

Issues, status and trends in deep-sea fishery genetic resources

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1. SUMMARY

The deep sea is the largest habitat on earth, covering around 53% of the sea's surface, from the poles to the tropics. The deep-sea region starts at the shelf break at the continental margins, around 200 m, and extends down the continental slope and the continental rise to the abyssal plain at around 6 000 m, and the deep trenches. Deepwater fisheries occur on the continental slopes and on seamounts and exploit resources down to ~2 000 m. The continental slopes cover about 8.8% of the world's surface, an area greater than all the continental shelves and shallow seas, and include the most variable habitats in the deep-sea with canyons, ridges, seamounts, hydrothermal vents, and cold seeps.

Definitions of deepwater fisheries vary geographically, but generally occur at depths greater than 400-500 m; trawl fisheries for orange roughy (*Hoplostethus atlanticus*) and oreos (*Pseudocyttus maculatus*, *Alloctytus niger* and *Neocyttus rhomboidalis*) occur between 600-1 800 m, while long-line fisheries for toothfish (*Dissostichus* spp.) in the Southern Ocean operate down to ~1 800 m. Landings of deepwater fishes have risen from <0.5 m tonnes a year in the 1960s to >3 m tonnes by the late 1990s, with more than half of the annual catch taken from the Atlantic Ocean, but account for only ~5% of the total fish catch. The landing statistics are likely to be under estimates due to illegal, unreported and unregulated (IUU) fishing operations, and discards of bycatch species. Several deepwater fisheries have been characterized by "boom and bust" cycles. Catches of the armourhead (*Pseudopentaceros wheeleri*) on the North Hawaiian Ridge were estimated to have exceeded 150 000 tonnes a year during the late 1960s to 1970s where today no fishery exists. During the late 1990s a new fishery developed for orange roughy and alfonsino (*Beryx* spp.) in the South Indian Ocean with annual landings rising from <1 000 tonnes, peaking at 39 400 tonnes in 2000, and declining to <5 000 tonnes by 2002. In other regions orange roughy fisheries have been closed to commercial fishing, following a cycle of rapidly rising and declining catches. High catches of orange roughy in some areas have been maintained, at least temporarily, through local scale serial depletion as neighbouring seamounts and hills are fished down.

Deep-sea fishes include a large number of diverse species. Not all deepwater fishes are well described and molecular tools are being used to resolve taxonomic questions of species identity. Species exploited by deepwater fisheries include both shelf species, that extend down the continental slopes, and species restricted to depths >400-500 m. Most species are caught by trawls on seamounts and ridges, although line fishing and gillnets, and traps for invertebrates are used; toothfish (*Dissostichus* spp.) in the Southern Ocean are taken by trawl and long-line fisheries. An artisanal long-line fishery has existed for the black scabbard fish *Aphanopus carbo* for more than a century off Maderia, but most deepwater fisheries are relatively new and capital-intensive. A few small-scale

deepwater fisheries occur where the shelf is narrow and the fishery areas are accessible by small vessels using drop lines. The sustainable yields from such fisheries may be only a few hundred tonnes a year, but are important for small island states.

Deepwater fisheries generally target teleosts, with sharks taken as bycatch; only a few target invertebrates. In the North Atlantic deepwater fisheries, 22 species of teleosts 10 species of shark and two invertebrates (the red crab *Chaecon affinis* and the shrimp *Aristeomorpha foliacea*) make up the most important commercial species. Major species associated with seamounts include orange roughy, oreos, alfonsinos, and the roundnose grenadier (*Coryphaenoides rupestris*). A high degree of endemism has been reported for seamount invertebrates and fishes, but many of the targeted fish species have extensive ocean-wide and even cosmopolitan distributions.

As with coastal and shelf fisheries, conserving genetic diversity at the population, species, and ecosystem levels should be major goals for managing genetic resources in wild populations. Genetic issues identified for shelf species are likely to be magnified for deepwater species. Many slope and seamount species exhibit traits such as high longevity, slow growth rate, and late maturity, that make them more vulnerable to exploitation than most shelf species.

Marine fish tend to have higher levels of intraspecific genetic diversity than anadromous species, which in turn are more variable than freshwater species; a trend relating to larger evolutionary effective population sizes in marine fishes. Low levels of genetic diversity have been reported in the Antarctic toothfish *Dissostichus mawsoni*. Marine fishes show less spatial genetic differentiation than anadromous and freshwater species, due to the fewer barriers to gene flow in the marine environment. A negative relationship reported between genetic differentiation and dispersal potential in coastal fishes appears to apply to deepwater fishes. Recent developments with new molecular tools, coupled with new analytical approaches, have revealed finer scale population structure within ocean basins for the Patagonian toothfish *D. eleginoides*, but for many deepwater fishes there is little or no information on genetic diversity within and among regions, and the scale of appropriate management units remain uncertain. Local declines among orange roughy fisheries on neighbouring seamounts suggest that they may be independent units in the ecological time frame of fisheries management, in the absence of detectable genetic differentiation at small spatial scales.

Directional selection, through size-selective harvesting, has been implicated in changes in life history traits in heavily exploited stocks of shelf species, but has not been demonstrated in deepwater fishes, in part due to the limited time series of appropriate data. The genetic composition of a population can also change over generations due to random events. Changes due to genetic drift are most likely in small populations and are expected to be weak in marine fishes with large populations ($N > 10^7$). However 'sweepstake' events, due to high larval mortalities, can result in a small effective population size (N_e) several orders of magnitude smaller than the census population (N). Low N_e/N ratios have been demonstrated in several shelf species and are equally likely to occur in some deepwater species, and potentially lead to loss of genetic diversity in collapsed stocks

There is a general perception that the risk of extinction is low for commercially important marine fishes due to their large population sizes and wide geographical distributions. Only a few marine fishes have been listed as endangered and fewer appear to be close to extinction. Several traits of deepwater species (long life span, large body size, low natural mortality, and late sexual maturity) make them more vulnerable to extinction than shelf species, in particular those species that aggregate on seamounts. Deepwater fisheries have only been operating in the Northwest Atlantic Ocean since the 1970s, but already several species appear to meet the criteria of being critically endangered. Non-target species, that include teleosts endemic to

seamount complexes and elasmobranchs with low reproductive potentials, are also likely to be endangered.

Currently discarded fish waste from processing is used for low value products such as fish-oils, meals, pet foods, and silage. Bioactive compounds may be extracted from left-over fish-frames, internal organs, and invertebrate bycatch species for biotechnological and pharmaceutical applications, offering the opportunity to add value to fisheries. Some compounds derived from fish waste have been identified as potential nutraceuticals. Marine invertebrates that occur around hydrothermal vents may provide enzymes and biochemicals for the biotechnology industries and become target species in the future, raising further issues over exploitation of specialised deepwater habitats.

Genetic resources at the species and ecosystem levels are equivalent to ecological resources for which the management issues are well documented in the fisheries literature. The rapid development, and in some cases rapid depletion, of deepwater fisheries is of major concern to fisheries managers around the world, and has been identified repeatedly at local, regional, and international meetings. ICES have recognised that most exploited deepwater fishes are harvested unsustainably and radical reductions in fleets, in particular trawlers, are required to reduce effort and to conserve vulnerable habitats.

NGOs have expressed concern over the mortality of macro invertebrates taken as bycatch in deepwater trawl fisheries on seamounts, and for seabirds taken in toothfish trawl and long-line fisheries, although mitigation measures have been put in place to reduce the bird catch. The fragile and ancient coral “forests” found on seamounts that are amenable to trawling are quickly reduced to rubble by heavy trawl gear. Improvements to trawl gear and monitoring may allow the operation of deepwater pelagic trawls that avoid contact with bottom features. In the short term, one mitigation measure to protect vulnerable and unique habitats is to close selected areas to bottom trawling.

Many deepwater fisheries occur in high-seas areas compounding the problem of management and regulation. IUU fishing has been widespread in high seas fisheries. Increased surveillance and the introduction of a catch documentation scheme have reduced IUU fishing for toothfish within and outside the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Area in the Southern Ocean. Removal of fisheries subsidies should relieve pressure on deepwater stocks to some extent, but will need to be considered in parallel with other management tools. Regional Fishery Management Organisations (RFMOs) are being developed that cover high seas fisheries, and urgent action is required at the global level, to avoid shifting the deepwater fishing problem from one region to another. The inertia in developing and implementing international fisheries legislation, has led to NGOs calling for the designation of large scale protected areas, and for a moratorium on bottom trawling. Recent initiatives have seen the establishment of a high seas benthic protected area in the Southern Indian Ocean, with further proposals for a network of large Marine Protected Areas or Benthic Protected Areas in waters around Australia and New Zealand, and in the Southern Ocean.

2. INTRODUCTION

The impacts of large scale industrial fishing on coastal ecosystems are well known. In some shelf and open ocean fisheries the community biomass has been reduced by up to 80 per cent within 15 years of exploitation (Myers and Worm, 2003). For the recorded species of coastal and oceanic sharks in the Northwest Atlantic Ocean fisheries, all except one have shown declines in relative abundance of >50% since the mid 1980s (Baum *et al.*, 2003). Extinctions of marine species were thought to be rare events, but two species of skate are near extinction in the North Atlantic (Brander, 1981; Casey and Myers, 1998); in coastal fisheries the Pacific abalone *Haliotis sorenseni* is in a

perilous condition (Davis *et al.*, 1998), and some populations of giant clams, *Tridacna*, are locally extinct (Awaya and Lee, 2005).

Compared to the rest of the planet, much of the deepsea appears to be relatively unimpacted by human activities. International regulations prohibit the dumping of structures and radioactive waste in the deep-sea; and oil and gas extraction has been limited (Glover, AGS, C R 2003). However, the expansion of commercial fisheries into deep waters (>400 m) especially those in high seas outside coastal jurisdictions has been a major development in world fisheries in recent years (Watson, R and Morato, T 2004). Landings of deeper water species have increased, driven by technological developments, that enable fishers to target localised feeding and spawning aggregations of fishes in deepwater, and by catch-limits imposed in coastal fisheries. The biological issues of overfishing deepwater species are well documented and there is general agreement that many deepwater fishes are exploited beyond sustainable levels (Koslow, *et al.*, 2000; Haedrich *et al.*, 2001; Watson and Morato, 2004; FAO, 2005b; Devine, *et al.*, 2006; Morato *et al.*, 2006a and 2006b). Urgent action is required at the global level to reduce effort in deepwater fisheries and to protect fragile ecosystems from the impact of bottom trawling.

The impacts of fishing on deep-sea genetic resources are likely to be similar to those observed in shelf fisheries at the population, species, and ecosystem levels. In general, the effects of fishing on intra-specific genetic diversity are more difficult to detect than ecological impacts (Kenchington, E. 2003), but include loss of diversity through size-selective fishing favouring early maturity and slow growth (Dieckmann *et al.*, 2006 in press), and through reduction in numbers of breeding fish (Hauser *et al.*, 2002). Patterns of genetic diversity and population structure are not well known for most deepwater fishes. The life history traits of some deepwater fishes, in particular high longevity, slow growth, and late maturity, make them more vulnerable to fishing than coastal species (Morato *et al.*, 2006a and 2006b), such that they may require different management systems (Clarke, M. *et al.* 2003). Some deepwater fishes already qualify as endangered species following <20 years of exploitation (Devine *et al.*, 2006).

3. THE DEEP-SEA AND DEEPWATER FISHERIES

The deep-sea is the largest habitat on earth, covering around 53% of the sea's surface from the poles to the tropics. The deep-sea region is generally recognised as starting at the shelf break at the continental margins (around 200 m) and extending down the continental slopes and the continental rises to the abyssal plains at around 6 000 m, to include the trenches. Much of the continental slope and the abyssal plain regions are covered by soft mud substrates, but the slopes include the most variable habitats in the deep-sea with canyons, ridges, seamounts, hydrothermal vents, and cold seeps. Four depth zones are recognised in the deep-sea: mesopelagic (200-1 000 m); bathypelagic (1 000-4 000m); abyssopelagic (4 000-6 000 m); and the hadalpelagic below 6000 m depth, in the deep ocean trenches.

