponentially with increasing rarity. For bycatch species the additional costs of capturing such species alongside the primary target are negligible, and the value of bycatch is slightly less than for the primary target species. Hence the point of economic extinction is closer to biological extinction than for the primary target species. Note generally that as profit (value per fish – cost per fish) increases the economic extinction point moves closer to the biological point of extinction, to the extreme case where economic extinction occurs almost at the point of biological extinction for species with rarity value.

costs per day equal the total catch value per day, and this is labelled 'economic extinction'. The good news from this model is that economic extinction will

indeed occur well before biological extinction. The bad news comes when we account for other factors.

There are few single-species fisheries

Almost all fisheries are unselective multispecies affairs even when they target particular species (e.g. shrimp trawl fisheries). There are exceptions, such as those involving whales, certain pelagic fishes, and specialized seahorse, live food fish or deepwater aquarium fish fisheries, but most others take numerous by-catch species, some of which are discarded while others may have market value (Jennings *et al.* 2001b; Sadovy and Vincent 2002). For these by-catch species, the point of economic extinction may be closer to the point of biological extinction because it is still economical to continue capturing rare by-catch species so long as the target species is still viable (Sadovy and Vincent 2002). This is illustrated in Fig. 5(b), which shows that although by-catch species may have a lower total value per day's fishing, the added incidental total costs of fishing for such species will also be quite low. Therefore, the population size at which economic extinction occurs will move down closer to biological extinction than in the case of targeted species.

There are many examples of this process at work. Brander (1981) concluded a paper documenting the first clear case of a fish brought to the brink of extinction by commercial fishing by saying, 'it has to be accepted that this species (the common skate) and others like it will be fished out as a consequence of the exploitation of other demersal fish'. This proved to be prophetic, as two more species of skate and an angel shark have since disappeared from the Irish Sea (Dulvy *et al.* 2000; Rogers and Ellis 2000). The Irish Sea skate and ray fishery is worth approximately US\$ 1.6 million per year. It is a by-catch of a more valuable trawl fishery for Atlantic cod, European plaice (*Pleuronectes platessa*, Pleuronectidae), common sole (*Solea solea*, Soleidae) and other demersal species worth US\$ 11 million each year (Anonymous 1996).

Some fish are more valuable when rare

The economic extinction hypothesis relies on declining economic benefit per unit cost of fishing as stocks decline. However, if the value of a species increases as its abundance declines, the species may remain profitable if caught in a targeted fishery or opportunistically (Fig. 5c). This has been observed in a multi-species fishery in the Celtic Sea, where large piscivorous species have been rapidly depleted and

these species have exhibited greater price rises than other less-depleted species at lower trophic levels (Pinnegar *et al.* 2002). A number of species are targeted for their status as luxury food, highly valued for taste or texture, such as reef groupers (Serranidae) and Napoleon wrasse taken for the live reef food fish trade or the southern bluefin tuna captured for the Japanese sashimi market. Seahorses (Syngnathidae) and the Chinese bahaba are captured for their medicinal value. Higher value is also associated with rarity for many species taken in the aquarium trade (Wood 2001; Sadovy and Vincent 2002). Difficulties in obtaining highly valued gourmet fish for the live reef food fish trade in south-eastern Asia have not halted their exploitation. The Napoleon wrasse fetched a retail price of over US\$ 100/kg in the mid-1990s when the regional economy was thriving (Johannes and Riepen 1995; Lau and Parry-Jones 1999). Given declining supplies of this species in the seas around the major consumer market (Hong Kong), importers and traders initially sought it more widely from the South China Sea, the Philippines and Indonesia. As availability declined, more distant sources in the Indian and Pacific Oceans were explored (Sadovy and Vincent 2002). The increasing difficulty in procuring this vulnerable species is at least partly reflected in the current predominance of juveniles in the retail sector of Hong Kong's live reef food fish trade and an increase in the number of source countries, although demand could also be an important factor (Lee and Sadovy 1998). These signs of depletion have not diminished trade in this species, indeed, its rarity is likely to increase its appeal. The Chinese bahaba is one of the largest of all sciaenids and was first known to western scientists in the 1930s. It is now almost extinct throughout its limited geographical range (Sadovy and Cheung 2003). Long valued for the medicinal properties of its swimbladder, its price rose astronomically as its numbers plummeted and a large swimbladder recently fetched US\$ 64 000/kg (Sadovy and Cheung 2003). The high cultural and economic values associated with such species mean they will not necessarily become economically extinct much before their global extinction. We wonder what might the last southern bluefin tuna, Chinese bahaba or Napoleon wrasse be worth?

The global retail value of the trade in marine aquarium fishes in the last decade has been estimated at anywhere between US\$ 90–300 million (Wheeler 1996; Biffar 1997; Warmoult 2000). Prices are dictated by consumer preferences for particular species,

as well as by colours and sizes within species, availability, ease of shipping, market forces and source country (Sadovy and Vincent 2002). Increasing rarity often means even higher prices; the peppermint angelfish (*Centropyge boylei*, Pomacanthidae) may fetch as much as US\$ 10 000 in some markets because of its scarcity (Wood 2001). Whether or not such species are truly rare, or supply is kept low by traders or fishers to keep prices high, they are likely to be expensive if they are difficult to obtain (e.g. deepwater species) or available from only a few fishers/divers. In any event, rarity confers higher value.

Depleted populations will recover

It was widely believed that fish populations could recover to former densities once exploitation halts. Sometimes this is true, as shown by the rapid recovery of target fish biomass following the cessation of fishing during the First and Second World Wars, and the well-known recoveries of several mammals such as sea otters and northern elephant seals (Table 1). Less well known is that both the common and the lesser black-backed gulls also declined sharply in the Wadden Sea in the 19th century, as a result of over-exploitation, and subsequently recovered (Table 1). But there are many counter-examples. Recent analyses of fish stock recovery rates after the point of maximum population decline are not encouraging. Only approximately 7% of stocks ($n = 90$) recovered within about one average generation (5 years) and only three stocks (12%) recovered after three generations (15 years) (Hutchings 2000a, 2001a). The failure of some stocks to recover can partly be attributed to continued fishing after the time of maximum population decline. For other stocks where fishing ceased after the decline, other biotic factors may contribute to the lack of recovery. Even heavily depleted populations still contain numerous individuals, possibly numbering in the thousands or even millions, yet numerical abundance alone appears insufficient to ensure recovery (Hutchings 2001a). But will they ever become extinct globally? We suspect the answer depends on whether they become vulnerable to Allee effects or ecosystem shifts.

