Chapter 3
Unnatural Selection of Antarctic Toothfish in the Ross Sea, Antarctica

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3.1 Fishing Further and Deeper

Historically, fishermen targeted fish in shallow, nearshore waters relatively close to port (Pauly et al. 2005). As these species became depleted, to meet growing demands, fishermen were forced to move offshore and into deeper waters (Hutchings and Reynolds 2004; Koslow et al. 2000; Morato et al. 2006; Hilborn et al. 2003; Pauly et al. 2002, 2005). Steady advances in fishing technology facilitated the exploitation of previously inaccessible fish stocks (Hutchings and Reynolds 2004; Koslow et al. 2000; Morato et al. 2006; Hilborn et al. 2003; Pauly et al. 2002, 2005), and by the mid-1980s fishermen began longline fishing in the northern Southern Ocean for the deep-living Patagonian toothfish *Dissostichus eleginoides* (Knecht 2006). Despite international efforts to regulate this fishery, extensive illegal, unregulated, and unreported (IUU) fishing compromised management and caused severe population declines, leading to localized depletions and stock closures within 10 years (Agnew et al. 2002). In search for other profitable toothfish stocks, fishermen soon moved into the southernmost marine regions of the Antarctic, to the freezing waters of the Ross Sea, this time in pursuit of the Antarctic toothfish, *Dissostichus mawsoni*. Reflecting market forces, both toothfish species are sold in industrialized countries under the market name "Chilean sea bass" and cost $25 or more a pound, a price that few can afford.

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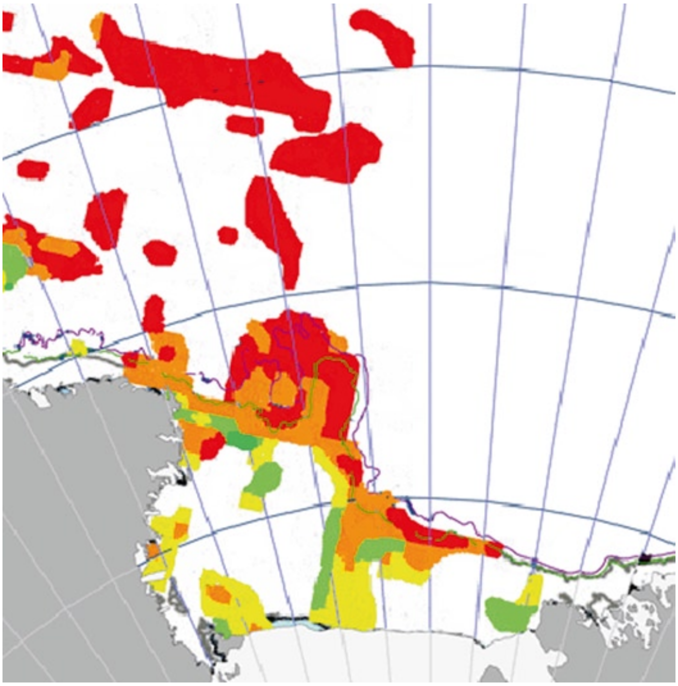


Fig. 3.1 The distribution, on average, of Antarctic toothfish, by size class (total length, TL), as taken in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Area 88.1 fishery: *green*, 40–80 cm; *yellow*, 80–100 cm; *orange*, 100–120 cm; *red*, >120 cm. (Redrawn from Hanchet et al. 2008). Area 88.2, for which even fewer data are available, is in the eastern half of this mapped area

Industrial-scale exploitations of large deep-sea predatory fish, such as the adult toothfish, have repeatedly been shown to be unsustainable (Baum et al. 2003; Myers and Worm 2003; Cheung et al. 2007). The typical life history characteristics of these fish, as reviewed here in detail for Antarctic toothfish, result in slow stock recovery times and render populations particularly vulnerable to overfishing (Koslow et al. 2000; Clark 2001; Haedrich et al. 2001; Devine et al. 2006; Morato et al. 2006). Industrial-scale fishing allows ships to take large quantities of these fish within a season. For example, one ship can catch as much as 40 t of these fish in a single haul and 300 t on a typical voyage (Knecht 2006). Thus, it is not surprising that Patagonian toothfish populations, similar to other deep-sea, *k*-selected fish stocks (Cheung et al. 2007), became rapidly depleted, with the industry then turning to Antarctic toothfish.

