

Continental slope and deep-sea fisheries: implications for a fragile ecosystem

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Exploited deepwater (>500 m) species generally exhibit clear “K-selected” life-history characteristics markedly different from most shelf species: extreme longevity, late age of maturity, slow growth, and low fecundity. Many also aggregate on restricted topographic features such as seamounts, and as a consequence are notably unproductive, highly vulnerable to overfishing, and have potentially little resilience to overexploitation. Since 1964, deepwater fisheries have contributed 800 000–1 000 000 t annually to global marine fish landings. Underlying this apparent overall stability is the “boom and bust” cycle that has characterized many individual fisheries. The accumulated biomass of previously unfished stocks is typically fished down, often within 5–10 years, to the point of commercial extinction or very low levels. Most deepwater stocks are today overfished or even depleted. Depletion of species from deep-sea environments that dominate mid to upper trophic levels may have long-term ecological implications, but the risks of reduced stock size and age structure to population viability, the potential for species replacement, and the impacts on prey and predator populations are not generally known. However, trawl fisheries have been shown to have potentially severe impacts on the benthic fauna of seamounts, where these fish aggregate. This fauna, dominated by suspension feeders, such as corals, is typically restricted to the seamount environment and is characterized by high levels of endemism, which suggests limited reproductive dispersal. The ability of the benthic community to recover, following its removal by trawling, is not known.

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Introduction

Deepwater fisheries may be defined as fisheries deeper than about 500 m, near the lower limits of the upper slope. However, some fisheries are carried out across upper-slope depths, and species such as hakes may vertically migrate from below 500 m to near-surface waters. The implications of these differences in depth distribution for the species' ecology and life history may be profound.

With the exception of a few traditional deepwater fisheries, such as the South Pacific handline fishery for *Ruvettus* and the dropline fishery around the Azores and Madeira for black scabbardfish (*Aphanopus carbo*), all major deepwater fisheries developed after World War II. Indeed, until relatively recently, there was scientific consensus that significant fisheries were unlikely to develop for species confined to deep water, and deep-water fisheries were not covered in reviews of fisheries and deep-sea biology up to the 1980s (e.g. Gulland,

1971; Rowe, 1983). Ecological conditions in the deep sea were considered depauperate, based on the general exponential decline in organic sedimentation, zooplankton, and benthic biomass with depth (Vinogradov and Tseitlin, 1983; Rowe, 1983). While overall production of mesopelagic fishes was estimated to be very large (in the order of hundreds of millions of tonnes; Gulland 1971, pp. 175–177), the resources were generally too scattered and of too little value to justify commercial exploitation.

The development of deepwater fisheries may be understood, at least in part, as a late stage of the “fishing up” process (Deimling and Liss, 1994). As traditional fisheries on the continental shelf declined, distant water fleets developed to exploit less accessible populations, followed by shifts to less desirable species and more marginal fishing grounds. The global expansion of fisheries, particularly by the Soviets, soon uncovered deepwater habitats, such as seamounts, with substantial aggregations of benthopelagic fishes. Many of the dominant species in these environments, such as orange roughy, oreosomatids, Patagonian toothfish, and pelagic armorhead, were previously considered rather obscure taxa (Boehlert and Sasaki, 1988; Koslow, 1996). However, their size, flesh characteristics and abundance within these habitats made them highly suitable for commercial exploitation.

First, we briefly examine the life-history and ecological characteristics of the major exploited groups, because their traits are virtually unique and underlie key fishery impacts. We then review the development and direct impact of deepwater fisheries by major taxa and conclude with a brief review of the secondary impacts of these fisheries, in particular on deepwater habitats.

Ecological and life-history patterns

Of the primary families of fishes commercially exploited on the continental shelf – the Gadidae (cods), clupeoids (sardines and anchovies), Salmonidae (salmons), Scombridae (tunas and mackerels), and Pleuronectidae (flounders) – only species belonging to the Pleuronectidae are commonly exploited in deep water. Many deepwater fisheries are based on entirely different orders, such as the Beryciformes, Zeiformes, and Scorpaeniformes. Differences at this taxonomic level indicate fundamental shifts in body plan and ecological strategy, as well as in evolutionary lineage.