The deep-sea is a dark, cold environment. There is no primary productivity via photosynthesis; even at depths of 150m light levels are just 1% of those at the surface and are insufficient to support photosynthesis. Concentrations of organic material decrease exponentially with depth, but the deep-sea is fuelled by a rain of sinking dead phytoplankton and nekton, and by many species that perform extensive vertical migrations, transferring surface production into deeper waters. Specialist habitats are maintained by organic material derived from sinking wood and from whale carcasses and have lead to the evolution of unique fauna (Distel *et al.*, 2000) which along with fauna on hydrothermal vents and cold seeps are dependent on chemoautotrophic primary production (VanDover, 2000).

Limited resources in shelf fisheries lead to an expansion of fishing effort into deeper waters during the 1980s. Some shelf fisheries expanded into deeper waters on the continental slope as technologies developed, e.g. the North Atlantic fishery for Greenland halibut *Reinhardtus hippoglossoides*. Other deepwater fisheries are relatively new and target species that are restricted to deepwater, e.g. the orange roughy *Hoplostethus atlanticus* found in the Atlantic, Indian and Pacific Oceans between 600–1 600 m.

Deepwater fisheries occur on the continental slope and on seamounts (see Box 1) and exploit resources down to ~2 000 m. The continental slopes cover about 8.8% of the world's surface, an area greater than all the continental shelf and shallow seas (~7.5% of the world's surface). Definitions of deepwater fisheries vary geographically; ICES uses the term deepwater fisheries for those in depths >400m; others define deepwater fisheries as those occurring deeper than ~500 m (Koslow *et al.*, 2000). Around New Zealand deepwater trawl fisheries occur between 750–1 500 m, while middle depths fisheries are recognised between 200–750 m.

Most deepwater species are caught by trawls on seamounts and ridges, although line fishing and gillnets are used, as are traps for invertebrates; toothfish *Dissostichus* spp. in the Southern Ocean are taken by trawl and long-line fisheries. An artisanal long-line fishery has existed for the black scabbard fish *Aphanopus carbo* for more than a century off Maderia, but most deepwater fisheries are relatively new, technology-dependent and capital-intensive. The Spanish deepwater fisheries are opportunistic with target species changing according to availability of other commercial species (Pineiro *et al.*, 2001). A few small-scale deepwater fisheries occur where the shelf is narrow and the fishery areas are accessible by small vessels using drop lines. The sustainable yields from such fisheries maybe only a few hundred tonnes a year, but are important for small island states.

Several deepwater fisheries have been characterized by “boom and bust” cycles. Catches of the armourhead *Pseudopentaceros wheeleri* on the North Hawaiian Ridge were estimated to have exceeded 150 000 t a year during the late 1960s to 1970s (Boehlert, 1986; Boehlert and Sasaki, 1988; Somerton and Kikkawa, 1992): today no fishery exists. Catches of the Pacific Ocean perch (*Sebastes alutus*) peaked at around 450 000 tonnes in the mid 1960s and have since fluctuated at 5–30 000 tonnes a year (Ianelli and Zimmerman, 1998). During the late 1990s a new fishery developed for orange roughy and alfonsino (*Beryx* spp.) on the Southwest Indian Ridge with annual landings rising from <1 000 tonnes, peaking at 39 400 tonnes in 2000, and declining to <5 000 tonnes by 2002 (FAO, 2002). In other regions orange roughy fisheries have been closed to commercial fishing, following a cycle of rapidly rising and declining catches. High catches of orange roughy in some areas are maintained, at least temporarily, through local scale serial depletion as neighbouring seamounts and hills are fished down.

The top fish species by landings (>1 m tonnes a year) that account for 30% of the total world capture fisheries are shelf and pelagic species, and of these 7 are fully exploited or overexploited (FAO 2005c). Furthermore, the top 71 species of fish and invertebrates, which account for ~50% of capture production by tonnage are shelf and pelagic species, with only two middle depths (300–700 m) species, the grenadiers, *Macruronus novaezelandiae* and *M. magellanicus* (both >200 000 tonnes in 2003). China's landings of deepwater fishes are dominated by the largehead hairtail *Trichiurus lepturus* (which accounted for 1.5% of the total world marine fish landings in 2002), and although sometimes listed as a deepwater species, is more correctly a shelf species found in depths <400 m.

Landings of deepwater fishes have risen from <0.5 m tonnes a year in the 1960s to >3 m tonnes by the late 1990s, with more than half of the annual catch taken from the

BOX 1 Seamounts

Seamounts, steep sided undersea mountains, are widely distributed in the world's oceans and usually associated with volcanic activity (Rogers, 1994). Some definitions describe seamounts as features with an elevation greater than 1 000 m, but in practice "seamount" is applied to knolls (elevation 500-1 000 m) and hills (elevation <500 m) that contrast with the surrounding seafloor. Seamounts often occur in clusters along ridges leading to island groups or chains that are physically isolated from other island chains. Seamounts (and oceanic islands) enhance productivity, due to Taylor columns and upwelling of nutrient rich water (Rogers, 1994), and provide a unique deep-sea environment for fishes and invertebrates that are not found in the open ocean (Boehlert and Mundy, 1993; Koslow *et al.*, 2000; Richer-de-Forges *et al.*, 2000). Several teleosts spawn above seamounts where they form dense seasonal aggregations (Koslow *et al.*, 2000).

A high degree of endemism has been reported for benthic invertebrates (~30%) and fishes (12%) on seamounts (Wilson and Kaufman, 1987; Richer-de-Forges *et al.*, 2000; Froese and Sampang, 2004). The macro invertebrates on seamounts tend to be dominated by suspension feeding corals (Rogers, 1994) which are most abundant along the sides and ridges of seamounts and provide habitat for a diverse facultative fauna (Jensen and Frederiksen, 1992). Recent exploration using acoustics and submersibles has revealed unexpectedly widespread and diverse coral ecosystems in deepwaters on continental shelves, slopes, seamounts, and ridge systems around the world (Roberts *et al.*, 2006). In the New Zealand Exclusive Economic Zone macro-invertebrates in trawl samples are made up of Cnidaria (black corals, hard corals, and sea fans), Echinodermata (starfish, sea lilies, and brittlestarfish), Arthropoda (stone crabs and true crabs), and Mollusca (gastropods, octopus and squid); but the greatest invertebrate biomass has been corals (Probert *et al.*, 1997). These large epibenthic organisms are vulnerable to trawling, and corals have been the dominant bycatch in the development of trawl fisheries on some newly discovered seamounts (Anderson and Clark, 2003). On Tasmanian seamounts major impacts were recorded within a few years of the development of the orange roughy *Hoplostethus atlanticus* fishery; on heavily trawled seamounts (>1 000 trawls) reef aggregate was removed or reduced to rubble, and the invertebrate biomass was 83% lower than on lightly fished seamounts (Koslow and Gowlett-Holmes, 1998). The recovery of these deep-sea corals that may live for centuries (Andrews *et al.*, 2005) is likely to be extremely slow.

Fisheries for teleosts and to a lesser extent for crustacea occur on and around seamounts in the North Pacific Ocean along the southern Emperor and northern Hawaiian Ridge in the North Pacific, in the southwest Pacific Ocean around New Zealand, New Caledonia and Tasmania, and the SE Pacific off Chile, in the North Atlantic around the Azores and on the Mid Atlantic Ridge, and in the South Atlantic. Fisheries have expanded for toothfish around sub Antarctic islands and seamounts in the Southern Ocean and for orange roughy and alfonsino on the Southwest Indian Ocean Ridge.

Atlantic Ocean, but still accounts for only ~5% of the total fish catch. The landing statistics are likely to be under estimates due to illegal, unreported and unregulated (IUU) fishing operations, and discards of bycatch species.

Currently discarded fish waste from processing is used for low-value products such as fish-oils, meals, pet foods, and silage. Bioactive compounds may be extracted from left-over fish-frames, internal organs, and invertebrate bycatch species for biotechnological and pharmaceutical applications, offering the opportunity to add value to fisheries. Some compounds derived from fish waste have been identified as potential nutraceuticals (Kim, S-K. and Mendis, E. 2006). Marine invertebrates that occur around hydrothermal vents may provide enzymes and biochemicals for the biotechnology industries and become target species in the future, raising further issues over exploitation of specialised deepwater habitats.

Deepwater fisheries and genetic resources

Aquatic genetic resources have been defined by the 1993 UN Convention on Biological Diversity (CBD) as genetic material of actual or potential value. It has been assumed that such a broad definition encompasses the sum total of all aquatic plants and animals on the planet and that aquatic biodiversity and aquatic genetic resources are almost synonymous terms (Bartley and Pullin, 1999; Pullin, 2000). Fish stocks and bycatch that are exploited, or potentially exploited, by fisheries are all considered as genetic resources (Bartley and Pullin, 1999). However, unlike the terrestrial genetic resources based on plants (PGR), livestock (AnGR), and even aquaculture genetic resources (FiGR, after Pullin, 2000), the deep-sea genetic resources are based on capture from natural ecosystems.

Much of fisheries management has been and continues to be directed towards population and ecosystems management and incorporates genetic resources by default (FAO, 2005b).

The specific application of genetic tools in the management of capture fisheries has been limited to stock identification. Awareness is growing of the genetic structure of fish stocks and the impact of fishing on genetic diversity (Pullin, 2000), but for many marine species the patterns of genetic diversity are poorly understood. The short term pragmatic stock assessment goals to estimate maximum sustainable yields, by necessity have overlooked the long term goals of conserving genetic diversity.

Deepwater fishes

Deepwater fishes comprise three major groups: pelagic fish living largely in midwater, with no dependence on the bottom; demersal fish, living close to and depending on the bottom; and benthopelagic fish, living close to the bottom but undertaking vertical migrations in the water mass (e.g. for feeding). Much remains unknown about the biology and distribution of deepwater fishes and new species continue to be discovered (Roberts and Paulin, 1997; Roberts *et al.*, in press). Species exploited by deepwater fisheries include both shelf species, that extend down the continental slopes, and species restricted to depths >400-500 m, and have been grouped into those that aggregate on seamounts and ridges and those more generally dispersed on the continental slope (see Box 2). Many of the commercially targeted species are widespread horizontally, but zoned by depth (e.g. alfonso and orange roughy), and exhibit specialist adaptations for dispersal and recruitment (Boehlert and Mundy, 1993).

Species diversity is high in the deep-sea and many fishes exhibit unique adaptations, such as bioluminescent organs, modified swim bladders, jaws, and eyes for the deep-sea environment. FishBase lists 1276 bathypelagic species and 2103 bathydemersal species; 798 species of fish have been classified as seamount species (Froese and Sampang, 2004; Morato *et al.*, 2006a). Not all deepwater fishes are well described and molecular tools

BOX 2

Deepwater fishes

Species associated with seamounts

The **orange roughy** *Hoplostethus atlanticus* has a wide distribution in the Atlantic, Indian and South Pacific Oceans, where it is found between 500-1 800 m, but is most abundant from 750 to 1 100m. Fisheries have developed around New Zealand, south-east Australia, in the southwest Indian Ocean, off Namibia, Chile, and on the Mid Atlantic Ridge, but the bulk of the catch has been made in the southern hemisphere. The New Zealand fisheries initially concentrated on flat bottom and slope edges, but technical developments, such as GPS navigation, net monitoring, and swathe mapping, coupled with increasing experience in the deepwater fisheries lead to the targeting of orange roughy spawning aggregations on seamounts. The catch of orange roughy from seamounts has increased from about 30% of the total catch in 1985 to 80% by 1995 and has stabilized at 60-70% (Clark, 1999; Clark, and O'Driscoll, 2001).

In spite of the extensive distribution, adults are not highly migratory and movement, inferred from seasonal catches and changes in distribution, is only hundreds of kilometres. Orange roughy eggs remain in the plankton for only about 10 days before descending and hatching near the bottom and the larvae are assumed to be epibenthic (Zeldis *et al.*, 1994). Relatively few juveniles (<1 000) have been caught in bottom trawls around New Zealand (Mace *et al.*, 1990) where the fishery peaked at more than 50 000 tonnes a year (Annala *et al.*, 2000). The species is slow-growing, reaching maturity at 25-30 years of age, and may live for more than 100 years (Smith *et al.*, 1995).