To date the main fishing grounds for Antarctic toothfish have been in FAO Area 88, the Ross Sea region (Fig. 3.1).

The Antarctic toothfish fishery in the Ross Sea region (FAO Area 88; see Fig. 3.1) is still considered “exploratory” by CCAMLR (The Commission for the Conservation of Antarctic Marine Living Resources) because insufficient data are available for management. This provision places CCAMLR managers in a unique position to apply precautionary practices before full, or "assessed," exploitation is allowed. Too often, as recognized by CCAMLR, fisheries have crashed when full-scale harvesting proceeded before understanding the life history traits and ecological needs of the fish species. A classic example is the orange roughy *Hoplostethus atlanticus*: this deep sea-mount fishery was managed assuming a 20- to 30-year longevity, but later age validation studies showed that orange roughy live more than 100 years and have an extremely slow growth rate (Smith et al. 1995; Andrews et al. 2009). By the time this essential information was available, fishermen had exploited this resource beyond levels of long-term sustainability and the fishery collapsed. Similarly, in the Northern Hemisphere, deep-living benthic rockfishes (*Sebastes* spp.) off the west coast of North America were fished in excess before accurate life history information was obtained. After populations crashed, age validation studies revealed that longevity and age at maturity, upon which management was based, had been drastically underestimated (see summary in Ainley and Blight 2009). As reviewed here, very little is known about the life history of the Antarctic toothfish. If responsible and precautionary management is implemented now, we can avoid adding this species to the growing list of overexploited deep-sea fishes.

3.1.1 Antarctic Toothfish: The Shark of the Antarctic

The fish fauna south of the Antarctic Polar Front (APF) is dominated mainly by an impressive radiation of perch-like species within several families, most notably the Nototheniidae. Among these is the Antarctic toothfish, also known as Antarctic cod, which is by far the largest and most trophically dominant fish in the Southern Ocean. Adults grow to 2.0 m in length and 140 kg in mass, whereas most other Antarctic fishes rarely become larger than 60 cm (a few, e.g., the marbled rockcod *Notothenia rossii*, reach 90 cm). Sharks, the typical top predators in most ocean ecosystems, are sparse in the Southern Ocean, occurring only at the northern periphery (close to the APF in the waters around Kerguelen and South Georgia Islands). The Antarctic toothfish's life history, size, and ecological role have led ichthyologists to refer to it, when adult, as "the greatest universal predator" of the region (Andriashev 1962, p. 150), the "largest midwater fish predator in the Southern Ocean … filling the ecological role of sharks in other oceans" (DeVries and Eastman 1998, p. 5), and "the most important piscine predator in the water column of the Southern Ocean" (Eastman 1993, p. 77).

As is typical of other top predators, the Antarctic toothfish is *k*-selected (as defined by MacArthur and Wilson 1967), being long lived (almost to 50 years), slow growing (2.3 cm and 1 kg per year, except in early years), late to mature (50% of females by 17 years, at about 100–120 cm total length), and likely of low fecundity (DeVries and Eastman 1998; Eastman and DeVries 2000; Horn 2002; Parker and Grimes 2009; Brooks et al. 2010). The fecundity of Antarctic toothfish has proved difficult to assess because no eggs, larvae, or small juveniles (young of the year, YOY) have been found in the Ross Sea or anywhere else. In fact, no toothfish smaller than 50 cm has ever been caught in the Ross Sea region (Hanchet et al. 2010). However, from what is known, Antarctic toothfish do not appear to be prolific spawners, in part because they do not spawn annually (Yukhov 1971; DeVries and Eastman 1998; Eastman and DeVries 2000; Brooks 2008; Parker and Grimes 2009). In contrast, the Atlantic cod *Gadus morhua*, another demersal, *k*-selected species, is among the most prolific fish species, with single females (100 cm long) annually producing 4–8 million eggs each measuring 1.2–1.7 mm in diameter (Collette and Klein-MacPhee 2002). For *D. mawsoni*, it is yet not known how many eggs a large female can produce, but it is estimated that they lay 2- to 4.5-mm-sized eggs (Hanchet et al. 2008), suggesting Antarctic toothfish invest more in their egg production than other ecologically similar fish.