Bank and seamount aggregating species

Many deepwater species aggregate on seamounts and banks, where they can be readily targeted and provide high yields per unit of effort. These aggregating species have evolved from distinct groups in the different major

biogeographic provinces of the world ocean: orange roughy (*Hoplostethus atlanticus*) (Trachichthyidae) and the oreosomatids (Zeiformes) in the temperate South Pacific; alfoncino (*Beryx* spp.) (Berycidae) in the tropics and sub-tropics; Patagonian toothfish (*Dissostichus eleginoides*) (Nototheniidae) in the Subantarctic Southern Ocean; pelagic armorhead (*Pseudopentaceros wheeleri*) (Pentacerotidae) in the open North Pacific; and several species of *Sebastes* (Scorpaenidae) along the continental slope of the North Pacific and North Atlantic. These bank and seamount-aggregating species form a distinct guild based on common features of their body plan, proximate composition, physiology and metabolism, ecology, and life history (Koslow, 1996, 1997). They tend to be robust and deep-bodied in order to manoeuvre in the strong currents characteristic of this environment. The flesh is usually firm with a water content typically <80%, which contributes to their relatively high palatability and marketability. These fish generally do not migrate vertically. Rather, they depend on the flux of meso- and bathypelagic organisms past the seamount and on intercepting mesopelagic migrators on their downward migration, which enables them to maintain high population densities, despite the low productivity of the deep sea (Isaacs and Schwartzlose, 1965; Genin *et al.*, 1988; Tseitlin, 1985; Koslow, 1997). Many are exceptionally long-lived: orange roughy and oreosomatids apparently live to 100+ years (Tracey and Horn, 1999; Smith and Stewart, 1994) and deepwater *Sebastes* spp. to over 50 years (Chilton and Beamish, 1982; Campana *et al.*, 1990). Natural mortality rate (M) is thus exceptionally low, in the order of 0.05 or less. Growth is also very slow and maturity may be delayed to >20 years, particularly in species like the orange roughy (and unlike *Sebastes* spp.), which develop as juveniles in deep water (Table 1).

Slope and open seafloor-associated species

The other major group exploited in deep water belong to the Gadiformes, the most speciose order of deepwater fishes. The Macrouridae, in particular, generally dominate over relatively flat portions of the deep sea. These species are generalized predators and scavengers, feeding both in the water column and over the bottom (Haedrich and Henderson, 1974; Mauchline and Gordon, 1986). Several species have been aged to approximately 60 years and their growth rates are very low (Bergstad, 1990), although their life-history characteristics are generally not as extreme as the seamount-aggregating species (Table 1).

Morids (Moridae), cusk-eels (Brotulidae), and hakes (Merlucciidae) are more robust-bodied Gadiformes than the macrourids and are more active predators. Morids are generally benthopelagic, while cusk-eels are benthic. The hakes form a small but widely distributed family.

Table 1. Proximate body composition and some life-history parameters (ED: egg diameter in mm; A_m : age-at-maturity in years; A_{max} : longevity in years) of exploited deepwater fish.

Species	% composition			Life-history param.		
	Water	Protein	Lipid	ED	A_m	A_{max}
Slope and open seafloor associated spp.						
<i>Coryphaenoides rupestris</i> ^a	85	14	1	2.3	10	60
<i>Anoplopoma fimbria</i> ^b	79	11	6	1.5–2	5	53
Seamount and bank associated spp.						
<i>Hoplostethus atlanticus</i> ^c	76	13	10	2.2	25	125
<i>Pseudocyttus maculatus</i> ^d	79	13	6	2–2.5	23	78
<i>Allocyttus niger</i> ^d	74	17	8	2–2.5	20	100
<i>Sebastes alutus</i> ^e	75	21	3	5–7 ^f	10	90

^a% c.: Siebenaller *et al.*, 1982; A_m , A_{max} : Bergstad, 1990; ED: Scott and Scott, 1988.

^b% c.: Sullivan and Smith (1982); ED: Thompson, 1941, Hunter *et al.*, 1989; A_m : Mason *et al.*, 1983;

A_{max} : Chilton and Beamish, 1982.

^c% c.: Koslow, 1996; ED: Bulman and Koslow, 1995; A_m , A_{max} : Tracey and Horn, 1999.

^d% c.: Koslow, 1996; ED: Pankhurst *et al.*, 1987; A_m , A_{max} : Smith and Stewart, 1994.

^e% c. for female *Sebastes flavidus* muscle: Norton and McFarlane, 1995; A_m : Leaman and Beamish, 1994; A_{max} : Chilton and Beamish, 1982.

^fSize of larvae at extrusion: Leaman and Beamish, 1994.

They are often the dominant piscivores over upper portions of the continental slope and typically migrate vertically into the upper waters at night to feed (Bulman and Blaber, 1986). Their productivity is thereby linked directly to the near-surface food web, and their life history is similar to that of shelf-dwelling cods: blue grandier (*Macrouronus novaezelandiae*), for example, matures at 4 to 7 years old and lives to a maximum of 25 years (Kenchington and Augustine, 1987).