The Oreosomatids, the **black oreo** (*Alloctytus niger*) and the **smooth oreo** (*Pseudocyttus maculatus*), support fisheries in the New Zealand and Australian EEZs. In the New Zealand EEZ black and smooth oreo, together with the less abundant **spiky oreo** (*Neocyttus rhomboidalis*), have been managed under a combined quota. The proportion of oreo catch derived from seamount fisheries increased from ~20% in the 1980s to 65% in the 1990s. Oreos aggregate in the mid slope region and above seamounts at 600-1800 m, and are long lived with estimated maximum ages of 86 years for *P. maculatus* and 150 years for *A. niger* (Doonan *et al.*, 1995). Smooth oreo adults are generally found north of 52° S, but most of the few recorded juveniles have been found between 60 and 68° S (James *et al.*, 1988); only 23 black oreo juveniles have been recorded from the New Zealand EEZ (McMillan, NIWA, unpub.obs.), despite annual catches >25 000 t within the New Zealand EEZ (Annala *et al.*, 2000). Juveniles of both black and smooth oreos are pelagic (James *et al.*, 1988) and settle at approximately 4 and 6 years respectively. The pelagic features and their low $\Delta^{14}\text{C}$ levels were interpreted as indicating a high latitude origin for black and smooth oreo juveniles (Morison *et al.*, 1999). It is possible that there are single genetic stocks of both species, and that juveniles recruit northwards, after which they show little dispersal and may form discrete ecological stocks.

Alfonsino (*Beryx splendens*) has a wide distribution in tropical and temperate waters of the Atlantic, Indian and Pacific Oceans and the Mediterranean Sea (Kotylar 1996), and occurs over seamounts and the continental slope in depths between 25-1300 m, but is most abundant between 300-500 m. Maximum age is 20 years and age at maturity is from 6 to 8 years. The adults do not appear to make extensive adult migration to spawning areas (Lehodey *et al.*, 1997), but the larvae and juveniles disperse widely in the pelagic environment for several months before settling on shallow seamounts (Boehlert and Sasaki, 1993). *B. decadactylus* has a wide distribution in tropical and temperate waters of except the eastern Pacific Ocean (Kotylar 1996), and occurs on the continental slope and ridges. Relative proportions of *B. splendens* and *B. decadactylus* are unknown.

BOX 2 (cont.)

Black cardinalfish (*Epigonus telescopus*) is widely distributed in the North Atlantic from Iceland to the Canary Islands, in the western Mediterranean, and in the South Atlantic, Indian, and southwest Pacific Oceans. The species occurs between 200–1400 m but is most common between 600–900 m. The juveniles are pelagic and undergo major ontogenetic changes; little is known of adult movements. Unvalidated otolith readings indicate slow growth and longevity, with maximum ages ~100 years. Around half the New Zealand catch (~2 000 tonnes year) has been taken as bycatch, with 80% taken in the orange roughy fisheries. In the North Atlantic black cardinalfish are taken as bycatch in trawl and long-line fisheries (Pineiro *et al.*, 2001).

Toothfish are large notothenoids living in Antarctic and sub-Antarctic waters. The two species are circumpolar, the **Antarctic toothfish** (*Dissostichus mawsoni*) is found at high latitudes south of the Antarctic Convergence around 60° S, while the **Patagonian toothfish** (*D. eleginoides*) ranges from about 50° S to 65° S, around sub Antarctic Islands and seamounts, between 50–60° S, and on the Patagonian Shelf and the southern coast of Chile to 30°S (Gon and Heemstra, 1990). *D. eleginoides* reaches a large size >200 cm and age of 50 years (Horn, P. 2002). It is targeted by trawl and long-line fisheries between 70 -1 800m, and was lightly exploited until the mid 1980s, with catches around several hundred tonnes a year. Catches increased rapidly during the 1990s; unofficial estimates suggested that catches reached more than 80 000 tonnes in 1996–97, with large IUU fishing activities (ISOFISH 1998), which have subsequently declined following the introduction of a catch documentation scheme. *D. mawsoni* reach a length of 175 cm and age of ~35 years (Horn, 2002) and have become the target of a number of new and exploratory fisheries since the mid 1990s, with TACs determined by CCAMLR.

Large catches of the **pelagic armourhead** (*Pseudopentaceros wheeleri*) were taken from seamounts (with summits 250–600 m) along the Emperor-Northern Hawaii Ridge in the central North Pacific during the 1970s. Annual catches were estimated at 50 000–200 000 tonnes, but were reduced to a few thousand tonnes in the late 1970s (Boehlert, 1986; Somerton and Kikkawa, 1992). The species is fast growing with a long pelagic juvenile phase and maximum age of 4 years.

Roundnose grenadier (*Coryphaenoides rupestris*) is abundant in the North Atlantic north of 50° N, from Newfoundland Banks to Rockall at 600–800 m, and occurs down to 2 000 m; long lived > 60 years; matures at age 8–10 years. *C. rupestris* is caught in mixed trawl fisheries with black scabbard fish in the NE Atlantic. Geographically distinct populations exist on the Mid-Atlantic ridge and the Hatton Bank, but its genetic relationships are unknown. A fishery developed in the Northeast Atlantic in the mid 1970s peaked at ~80 000 tonnes and declined rapidly to ~6 000 tonne a year by 1980; the fishery began in the north of the range and moved southwards in the NW Atlantic (Atkinson, 1995). *C. rupestris* has recently been identified as critically endangered (Devine *et al.*, 2006).

Sebastes spp. (**redfish** and **ocean perch**) have supported the longest deepwater fisheries in both the Atlantic and Pacific Oceans. Many species are long lived (up to 100 years), with slow growth rates and late maturity (> 20 years). *Sebastes alutus* is found <50–825 m in the North Pacific, from Honshu, Japan through the Bering Sea to California, with a maximum age of 100 years (Leaman, 1991). The primary focus of deepwater fisheries has been on the upper slope off North America, with catches peaking in the 1960s at around 450 000 tonnes, and since fluctuating at 5 000–30 000 tonnes (Ianelli and Zimmerman, 1998). The fishery has extended into deepwater and exploits several other species of scorpaenids (Ianelli and Zimmerman, 1998)

The *Sebastes* fishery in the Northwest Atlantic is based on the redfish complex *S. fasciatus*, *S. mentella*, and *S. marinus*, which are caught on the shelf edge and the upper

BOX 2 (cont.)

slope. The species are characterized by longevity, episodic recruitment, and low fecundity due to ovoviparous reproduction (Leaman, 1991). The Northwest Atlantic fishery peaked at 400 000 tonnes in the late 1950s and has recently declined. In the Northeast Atlantic the fishery has fluctuated between 150 000-300 000 tonnes since the early 1950s; this figure might mask serial depletion as *S. marinus* has been replaced in the landings by the deepwater *S. mentella*.

Continental slope species

The **ling** (*Molva molva*) is found in the Northwest and Northeast Atlantic on the continental shelf, and is common between 100-400 m; it is found down to 1000 m. The only significant fisheries are in the Northeast Atlantic, where landings have been around 50-60 000 tonnes since the 1970s, but recent CPUE data indicate severe depletion (ICES, 2005a). Ling reach 30 years of age and grow to 200 cm in length.

The **blue ling** (*Molva dypterygia*) is common between 350-500 m, and ranges between 150-1 000 m in the Northeast and Northwest Atlantic. Landings peaked at 35 000 tonnes in the 1980s, but declined to <10 000 tonnes. It reaches 20 years of age and 155 cm in length. Recent CPUE data indicate a severe depletion. Its growth rate is unknown (ICES, 2005a).

The **tusk** (*Bromse bromse*) is found in the Northwest and Northeast Atlantic on the continental shelf to 1 000 m, but the only fisheries are in the Northeast Atlantic. It reaches a maximum size 120 cm and a reported age of 20 years. Its landings are in decline and CPUE indicates a severe depletion. Its growth rates are unknown (ICES, 2005a).

Hoki or blue grenadier (*Macruronus novaezelandiae*) support the largest fishery in the New Zealand EEZ and are caught between 300-700 m. It occurs from 10-900 m, matures at 4-5 years and has a maximum age of 20-25 years. It is found around New Zealand and Tasmania. Annual catches in New Zealand peaked at 269 000 tonnes in 1997-98; the current TAC has been reduced to 100 000 tonnes. The **whiptail hake** (*Macruronus magellanicus*) supports trawl fisheries in the South Atlantic and South Pacific around South America from Punta Medanos Argentina to Valparaíso Chile. It is caught by the purse-seine fleet off central-south Chile. It reaches maximum age of ~20 years.

Greenland halibut (*Reinhardtius hippoglossoides*) is found in the North Pacific and North Atlantic Ocean on the shelf down to 2000 m; it reaches a maximum age of 30 years and length of 120 cm. The Northwest Atlantic fishery for *R. hippoglossoides* remained high over the 1960s to 1990s, but grew rapidly during the early 1990s with the entry of Spanish vessels into the fishery, leading to the much publicised Canada-Spain “turbot war” in 1993. The mean size of fish has declined rapidly and the bulk of the catch is made up of fish smaller than the size at maturity. A major collapse of the fishery appears likely (Haedrich *et al.*, 2001).

Black scabbardfish (*Aphanopus carbo*) has a wide distribution in the Northeast Atlantic in 200-1 600 m. There are longline fisheries off Madeira and Portugal and more recently *A. carbo* has become an important species in the mixed bottom-trawl fishery that developed in the Rockall Trough in the 1990s where it is caught with *C. rupestris*. Age estimates vary from 8-25 years with a maximum length of 110 cm. The stock composition of this species is unknown, but element composition of its otoliths indicates differences between the northern and southern areas of the Mid-Atlantic Ridge (Swan *et al.*, 2003). The eggs, larvae and small juveniles are unknown.

The sablefish (*Anoplopoma fimbria*) is found in the North Pacific: Bering Sea coasts of Kamchatka, Russia and Alaska southward to southern Japan and central Baja California.

BOX 2 (cont.)

It supports major fisheries in the NE and NW Pacific and reaches a maximum size of 200 cm, and maximum reported age of 114 years. It is found from the surface to 2 700 m: the juveniles are pelagic and migratory.

Deepwater sharks

In the Northeast Atlantic 12 species of shark are caught in the deepwater fisheries. The wide distribution of deepwater sharks means that fishers in deepwater areas cannot avoid catching them and the catch has risen from <100 t a year in the late 1980s to ~11 000 tonnes by 2003. The **Portuguese dogfish** (*Centroscymnus coelolepis*) and the **leafscale gulper shark** (*Centrophorus squamosus*) are target species in long-line and gill net fisheries but they, and other sharks, are taken as bycatch in trawl fisheries targeting orange roughy, roundnose grenadier, blue ling and longline fisheries for black scabbard fish. As trawlers have started to fish further down the continental slope the species mix of sharks has changed from that dominated by leafscale gulper shark in the early stages of the fishery to the Portuguese dogfish (ICES 2005b); more than 95% of the ICES shark catch probably consists of these two species; the other shark species have low commercial value and are discarded. A combined TAC applies to all deepwater shark species for 2006-07 (ICES, 2005b). The lack of species-specific catch data may have disguised an extreme decline of vulnerable species. Although it has been difficult to advise on a sustainable catch with limited information, the current fishing effort in the North Atlantic is recognised as too high (ICES, 2005b).

Both *C. squamosus* and *C. coelolepis* have wide distributions and depth ranges. *C. squamosus* is found between 150–2 400 m in the Eastern Atlantic, the Western Indian Ocean and Western Pacific, and although caught on the bottom 600–1 000 m it is pelagic above deepwater (4 000 m). It reaches a maximum age of 60–70 years and size of 160 cm. *C. coelolepis* is caught between 500–1 500 m and are found between 270–3 600 m in the Western and Eastern Atlantic, the Mediterranean and Western Pacific. It reaches a maximum size of 120 cm; Its maximum age is unknown, and it is near threatened.¹

Deepwater sharks in other fisheries are vulnerable, whether taken as targeted species or as bycatch. The dumb gulper shark (*Centrophorus harrissoni*), which is possibly restricted to Western Australia, Tasmania and New South Wales and caught in a deepwater trawl fishery off New South Wales, is critically endangered (FishBase).

¹ A general term used to cover taxa whose survival is uncertain (FishBase).

are being used to resolve taxonomic questions of species identity. DNA barcoding initiatives (Hebert *et al.*, 2003) will provide tools for the rapid identification of species in processed products.