Allee effects

The Allee effect, also known as depensation in the fisheries literature, is positive density-dependence. It can be defined as a positive relationship between fitness (of individuals) or per capita growth rate (of populations) and population size, at low-population

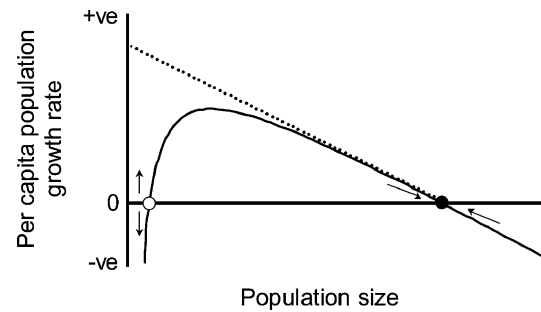


Figure 6 The Allee effect. The per capita rate of population growth indicates whether a population will grow (positive values) or decline (negative values) or remain stable (0). With logistic growth (dotted curve) there is only one equilibrium which is stable (●) at the carrying capacity, and population growth is negative above this carrying capacity and positive below, stabilising this equilibrium (as indicated by the arrows). If an Allee effect occurs (solid curve) then there is a positive relationship between population growth rate and population size at low population sizes and there is a second, lower, unstable equilibrium (○). This lower equilibrium is unstable because if the population drops below this equilibrium size (due to environmental variation, exploitation, predation or zero reproduction) negative population growth rates occur, causing the population to spiral toward extinction.

sizes or densities (Fig. 6) (Stephens *et al.* 1999; Petersen and Levitan 2001). Typically, under logistic dynamics there is one stable equilibrium population size at the so-called carrying capacity of the environment. If Allee effects are strong, one can get a second, unstable equilibrium at low-population sizes or densities (Fig. 6). Once a population is at the lower (unstable) equilibrium it takes little to tip it into the domain of negative population growth whereupon the species can spiral toward extinction (Fig. 6).

There are three general mechanisms for Allee effects: reduced reproductive output, predator saturation and conditioning of the environment (Liermann and Hilborn 2001). Fertilization, mating and consequently reproductive success can be reduced disproportionately at low densities. Low densities of sessile broadcast spawning invertebrates, for example, may produce gamete densities below the threshold for successful fertilization (Petersen and Levitan 2001). At high-prey densities predators are saturated and impose a relatively low per capita mortality on prey but as fishing reduces prey shoal sizes, an increasing proportion of prey can be killed, pushing the population into a predator pit from which it cannot readily escape (e.g. Courchamp *et al.* 1999; Liermann and Hilborn 2001). Similar argu-

ments can be applied to broadcast-spawning fishes. Adult fish of large populations often prey upon species that in turn prey upon or compete with their juveniles. Depleting a fish population may, therefore, reduce the survival of its juveniles, resulting in an Allee effect (Walters and Kitchell 2001).

Analysis of stock-recruitment curves of 128 stocks from four taxa (salmonids, gadiforms, clupeiforms and pleuronectiforms) detected only three stocks with Allee effects (Myers *et al.* 1995). A reanalysis of these data, although not confirming overall Allee effects, noted that the tails of the Bayesian probability density functions extended well into the Allee range, indicating low power to discriminate among hypotheses (Liermann and Hilborn 1997). Low detection power could be due to the scarcity of data points at low stock sizes and/or the difficulty of statistically quantifying the strength of the effect (Liermann and Hilborn 1997). In the Myers *et al.* analysis only 26 stocks had sufficient data to allow statistically powerful tests for Allee effects (Myers *et al.* 1995). By comparison, many more stocks appear to exhibit Allee effects if the data are qualitatively 'eyeballed' (Walters and Kitchell 2001). Statistical description of Allee effects may be hampered by the use of stock-recruitment models constrained to a zero origin, or where there is no clear spawner–recruit relationship. In such models recruitment is assumed to reach zero only when there are no fish, whereas Allee effects can result in zero recruitment even when fish are still present (Frank and Brickman 2000; Chen *et al.* 2002). More data and better methods are needed to evaluate possible Allee effects in marine organisms and establish whether they might be linked to recovery potential and extinction risk.

Direct links between Allee effects and extinction risk come from sessile broadcast spawners (Petersen and Levitan 2001). The white abalone is a long-lived slow-growing broadcast spawner that has been depleted throughout its range due to intense fishing (Davis *et al.* 1996; Tegner *et al.* 1996). Adult densities declined to a point where relatively sedentary adults evidently lost the ability to aggregate in sufficient densities to achieve fertilization. While adults can produce millions of eggs, at population densities of below approximately 1 animal per square metre fertilization does not occur (McShane 1995; Davis *et al.* 1996). Only eight individual white abalone now persist in an area where 16 000–820 000 animals were found 20 years ago. The last successful breeding event was in 1969 and the remaining senescent animals are not reproducing, hence we have referred to

them as extinct in Table 1. Threshold fertilization densities have been measured in another relatively immobile mollusc – the queen conch (*Strombus gigas*, Strombidae) (Stoner and Ray-Culp 2000). Mating behaviour was not observed where conch densities were below 56 individuals ha^{-1} and spawning never occurred below 48 individuals ha^{-1} , indicating a possible Allee effect.

Ecosystem shifts

There is increasing evidence of rapid and nonlinear shifts from one ecosystem state to another that could hinder species recovery in some ecosystems (Scheffer *et al.* 2001). These shifts can result from the functional removal of species, disrupting indirect interactions which have a stabilising role in communities, causing species replacements, trophic cascades and phase shifts (Yodzis 1988; Wootton 1994; Pinnegar *et al.* 2000). The removal of predatory benthic fishes by fishing has led to their unexpected replacement by species such as cephalopods, crustaceans, sea combs and jellyfishes, resulting in a global shift from groundfish to invertebrate catches (Caddy and Rodhouse 1998; Worm and Myers 2003). The depletion of predators has increased the abundance of grazing invertebrates, resulting in algal phase shifts on coral and rocky reefs (Lessios 1988, 1995; McClanahan and Muthiga 1988; Hughes 1994; McClanahan 1994; McClanahan 1995; Estes 1998; McClanahan *et al.* 2002; Steneck *et al.* 2002).