Other important continental slope species include the Greenland halibut (*Reinhardtius hippoglossoides*) (Pleuronectidae) and sablefish (*Anoplopoma fimbria*) (Anoplopomatidae). Sablefish is long-lived, but the juveniles grow rapidly in near-surface waters and they mature relatively early (Chilton and Beamish, 1982; Mason *et al.*, 1983).

Demographic implications

Benthopelagic fish species, unlike most meso- and bathypelagic fishes, are generally at the far K-selected end of the life-history spectrum. With their exceptional longevity, slow growth and delayed maturity (particularly when the juveniles grow up in deep water), these species fill a gap in the distribution of teleost life-history patterns (Roff, 1984).

Many exploited deepwater species also have relatively large eggs. Whereas pelagic eggs of most marine teleosts have a diameter of approximately 1 mm (Ware, 1975), the diameter for most species cited above is in excess of 2 mm (Table 1), with a consequent relatively low specific fecundity (Pankhurst and Conroy, 1987; Conroy and Pankhurst, 1989).

For the few species in which recruitment variability has been examined, recruitment appears to be highly episodic. Populations of orange roughy and *Sebastes* spp. undergo extended periods (in the order of a decade or more) of very low recruitment to the adult population (Leaman and Beamish, 1984; Clark, 1995). An evolutionary link between longevity and recruitment variability has been hypothesized (Murphy, 1968; Stearns, 1976).

These extreme life-history characteristics have profound implications for conservation and management. Slow growth and low natural mortality lead to an exceptionally low productivity. The sustainable yield for orange roughy has been estimated at only about 1–2% of pre-exploitation biomass (Clark, 1995). Low fecundity may contribute to reduced resilience and a reduced density-dependent response to low population size. Highly autocorrelated recruitment variability increases the risk of stock collapse, if the number of mature age classes is reduced below the interval between good recruitment events (Koslow, 1989). Therefore, assessment models assuming a mean annual recruitment to the population with random (i.e. non-autocorrelated) variability around the mean are inappropriate.

Development and status of deepwater fisheries

Landings from the major deepwater fisheries since 1950, defined as those with landings >10 000 t in any year, are shown by species group in Figure 1. Following the initial period of rapid expansion in the 1950s and early 1960s, landings have generally varied from 800 000 to

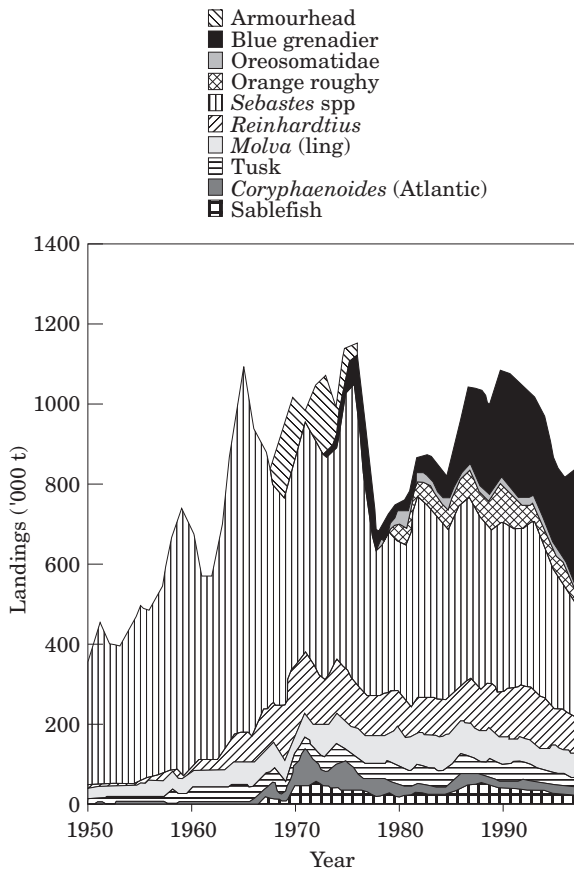


Figure 1. Total landings ('000 t) from deepwater fisheries world-wide by major species (groups), 1950–1997 (data: FAO).

somewhat over one million tonnes. However, the apparent stability of global deepwater landings is belied by the patterns for individual fisheries, which show that progressively new fisheries developed as traditional stocks and species within these groups were fished down (Fig. 2).

Sebastes spp.