Antarctic toothfish reside at depths from the surface to > 2,200 m deep (Fuiman et al. 2002; Hanchet et al. 2003), with subadult toothfish residing over the shallower inner Ross Sea Shelf and most larger fish moving to waters overlying the deeper continental slope and the seamounts and ridges in the north of Area 88 (north of 70° S; Prutko 2004; Brooks and Ashford 2008; Hanchet et al. 2008; see Fig. 3.1). This ontogenetic shift in habitat coincides with the adults (fish >115–130 cm) achieving neutral buoyancy, one of only five nototheniid species to do so, which allows them to occupy the entire water column.

Over the Ross Sea continental shelf, large subadult and adult toothfish prey heavily on Antarctic silverfish (*Pleuragramma antarcticum*), a species with life history traits similar to those of clupeids (loosely swarming baitfish; DeWitt and Hopkins 1977; Fuiman et al. 2002). Sampling of stomachs from adult and subadult toothfish caught in McMurdo Sound, on the southern Ross Sea Shelf, showed that silverfish were the primary prey item by both occurrence (71.2%) and dry weight (89.2%; Eastman 1985a). However, adult toothfish that occupy benthic waters of the continental slope forage principally upon macrourids and icefish (Fenaughty et al. 2003; La Mesa et al. 2004), as well as other species (Arana and Vega 1999; Prutko 2004). Occasionally, they feed on Adélie penguins (*Pygoscelis adéliae*), and, so far as is known, only rarely on subadult toothfish (Fenaughty et al. 2003; Prutko 2004; Petrov and Tatarnikov 2010). This seeming lack of widespread cannibalism in Antarctic toothfish is very unusual for these types of fish, in which adults usually prey on eggs, larvae, and small fish to an extent very much density dependent (e.g., it is rampant in Atlantic cod; Longhurst 2010). Although no sampling of Antarctic toothfish has ever been conducted in pack ice-covered seas of the winter, when the species is thought to spawn (Hanchet et al. 2008), the apparent lack of density-dependent cannibalism would increase the uncertainty of fishery models aimed toward managing toothfish "surplus production" (Longhurst 2010). Instead, the toothfish diet is more similar to that of large sharks, changing ontogenetically: adult toothfish feed on large prey items, whereas subadult toothfish (20–100 cm) eat smaller prey, such as prawns (*Nauticaris* sp.; Fenaughty et al. 2003), and the smallest toothfish (<20 cm) likely prey on zooplankton (however, very few fish <20 cm have ever been collected; see Foster and Montgomery 1993).

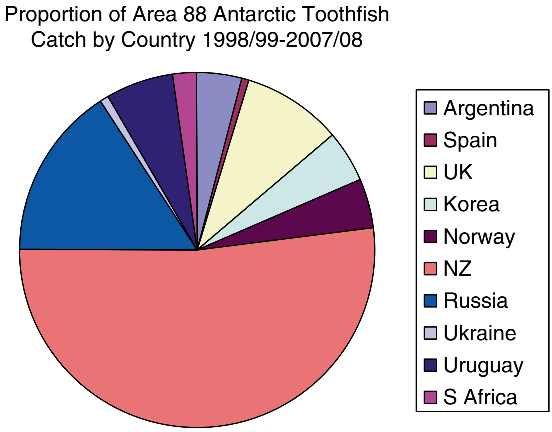
Recent evidence suggests that fish in Area 88 make a remarkable spawning migration, traveling thousands of kilometers from the continental shelf or slope of the Ross Sea to spawn along the Pacific Antarctic Ridge system in winter (Prutko 2004; Brooks and Ashford 2008; Hanchet et al. 2008), moving perhaps as fast as 6 km per day (Petrov and Tatarnikov 2010), before returning to the Ross Sea in summer. Much remains unknown of this migration, including whether it is an annual event for a given individual (Parker and Grimes 2010). Antarctic toothfish captured by sperm whales (*Physeter macrocephalus*) and by fishermen among the seamounts and ridge system north of the Ross Sea have often been extremely emaciated, which is consistent with being in a postspawning mode (Yukhov 1970, 1971; Prutko 2004; Fenaughty et al. 2008), further evidence of this spawning migration.