Some of the commercially important deepwater fishes exhibit extreme life history traits with slow growth rates, high longevity (~100 years) and late maturity (15–25 years), see Box 2. In addition some species appear to exhibit long periods of low recruitment (Koslow *et al.*, 2000). For species with episodic recruitment the removal of older fishes may reduce the ability of populations to withstand extended periods of very low recruitment (Koslow *et al.*, 2000); for example the Pacific Ocean perch (*Sebastes alutus*) in lightly and heavily fished populations shows 73% and 7% respectively of fish older than 20 years (Leaman, B.M. 1991).

4. STATUS AND TRENDS OF THE GENETIC RESOURCES

Genetic resources and stock structure

A knowledge of the stock structure of marine fishes is important for the management and conservation of genetic resources. Several approaches are used to measure relationships among spatially isolated populations, most are based on ecological measures, such as a parasite load (McKenzie, 2002) or accumulation of trace elements (Thresher, 1999), or environmentally sensitive characters such as morphometrics and meristics (Cadrin, 2000). Molecular tools provide an alternative, indirect measure of dispersal and gene flow. Genetic diversity measured with most molecular methods is assumed to be selectively neutral and non-adaptive with respect to fitness. In general marine fishes have higher levels of genetic diversity than anadromous species, which in turn have higher levels than freshwater species (Gyllenstein, 1985; Ward *et al.*, 1994), a trend that probably results from larger evolutionary effective population sizes in marine fishes (Dewoody and Avise, 2000).

Marine fishes on average show less spatial genetic differentiation than anadromous and freshwater species, due to the fewer barriers to gene flow in the marine environment. Marine dispersal is constrained by the length of time of the pelagic larval and juvenile stages, by behavioural mechanisms, and by physical barriers such as gyres and ocean fronts. An inverse relationship has been reported between genetic differentiation and dispersal potential in small shelf fishes (Waples, 1987; Doherty *et al.*, 1995), but many of the larger shelf fishes show little genetic differentiation over ocean wide scales (Hauser, and Ward, 1998), possibly due to a combination of large population sizes and high mobility.

Deepwater species with potential for extensive dispersal through pelagic juvenile stages, such as the Pacific armourhead, (*Pseudopentaceros wheeleri*) (Martin *et al.*, 1992), the alfosino (*Beryx splendens*) (Hoarau and Borsa, 2000; Aboim, 2005), the wreckfish (*Polyprion americanus*) (Sedberry *et al.*, 1996; Ball *et al.*, 2000), and the silver roughy (*Hoplostethus mediterraneus*) (Smith unpublished observations) exhibit ocean-wide genetic population structures. In the wreckfish, microsatellite allele frequencies were homogeneous in the eastern and western North Atlantic and Mediterranean, but heterogeneous between the North and South Atlantic Ocean (Ball *et al.*, 2000), a genetic discontinuity supported by differences in mitochondrial (mt) DNA haplotype frequencies; and by implication there is little contemporary gene flow across the tropics (Sedberry *et al.*, 1996). In the redfish (*Sebastes mentella*) genetic homogeneity observed over 6 000 km probably results from larval gene flow in the cyclonic circulation of the central North Atlantic, although at wider spatial scales there is evidence for three genetically differentiated groups around the Gulf of St Lawrence/Newfoundland; the Grand Banks to the Faroes; and the eastern Atlantic and the Barents Sea (Roques *et al.*, 2002). In the hoki (*Macruronus novaezelandiae*) there is no genetic differentiation among spawning stocks within the New Zealand EEZ (Smith *et al.*, 1996), but there is genetic differentiation across the Tasman Sea (Milton and Shaklee, 1987).

Likewise for the black oreo (*Allocyttus niger*) and smooth oreo (*Pseudocyttus maculatus*) which have extensive pelagic dispersal during the juvenile stages, no significant genetic differentiation was found among black oreo and among smooth oreo samples from the New Zealand EEZ (Smith *et al.*, 2002). At wider scales a lack of genetic differentiation was reported in smooth oreo samples from Western Australia, Tasmania, and New Zealand, with a different suite of allozyme and mtDNA markers, and little evidence for genetic differentiation between black oreo samples from New Zealand and Tasmania (Ward *et al.*, 1998).

Mitochondrial DNA haplotype data indicated a strong genetic differentiation between populations of the viviparous blackbelly rosefish (*Helicolenus dactylopterus*) from the NE and NW Atlantic Ocean (Aboim, 2005; Aboim *et al.*, 2005). The

application of microsatellite DNA markers has revealed finer population structure within the central NE Atlantic Ocean off Portugal and around the Azores archipelago (Aboim, 2005).

Contrasting patterns of genetic differentiation have been reported in some congeneric pairs of species. In the Patagonian toothfish (*D. eleginoides*) a study of allozyme markers showed no significant regional differentiation among samples from the Southern Ocean, while microsatellite DNA markers showed significant heterogeneity, rejecting the null hypothesis of a single stock (Smith and McVeagh, 2000). Samples from the Indian Ocean were homogeneous for both mitochondrial DNA and microsatellite markers (Appleyard and Williams, 2004), but heterogeneity was found among samples from Macquarie Island, Heard and MacDonal Islands (Appleyard *et al.*, 2002). A major genetic break has been reported north and south of the convergence zone in the Atlantic Ocean (Smith and Gaffney, 2000a; 2000b; Shaw *et al.*, 2004). Recent studies with single nucleotide polymorphisms (SNPs) in *D. eleginoides* have revealed finer population structure with differentiation within ocean basins (Gaffney, University of Delaware pers.com.). In contrast, populations of the Antarctic toothfish (*D. mawsoni*) appear to be characterized by very low mitochondrial sequence diversity, and homogeneous frequencies of nuclear alleles and mitochondrial haplotypes among sea areas. These preliminary genetic data provide little support for the hypothesis of separate regional stocks of (*D. mawsoni*) (Smith and Gaffney, 2005).

In the congeneric alfonosinos (*Beryx splendens*) and (*B. decadactylus*) analyses of mtDNA haplotype data revealed major differences in the structure and history of the populations of the two species. *B. splendens* appears to have one population in the Northeast Atlantic, while *B. decadactylus*, exhibits lower genetic diversity but strong genetic differentiation between Cape Verde and the other populations in the NE Atlantic Ocean (Aboim, 2005).

The orange roughy (*Hoplostethus atlanticus*) and silver roughy (*H. mediterraneus*) have wide distributions in the North Atlantic, Indian and Pacific Oceans, but different dispersal potentials. Orange roughy have weak dispersal potential: their pelagic eggs sink and hatch near the bottom (Zeldis *et al.*, 1994) and exhibit genetic differentiation at small spatial scales in the SW Pacific Ocean and Tasman Sea (Smolenski *et al.*, 1993; Smith *et al.*, 1996; Smith and Benson, 1997; Smith *et al.*, 1997). In contrast silver roughy have a long pelagic phase and show little genetic differentiation at the oceanic scale (Smith, unpublished results). Local declines among orange roughy fisheries on neighbouring seamounts suggest that they may be independent units in the ecological time frame of fisheries management, in the absence of detectable genetic differentiation.

Genetic diversity in deep-sea soft sediment invertebrates and deep-sea corals

The deep-sea soft-sediment environment hosts a diverse and often highly endemic fauna of uncertain origins. Little is known of the genetic resources and the impact of trawling on these soft substrates, but some broadly distributed invertebrates exhibit genetically divergent populations in the absence of morphological divergence, and may represent cryptic species (Etter, 1999; Zardus *et al.*, 2006). High levels of genetic diversity were found in the protobranch bivalve (*Demimticula atacellana*), which is widespread throughout the Atlantic Ocean in soft sediments at bathyal and abyssal depths. Samples from localities in the North American, West European and Argentine basins were divided into four major clades, with DNA haplotypes unique to each basin (Zardus *et al.*, 2006). Genetic divergence was greater among populations at different depths within basins, than among those at similar depths in separate basins, indicating population differentiation at small (100s kms) spatial scales (Chase *et al.*, 1998; Zardus *et al.*, 2006). Depth-related divergence has also been reported in the deepwater amphipod (*Eurythenes gryllus*) (Bucklin *et al.*, 1987; France and Kocher, 1996), and this general finding may reflect historical patterns of colonization, or strong environmental

selective gradients, or horizontal dispersal in the deep-sea (Bucklin *et al.*, 1987; Etter *et al.*, 2005; Zardus *et al.*, 2006).

There have been few genetic studies on deepwater corals to identify dispersal and connectivity among seamounts (Baco *et al.*, 2006); yet such data are required for the development of management strategies for these species that dominate the fragile ecosystems. Low-sequence divergences were found among some deep-sea octocorals, but preliminary results for the bamboo corals (Keratoisidinae) in the SW Pacific suggest that some species are widespread and are not restricted to seamounts (France, and Hoover, 2002; Smith *et al.*, 2003). Genetic data for the scleractinian coral (*Lophelia pertusa*), the main framework-building species in the Northeast Atlantic at depths between 200 and 1 000 m, have revealed distinct offshore and fjord populations. The levels of genetic diversity in *L. pertusa*, and the contribution of asexual reproduction to the maintenance of the subpopulations were highly variable among sites (Goff-Vitry *et al.*, 2004).

Potential loss of genetic diversity in small populations

The genetic composition of a population can change over generations due to random events. Changes due to genetic drift are most likely in small populations and are expected to be weak in marine fishes with large populations ($N > 10^7$). However, sweepstake events driven by very high larval mortalities can reduce N_e (the number of individuals contributing to the next generation) by several orders of magnitude from the census population size, N (Hedgcock, 1994). Estimates of N_e in several shelf fishes are considerably smaller than census sizes (Bagley *et al.*, 1999; Chapman *et al.*, 2002; Hauser *et al.*, 2002; Turner *et al.*, 2002). Long-lived fishes with overlapping generations and annual spawning events are protected from loss of genetic variability due to drift, through the “storage effect” of year classes that buffer annual decreases in N_e (Gaggiotti and Vetter, 1999). However, additional pressures from fishing practices that lead to population declines and loss of juvenile habitat, imposed on sweepstake recruitment events, may lead to loss of genetic diversity (Chapman *et al.*, 1999b; Hauser *et al.*, 2002). Temporal genetic variation maybe enhanced in deepwater fishes, because the low productivity environment may restrict individual fish from spawning annually, leading to low and patchy recruitment (Leaman and Beamish, 1984).

Within-area temporal variation has been reported in orange roughy (Smolenski *et al.*, 1993; Smith and Benson, 1997); grouper (*Mycteroperca microlepis*) (Chapman *et al.*, 1999b); and hake (*Merluccius merluccius*) (Lundy *et al.*, 2000); and may result from stochastic events in progeny survival (Chapman *et al.*, 1999a). The low N_e/N ratios demonstrated in several shelf species are equally likely to occur in some deepwater species, and potentially lead to loss of genetic diversity in collapsed stocks.

Genetic diversity and selective fisheries

Substantial changes in life history traits, in particular age and size at maturity, have been reported in heavily exploited stocks on the continental shelves in the North Atlantic (Smith, 1994; Stokes and Law, 2000; Dieckmann *et al.*, 2006 in press). These changes may result from environmental change, the direct selective effects of fishing, or a compensatory response to reduced stock densities (Law, 2000). The compensatory response to a reduction in stock size promotes growth rate, resulting in a decrease in the age at maturity but an increase in the size at maturity, and may conceal long-term selection effects that would favour early maturing genotypes (Rochet, 1998). These responses may be non-exclusive making it difficult to untangle the compensatory and evolutionary components of these observed changes (Law, 2000).

Reaction norms for age and size at maturation have been used to estimate the probability of maturing at each relevant age and size, and thereby separate the genetically determined character from the plasticity in maturation that results

from changes in growth rate (Heino *et al.*, 2002; Engelhard and Heino, 2004). Growth-related phenotypic plasticity appears to have been largely responsible for recorded changes in early maturity in the Norwegian spring herring (*Clupea harengus*) (Engelhard and Heino, 2004), but in Atlantic cod (*Gadus morhua*) (Heino, 2002) and plaice (*Pleuronectes platessa*) (Rijnsdorp *et al.*, 2005) evolutionary changes appear to have occurred in response to heavy fishing (Law, 2000). These evolutionary changes are supported by controlled selection experiments that have demonstrated that fisheries have the potential to cause rapid evolution in life history traits (Conover, 1998; Conover *et al.*, 2005). Life history traits in populations of Atlantic cod off southern Labrador and eastern Newfoundland continually shifted towards maturation at earlier ages and smaller sizes, before the fishery finally collapsed in the 1990s. These changes in life history could provide a tool to give warning signals before more overt changes occur to populations (Olsen *et al.*, 2004).