Initiated prior to 1950 in both the Atlantic and Pacific Oceans, fisheries for species of *Sebastes* are the largest and longest standing deepwater fisheries (Fig. 2A). In the Pacific, the primary species of interest was initially Pacific Ocean perch (*S. alutus*), but several other species comprise the bulk of the catch at present. In the Atlantic, the primary commercial species are represented by the redfish complex, *S. fasciatus*, *S. marinus*, and *S. mentella*. These species are largely fished at the shelf-edge and along the upper slope – *S. mentella* lives deepest and is fished predominantly between 350 and 700 m – but they are included because they share many of the key ecological and life-history characteristics of

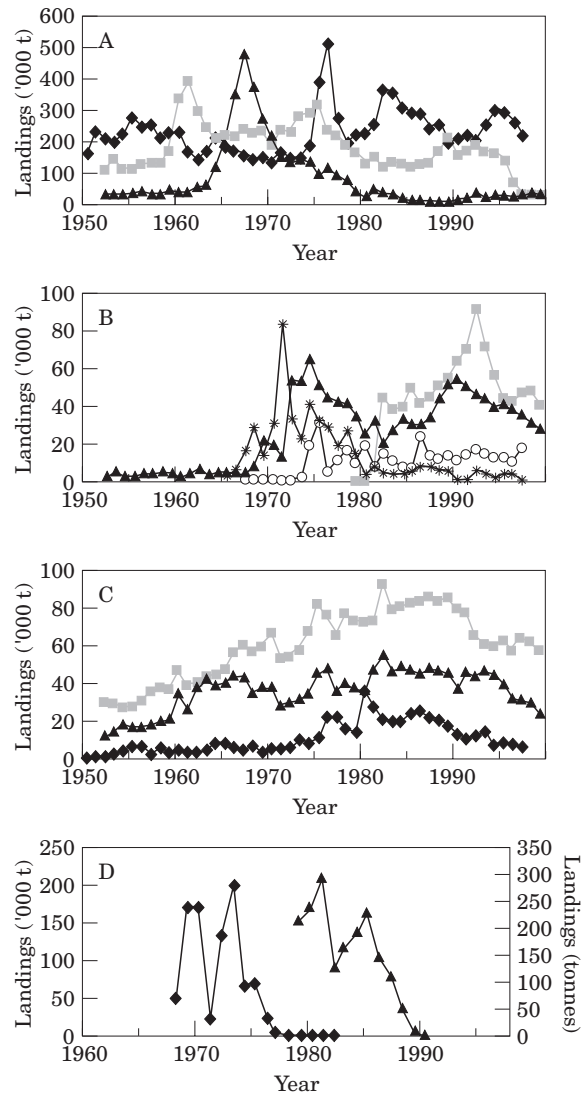


Figure 2. Landings ('000 t) for individual deepwater fisheries, 1950–1997 (data: FAO): (A) *Sebastes* spp. from NE Atlantic (diamonds), NW Atlantic (squares), and of *S. alutus* from Pacific Ocean (triangles); (B) orange roughy (squares); sablefish (triangles), and *Coryphaenoides rupestris* from the NE Atlantic (diamonds) and NW Atlantic (×); (C) ling (squares), blue ling (diamonds) and tusk (triangles); (D) pelagic armorhead (diamonds); precious pink coral *Corallium* sp. (triangles; landings in tonnes) from North Pacific Ocean (data from Grigg, 1993).

true deepwater species, i.e. longevity, episodic recruitment (Leaman and Beamish, 1984), and relatively low fecundity, due to their ovoviviparous reproduction.

In the Northwest Atlantic, the redfish fishery peaked in the late 1950s at almost 400 000 t and collapsed recently. Although relatively high catches were maintained over most of the period, there are signs that the fishery was overfished in the 1990s, when c.p.u.e. in

scientific surveys declined dramatically to <10% of the level in 1978–1985, and the mean weight of fish sampled was only about half the weight of the fish landed during the 1980s (Haedrich and Barnes, 1997).

In the Northeast Atlantic, the apparent stability in landings, which have fluctuated between about 150 000 and 300 000 t since the early 1950s, again masks more disconcerting shifts in the fishery. In the early 1980s, *S. marinus* represented 40% of the redfish catch. This species was gradually replaced by the deeper living and more oceanic *S. mentella* in the 1990s, such that *S. marinus* now comprises less than 20% of the catch. The major stocks have been overexploited (ICES, 1997), and the more offshore and deeper fishing grounds appear to support smaller stocks that can be quickly fished down.

There have been deepwater fisheries for several scorpaenids in the North Pacific, including several thornyheads (genus *Sebastolobus*). The largest scorpaenid fishery was for Pacific Ocean perch on the upper continental slope, primarily off North America. This fishery peaked at about 450 000 t in 1965, due to massive removals by distant water trawlers, and declined thereafter; since 1978, the fishery has fluctuated between about 5000 and 30 000 t (Ianelli and Zimmerman, 1998). The fishery subsequently extended deeper to exploit a complex of scorpaenids, some of which had previously been discarded or used for animal food.