Although being the dominant piscine predator in the Ross Sea, Antarctic toothfish, including adults and large subadults (>100 cm), can be important prey of Weddell seals (*Leptonychotes weddelli*) and Ross Sea killer whales (*Orcinus orca*), especially in waters overlying the shelf (Ainley and Siniff 2009; Ainley et al. 2009). The seals may take as many as 0.8–1.3 large toothfish each per day. In shelfbreak and deeper waters, toothfish, including adults, are also consumed by sperm whales (Yukhov 1971) and elephant seals (*Mirounga leonina*) (Reid and Nevitt 1998; Goldsworthy et al. 2001), especially so around the seamounts in the northern part of Area 88 and typically during the ice-free months (see Fig. 3.1). Both sperm whale and elephant seal populations are severely reduced in the Pacific sector as a result of past exploitation and depression of prey (by fishing), respectively (reviewed in Ainley and Blight 2009), and although the sperm whale population is slowly recovering (Branch and Butterworth 2001), their numbers are still low relative to historical populations. Weddell seal and Ross Sea killer whale populations currently remain at or near levels attained through past millennia (Ainley et al. 2009; Ainley 2010).

3.1.2 The Most Remote Fishery

The Area 88 toothfish fishery is the most remote fishery on the planet, taking place between 150° E (longitude of Victoria Land) and 105° W (Marie Byrd Land) and south of 60° S (see Fig. 3.1). This fishing zone extends as much as 3,250 km south of Bluff or Dunedin, New Zealand, the closest ports of departure for many fishing vessels. The fishery officially began in 1997 (1996–1997 austral summer) when CCAMLR permitted one New Zealand vessel to explore the feasibility of catching toothfish, traveling as far south as the Ross Ice Shelf (78° S; Waterhouse 2001). Subsequently, the number of vessels and participating countries swiftly increased, up to the current annual average of 15 (in 2010: Argentina 1, New Zealand 4, Republic of Korea 4, Russia 2, Spain 1, United Kingdom 2, Uruguay 1; Fig. 3.2). Each year, the fishery commences roughly in December, when the seasonal ice is sufficiently broken to allow fishing vessels into waters overlying the Ross Sea slope. Vessels fish using longlines, and in recent years have started targeting the Ross Sea slope at depths between 800 and 1,700 m (Figs. 3.3 and 3.4). Competing boats fish

Fig. 3.2 The take of Antarctic toothfish by country in Area 88, 1998–2007



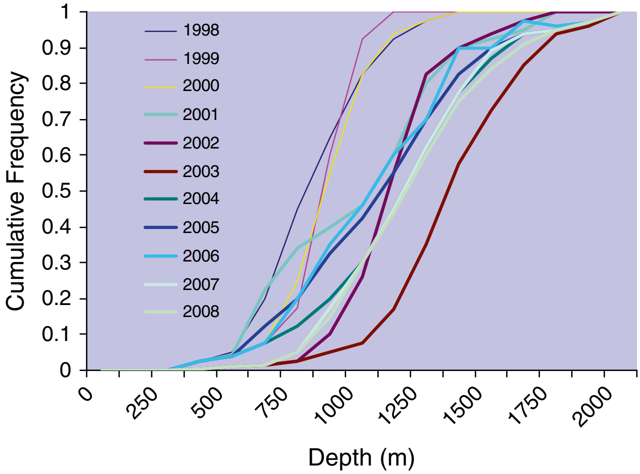


Fig. 3.3 The deepening of fishing effort, 1998–2008, in Area 88.1. After a few years of fishing at a wide range of depths, and then 1 year at very deep depths (2003), the fleet has concentrated sets between 1,000 and 1,250 m mainly over the Ross Sea continental slope in SSRUs (small scale research units) 88.1H and 88.1I (see Fig. 3.1). [Figure redrawn from Stevenson et al. (2008), their Fig. 3.2]

until the Total Allowable Catch for Area 88 is reached (TAC, in tons; most recently, ~3,500 t per year), or until the autumn growth of sea ice impedes the fishery. Some vessels (particularly those from relatively nearby New Zealand) are able to return to this region, and especially the seamounts in the north, for a second time at the end of the season after having dropped off their initial catch in port (Hanchet et al. 2007). Fishing vessels can no longer access the deep troughs of the westernmost shelf, in part owing to CCAMLR's prohibition of fishing along the Victoria Land coast (CCAMLR Conservation Measure 41-09), apparently to protect small fish. Despite these environmental and policy restrictions, fishing vessels have easily reached the annual TAC limit since 2005 (Fig. 3.5).