There are two key problems with interpreting ecosystem shifts in relation to extinction biology. First, we do not know which species, or groups of species, are the keystone players until they are lost or decline to a point where their functional role is diminished. Second, we have little idea how a change in ecosystem state will affect the recovery of species.

Marine fish populations are more variable and resilient than terrestrial populations

Great natural variability in population size is sometimes invoked to argue that IUCN *Red List* criteria, as one example, are too conservative for marine fishes (Hudson and Mace 1996; Matsuda *et al.* 1997; Musick 1999; Powles *et al.* 2000; Hutchings 2001a). For the (1996) IUCN list, a decline of 20% within 10 years or three generations (whichever is longer) triggered a classification of 'vulnerable', while declines of 50 and 80% led to classifications of 'endangered' and 'critically endangered', respectively. These criteria were designed to be applied to all animal and plant taxa,

but many marine resource biologists feel that for marine fishes 'one size does not fit all' (see Hutchings 2001a). They argue that percent decline criteria are too conservative compared to the high natural variability of fish populations. Powles *et al.* (2000) cite the six-fold variation of the Pacific sardine population (*Sardinops sagax*, Clupeidae) and a nine-fold variation in northern anchovy (*Engraulis mordax*, Clupeidae) over the past two millennia to suggest that rapid declines and increases of up to 10-fold are relatively common in exploited fish stocks. It should, however, be borne in mind that the variation of exploited populations must be higher than unexploited populations because recruitment fluctuations increasingly drive population fluctuations when there are few adults (Pauly *et al.* 2002).

While recruitment is indeed highly variable in marine fishes, there are weak links among fecundity, recruitment variability, maximum reproductive rate, and therefore, fitness (see section on 'Fecund species are less vulnerable', Myers *et al.* 1999; Hutchings 2000b, 2001a,b; Rickman *et al.* 2000; Denney *et al.* 2002). Furthermore, it has not been clear whether variability in breeding population sizes of marine fishes exceeds that of other taxa (Hutchings 2001b). To assess variability in the size of the breeding population, Hutchings (2001b) used the ratio of maximum to minimum spawner biomass: $N_{\max}:N_{\min}$. For 90 marine fish stocks, the back transformed mean of the \log_{10} -transformed ratio was 13 (± 1.2 SE). However, this figure was heavily influenced by herring-like fishes (Clupeidae $N_{\max}:N_{\min} = 14.2$, $n = 38$), which were almost twice as variable as cods (Gadidae $N_{\max}:N_{\min} = 8.2$, $n = 36$) and mackerels (Scombridae $N_{\max}:N_{\min} = 7.6$, $n = 12$) and much more variable than rockfishes (Scorpaenidae $N_{\max}:N_{\min} = 4.9$, $n = 9$) and flatfishes (Pleuronectidae $N_{\max}:N_{\min} = 4.6$, $n = 24$). Hutchings concluded that, with the exception of clupeids, the ratio varied between about 4 and 8 and noted that there are many species of birds and mammals for which $N_{\max}:N_{\min} > 4-8$. This suggests that the breeding component of exploited marine fish populations is not more variable than that of largely nonexploited bird and mammal populations. This is a conservative comparison because most of the nonmarine species were not exploited, therefore, one might expect virgin fish populations to be less variable than bird and mammal populations.

This conclusion was supported by a recent systematic analysis of the population parameters of 758 mammal, bird, fish and butterfly species. Three population parameters, the intrinsic rate of population

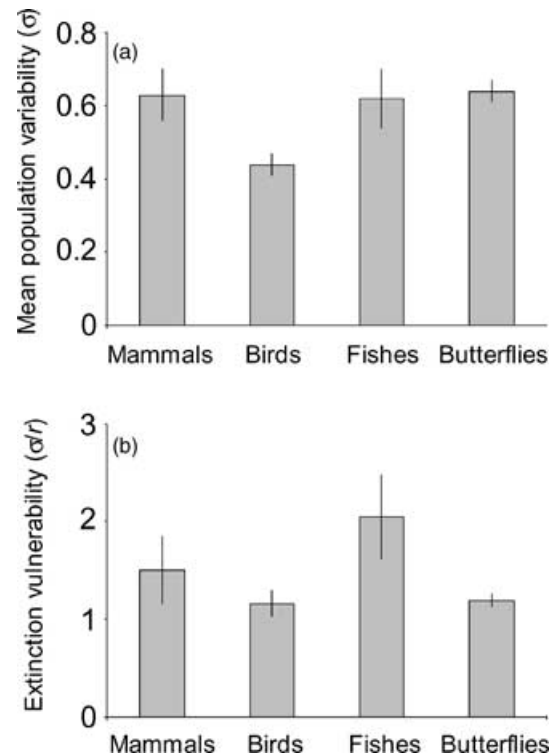


Figure 7 (a) Population variability σ , and (b) extinction vulnerability which was measured as the ratio of population variability to the intrinsic rate of population increase (σ/r) for mammals ($n = 86$), birds ($n = 166$), fishes ($n = 91$) and butterflies ($n = 415$). The bars represent 95% CI (Fagan *et al.* 2001).

increase (r), population carrying capacity (K) and the degree of population fluctuation (σ) were calculated by fitting a Ricker model (Fagan *et al.* 2001). There was no significant difference in population variability (σ) among mammals, fishes and butterflies (Fig. 7a). Together, these analyses refute the argument that marine fishes are inherently more variable than other taxa, with the possible exception of clupeids. Fagan *et al.* (2001) also calculated a measure of extinction vulnerability, as the ratio of population variability to the intrinsic rate of population increase (σ/r) and argued that high σ/r ratios predispose a species to extinction. By this criterion fishes were the most extinction-prone taxon, with significantly higher vulnerability than that of both birds and butterflies, but not significantly different from mammals (Fig. 7b). Therefore, there is no compelling evidence to suggest that fishes deserve special treatment by the IUCN's decline criterion on the basis of higher population variability than other taxa (Hutchings 2000b, 2001a,b).