Stock size for the Washington-Oregon stock of Pacific Ocean perch is currently at 13% of the 1960 value (Ianelli and Zimmerman, 1998). Leaman (1991) compared lightly and heavily fished populations and found that 73% and 7%, respectively, were older than 20 years old. Given the episodic recruitment, elimination of the older mature year classes may significantly impair the population's ability to withstand extended periods of poor recruitment.

The large sustained landings of deepwater rockfishes are still surprising. However, uncertainties about the unit stocks, and in the North Atlantic even the taxonomic composition of the catch, appear to have masked the progressive fishdown of successive *Sebastes* populations around the rim of both the North Pacific and the Atlantic.

Greenland halibut

Greenland halibut is a Subarctic species fished below 400 m across the North Atlantic and North Pacific, but 96% of the landings since 1950 have been from the Atlantic. Like redfish, landings of Greenland halibut have exhibited considerable stability, the fishery developing in the 1960s and peaking at 180 000 t in 1970 and subsequently being maintained at about 100 000 t. However, the mean size has declined dramatically in the Northwest Atlantic sector from a mean weight of

~1.0 kg in the early 1980s to just above 200 g since 1992, which is substantially below the size at 50% maturity (Merrett and Haedrich, 1997). The stock in the Northeast Atlantic is considered to be outside safe biological limits (ICES, 1997).

Coryphaenoides

There is a small growing fishery for *Coryphaenoides acrolepis* in the North Pacific and a substantial but diminishing fishery for *C. rupestris* in the North Atlantic (Fig. 2B; Merrett and Haedrich, 1997). The Soviets initially developed a fishery for *C. rupestris* (most abundant between 600 and 800 m) in the late 1960s in the Northwest Atlantic. Landings rapidly peaked in 1971 at over 80 000 t and then declined as quickly. Since 1980, landings have remained below 10 000 t and in 1997 dropped to only a few hundred tonnes.

In the Northeast Atlantic, the fishery developed in the mid-1970s and again quickly peaked, 30 000 t being landed in 1975, after which the fishery fluctuated mostly between 5000 and 20 000 t. The present status is not certain but appears to be poor. C.p.u.e. from the most productive fishing grounds to the west of Scotland declined by almost 50% from 1991 to 1996 (Lorance and Dupouy, 1998). The fishery on the mid-Atlantic ridge, the other major fishing ground, is also much reduced: landings since the early 1990s are only a few thousand tonnes, compared with 30 000 t in 1975. The species' longevity (>60 years; Bergstad, 1990) and a substantial by-catch of small individuals do not augur well.

Lings and tusk

Ling (*Molva molva*), blue ling (*M. dypterygia*), and tusk (*Brosme brosme*) are found across the North Atlantic but only the fisheries in the northeast sector are significant (Fig. 2C). Blue-ling landings peaked at 35 000 t in the early 1980s but are presently below 10 000 t (Bergstad and Hareide, 1996). Landings of ling have been stable, fluctuating between 50 000 and 60 000 t since 1975, whereas landings of tusk have declined steadily since the late 1980s (Bergstad and Hareide, 1996). Declining c.p.u.e. suggests severe depletion for all three species (Lorance and Dupouy, 1998).

Pelagic armorhead

In 1967, the Soviets discovered abundant stocks of pelagic armorhead (*Pseudopentaceros wheeleri*) on seamounts in the central North Pacific. For the ensuing eight years, Soviet and, to a lesser extent, Japanese trawlers landed 50 000–200 000 t annually (Fig. 2D) from the relatively few seamounts in the southeast Emperor-Northern Hawaiian Ridge system with summit depths between 260 and 600 m (Boehlert, 1986). Fishing

effort in this restricted area was very intense: 18 000 trawler days by the Soviet fishing fleet alone in the period 1969–1975 (Borets, 1975). By 1977, the fishery was reduced to a few thousand tonnes and there have been only minor landings since 1982, the species having been fished to commercial extinction.

Orange roughy and oreosomatids

Orange roughy (Fig. 2B) is fished predominantly on seamounts and deep plateaus at 700–1200 m depth around New Zealand and Australia; smaller fisheries are found in the Northeast Atlantic and off Namibia in the Southeast Atlantic. The first fishery was developed in the early 1980s on the Chatham Rise, east of New Zealand. The fishery peaked in 1990 at just over 90 000 t, following the discovery of aggregations on seamounts off Tasmania. However, these were fished down within several years. Since 1993, the fishery has fluctuated between 40 000 and 50 000 t.