Directional selection, through size-selective harvesting has not been demonstrated in deepwater fishes, in part due to the lack of long term data sets and, for long-lived species the long response time of the population to fishing. A number of changes were observed in a major orange roughy fishery on the Chatham Rise (New Zealand) over a 19-year period. The species distribution showed a marked contraction, with aggregations becoming centred around seamounts, or localised areas of the slope, and the biomass declined substantially to about 20% of virgin levels (Clark *et al.*, 2000). However size structure and size or age at maturity did not change markedly over the same period. Biological changes may not have been apparent because orange roughy is a long-lived, slow-growing species, with low productivity (Clark *et al.*, 2000).

Deepwater fisheries have only been operating in the Northwest Atlantic Ocean since the 1970s, but already four out of five species (the roundnose grenadier [*Coryphaenoides rupestris*], the onion-eye grenadier [*Macrourus berglax*], the blue hake [*Antimora rostrata*], and the spinytail skate [*Bathyraja spinicauda*]) have declined by 25-57% in mean size over 17 year period, so that fewer fish reach maturity and breed (Devine *et al.*, 2006). In the Northwest Atlantic fishery for Greenland halibut *R. hippoglossoides* the mean size of fish has declined rapidly and the bulk of the catch is made up of fish smaller than the size at maturity, and a major collapse of the fishery is likely (Haedrich *et al.*, 2001).

Endangered species

Only a few marine fishes have been listed as endangered (although the list is growing) and fewer appear to be close to extinction, e.g. skates (Brander, 1981; Casey and Myers, 1998). Traits of several deepwater species, such as long-life span, large body size, low natural mortality and late sexual maturity, are likely to make them more vulnerable to extinction than shelf species, in particular species that aggregate above seamounts. A review of the extinction risk in marine fish found that large body size and late maturity were the best predictors of vulnerability to fishing; there was no evidence that high fecundity conferred increased resilience (Reynolds *et al.*, 2005). Much of the evidence for extinction risk comes from shelf species, where inshore sub-populations of Atlantic cod and herring have been driven to extinction or have had insufficient time to recover from severe depletions (Smedbol and Stephenson, 2001).

Different criteria have been used to express the risk of extinction. The widely used IUCN system uses the graded terms vulnerable, endangered, and critically endangered and is applied to all organisms regardless of life history strategy. The IUCN criteria may overestimate the extinction risk for many marine fishes with their high intrinsic rates of increase, and for which management plans allow for stock biomass targets of 20-30% of the virgin biomass (Musick, 1999). Stocks of some pelagic shelf fishes have collapsed with severe reductions (1/3000) in population size, but have shown evidence of recovery. In general these species are characterized by small body size and early

maturity, the converse of traits that were the best predictors of vulnerability to fishing (Reynolds *et al.*, 2005). Pelagic species showing the greatest declines have shown the slowest recoveries (Beverton, 1990). The American Fisheries Society (AFS) developed a precautionary set of criteria to predict the risk of extinction in marine fishes, which includes rarity, specialization in habitat requirements, endemism or small range, and population decline, and also aims to recognise distinct population segments (DPS) when data are available (Musick, 1999). Rare species, because of evolutionary or ecological factors or crypsis, would be classified as vulnerable until further data were available. Species that are endemic or occur over a small range where the habitat is under threat from degradation would be classified as vulnerable, and where habitat loss has occurred they would be classified as endangered or threatened. Species with specialised habitat requirements, but that occur over wide geographic ranges, may also be vulnerable when the specialised habitat is subject to degradation or destruction (Musick, 1999). However the lack of knowledge about critical minimum population size and possibility of depensation create the greatest problems in assessing the extinction risk in marine fishes (Musick, 1999). Consequently the AFS proposed evaluating the resilience of the DPS using four levels of productivity: high, medium, low, and very low. Fish with late maturity (5-10 years), a long life span (>30 years), and high fecundity (>10⁴), typical of some deepwater fishes (and some show even later maturity and greater longevity), would be classified as very low productivity and would have a lower threshold to extinction than a species with medium or high productivity (Musick, 1999). Non-target species, that include teleosts endemic to seamount complexes and elasmobranchs with very low productivity, are likely to be vulnerable. For the few seamount fishes for which there are adequate biological data, most species have a low or very low productivity, and low resilience to exploitation (Froese and Sampang, 2004). It has been predicted that more seamount populations will be depleted and some will be extirpated if fishing continues at current levels (Morato *et al.*, 2006a).

Five deepwater species (the roundnose grenadier *C. rupestris*, the onion-eye grenadier *M. berglax*, the blue hake *A. rostrata*, the spinytail skate *B. spinicauda*, and the spiny eel *Notocanthus chemnitzii*) in Northwest Atlantic fisheries appear to meet the IUCN and AFS criteria of being critically endangered (80% decline in 10 years or three generations, or whichever is longer), showing overall declines in relative abundance of 87-98% in <20 years of exploitation, and higher estimated declines over three generations (Devine *et al.*, 2006). If the IUCN criteria are applied, the Dumb gulper shark (*Centrophorus harrissoni*) caught in the deepwater fishery of New South Wales is critically endangered; the deepwater bluntnose sixgill shark (*Hexanchus griseus*), circumglobal in tropical and temperate seas, is vulnerable (20% decline in 10 years or three generations or whichever is longer) while the kitefin shark (*Dalatias licha*) and the leafscale gulper shark (*Centrophorus squamosus*) are at lower risk, near threatened (i.e., survival is uncertain), along with several other species of shark in shelf waters (IUCN Red List).

The blue skate (*Dipturus batis*) is endangered and extirpated by trawling over much of its range in the eastern North Atlantic. The shallow water bocaccio (*Sebastes paucispinis*) found on seamounts in the eastern Pacific is critically endangered, while the deepwater shortspine thornyhead (*Sebastolobus alascanusis*) in the North Pacific is endangered. The Atlantic halibut (*Hippoglossus hippoglossus*) caught in shelf and slope fisheries in the North Atlantic is also endangered (see FishBase).

5. MAJOR INTERNATIONAL INITIATIVES, AGREEMENTS AND INSTRUMENTS

Genetic resources at the species and ecosystem levels are equivalent to ecological resources for which the management issues are well documented in the fisheries literature. The rapid development, and in some cases rapid depletion, of deepwater fisheries is of major concern to fisheries managers around the world, and has been

identified repeatedly at the local, regional and international levels (Koslow *et al.*, 2000; Haedrich *et al.*, 2001; Molenaar, 2004; FAO, 2005b; Morato *et al.*, 2006b). ICES have recognised that most exploited deepwater fishes are harvested unsustainably and radical reductions in fleets, in particular bottom trawlers are required to reduce effort and to conserve vulnerable habitats (ICES, 2005a).

Many deepwater fisheries occur in high seas areas adding to the problem of management and regulation. Urgent action is required at the global level, to avoid shifting the deepwater fishing problem from one region to another. Concerns about the apparent inertia in developing and implementing fisheries legislation, especially in the international arena, have led to NGOs calling for the designation of large-scale protected areas, and for a moratorium on bottom trawling until area management regimes can be implemented. Several countries have small-scale closures for deepwater fisheries within their territorial waters.

1995 UN Fish Stocks Agreement (FSA)

The 1995 UN Fish Stocks Agreement sets out the principles for the conservation and management of straddling fish stocks and highly migratory fish stocks and establishes that management be based on the precautionary approach and the best available scientific information (UN, 1995). The Agreement builds on the fundamental principle, established in the 1982 UN Convention of the Law of the Sea that States should cooperate to ensure conservation and promote the objective of the optimum utilization of fisheries resources both within and beyond the EEZs. The 1995 UN Fish Stocks Agreement was signed by 59 States and entities, but some major fishing nations, such as China and the Republic of Korea have not yet ratified the Agreement. The Agreement does not cover deepwater stocks found exclusively outside the 200 mile EEZs (i.e. discrete high seas stocks), but in practice States have been applying it to discrete high seas stocks (e.g. the South East Atlantic Fisheries Organisation).

A review meeting of the FSA in May 2006 identified a series of actions for States individually, and collectively through regional fisheries management organizations, to ensure the conservation and sustainable use of straddling fish stocks and highly migratory fish stocks, and that these principles should be applied to fish stocks in the high seas.¹

1995 FAO Code of Conduct for Responsible Fisheries

The 1995 FAO Code of Conduct for Responsible Fisheries (FAO, 1995) is a voluntary comprehensive instrument that sets out the principles and standards for the conservation and management of all fisheries and aquaculture including processing and trade in fish and fishery products, research and the integration of fisheries and aquaculture into coastal management areas. The Code refers to the role of Regional Fisheries Bodies to establish responsible international fisheries regimes.

Regional fisheries management organizations or arrangements (RFMOs)

There are 44 regional fisheries bodies that cover three categories: RFMOs, Advisory bodies, and Scientific bodies (FAO, Fisheries). Of these, 17 RFMOs are responsible for establishing management measures and some have regulatory powers in their jurisdictions, although many have a purely advisory role. Major problems for the current RFMOs relate to decision making, the allocation of resources to new entrants (principally developing countries that do not have a historical catch record) and the impacts of IUU fishing.²

¹ http://www.un.org/Depts/los/convention_agreements/review_conf_fish_stocks.htm

² <http://www.fao.org/docrep/008/a0098e/a0098e06.htm>

Most RFMOs have common responsibilities (Devaney, PL 2005) to:

- collect and distribute fishery statistics,
- provide evaluations of the state of fish stocks in their area of jurisdiction,
- determine the total allowable catch (TAC) quotas,
- set limits on the number of vessels allowed to exploit the fishery,
- control fishing opportunities by RFMO participants using such measures as area and seasonal closures and bycatch limits,
- regulate the types of gear used and conduct inspections to ensure compliance,
- monitor and enforce adherence to the rules of the RFMO and
- oversee the scientific research conducted within the fishery.

Australia, Chile, and New Zealand are promoting the development of a South Pacific Regional Fisheries Management Organisation (SPRFMO) to address governance of high-seas fisheries from the eastern Southern Indian Ocean, across the Tasman Sea and South Pacific Ocean to the Pacific EEZ's of South America. Several other countries have fishery interests in the area, notably Russian Federation, Ukraine, China, the Republic of Korea and the European Union. Currently there is little or no control over fishing methods or the management of fish stocks, other than for highly migratory tunas, in this extensive region. Other RFMOs, such the Western and Central Pacific Fisheries Convention (WCPFC) and the Inter-American Tropical Tuna Convention (IATTC) cover parts of this region, but their mandates relate only to highly migratory species.

The High Seas Task Force

The High Seas Task Force was established in 2003 to develop an action plan to combat IUU fishing (see below) on the high seas; membership consists of a group of fisheries ministers from Australia, Canada, Chile, Namibia, New Zealand, and the UK; and international NGOs – WWF, the World Conservation Union (IUCN) and the Earth Institute. Although established in 2003 the first report was not released until 2006. The High Seas Task Force aims, inter alia, to develop a Global Information System (GIS) on high seas fishing vessels that will make available information on the characteristics, ownership, and operations of all high seas fishing vessels. The GIS will also identify vessels previously black-listed by RFMOs, with the intention to make it difficult for IUU operators.

The Marine Stewardship Council (MSC) and ecolabelling of fish products

The MSC is an independent non-profit organisation that aims to use consumer purchasing power to enhance responsible management of seafood resources to ensure the sustainability of global fish stocks and the health of the marine ecosystem. The MSC has developed an environmental standard for sustainable and well-managed fisheries and uses a product label to reward responsible fishery management and practices. Certification is only granted if there is consensus amongst independent assessors that the fishery meets the MSC standard. Consumers, concerned about overfishing and its environmental impacts are able to choose seafood products which have been given MSC certification. The New Zealand hoki (*Macruronus novaezelandiae*) was the first large whitefish and only deepwater fishery to achieve MSC certification, for a period of five years.

Other NGOs have developed eco-labels that rank fish species by the sustainability of the fisheries so as to provide information to consumers. Eco-labels may be in conflict with the MSC, for example the New Zealand Forest and Bird Society's *Best Fish Guide* advises consumers to avoid eating hoki, and lists this as a worst choice species, due to the bycatch of fur seals, albatrosses and petrels and management practices in the fishery.