Improving detection of extinctions

Eighty percent of the 133 local, regional and global extinctions that we have listed were discovered long after the event, usually by comparing historical species lists with the present day fauna. In only one case, the barndoor skate, was there a long time-series of abundance data sampled over most of the species' geographical range and even these data and survey design have been queried (Kulka 1999). Clearly, there is a need to evaluate methods of detecting extinctions at sea. Currently, this is achieved through one or a combination of ecological surveys, historical faunal comparisons, questionnaires and informal or anecdotal information gathering.

Ecological surveys

Ecological censuses have limited utility for detecting extinctions both because it is difficult to sample marine habitats effectively and because rare species require a large number of samples to determine their status with any accuracy. On coral reefs, the main fish census technique, underwater visual census (UVC), is limited by the amount of time that can be spent underwater with SCUBA. For example, it has been estimated that a basic fish census of Indonesia's coral reef fishes would take 400 person-years (Johannes 1998). Local extinctions have gone unnoticed for years even in well-sampled habitats; it was at least a decade and possibly much more before the realization that at least 5 and 31 species have disappeared from the Irish and Wadden Seas, respectively (Table 1).

These sampling difficulties produce data with a high degree of uncertainty. As species decline the variance of abundance estimates increases for a number of reasons. First, spatial variance increases as a species retracts to small patches of higher quality habitat, resulting in a patchy distribution – the buffer effect (Swain and Sinclair 1994; Myers and Cadigan 1995; Hutchings 1996; Brodie *et al.* 1998; Gill *et al.* 2001). Second, temporal variability increases as exploited fishes become rarer, because most of their age structure has been truncated by fishing, so total abundance becomes dominated by infrequent pulses of recruitment (e.g. Leaman and Beamish 1984; Jonzén *et al.* 2001). Such sources of intrinsic variation (process errors) are distinct from the methodological errors or biases associated with sampling (observational errors) (Hutchings 1996; Meir and Fagan 2000). Little can be done about process errors. How-

ever, observational errors can be reduced by increasing the temporal and spatial extent of replication.

Ecology matters too. As a general rule large-bodied species tend to be less abundant than smaller ones (Gaston and Blackburn 2000). An example comes from census data for 182 species of coral reef fishes in the Lau Islands, Fiji (Fig. 8). The relationship becomes particularly clear when phylogenetic relationships among taxa are accounted for in the analyses (Fig. 8b). Since vulnerable species tend to be rarely encountered, this means that greater replication is required to monitor them and to reach a confident conclusion about their status (Fig. 8c–f). An example illustrates this problem.

Is the barndoor skate recovering?

A severe decline in numbers of barndoor skates in the northwest Atlantic illustrates problems with interpretations of surveys of rare species. Casey and Myers (1998) raised the alarm about the precarious status of this species, leading to consideration for its protection under the US Endangered Species Act. The Stock Assessment Review Committee charged with assessing the status of the barndoor skate concluded that there was, 'no evidence that they were in danger of extinction or likely to become endangered within the foreseeable future' (NEFSC 2000). The conclusion was based partly on recent evidence that, 'barndoor skate abundance and biomass have begun to increase in surveys in USA and Canada' (Fig. 9). Our regression analysis suggests significant increase in the biomass index between 1983 and 1998 (Fig. 10a). Based on this increase it was concluded that, 'the small but sustained increase in research survey catches indicates that annual survival rates are currently high enough to allow for some recovery'. Consequently, the skate was not listed for protection. However, the power of the estimates of barndoor abundance trends was not considered. Not one barndoor skate was captured in the first 3 years of this time series and after 1983 the 95% confidence intervals encompass zero abundance for 13 out of the following 15 years (Fig. 10b). This suggests the abundance of the barndoor skate is statistically indistinguishable from zero. It should also be noted that the abundance index is composed of all size classes, rather than just mature adults, which would be preferred. The apparent recent increase in abundance may be a function of increased catches of juveniles and/or the tendency for recent surveys to have been done in areas that had been lightly exploited, including deeper waters, where the skates appear to be common (Kulka 1999). We suggest