To date, orange roughy landings have been maintained through progressive serial depletion of a number of stocks, primarily between southeastern Australia and New Zealand: newly-discovered stocks were typically fished down within 5–10 years to 15–30% of their initial biomass (Koslow *et al.*, 1997; Clark, 1999). The main stocks are now monitored with acoustic, egg, and trawl surveys; following the initial fishdown, their annual harvest is reduced to sustainable levels: 1–2% of the virgin biomass (Clark, 1995). It is doubtful whether the fishery can be sustained at present levels, given the lack of further seamount features to be exploited. Stocks too small to be actively managed, or those in international waters, are still at risk of depletion.

Recruitment to orange roughy stocks appears to be highly episodic. Despite the ~80% reduction in stock size, the size structure on the Chatham Rise and Challenger Plateau appeared unchanged over the first 15 years of the fishery (Clark, 1995), indicating no significant recruitment over this period. For the Tasmanian stock, the mode in the catch curve was initially for fish at about 50 years of age, rather than at 30 years, when the fish enter the fishery. However, current stock assessment models for orange roughy assume stochastic recruitment variability, which underestimates the risk of stock collapse.

Two oreosomatid species are landed in significant quantities in Australia and New Zealand: smooth oreo (*Pseudocyttus maculatus*) and black oreo (*Alloctytus niger*). Like orange roughy, they aggregate at mid-slope depths (850–1150 m) on rough ground and seamounts at temperate latitudes. Their longevity and productivity are also similar to that of orange roughy, so annual sustainable yield is estimated at <2% of virgin biomass. Since the early 1980s, the New Zealand catch has generally fluctuated between 15 000 and 25 000 t annually (Annala

et al., 1998). Stock structure, sustainable yield and stock status are generally not known, and there is considerable uncertainty whether current landings are sustainable. Oreo landings in Australia are about an order of magnitude smaller than in New Zealand, and the fishery is unmanaged.

Sablefish

Sablefish are fished across the North Pacific but there is a major fishery only along the continental slope of North America, where landings since 1970 have generally ranged between 20 000 and somewhat over 50 000 t (Fig. 2B). Sablefish have been managed intensively since 1982, but since then estimated stock biomass has declined from 78% of the earliest estimate available to 41% in 1998 (Methot *et al.*, 1998). In some regions, biomass may be depleted. This is the case off Southern California, for example, where photographic surveys 20 years ago indicated a high biomass of sablefish at 800–1500 m (Isaacs and Schwartzlose, 1975).

Blue grenadier

Blue grenadier, a hake fished between 300 and 600 m, is perhaps the only species that today sustains a large, sustainable deepwater fishery, possibly because it shares many ecological and life-history characteristics with shallower-water fishes (see above). Blue grenadier is fished primarily around New Zealand. Catches and quotas (TACs) have ranged between about 200 000 and 250 000 t since 1987 (Coombs and Cordue, 1995).

Community and ecosystem-scale impacts

What are the long-term ecological implications of depleting species that generally dominate mid- to upper trophic levels in deep-sea environments? Will these species be replaced by other, perhaps more opportunistic species? What will be the impacts on prey and predator populations? What are the risks of severely reduced abundance and elimination of the older age classes to population viability for long-lived species with highly episodic recruitment?

There is considerable potential to examine these questions. Because deepwater fisheries have often developed quite recently, data for many ecosystems may be obtained near their pristine state, which is generally not possible for shelf ecosystems. However, there are few answers to these questions at present.

Possible shifts in the demersal fish community were examined in relation to the orange roughy fisheries on the Chatham Rise and Challenger Plateau, where abundance is monitored with trawl surveys, but no significant

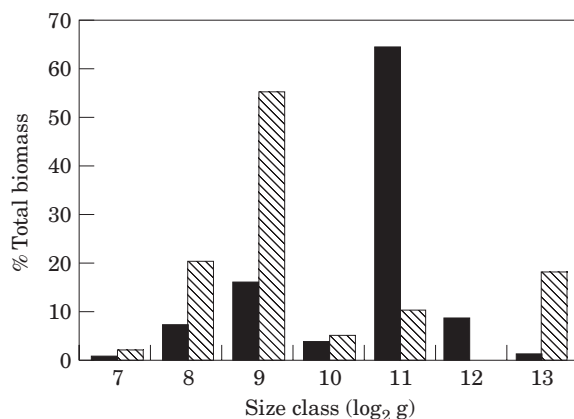


Figure 3. Percent biomass distribution of the Newfoundland deepwater fish assemblage by \log_2 size classes (g), 1981 (black) and 1991 (hatched).

shifts have been observed (Clark and Tracey, 1994; Clark, 1995, 1999). On the Chatham Rise, 9 out of 17 species showed a downward trend between 1984 and 1994, with a median decline of 50%. Only one species, *Centroscymnus crepidater* (a dogfish), increased significantly. The general decline of most species was not unexpected, since the trawl fishery operated on both flat areas of the continental slope and the seamounts. Similarly, trawl surveys in the Northeast Atlantic carried out on the continental slope before and after the onset of deepwater trawling showed no significant shift in species composition, although sharks may have declined more than other species groups (Lorance, 1998).