Guidelines for ecolabelling fish products have been developed by the FAO Committee of Fisheries (COFI) for governments and organizations that maintain, or

are establishing, labelling schemes for fish and fishery products from well-managed marine capture fisheries (FAO, 2005a). The general principles for ecolabelling schemes include the need for reliable and independent auditing, transparency of standard-setting and accountability and the need for the standards to be based on good science.

6. KEY SCIENTIFIC AND MANAGEMENT ISSUES TO BE ADDRESSED

Many deepwater species differ from shelf species in that they exhibit high longevity and late maturity; some have extensive but localised distributions in a low productivity environment. However there are limited scientific data available for many species. Working Groups at the Deep-sea 2003 conference identified several scientific areas where additional data are desirable for the management of deepwater species (FAO 2005b):

- accurate catch data,
- time series of abundance,
- stock identity and distribution information,
- life-history information,
- population biology statistics and age-frequency data,
- ability to make use of the most recent developments in fisheries resource management

Fishery subsidies

One component of reducing fishing capacity is the reduction or removal of subsidies (Pauly *et al.*, 2002). In general, the provision of subsidies increases the net returns from fishing and leads to an increased pressure on deepwater fish stocks, although simply removing subsidies will be ineffective in the absence of other management regimes (Cox, 2005). Subsidies, and other incentives such as accelerated depreciation for vessels, that encourage the expansion of capacity, such as vessel construction, may lead to increased pressure on deepwater fisheries that are technology driven. The converse, subsidies for vessel decommissioning, will only be effective if the vessels are scrapped (to avoid transfer to another fishery) and not replaced by new vessels (Cox, 2005). Rising fuel prices might also contribute to the restriction of some deepwater fishing operations.

Illegal, unreported and unregulated (IUU) fishing

The global excess of fishing capacity has contributed to illegal, unreported and unregulated (IUU) fishing and is recognized as a major threat to the long term sustainability of the world's fish stocks (FAO, 2004a). IUU fishing on the high seas is generally described as any fishing that takes place within the jurisdiction of a RFMO, but not in compliance with its regulations. IUU fishing is more broadly defined by the FAO as fishing activities in the area of application of a relevant RFMO that are conducted by vessels without nationality, vessels flagged to a State not party to that organization, or by a fishing entity, in a manner that is not consistent with, or contravenes, the conservation and management measures of that organization (FAO 2004a).

A number of measures aimed at combating IUU fishing, have been adopted by States and RFMOs, but despite these measures IUU fishing appears to continue because mobile fishing fleets are able to move rapidly between areas. FAO have developed a voluntary instrument within the framework of the Code of Conduct, the 2001 FAO International Plan of Action to Prevent, Deter and Eliminate Illegal, Unreported, and Unregulated Fishing (IPOA-IUU).³

³ <http://www.fao.org/docrep/005/y3554e/y3554e00.HTM>

IUU fishing for toothfish has consisted largely of illegal fishing within the EEZs of sub-Antarctic island territories within the CCAMLR Area and unregulated and unreported fishing both within and outside the CCAMLR Area. Most IUU fishing is thought to have occurred in the Indian Ocean sector around Crozet, Heard, Kerguelen and Prince Edward Islands. Increased surveillance activity in these areas has forced illegal operators to more remote areas, such as the waters around Ob and Lena Banks, and the waters around South Georgia.⁴

CCAMLR introduced a catch documentation scheme (CDS)⁵ that became binding on its members in May 2000. The Scheme tracks the landings and trade flows of toothfish caught in the CCAMLR Area by requiring landings and trans-shipments of toothfish to be accompanied by a valid CCAMLR Catch Document. The CDS identifies the origin of toothfish entering the markets of all participants in the Scheme. CDSs are a promising tool for other RFMOs to encourage legal fishing, and certify that fish entering the markets were caught in compliance with regional fishing regulations. However IUU fishers who land their catch into non-member port states will continue to undermine conservation measures.

In addition, CCAMLR maintains a list of vessels with a history of IUU fishing and has passed a resolution to avoid flagging and licensing non-Contracting Party vessels to fish in CCAMLR waters when the vessels have a history of IUU fishing. Several RFMOs have also instituted a system of black listing IUU fishers as a cost effective enforcement tool and prohibit black listed vessels from landing their catches in member ports.

New technologies are creating opportunities for RFMOs to better monitor vessels and catches and applications are supported by the High Seas Task Force. Vessel Monitoring Systems (VMSs) installed on fishing vessels allow RFMOs to receive up-to-the-minute data on the locations of member vessels. DNA barcoding of marine fish will provide tools for the rapid identification of species in processed products.

Protected areas

The international community, including NGOs, have expressed concern over the loss of macro invertebrates taken as bycatch in deepwater trawl fisheries on seamounts and for seabirds taken in toothfish trawl and long-line fisheries, although mitigation measures have been implemented to reduce the bird catch (FAO, 2004b). The fragile and ancient coral “forests” found on seamounts are reduced to rubble by heavy trawl gear and consequently habitat for numerous other invertebrate species is lost. Improvements to trawl gear and monitoring may eventually allow the operation of deepwater pelagic trawls that avoid contact with bottom features, but in the short term the most effective mitigation measure to protect vulnerable and unique habitats is to close relevant areas to bottom trawling. The application of marine protected areas is controversial, especially in areas outside national jurisdiction, and the subject is under debate within the IUCN and CBD;⁶ notably, IUCN Recommendation 3099 calls for the protection of seamounts, deep-sea corals and other vulnerable deep-sea habitats from destructive fishing practices, including bottom trawling, on the high seas.⁷ Zoning the oceans into unfished marine reserves and areas with limited levels of fishing effort is one mechanism that might allow sustainable fisheries to be maintained within the diverse deep-sea ecosystems (Pauly *et al.*, 2002). The inertia in developing and implementing international fisheries legislation has led to NGOs calling for the designation of large-scale protected areas and for a moratorium on high seas bottom trawling until area management regimes can be implemented.⁸

⁴ <http://www.ccamlr.org/pu/E/sc/fish-monit/iuu-intro.htm>

⁵ <http://www.ccamlr.org/pu/E/cds/intro.htm>

⁶ http://www.iucn.org/en/news/archive/2006/03/31_high_seas.htm

⁷ http://www.iucn.org/en/news/archive/2006/02/22_ungea_high_seas.htm

⁸ <http://www.savethehighseas.org/display.cfm?ID=136>

A recent survey estimated that 47% of seamounts fall inside EEZs and 53% in international waters (Alder and Wood, 2004). Several countries have limited closures in place within their territorial waters. The Tasmanian seamounts reserve was voluntarily established in the Australian EEZ in 1996 and formally declared in 1999. Below 500 m the reserve has a protected area (IUCN management category 1a) and represents ~20% of the total seamounts in the local region. In the Tasman Sea, the Lord Howe Marine Park covers all the waters around Lord Howe Island down to 1800 m. Nineteen seamounts around New Zealand were closed to bottom trawling in 2000 (Clark *et al.*, 2000). The closed seamounts were identified as being either representative of seamounts in their area or unique features in the EEZ. The faunal compositions of many seamounts are not known and selection of seamounts was based on geographical location and depth, rather than biodiversity. In the North Pacific the Bowie Seamount has a marine protected status that includes the conservation and protection of commercial and non-commercial fisheries. In Australia, the Department of Environment and Heritage have proposed establishing a network of large scale Marine Protected Areas (MPAs) in the SE marine region, that would cover 171 000 km² and close the major orange roughly fisheries (Buxton *et al.*, 2006). Recent initiatives have led to the establishment of a high seas Benthic Protected Area (BPA) in the Southern Indian Ocean,⁹ while representatives from the New Zealand fishing industry have proposed closing 31% of the seafloor (~1.2 m km²) in the New Zealand EEZ to bottom trawling,¹⁰ although the areas selected for closure need scientific review¹¹ to ensure that the areas that are representative of marine environments in the EEZ.

7. SUMMARY

The expansion of fisheries into deepwaters, especially those in high seas outside coastal jurisdictions, has been the most significant development in world fisheries in recent years. Several of the important deepwater species are characterised by high longevity and late age at maturity; these species have ocean-wide distributions within a depth range and exhibit weak genetic differentiation within oceans. Several species, especially elasmobranchs taken as bycatch, are endangered; some teleost species in the NW Atlantic appear to have become endangered following 20 years of heavy exploitation. There is general agreement that many deepwater fishes are exploited beyond sustainable levels and that urgent action is required at the global level to reduce effort and to protect fragile ecosystems from the impact of bottom trawling. Difficulties in managing deepwater fishes are compounded by the high seas nature of many fisheries and the limited regimes available for management in international waters.

8. ELECTRONIC BIBLIOGRAPHY

CCAMLR	http://www.ccamlr.org
Census of Marine Life	http://censeam.niwa.co.nz/
DNA barcoding, fish	http://www.fishbol.org/
FAO, Fisheries	http://www.fao.org/fi/default.asp
FishBase	http://filaman.ifm-geomar.de/home.htm
High Sea Task Force	http://www.high-seas.org/
ICES	http://www.ices.dk/advice/icesadvice.asp
ICES, sharks	http://www.ices.dk/marineworld/jaws.asp
IUCN Red List	http://www.redlist.org/
RFMOs	http://www.pon.org/downloads/ien14_4Devaney.pdf .
South Pacific RFMO	http://www.southpacificrfmo.org
Toothfish	http://www.traffic.org/toothfish/tooth2.html

⁹ http://www.iucn.org/en/news/archive/2006/07/2_qa_fishing_high_seas.htm

¹⁰ <http://www.seafood.co.nz/newscentre/press/2006pressreleases/closures.asp>

¹¹ <http://www.eco.org.nz/campaigns/benthicprotectedareas.htm>

9. REFERENCES

- Aboim, M.A.** 2005. *Population genetics and evolutionary history of some deep-sea demersal fishes from the Azores - North Atlantic*. PhD thesis University of Southampton, Faculty of Engineering Science and Mathematics, School of Ocean and Earth Science, PhD Thesis: 167 p.
- Aboim, M.A., Menezes, G.M., Schlitt, T. & Rogers, A.D.** 2005. Genetic structure and history of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809) inferred from mtDNA sequence analysis. *Molecular Ecology*, 14:
- Alder, J. & Wood, L.** 2004. *Managing and protecting seamount ecosystems*. In Seamounts: Biodiversity and Fisheries (ed) T. Morato and D. Pauly. Fisheries Centre Research Report: 67-73.
- Anderson, O.F. & Clark, M.R.** 2003. Analysis of bycatch in the fishery for orange roughy, *Hoplostethus atlanticus*, on the South Tasman Rise. *Marine and Freshwater Research*, 54: 643-652.
- Andrews, A.H., Cailliet, G., Kerr, L.A., Coale, K.H., Lundstrom, C. & DeVogeleare, A.** 2005. *Investigations of age and growth for three species of deep-sea coral from the Davidson Seamount off central California*. *Cold-water Corals and Ecosystems*. A. Freiwald and J.M. Roberts eds. Proceedings of the Second International Symposium on Deep-sea Corals. Erlangen, Germany. 965-982.
- Annala, J.H., Sullivan, K.J., O'Brien, C.J. & Iball, S.D.** 2000. Report from the Fishery Assessment Plenary, May 2000: *Stock Assessments and Yield Estimates*.
- Appleyard, S., Ward, R. and Williams, R.** 2002. Population structure of the Patagonian toothfish around Heard, McDonald and Macquarie Islands. *Antarctic Science*, 14: 364-373.
- Appleyard, S. & Williams, R.** 2004. Population genetic structure of Patagonian toothfish in the West Indian ocean sector of the Southern Ocean. *CCAMLR. Science*, 1: 21-32.
- Atkinson, D.B.** 1995. The biology and fishery of roundnose grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the northwest Atlantic. In Deepwater fisheries of the North Atlantic Oceanic Slope Kluwer Academic Publishers, Dordrecht the Netherlands: 51-112.
- Awaya, K.L. & Lee, C-S.** 2005. *Giant Clam*. American Fisheries Society Symposium, 46: 111-124.
- Baco, A.R., Clark, A.M. & Shank, T.M.** 2006. Six microsatellite loci from the deep-sea coral *Corallium lauense* (Octocorallia: Coralliidae) from the islands and seamounts of the Hawaiian archipelago. *Molecular Ecology Notes* 6: 147-153.
- Bagley, M.J., Lindquist, D.G. & Geller, J.B.** 1999. Microsatellite variation, effective population size, and population genetic structure of vermilion snapper *Rhomboplites aurorubens*, off the southeastern United States of America. *Marine Biology*, 134: 609-620.
- Ball, A.O., Sedberry, G.R., Zatcoff, M.S., Chapman, R.W. & Carlin, J.L.** 2000. Population structure of the wreckfish *Polyprion americanus* determined with microsatellite genetic markers. *Marine Biology*, 137: 1077-1090.
- Bartley, D.M. & Pullin, R.S.V.** 1999. *Towards policies for conservation and sustainable use of aquatic genetic resources*. ICLARM Conference Proceedings, 59: 1-16.
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A.** 2003. Collapse and Conservation of Shark Populations in the Northwest Atlantic. *Science*, 299: 389-392.
- Beverton, R.J.H.** 1990. Small marine pelagic fish and the threat of fishing: are they endangered? *Journal of Fish Biology*, 37 (Suppl A): 5-16.
- Boehlert, G. & Mundy, B.** 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. *Bulletin of Marine Science*, 53: 336-361.
- Boehlert, G. & Sasaki, T.** 1988. Pelagic biogeography of the armorhead *Pseudopentaceros wheeleri*, and recruitment to isolated sea mounts in the north Pacific Ocean. *Fishery Bulletin*, 86: 453-466.
- Boehlert, G. & Sasaki, T.** 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. *Bulletin of Marine Science* 53: 336-361.