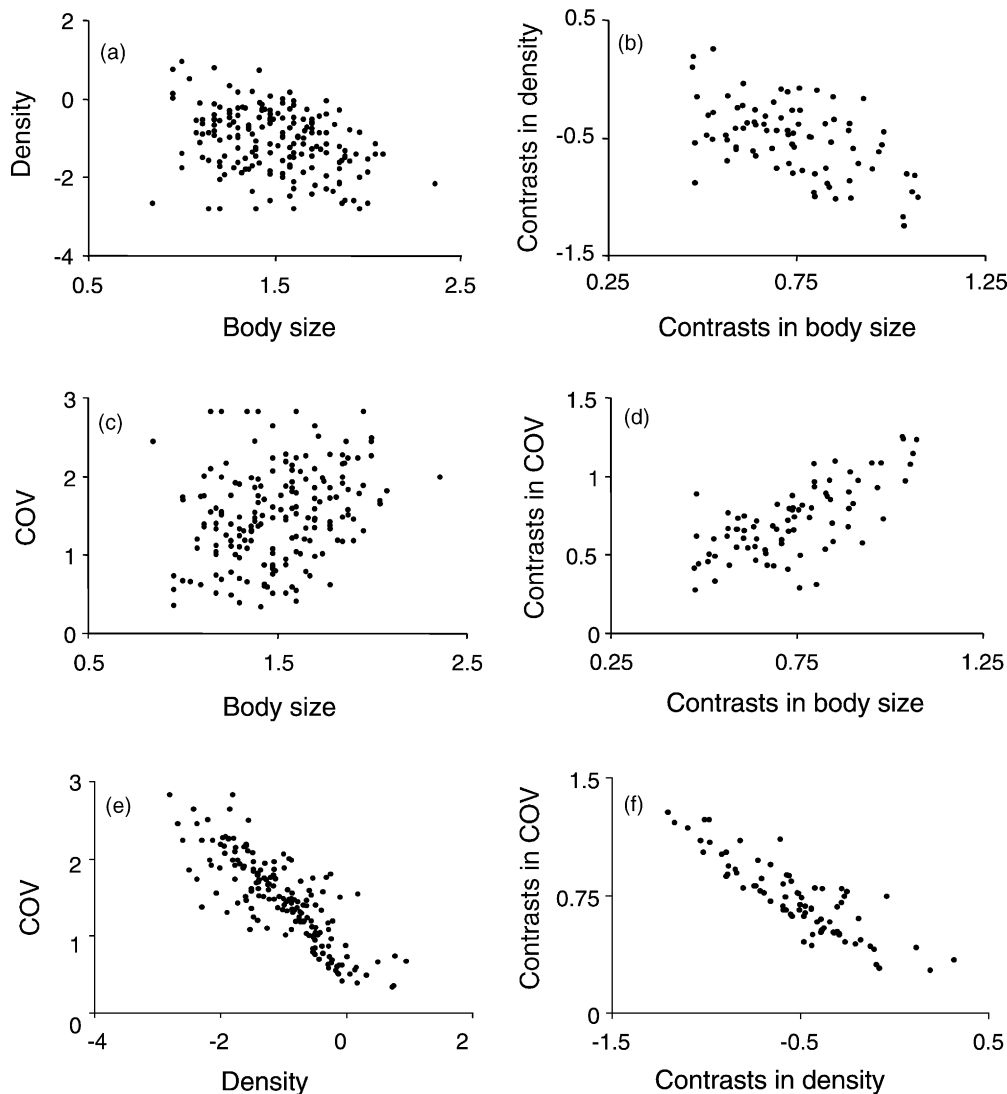


Figure 8 (a) Coral reef fish body size (\log_{10} cm) and density (\log_{10} number of individuals per count) relationships for all species and (b) the phylogenetically corrected relationship. (c) Body size and coefficient of variation (COV) for all species and (d) the phylogenetically corrected relationship. (e) Density and coefficient of variation (COV) for all species and (f) phylogenetically corrected relationship, $n = 182$ species (Dulvy and Polunin unpublished data).

that for large rare species the census power must be considered carefully in order to avoid nonprecautionary or erroneous conclusions about decline or recovery. Abundance trends should not be predicted when the point estimates of abundance are unreliable.

Historical faunal comparisons

Historical faunal comparisons typically attempt to compile a historical list of species presence or abun-

dance that can be compared to the modern faunal list based on museum collections or survey records. This method has detected by far the most extinctions (80%, from Table 1), despite the limited number of areas in which it can be used, e.g. Bermuda (Smith-Vanis *et al.* 1999), Wadden Sea (Wolff 2000a,b), and the Irish Sea (Dulvy *et al.* 2000; Rogers and Ellis 2000). This approach is limited by having at best only two data points: past and present. When more data are available an extinction probability can be calculated using data from incidental observations in an

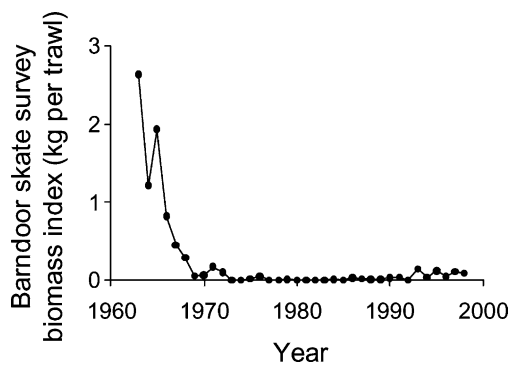


Figure 9 The overall decline in abundance of the barndoor skate from the Gulf of Maine to Southern New England. On average the biomass index of this species has declined by 96% between 1963–1965 and 1996–1998.

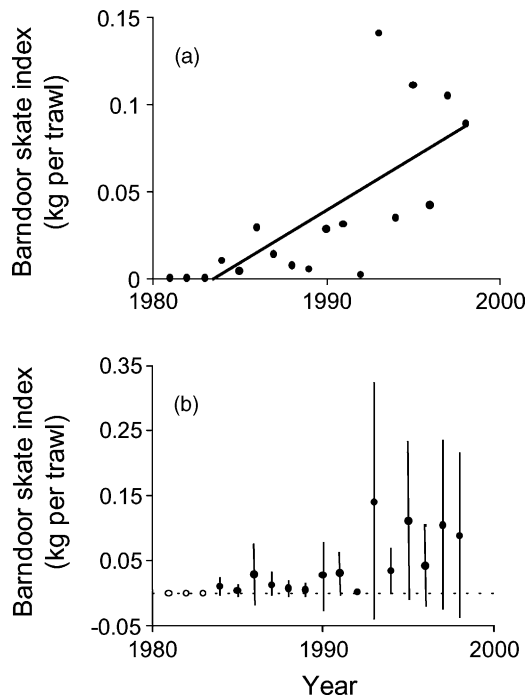


Figure 10 Two alternative interpretations of the recent status of the barndoor skate. (a) There has been a statistically significant increase in barndoor abundance since the early 1980s based on regression analysis upon mean abundance ($F_{1,14} = 13.8$, $P = 0.002$); and (b) the barndoor has been statistically extinct for 16 out of the past 18 years as demonstrated by either zero abundance or negative 95% confidence intervals.

informal data series, such as strandings, or a series of museum collections (Solow 1993; Reed 1996). One needs to know the number of time intervals in which the species was observed (n), the total number of

intervals in the survey series (T) and when the species was last observed (t_c) (Solow 1993; Burgman *et al.* 1995; Grogan and Boreman 1998). The probability that a species has disappeared at a particular spatial scale is

$$p = 1 - (t_c/T)^n \quad (1)$$

or where the total number of individuals recorded (k) is known,

$$p = 1 - (t_c/T)^k. \quad (2)$$

Grogan and Boreman (1998) suggest that minimum probability levels for declaring a species in danger of extinction, at the relevant spatial scale, should be $P = 0.75$, and as extinct should be $P = 0.95$. This approach was used to calculate the extinction probability of the Atlantic sturgeon from the James River, VA, USA. A total of 25 (k) sturgeon were captured in 9 (n) out of a total of 31 (T) years of annual surveying, and the last sturgeon was captured in the 25th year (t_c) of the data series. This results in sturgeon extinction probabilities of $P = 0.856$ for equation 1 and $P = 0.995$ for equation 2. It would be more prudent to use equation 2 because it is more sensitive to the frequency with which the species was collected prior to the last observation and also because it is more precautionary (Grogan and Boreman 1998).