Jennings and Kaiser (1998) drew the general conclusion that evidence for shifts among competing species due to the impact of fishing is weak. However, community change in the deep sea may operate on relatively long time scales, given the longevity, slow growth, and late maturation of many species, and most deepwater fisheries are probably too recent to reach firm conclusions regarding community stability.

The size structure of deepwater fish assemblages shifted to smaller sizes both in the Northeast Atlantic (Large et al., 1998) and off northeast Newfoundland (Haedrich, 1995), presumably as a consequence of the fishery (Fig. 3). This suggests a shift in the community structure to dominance by species or size classes that turn over faster and consume smaller prey (Merrett and Haedrich, 1997).

The evidence for density-dependent changes in deepwater fish populations has been examined in few stocks and the available evidence is somewhat equivocal. Fecundity for Tasmanian orange roughy increased 20% as stock biomass declined by about 50% (Koslow et al., 1995), but a similar change was not observed for orange roughy on the Challenger Plateau off New Zealand (Clark et al., 1994). Decreased biomass of Pacific Ocean

perch was associated with accelerated growth and an earlier age at maturity; it was also suggested that it led to increased growth rate in a lightly fished competitor, *S. diploproa* (Boehlert et al., 1989), causing increased egg production relative to age (Leaman, 1991).

There have been no studies of the impact of deepwater fisheries on predator or prey populations of the target species. However, species that aggregate on seamounts and near other local topographic features, such as armorhead, rockfish, and orange roughy, may require the production from an ocean area in the order of 10 times larger than the habitat that they physically occupy (Tseitlin, 1985; Koslow, 1997). Therefore, aggregations of these predators may affect the local abundance of their prey, where vertically migrating species are trapped by the shoal topography (Isaacs and Schwartzlose, 1965; Genin et al., 1988), but it is unlikely that they significantly regulate prey abundance over the range of their prey's distribution, given that these features represent a very small proportion of the available ocean area.

Coupling between the benthic and benthopelagic components of seamount ecosystems has not been examined. Presumably, resident fish aggregated over seamounts rain down a significant quantity of detrital material; fishing down these aggregations could potentially cut off a significant energetic input to the benthic community.

Fishery impacts on deepwater habitats

One of the clearest impacts of deepwater fisheries has been on benthic habitats. The benthic fauna of seamounts is typically distinct from that found on the surrounding seafloor, because the intensification of currents leads to a fauna dominated by suspension feeders, including scleractinian, antipatharian, and gorgonian corals. This fauna has been impacted both by fisheries directly targeting corals for the jewellery trade and indirectly by trawl fisheries targeting seamount-associated fish species.

The recorded landings of deepwater coral are low – in the order of 100 t per year – but their value is high and as many as 100 vessels operated in the distant-water coral fishery in 1981 (Grigg, 1993). The method most commonly in use (“tangle” netting, which involves hauling concrete blocks with attached netting along the bottom) is destructive of the environment and inefficient, only a fraction of the broken coral being recovered. The greatest development of coral fisheries occurred in the North Pacific after 1965, when new beds were discovered in the Emperor Seamounts (Fig. 2D). Although data are poor, the Japanese and Taiwanese harvest apparently reached a peak of 150 t in 1969 and then fell rapidly, until the discovery of a new species of *Corallium* at depths from 900 m to 1500 m. As this species was depleted, landings declined 100-fold from

1984 to 1991 (Grigg, 1993). There is no indication of major new harvests. Available age and growth estimates suggest that the exploited corals grow slowly and reach ages of some 75 years; best field estimates of natural mortality rates are between 0.04 and 0.07 (Grigg, 1984).

Deepwater trawling on seamounts may also severely impact the benthic fauna, owing to incidental damage and removal as by-catch. A study on seamounts around Tasmania found some 300 species of fish and invertebrate macrofauna, of which 24–43% were new to science and 16–33% restricted to the seamount environment (Koslow and Gowlett-Holmes, 1998; the ranges in the estimates reflect uncertain species identifications for this poorly-known fauna). Benthic biomass per dredge sample was reduced by 83% and the number of species per sample by 59% in a comparison of fished and unfished areas. Photographic transects indicated that 95% of the bottom was bare rock on a heavily fished seamount compared with about 10% on the most comparable unfished seamount (Fig. 4).