- Boehlert, G.W. 1986. Productivity and population maintenance of seamount resources and future research directions. NOAA Technical Report National Marine Fisheries Service, 43: 95-101.
- Brander, K. 1981. Disappearance of common skate *Raia batis* from Irish Sea. *Nature*, 290: 48-49.
- Bucklin, A., Wilson, R.R. and Smith, K.L. 1987. Genetic differentiation of seamount and basin populations of the deep-sea amphipod *Eurythenes gryllus*. *Deep-sea Research*, 34: 1795-1810.
- Buxton, C., Haddon, M. & Bradshaw, M. 2006. *Regional impact assessment for the marine protected areas proposed for the south-east region*. Fisheries Research and Development Corporation Final Report 2005/083: 141 p.
- Cadrin, S.X. 2000. *Advances in morphometric identification of fishery stocks*. Reviews in Fish Biology and Fisheries 10: 91-112.
- Casey, J.M. & Myers, R.A. 1998. Near extinction of a large, widely distributed fish. *Science* 281: 690-692.
- Chapman, R.W., Ball, A.O. & Marsh L.R. 2002. Spatial homogeneity and temporal heterogeneity of red drum (*Sciaenops ocellatus*) microsatellites: effective population sizes and management implications. *Marine Biotechnology*, 4: 589-603.
- Chapman, R.W., Sedberry, G.B. & McGovern, J.C. 1999a. The genetic consequences of reproductive variance: studies of species with different longevities. American Fisheries Society Symposium 23: 169-181.
- Chapman, R.W., Sedberry, G.R., Koenig, C.C. & Eleby, B.M. 1999b. Stock identification of gag, *Mycteroperca microlepis*, along the southeast coast of the United States, 1: 137-146.
- Chase, M.R., Etter, R.J., Rex, M.A. & Quattro, J.M. 1998. Bathymetric patterns of genetic variation in a deep-sea protobranch bivalve, *Deminucula atacellana*. *Marine Biology*, 131: 301-308.
- Clark, M. 1999. Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. *Oceanologia Acta* 22: 593-602.
- Clark, M. & O'Driscoll, R. 2001. Deepwater fisheries and aspects of their impact on seamount habitat in New Zealand. *Journal Northwest Atlantic Fisheries Science*, 31: 441-458.
- Clark, M., O'Shea, S., Wood, B. & Wright, I. 2000. Seamount management. A report on seamounts potentially suitable for consideration under the MFish seamount management strategy. Report prepared for the New Zealand Ministry of Fisheries April 2000: 82 p.
- Clark, M.R., Anderson, O.F., Francis, C. & Tracey, D. 2000. The effects of commercial exploitation on orange roughy (*Hoplostethus atlanticus*) from the continental slope of the Chatham Rise, New Zealand, from 1979 to 1997. *Fisheries Research*, 45: 217-238.
- Clarke, M., Kelly, C., Connolly, P. & Molloy, J. 2003. A life history approach to the assessment and management of deepwater fisheries in the Northeast Atlantic. *Journal Northwest Atlantic Fisheries Science*, 31: 401-411.
- Conover, D., Arnott, S., Walsh, M. & Munch, S. 2005. Darwinian fishery science: lessons from the Atlantic silverside (*Menidia menidia*). *Canadian Journal of Fisheries & Aquatic Sciences*, 62: 730-737.
- Conover, D.O. 1998. Local adaptation in marine fishes: evidence and implications for stock enhancement. *Bulletin of Marine Science* 62: 477-493.
- Cox, A. 2005. Subsidies and deep-sea fisheries management: policy issues and challenges. www.oecd.org/dataoecd/10/27/24320313.pdf 23 p.
- Davis, G.E., Haaker, P.L. & Richards, D.V. 1998. The perilous condition of white abalone *Haliotis sorenseni*, Bartsch, 1940. *Journal of Shellfish Research*, 17: 871-875.
- Devaney, P.L. 2005. Regional Fisheries Management Organizations. Papers on International Negotiation XIV: 18 pp.
- Devine, J.A., Baker, K.D. & Haedrich, R.L. 2006. Deep-sea fisheries qualify as endangered. *Nature*, 439: 29.

- Dewoody, J.A. & Avise, J.C. 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. *Journal of Fish Biology*, 56: 461-473.
- Dieckmann, U., Godo, O.R. & Heino, M. (Eds) JM 2006 in press. Fisheries induced adaptive change. International Institute for Applied Systems Analysis
- Distel, D.L., Baco, A.R., Chung, E., Morrill, W., Cavanaugh, C & Smith, C.R. 2000. Do mussels take wooden steps to deep-sea vents? *Nature*, 403: 725-726.
- Doherty, P.J., Planes, S. & Mather, P. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier reef. *Ecology*, 76: 2373-2391.
- Doonan, I., McMillan, P., Kalish, J. & Hart, A. 1995. *Age estimates for black oreo and smooth oreo*. New Zealand Fisheries Assessment Report 95/14: 26p.
- Engelhard, G.H. & Heino, M. 2004. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary response? *Marine Ecology Progress Series*, 272: 245-256.
- Etter, R., Rex, M., Chase, M. & Quattro, J. 2005. Population Differentiation Decreases With Depth In Deep-Sea Bivalves. *Evolution*, 59: 1479-1491.
- Etter, R.J., Rex, M.A., Chase, M.C. & Quattro, J.M. 1999. A genetic dimension to deep-sea biodiversity. *Deep-sea Research*, 46: 1095-1099.
- FAO. 1995. *Code of Conduct for Responsible Fisheries*. Rome, FAO. 41p.
- FAO. 2002. *Report of the Second Ad Hoc Meeting on Management of Deepwater Fisheries Resources of the Southern Indian Ocean. Fremantle, Western Australia. 20-22 May 2002*. FAO Fisheries Report. No. 677. Rome, FAO. 106p.
- FAO. 2004a. *Report of the Expert Consultation on Fishing Vessels Operating under Open Registries and their Impact on Illegal, Unreported and Unregulated Fishing. Miami, Florida, United States of America, 23-25 September 2003*. FAO Fisheries Report. No 722. Rome, FAO. 168p.
- FAO. 2004b. *Report of the FAO/BirdLife South American Workshop on Implementation of NPOA-Seabirds and Conservation of Albatrosses and Petrels. Valdivia, Chile, 2-6 December 2004*, by Lokkeborg, S. and Thiele, W. (eds.). FAO Fisheries Report. No. 751. Rome, FAO. 2004. 32p.
- FAO. 2005a. *Report of the Technical Consultation on International Guidelines for the Ecolabelling of Fish and Fishery Products from Marine Capture Fisheries. Rome, 19-22 October 2004*. FAO Fisheries Report. No. 760. Rome, FAO. 99p. (Trilingual)
- FAO. 2005b. *Report on DEEP SEA 2003, an International Conference on Governance and Management of Deep-Sea Fisheries. Queenstown, New Zealand 1-5 December 2003*. FAO Fisheries Report. No. 772. Rome, FAO. 84p.
- FAO. 2005c. *Review of the state of world marine fishery resources*, by Marine Resources Service, Fishery Resources Division. FAO Fisheries Technical Paper. No. 457. Rome, FAO. 235p.
- France, S. & Hoover, L. 2002. DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). *Hydrobiologia*, 471: 149-155.
- France, S. & Kocher, T. 1996. Geographic and bathymetric patterns of mitochondrial 16S rRNA sequence divergence among deep-sea amphipods, *Eurythenes gryllus*. *Marine Biology*, 126: 633-643.
- Froese, R. & Sampang, A. 2004. *Taxonomy and biology of seamount fishes*. In Seamounts: Biodiversity and Fisheries (ed) T. Morato and D. Pauly Fisheries Centre Research Report: 25-31.
- Gaggiotti, O. & Vetter, R. 1999. Effect of life history strategy, environmental variability, and overexploitation on the genetic diversity of pelagic fish populations. *Canadian Journal of Fisheries & Aquatic Sciences*, 56: 1376-1388.
- Glover, A.G.S., C R. 2003. The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. *Environmental Conservation*, 30: 219-241.

- Goff-Vitry, M.L., Pybus, O. & Rogers, A. 2004. Genetic structure of the deep-sea coral *Lophelia pertusa* in the northeast Atlantic revealed by microsatellites and internal transcribed spacer sequences. *Molecular Ecology*, 13: 537-549.
- Gon, O. & Heemstra, P. 1990. Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown
- Gyllenstein, U. 1985. The genetic structure of fish: differences in the intraspecific distribution of biochemical genetic variation between marine, anadromous, and freshwater species. *Journal of Fish Biology*, 26: 691-699.
- Haedrich, R., Merrett, N. & O'Dea, N. 2001. Can ecological knowledge catch up with deep-water fishing? A North Atlantic perspective. *Fisheries Research*, 51: 113-122.
- Hauser, L., Adcock, G., Smith, P., Bernal-Ramirez, J.H. & Carvalho, G.R. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings National Academy of Sciences* 99: 11742-11747.
- Hauser, L. & Ward, R.D. 1998. Population identification in pelagic fish: the limits of molecular markers. In Carvalho G (ed) *Advances in Molecular Ecology*. IOS, Amsterdam pp 191-224.
- Hebert, P., Cywinska, A., Ball, S. & deWaard, J. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B* 270: 313-322.
- Hedgecock, D. 1994. Temporal and spatial genetic structure of marine animal populations in the California Current. *Reports of California Cooperative Oceans Fisheries Investigations* 35: 73-81.
- Heino, M., Dieckmann, M.U. & Godo, O. 2002. Reaction norm analysis of fisheries induced adaptive change and the case of the Northeast Arctic cod. *ICES CM2002/Y:14*
- Hoarau, G. & Borsa, P. 2000. Extensive gene flow within sibling species in the deep-sea fish *Beryx splendens*. *Life Sciences*, 323: 315-325.
- Horn, P. 2002. Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) in waters from the subantarctic to the Ross Sea, *Antarctica. Fisheries Research*, 56: 275-287.
- Ianelli, J. & Zimmerman, M. 1998. Status and future prospects for the Pacific Ocean perch resource in waters off Washington and Oregon as assessed in 1998. In *Status of the Pacific coast groundfish fishery through 1998 and recommended acceptable biological catches for 1999 Pacific Fishery Management Council*, Portland Oregon: 53 p.
- ICES. 2005a. Advice on deepwater stocks (EC FISH). *ICES Report on Deepwater Fisheries Resources* 10: 10-20.
- ICES. 2005b. Deepwater sharks in the northeast Atlantic (ICES Sub-areas V-XIV, mainly Portuguese dogfish and leafscale gulper shark). *ICES Report on Deepwater Fisheries Resources* 10: 21-27.
- ISOFISH. 1998. The Vikings: the involvement of Norwegian fishermen in illegal and unregulated longline fishing for Patagonian toothfish in the Southern Ocean. *ISOFISH Occasional Report*, Hobart Australia 3:
- James, G., Inada, T. & Nakamura, I. 1988. Revision of the oreosomatid fishes (Family Oreosomatidae) from the southern oceans, with a description of a new species. *New Zealand Journal of Marine & Freshwater Research*, 15: 291-326.
- Jensen, A. & Frederiksen, R. 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe Shelf. *Sarsia* 77: 53-69.
- Kenchington, E. 2003. The effects of fishing on species and genetic diversity. *Responsible fisheries in the marine ecosystem Conf. on Responsible Fisheries in the Marine Ecosystem*, Reykjavik (Iceland), 1-4 Oct 2001. Sinclair, M and Valdimarsson, G (ed): 235-253.
- Kim, S-K. & Mendis, E. 2006. Bioactive compounds from marine processing byproducts - a review. *Food Research International*, 39: 383-393.
- Koslow, J., Boehlert, G., Gordon, J., Haedrich, R., Lorance, P. & Parin, N. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science*, 57: 548-557.