Historical comparisons depend on accurate historical identifications and some form of sampling, of known methodology, over time (Rogers and Ellis 2000). While this may be possible in parts of Europe and North America, such methods are difficult to apply to many regions where historical written records are unavailable; such as Africa, parts of Asia and the tropical Pacific.

Questionnaires

Often historical scientific records are absent, but where humans are present there is often a vast store of traditional ecological knowledge passed down through generations by oral histories (Johannes 1978, 1981, 1998). This knowledge can be tapped by careful questioning to determine the previous status of exploited species. The near loss of the Chinese bahaba was first hinted at by a historical faunal comparison in Hong Kong (Sadovy and Cheung 2003). Confirmation of the geographical extent of its disappearance and probable causes of decline were then uncovered by questionnaire surveys of fishers, biolo-

gists, government officials and traders (Sadovy and Cheung 2003). Detection of severe declines and extinctions using questionnaires (or historical comparisons) can occur too late for useful conservation initiatives. However, questionnaires are inexpensive and provide a more rapid answer compared to other methods.

Predicting and categorizing vulnerability

'We seem unable to predict . . . the susceptibility of fish stocks to collapse' (Hutchings 2000b). Given the vast number of marine organisms and the difficulty of assessing their status, there is increasing interest in predicting which species are likely to be most vulnerable and should, therefore, receive greater attention (Dulvy and Reynolds 2002). For example, the World Conservation Union shark specialist group has undertaken Red List assessments of the 105 better-known species, but it also aims to assess the remaining 900 + sharks, rays and ratfishes in the near future. Which species of sharks, rays and ratfishes should they assess first? This is a typical problem faced by all international and national agencies concerned with conservation.

Biological correlates of vulnerability

We assigned three correlates of extinction to 61 of the cases listed in Table 1: large body size, small geographical range/endemism and habitat specialization. When there was only a single correlate, large body size was the most prevalent extinction correlate (57%), followed by ecological specialization (28%), and small geographical range and endemism (7%). Ecological specialists included populations that had disappeared due to habitat loss, such as some of those previously found in Bermuda and the Wadden Sea. Large body size is proving to be a useful vulnerability correlate for exploited species in marine fishes (Reynolds *et al.* 2001), birds (Owens and Bennett 2000), and many other vertebrates (Reynolds 2003). This may be because large-bodied animals are more sought-after and apt to suffer greater mortality, and also because large size is often correlated with other factors associated with vulnerability such as low intrinsic rates of population increase, late maturity, dependence on vulnerable habitat, and behaviours that substantially increase catchability (Reynolds and Jennings 2000; Reynolds *et al.* 2002a). In fishes, body size appears to be directly linked to r , the intrinsic rate of natural increase of a population (and

various surrogates) (Frisk *et al.* 2001; Denney *et al.* 2002), and r is the parameter that ultimately determines a population's ability to sustain fishing mortality and recover from collapse (Hutchings 2000b, 2001a). Species with low intrinsic rates of increase are expected to be less able to withstand elevated mortality or exploitation (Adams 1980; Kirkwood *et al.* 1994; Jennings 2000; Pope *et al.* 2000; Reynolds *et al.* 2001). Unfortunately, measuring r in the wild is fraught with difficulties, including lack of stable age distribution and modification of observed population growth rates by density dependence (Reynolds *et al.* 2001). However, since r is an integration of age- or stage-specific survival and reproductive output across all ages or stages at low-population sizes, it can be predicted by other allometrically related life history traits (Charnov 1993). For example, at the species level, body growth is negatively related to natural mortality (and therefore lifespan), as well as maximum body size, size at maturity, and age at maturity (Beverton and Holt 1957; Beverton 1963; Pauly 1980; Froese and Binohlan 2000; Frisk *et al.* 2001; Denney *et al.* 2002).

Empirical studies are beginning to provide support for links between life histories (in particular body size), demography and vulnerability. For example, when differences in fishing mortality among NE Atlantic fish stocks were controlled for statistically, population trends were related to body size, age at maturity and a surrogate for r (r'), though surprisingly, population declines were not correlated with slow body growth rates (Jennings *et al.* 1998). Shark and skate life history traits are as tightly interrelated as those of teleosts, and body size is likewise negatively related to demographic parameters, such as r' (Walker and Hislop 1998; Cortés 2000; Frisk *et al.* 2001). So, it is not surprising to find that body size is also a good predictor of population trend (while controlling for fishing mortality) in exploited skates, with larger skates having declined more quickly than smaller species (Dulvy *et al.* 2000).

The finding that body size is correlated with population trends suggests that this characteristic might provide a benchmark within clades for predicting vulnerability (Reynolds *et al.* 2001, 2002a). For example, in well-studied Atlantic skate communities, species above approximately 130 cm maximum length have largely disappeared, species in the 80–130 cm range are declining, and the smallest species have exhibited either stable or increasing abundance trends (Walker and Hislop 1998; Agnew *et al.* 2000; Stevens *et al.* 2000). Skates (Rajidae) are the most

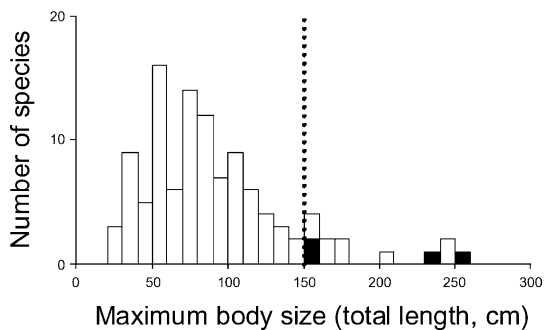


Figure 11 Frequency distribution of skate body sizes, $n = 109$. Locally extinct species are shaded and the benchmark (dotted line) is defined by the smallest locally extinct species (barndoor skate). All species to the right of this benchmark line exhibit sufficiently slow life histories to be vulnerable to extinction if exploited in a similar manner to the known locally extinct species (Dulvy and Reynolds 2002).

species-rich family of all elasmobranchs with over 230 described species, ranging in body size from 21 to 250 cm (McEachran and Miyake 1990; McEachran 1990; Dulvy and Reynolds 2002). The four species virtually eliminated from large areas are clustered at the upper end of the size spectrum (Fig. 11). The smallest of these is the barndoor skate, which is 152 cm long (Bigelow and Schroeder 1953; Scott and Scott 1988). If this species is used as a benchmark, then seven species enter the potentially vulnerable category (excluding the other species known to have completely or nearly disappeared from large areas) (Dulvy and Reynolds 2002). This priority list can be further shortened because so far three species inhabit deep waters that are beyond the reach of current fisheries. But it is important to identify such species now, before new fisheries appear.