The risk of severe depletion, and even extinction, of elements of the benthic seamount fauna is increased by their highly specific habitat requirements, localized distributions and high levels of local endemism. Their restricted distribution, in sharp contrast to the broad biogeographic range of most deepwater species, may arise from limited reproductive dispersal, coupled with larval retention along seamount chains (Parker and Tunnicliffe, 1994; Mullineaux and Mills, 1997). The high proportion of new species in the Tasmanian study indicates substantial differences in species composition between seamounts of Tasmania and New Zealand (cf. Probert *et al.*, 1997; Koslow and Gowlett-Holmes, 1998). Richer de Forges (1998) found only a 5% mean overlap in species between ridge systems at the same latitude and separated by only ~1000 kilometers in the Coral and Tasman Seas.

Concerns about the impacts of trawling on benthic seamount fauna led to one of the world's first deepwater marine reserves being established in 1995 over an area of 370 km² on the continental slope south of Tasmania. The reserve enclosed 14 seamounts in the vicinity of an orange roughy fishing ground. A study is currently underway to assess the impact of trawling on New Zealand seamounts. Given the high degree of endemism, adequate conservation will require a network of reserves both within areas of national jurisdiction and on the high seas. The size and distribution of the reserves should be based on a better understanding of the biogeography, reproductive strategies and ecology of the benthic fauna and its associated deepwater fishes. In some fisheries, changes in fishing practice, such as switching from trawling to long-lining, should be considered.

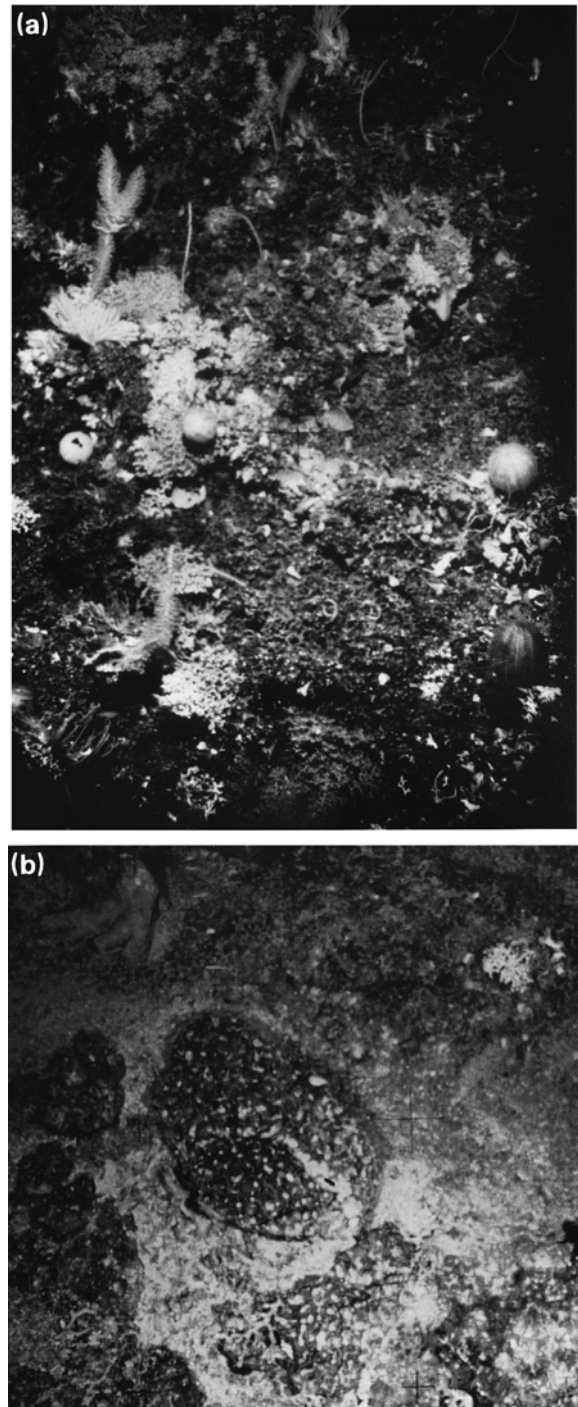


Figure 4. Photographs of seamount benthos, ~1000 m south of Tasmania: (a) unfished: scleractinian coral substrate with gorgonians, ophiuroids, urchins and sponges; (b) heavily fished: coralline community removed showing bare rock substrate with the broken base of a large bamboo coral in the upper left.

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