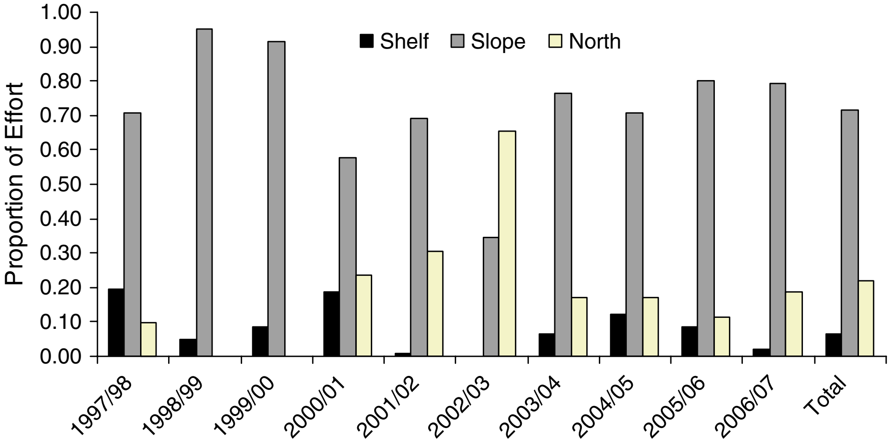


Fig. 3.4 Change in proportion of fishing effort over the Ross Sea continental shelf, its slope, and the seamounts to the north within Area 88.1, 1997–2007. When no real change in total landings (kg) was realized, the shelf waters became unimportant to the fishery after 2000 and the northern seamount waters after 2002. (Data from CCAMLR 2008)

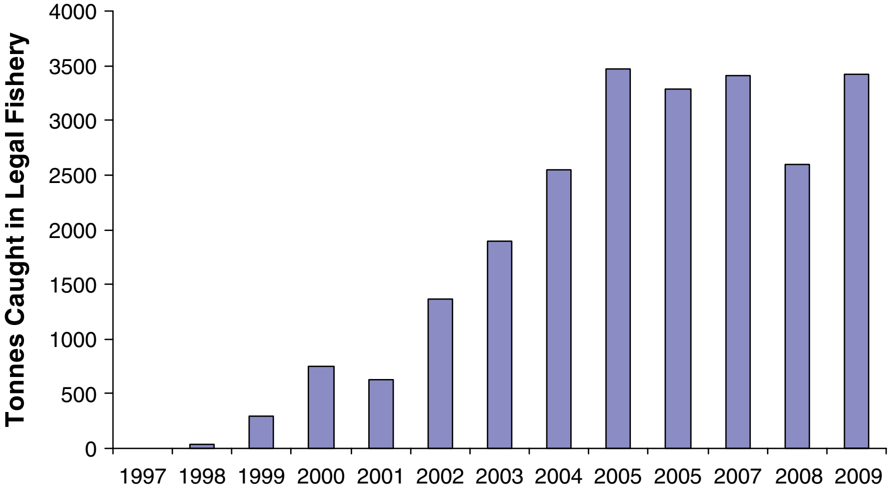


Fig. 3.5 History of the legal catch of Antarctic toothfish in Area 88. Only since 2005 has the fishery reached the allowable catch as determined by CCAMLR. (Data from CCAMLR 2009)

Illegal, unregulated, and unreported (IUU) vessels also target Antarctic toothfish in Area 88 (Barker 2008; MercoPress 2009). Although the history and level of extraction are not known, IUU catch in the Southern Ocean has been estimated by some, at least initially, to be three times that of the permitted catch as reported by CCAMLR (Clarke and Harris 2003; Hutchinson 2004; see also Agnew et al. 2009). Moreover, recent evidence suggests IUU fishermen are using deepwater gillnets in the Ross Sea region (TRAFFIC 2009). These nets are banned by CCAMLR and pose a significant environmental threat because of even higher by-catch levels than longlines and the risk of "ghost fishing," which refers to nets that have been left or lost in the ocean that continue fishing for years. The amount of toothfish caught in IUU gillnets remains unknown but is likely substantial (Österblom et al. 2010). For example, one net recently found by Australian officials spanned 130 km and had 29 t of Antarctic toothfish ensnared (TRAFFIC 2009), more than eight times the annual TAC for the area (outside of Area 88) where the net was retrieved.