Most of what we know of fish life histories comes from Atlantic species with simple life histories, but what about tropical reef fishes, many of which are sequential hermaphrodites or exhibit deterministic growth patterns? Despite these added complexities, relative body size was a good predictor of population trend for 33 intensively fished species of parrotfish (Scaridae), snappers (Lutjanidae) and groupers (Serranidae) in Fiji (Jennings *et al.* 1999b). Parrotfishes and groupers exhibit both sex change and a variety of growth trajectories (Thresher 1984; Sadovy 1996). Even when population trend is used without correcting for fishing effort (which is difficult to estimate in

general, but especially so in the tropics) the body size-vulnerability pattern still holds (Russ and Alcalá 1998; Jennings *et al.* 1999a).

Target species that aggregate in large numbers at locations that are consistent in time and space and which are easy to find can be readily overfished, leading to local depletions or extinctions (Vincent and Sadovy 1998; Reynolds and Jennings 2000). Examples include many exploited fishes that aggregate to spawn, such as orange roughy (*Hoplostethus atlanticus*, Trachichthyidae), blue ling (*Molva dipterygia*, Lotidae) and Nassau grouper (*Epinephelus striatus*, Serranidae) (Clark 1999; Sadovy and Eklund 1999; Roberts 2002). The pelagic slender armourhead (*Pseudopentaceros wheeleri*, Pentaceroideae) were fished over sea mounts. Some stocks collapsed in 1977 and have not recovered (Roberts 2002). Moreover, for a number of coral reef fish families, larger species are more likely to aggregate than smaller species (Sadovy 1996). It may be no coincidence that several species of croaker (Sciaenidae), often heavily targeted in their estuarine spawning areas, have attracted conservation concern (Sadovy and Cheung 2003). These include the massive totoaba (listed on CITES Appendix I in 1975 and a 'specially protected species' in Mexico), Chinese bahaba (Grade II protected in China) and the gulf weakfish (*Cynoscion othonopterus*) (Musick *et al.* 2000; Sadovy and Cheung 2003).

Dependence on particularly susceptible habitat, or behaviours that cause high and uncontrollable catchability in nontarget species, can contribute towards vulnerability, either alone or in combination with overfishing (Reynolds and Jennings 2000). Degradation of habitat and heavy by-catch of juveniles in the shrimp fishery threaten the totoaba (Cisneros-Mata *et al.* 1995). Three croakers listed as vulnerable in the US are particularly threatened by habitat degradation in inshore waters or estuaries, and many other vulnerable species listed by the American Fisheries Society were at risk partially due to life history limitation and habitat degradation (Musick *et al.* 2000). Nontarget species taken as by-catch in trawl fisheries, such as pipefishes and seahorses, may also be particularly susceptible.

Assessing vulnerability of communities

While univariate correlates of extinction may be the most objective way forward for assessing the vulnerability of clades (groups of species derived from a sin-

gle ancestor), there is often insufficient knowledge or time to tackle multispecies assemblages over large areas using rigorously underpinned approaches. For example, 82% of the northern Australian shrimp-associated catch is composed of a taxonomically diverse fauna that includes turtles, snakes and 411 fish species from 99 families including croakers, groupers, triggerfishes, sharks, rays, and sawfishes (Stobutzki *et al.* 2001a). The by-catch mortality rate is >90% for teleost fishes and may be greater for elasmobranchs (Stobutzki *et al.* 2001b). Which of these by-catch species are most vulnerable to the additional fisheries mortality, and should therefore be prioritized for conservation or management action?

One possible approach to this problem is to qualitatively rank species both according to their susceptibility to capture and with regard to their ability to recover (Stobutzki *et al.* 2001a). Teleost species were scored on a 1–3 scale for each criterion, with 1 representing most susceptible. The perceived relative importance of each criterion was also weighted. Susceptibility criteria included: height in water column, habitat, probability of survival, geographical range within the fishery area, catchability, diet and depth range. Recovery criteria included probability of breeding, maximum size, removal rate, reproductive strategy, hermaphroditism and mortality index. The total susceptibility or recovery rank was calculated by summing weighted ranks of criteria to provide an overall measure of relative vulnerability of each species. The teleost species least likely to be sustainably exploited included pufferfishes and porcupinefishes (Tetraodontidae and Diodontidae), dragonets (Callionymidae), wrasse (Labridae) and parental caring members of the catfishes (Ariidae, Congridae and Plotosidae), jawfishes (Opisthognathidae), cardinalfishes (Apogonidae) and benthic egg-layers such as lizardfishes (Synodontidae) (Stobutzki *et al.* 2001a). While this approach is arguably subjective it may be the only one available for researchers and managers of such fisheries.

Conflicts over categorizing vulnerable species

'Rule of thumb' approaches based on biological correlates of vulnerability are useful for focusing research or conservation attention but they cannot compete with more formalized assessments if the data are available. Several formal systems for assessing extinction risk have been developed, including the

World Conservation Union *Red List* guidelines, and various national guidelines. Criteria variously include rate of decline in abundance, low population size, small and/or declining range, fragmentation and fluctuations (e.g. World Conservation Union *Red List*). They may also include productivity indices, such as intrinsic rate of increase, body growth rates, fecundity, age at maturity and longevity or some combination of these (e.g. American Fisheries Society).