- Koslow, J. & Gowlett-Holmes, K. 1998. The seamount fauna off southern Tasmania: benthic communities, their conservation and impacts of trawling. Report to the Environmental Australia Fisheries Commission 95/058: 104 p.
- Law, R. 2000. Fishing, selection, and phenotypic plasticity. *ICES Journal of Marine Science* 57: 659-668.
- Leaman, B., Beamish, R. 1984. Ecological and management implications of longevity in some Northeast Pacific groundfishes. *International North Pacific Fisheries Commission Bulletin* 42: 85-97.
- Leaman, B.M. 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Environmental Biology of Fishes*, 30: 253-271.
- Lehodey, P., Grandperrin, R. & Marchal, P. 1997. Reproductive biology and ecology of a deep-demersal fish, alfoncino *Beryx splendens* over the seamounts off New Caledonia. *Marine Biology*, 128: 17-27.
- Lundy, C., Rico, C. & Hewitt, G. 2000. Temporal and spatial genetic variation in spawning grounds of European hake (*Meluccius merluccius*) in the Bay of Biscay. *Molecular Ecology*, 9: 2067-2079.
- Mace, P., Fenaughty, J., Coburn, R. & Doonan, I. 1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the North Chatham Rise. *New Zealand Journal of Marine & Freshwater Research* 24: 105-119.
- Martin, A., Humphreys, R. & Palumbi, S. 1992. Population genetic structure of the armourhead *Pseudopentaceros wheeleri* in the North Pacific Ocean: application of the polymerase chain reaction to fisheries problems. *Canadian Journal of Fisheries & Aquatic Sciences* 49: 2386-2391.
- McKenzie, K. 2002. Parasites as biological tags in population studies of marine organisms: an update. *Parasitology* 124: 153-163.
- Milton, D. & Shaklee, J. 1987. Biochemical genetics and population structure of blue grenadier, *Macruronus novaezelandiae* (Hector) (Pisces: Merluccidae), from Australian waters. *Australian Journal of Marine and Freshwater Research* 38: 727-742.
- Molenaar, E. 2004. Unregulated deep-sea fisheries: a need for a multi-level approach. *International journal of marine and coastal law* 19: 223-246.
- Morato, T., Cheung, W. & Pitcher, T. 2006a. Vulnerability of seamount fish to fishing: fuzzy analysis of lifehistory attributes. *Journal of Fish Biology* 68: 209-221.
- Morato, T., Watson, R., Pitcher, T. & Pauly, D. 2006b. Fishing down the deep. *Fish and Fisheries* 7: 24-34.
- Morison, A., Kalish, J., Green, C. & Johnston, J. 1999. Estimation of orange roughy, black oreo and smooth oreo and natural mortality of black and smooth oreo. Final Research report to the New Zealand Ministry of Fisheries, project DEE9702
- Musick, J. 1999. Criteria to define extinction risk in marine fishes. *Fisheries* 24: 6-14.
- Myers, R. & Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, 423: 280-283.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B. & Dieckmann, U. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 428: 932-935.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R & Zeller, D. 2002. Towards sustainability in world fisheries. *Nature*, 418: 689-695.
- Pineiro, C.G., Casas, M. & Banon, R. 2001. The deep-water fisheries exploited by Spanish fleets in the Northeast Atlantic: a review of the current status. *Fisheries Research* 51: 311-320.
- Probert, P.K., McKnight, D.G. & Groove, S.L. 1997. Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems* 7: 27-40.
- Pullin, R.S.V. 2000. Management of Aquatic Biodiversity and Genetic Resources. *Reviews in Fisheries Science* 8: 379-393.

- Reynolds, J.D., Dulvy, N.K., Goodwin, N.B. & Hutchings, J.A. 2005. Biology of extinction risk in marine fishes. *Proceedings of the Royal Society of London B* 272: 2337-2344.
- Richer-de-Forges, B.R., Koslow, J.A. & Poore, G.C.B. 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405: 944-947.
- Rijnsdorp, A.D., Grift, R.E. & Kraak, S.B.M. 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Canadian Journal of Fisheries & Aquatic Sciences* 62: 833-843.
- Roberts, C., Paulin, C., Stewart, A., McPhee, R. & McDowall, R. in press. Appendix. Checklist of living lancelets, jawless fishes, cartilaginous fishes and bony fishes. In: D. P. Gordon (ed.). *The New Zealand Inventory of Biodiversity. Volume 1. Kingdom Animalia*. Canterbury University Press, Christchurch.:
- Roberts, C.D. & Paulin, C.D. 1997. Fish collections and collecting in New Zealand. *Ichthyology and Herpetology* 207-229.
- Roberts, J.M., Wheeler, A.J. & Freiwald, A. 2006. Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems. *Science*, 312: 543-547.
- Rochet, M.-J. 1998. Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science* 55: 371-391.
- Rogers, A.D. 1994. The Biology of seamounts. *Advances in Marine Biology* 30: 305-350.
- Roques, S., Sevigny, J.M. & Bernatchez, L. 2002. Genetic structure of deepwater redfish, *Sebastes mentella*, populations across the North Atlantic. *Marine Biology* 140: 297-307.
- Sedberry, G.R., Carlin, J.L., Chapman, R.W. & Eleby, B. 1996. Population structure in the pan-oceanic wreckfish *Polyprion americanus* (Teleostei: Polyprionidae), as indicated by mtDNA variation. *Journal of Fish Biology* 49: 318-329.
- Shaw, P., Arkhipkin, A. & Al-Khairulla, H. 2004. Genetic structuring of Patagonian toothfish populations in the Southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Molecular Ecology*, 13: 3293-3303.
- Smedbol, R.K. & Stephenson, R. 2001. The importance of managing within-species diversity in cod and herring fisheries of the north-wetsern Atlantic. *Journal of Fish Biology*, 59: 109-128.
- Smith, D.C., Fenton, G.E., Robertson, S.G. & Short, S.A. 1995. Age determination growth of orange roughy (*Hoplostethus atlanticus*): A comparison of annulus counts with radiometric ageing. *Canadian Journal of Fisheries & Aquatic Sciences* 52: 391-401.
- Smith, P. 1994. Genetic diversity of marine fisheries resources: possible impacts of fishing. *FAO Fisheries Technical Paper* 344: 53 pp.
- Smith, P. & Benson, P. 1997. Genetic diversity in orange roughy from the east of New Zealand. *Fisheries Research* 31: 197-213.
- Smith, P., Benson, P. & McVeagh, S. 1997. A comparison of three genetic methods for stock discrimination of orange roughy, *Hoplostethus atlanticus*: allozymes, PCR amplified mitochondrial DNA and random amplified polymorphic DNA. *Fishery Bulletin* 94: 800-811.
- Smith, P. & Gaffney, P. 2000a. Population genetics of Patagonian toothfish (*Dissostichus eleginoides*) and fillet identification of Patagonian toothfish and Antarctic toothfish *D. mawsoni*. *CCAMLR WG-FSA-00/53* 13pp.
- Smith, P. & Gaffney, P. 2000b. Toothfish. *Water & Atmosphere* 8: 17-18.
- Smith, P. & Gaffney, P. 2005. Low genetic diversity in the Antarctic toothfish *Dissostichus mawsoni* observed with mitochondrial and intron DNA markers. *CCAMLR Science* 12: 43-51.
- Smith, P., McMillan, P., Bull, B. & McVeagh, S. 2002. Genetic and meristic variation in black and smooth oreos in the New Zealand EEZ. *New Zealand Journal of Marine & Freshwater Research* 36: 737-750.
- Smith, P. & McVeagh, M. 2000. Allozyme and microsatellite DNA markers of toothfish population structure in the Southern Ocean. *Journal of Fish Biology* 57: 72-83.

- Smith, P.J., McVeagh, S.M. & Ede, A. 1996. Genetically isolated stocks of orange roughy (*Hoplostethus atlanticus*) but not hoki (*Macruronus novaezelandiae*) in the Tasman Sea and Southwest Pacific Ocean around New Zealand. *Marine Biology*, 125: 783-793.
- Smith, P.J., McVeagh, S.M., Mingoia, J.T. & France, S.C. 2003. Mitochondrial DNA sequence variation in deep-sea bamboo coral (Keratoisidinae) species in the southwest and northwest Pacific Ocean. *Marine Biology*, 144: 253-261.
- Smolenski, A.J., Ovenden, J.R. & White, R.W.G. 1993. Evidence of stock separation in southern hemisphere orange roughy (*Hoplostethus atlanticus*), Trachichthyidae) from restriction-enzyme analysis of mitochondrial DNA. *Marine Biology*, 116: 219-230.
- Somerton, D.A. & Kikkawa, B.S. 1992. Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on southeast Hancock seamount. *Fishery Bulletin* 90: 756-769.
- Stokes, K. & Law, R. 2000. Fishing as an evolutionary force. *Marine Ecology Series* 208: 307-309.
- Swan, S.C., Gordon, J.D.M. & Shimmield, T. 2003. Preliminary investigations on the uses of otolith microchemistry for stock discrimination of the deep-water black scabbardfish (*Aphanopus carbo*) in the Northeast Atlantic. *Journal Northwest Atlantic Fisheries Science* 31: 221-231.
- Thresher, R.E. 1999. Elemental composition of otoliths as a stock delineator in fishes. *Fisheries Research* 43: 165-204.
- Turner, T.F., Wares, J.P. & Gold, J.R. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine dependent marine fish (*Sciaenops ocellatus*). *Genetics*, 162: 1329-1339.
- UN. 1995. Agreement for the implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks. United Nations Conference on Straddling Fish Stocks and Highly Migratory Fish Stocks Sixth session New York, 24 July-4 August 1995. <http://daccessdds.un.org/doc/UNDOC/GEN/N95/274/67/PDF/N9527467.pdf?OpenElement>
- VanDover, C.L. 2000. The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton, NJ.
- Waples, R.S. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. *Evolution* 41: 385-400.
- Ward, R.D., Elliott, N.G., Grewe, P., Last, P.R., Lowry, P.S., Innes, B.H. & Yearsley, G.K. 1998. Allozyme and mitochondrial DNA variation in three species of oreos (Teleostei: Oreosomatidae) from Australasian waters. *New Zealand Journal of Marine & Freshwater Research* 32: 233-245.
- Ward, R.D., Woodwark, M & Skibinski, D.O.F. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *Journal of Fish Biology*, 44: 213-232.
- Watson, R. & Morato, T. 2004. Exploitation patterns in seamount fisheries: a preliminary analysis. In *Seamounts: Biodiversity and Fisheries* (ed) T. Morato and D. Pauly Fisheries Centre Research Report: 61-65.
- Wilson, R. & Kaufman, R. 1987. Seamount biota and biogeography. *Geophysics Monographs*, 43: 355-377.
- Zardus, J.D., Etter, R.J., Chase, M.R., Rex, M.A. & Boyle, E.E. 2006. Bathymetric and geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula atacellana* (Schenck, 1939). *Molecular Ecology*, 15: 639-651.
- Zeldis, J.R., Grimes, P.J. & Ingerson, J.K.V. 1994. Ascent rates vertical distribution, and a thermal history model of development of orange roughy *Hoplostethus atlanticus* eggs in the water column. *Fishery Bulletin*, 93: 373-385.