3.2 Precautionary Management, Wise Use, or Blind Exploitation?

In this age of ecosystem-based fishery management (EBFM), designed to achieve rational or "wise use" (Leopold 1949), precautionary strategies are critical to ensure normal ecosystem functioning in the absence of adequate data (Constable et al. 2000; Croxall and Nicol 2004). In true EBFM, according to Pikitch et al. (2004, p. 346), "the overall objective … is to sustain healthy marine ecosystems and the fisheries they support. In particular, EBFM should (i) avoid degradation of ecosystems, as measured by indicators of environmental quality and system status; (ii) minimize the risk of irreversible change to natural assemblages of species and ecosystem processes; (iii) obtain and maintain long-term socioeconomic benefits without compromising the ecosystem; and (iv) generate knowledge of ecosystem processes sufficient to understand the likely consequences of human actions." EBFM is an approach to ensure that an appreciable portion of the fish population remains in the ecosystem, whereas many modern fishery models assume that there are "surplus" fish within an ecosystem which are there to take without any effects on the ecosystem (Longhurst 2010).

Heeding lessons learned from other collapsed deep-sea fisheries from around the world (Pauly et al. 2005; Cheung et al. 2007), "precautionary management" has become the watchword of CCAMLR (Constable et al. 2000). The CCAMLR charter clearly states precautionary rules to allow only conservative or low extraction levels to prevent damaging food web relationships and to ensure that stock levels can recover within 20–30 years if necessary (see treaty on CCAMLR website). Employing what is claimed to be a precautionary management strategy is admirable, particularly in a region where critical data for use in fishery models are often meager or missing (see above) owing to logistical difficulties of obtaining such data (reviewed in White 2010). However, despite the history of overexploitation of other toothfish fisheries, the lack of much data about toothfish natural history, and against its own precautionary rules, CCAMLR is aiming for the Ross Sea toothfish spawning stock to be reduced by 50% in the next 20 years. This extraction plan is applied by CCAMLR to all fish that are considered mainly as predatory species within an ecosystem; prey species, for example, krill, are allowed to be fished just to 75% pre-exploitation biomass (Constable et al. 2000; Pinkerton et al. 2007). As already noted, toothfish are important prey to several large mammal species.

Effectively, this management aims for maximum sustainable yield (MSY), a harvesting strategy that has been used for decades to manage other fisheries elsewhere (FAO 1998) and which has led to the declining harvest rates and populations of fish stocks worldwide (Longhurst 2010). Currently, there is no combined, formal research effort by CCAMLR to obtain ecosystem data of the Ross Sea and how this fishery affects the ecosystem, other than what can be acquired opportunistically by collecting data from commercially caught fish and by-catch. Nor is there dedicated research to understand the role of toothfish within its ecosystem or any attempt to verify what might be precautionary fishing in the Ross Sea. In reality, CCAMLR pays little attention to the Pikitch et al. (2004) EBFM points i, ii, and iv. Thus, the management of this fishery appears to be a single-species plan rather than EBFM.

Under the hypothetical MSY strategy, models predict that recruitment, growth, and rate of turnover of young fish increase from the removal of supposedly competing large fish from the population. Removal of the latter presumably frees up prey for the remaining younger, smaller fish and, in turn, increases growth rate and survival of those fish; this is the supposed “surplus production” that a fishery theoretically should be able to exploit without harming the ecosystem (see various chapters in Steele 1977; FAO 1998; Longhurst 2010). Under such a strategy, the only aspect that is predicted to change for the target species and the ecosystem is the density-dependent intraspecific competitive relationships (Steele 1977), which likely does not apply to toothfish, as reviewed here. The increased food availability, in part dependent on a species tendency toward cannibalism, is also predicted to affect other species within the food web positively if it is a competitor (competitive release) or predator of the target species (increased availability of alternate prey that the target species no longer consumes: Steele 1977; Longhurst 2010). Yet these models predicting target species and ecosystem responses to extraction under a MSY strategy do not account for many aspects of toothfish biology, including ontogenetic changes in their distribution, nor the differences in the sizes of prey taken by them (see Longhurst 2010). Finally, these models do not apply very well to long-lived species in general (Cheung et al. 2007). As we have shown earlier, there is considerable evidence that the vertical and horizontal distribution of Antarctic toothfish and their diet varies with age. If young and old fish do not share the same distribution and occupy different ecological niches, how can young fish experience a competitive release when the older fish are removed, other than by genotypic alteration? Moreover, taking out the larger, strictly “predatory” members of the stock, leaving just the smaller adults and subadults to the predators (including humans as predators), effectively alters the functionality of this fish within the ecosystem from being top predators to becoming only “prey.” Applying the MSY strategy to the Antarctic toothfish fishery raises doubts about whether this management strategy of reducing 50% of the spawning biomass is truly precautionary.