The primary criticism of IUCN Red Listing of species such as Atlantic cod and southern bluefin tuna was that in theory, the maximum sustainable yield (MSY) of a population occurs at 50% of virgin biomass. This is the same as the (1996) list's threshold for designating a species as endangered if the decline occurs over the last 10 years or three generations. The *Red List* published a caveat that such designations may not be appropriate for species subject to fisheries management. Despite the inclusion of this caveat many fisheries biologists still felt the list to be misleading because they believed that some of the commercially exploited species listed were actually at little risk of extinction (Matsuda *et al.* 1998, 2000; Powles *et al.* 2000). As an aside, it is worth noting that subsequent simulations have shown that if a population exhibits a strong Allee effect (depensation) then the point at which a population might be driven to extinction turns out to be close to MSY (Punt 2000). Nonetheless, the general point remains that productivity of any population will be maximized at a population size that is less than the virgin biomass, and a re-evaluation of the suitability of the *Red List* criteria for commercially exploited fishes was in order.

To address the concerns of fishery scientists, under the IUCN 2001 guidelines the decline thresholds were changed for cases where the causes of reduction are clearly reversible, understood and have ceased. Now a listing of 'vulnerable' is not triggered until such species have declined by at least 50% (instead of 20% in the 1996 list), 'endangered' is now set at 70% instead of 50% and 'critically endangered' requires a 90% decline instead of an 80% decline. As long as threatened species protocols such as the World Conservation Union *Red List* are aimed at a wide variety of taxa, there will always be limits to how well they can reflect every situation (Hudson and Mace 1996; Reynolds and Mace 1999). The World Conservation Union may still not have it right for commercially exploited fish species, which are examined with management reference points that are

much more complex and more conservative than the simple protocols of the IUCN (Powles *et al.* 2000). Powles *et al.* (2000) argue that, 'simple approaches are unlikely to work for marine species because of limited experience with extinctions to date and the wide variety of life history characteristics'. This is an interesting point because one might counter that such limited experience with marine extinctions might make a case for listening to scientists with greater experience with extinction biology from terrestrial systems. While threatened species criteria are indeed simplistic compared to the vast data gathering, assessment and management effort applied to a tiny fraction of the world's fish species, perhaps we need more comparisons between the two methods so that we can refine simple methods to assess the risks faced by the majority of fishes where so little is known about their biology.

It has been suggested that one possible source of the conflict is the use of World Conservation Union *Red List* categorization terminology which is potentially viewed as emotive, e.g. vulnerable, endangered and critically endangered (Hutchings 2001a). To overcome this problem Hutchings proposes renaming the categories according to priority, I–IV. However, he concedes this might not be possible because the current terms are more effective at grabbing the attention of the public and decision-makers.

In a sense, national and international threat categorization schemes represent the last benchmark for marine populations (Powles *et al.* 2000), but their adoption comes at the expense of allowing external conservation interests into the management process. Therein lies the conflict, but this is also the source of opportunity. The debate between resource biologists and conservationists can be seen as a chance to strengthen decision-making, management and policing of fisheries.

Conclusions

A charitable description of the quality of evidence underlying the extinctions at various scales listed in Table 1 is that it is 'variable'. So, we would not be surprised to see some readers question entries in this preliminary list and we will be happy to hear from you. Conversely, we are likely to have missed many extinctions, which we also hope to hear about so that we can update this table on the web (<http://www.uea.ac.uk/bio/updatehtml/marine/extinctions.htm>). Even if the reports of some of

these losses are eventually falsified, we predict that many such species will still be ecologically extinct in functional terms at the specified spatial scale. The analyses derived from this dataset suggest that while the ability to detect marine extinctions may be gradually improving, there is still a considerable way to go to identify which other species may be on the verge of disappearing or have done so already.

We find little evidence to suggest that marine taxa are less vulnerable than terrestrial taxa. While they may generally be more fecund, the high fecundity of broadcast spawners does not appear to result in higher maximum reproductive rates (Fig. 3), which are similar to those of similar-sized terrestrial taxa. Additionally, fishes are no more variable in abundance from year-to-year than are mammals and butterflies (Fig. 7a), and demographic analyses indicate they may actually be even more vulnerable than birds and butterflies, all other factors being equal, e.g. severity of threat (Fig. 7b). A barrier to precautionary thinking has been the hope that economic extinction would pre-empt biological extinction. However, this is unlikely to hold for non-target species caught in multispecies fisheries and for those fisheries targeting species with value that increases with rarity.

The ability to detect or falsify severe declines and extinctions will become increasingly important because of the conflicting viewpoints over extinction vulnerability. The determination of a species' status only begins with data collection. The hard part comes with the decision-making process. Beverton (1990) noted that decision making can be complicated and described how both sides of a resource conservation debate (pro-exploitation and pro-conservation) could end up in entrenched positions. Two issues arise from this uncannily prescient view, first, that both sides should simultaneously consider alternative hypotheses, rather than compiling evidence for their 'side'. To use a statistical metaphor each side should avoid opposing one-tailed tests of the same hypothesis. Second, this process will often result in deadlock, because as Beverton warned, decision making at this level is often an art form. So, if a qualitative judgement must be made, which way should the decision fall? Beverton was one of the first scientists to argue that the final decision should err on the side of precaution, i.e. assume the population or species may be in trouble, and then go on to simultaneously compile evidence to accept or refute the designated status of the species (Beverton 1990).

There are sound ecological reasons for applying a precautionary approach to extinctions.

The ecological context of extinctions may be important for decision making, but economics, politics and social development matter too. These social arenas are where prescription for changing the way people behave will succeed or fail. Despite the philosophical simplicity of the precautionary approach the case study of the barndoor skate suggests that there are still difficulties in its application. One possible approach toward minimizing the categorization conflict is for fisheries scientists to adopt a more proactive stance rather than the fire fighting approach often observed (Jennings *et al.* 2001b). Governments (and their scientists) rush from issue to issue in an attempt to placate pressure groups. While this provides a short-term fix, it does not necessarily resolve long-term issues or conflicts among groups. One area in which fisheries scientists could be more proactive is in the prediction of vulnerability, estimation of extinction risk and the prioritization of species for particular conservation or management attention. We have reviewed some initial progress in predicting vulnerability using both objective and subjective criteria in both data-rich and data-limited situations and for geographically and taxonomically diverse cases. While the utility of life history characteristics, in particular body size, as vulnerability indicators is becoming clearer, the relative importance of geographical range and endemism as potentially key correlates of extinction vulnerability has barely been explored in marine taxa (Hawkins *et al.* 2000). Those concerned with extinction risk need to join forces with resource managers to learn more about two things: the biology of the species of concern and the vital human dimension of both threats and solutions to conservation problems.

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