A historical case demonstrating our point involves the overexploitation to near collapse of *N. rossii*, which was the pioneer of commercially exploited fish in the Antarctic (>500,000 t taken in the first two fishing seasons, 1970–1971, around South Georgia alone; Koch 1992). This fishery began before the formation of

Fig. 3.6 Large, adult toothfish were once caught regularly under the ice of McMurdo Sound, the southernmost portion of the Ross Sea, and, presumably, the species occurs near the surface under other areas of heavy sea ice as well. Almost all McMurdo Sound fish were caught, tagged, and released, but no longer is it possible to catch such fish as those pictured (DeVries et al. 2008). The occurrence of large fish under the southern Ross Sea ice thus does not fit with the pattern of fish caught in the longline fishery, which now catches only small fish, on average, in the southern shelf waters (cf. Fig. 3.1)

CCAMLR; however, soon after CCAMLR was established, it immediately closed several areas to any finfishing (e.g., Antarctic Peninsula and South Shetland Islands, CCAMLR subarea 48.1, and South Orkney Islands, subarea 48.2; see Conservation Measures on CCAMLR website) to protect *N. rossii* stocks and other fish species. Now, even three decades post collapse, with no fishing allowed, the populations of *N. rossii* and also some by-catch species (e.g., *Gobionotothen gibberifrons*) have not recovered (Barrera-Oro et al. 2000; Barrera-Oro and Marschoff 2007; Marschoff et al. ms). This is just one of many examples of a fishery not recovering despite cessation of harvesting, particularly for deep-dwelling, long-lived species (Longhurst 2010). These cases point out that the 20–30 year recovery rule of CCAMLR will likely prove problematic for the Antarctic toothfish, especially if the pre-fished biomass was reduced by IUU fishing before any scientific assessment began.

Ichthyologists have been unable to catch large toothfish at the southern periphery of its range in McMurdo Sound since about 2001, something that was easily accomplished during the previous 35 years (DeVries et al. 2008) (Fig. 3.6). This detection of a reduced presence of large fish at the southern periphery of its range just 6 years after CCAMLR authorized a permitted, exploratory fishery has raised concern among Ross Sea scientists and has raised questions about how close the fishery is to the point that it cannot recover in 20–30 years, as dictated by the CCAMLR treaty. In addition, the presence of fish-eating killer whales, also known to consume large toothfish, has declined in that area (Ainley et al. 2009), while populations of predators that prey on small fish (including silverfish), such as Adélie penguins, have recently increased explosively (Lyver et al., unpublished data). This observation suggests that the zoogeographic range of at least large toothfish is contracting northward, to overlie just the Ross Sea shelfbreak region (see Fig. 3.1), as judged from fishery catch data (Hanchet et al. 2008).

3.3 Evolutionarily Enlightened Management

For EBFM to be truly precautionary and effective, it is important to employ "evolutionary enlightened" management (Ashley et al. 2003), which incorporates not only ecological but also evolutionary concepts into management decisions. We outline here reasons why management, as practiced by CCAMLR to date, may not be as precautionary as is hoped. We believe that evolutionary consequences, especially for long-lived, ontogenetically complex species, should be considered, along with ecological consequences, to make informed decisions and adjust extraction strategies for better management and wise use of the ecosystem.

To date numerous studies have shown that fishing can greatly accelerate evolution and thus cause considerable and irreversible life history changes in the target species within only a few generations (Haugen and Vøllestad 2001; Conover and Munch 2002; Olsen et al. 2004, 2005; Edeline et al. 2009; Greenberg 2010). Some of the most profound examples of contemporary evolution caused by fishing occurred when the largest, oldest, and most fecund individuals were removed (see reviews in Browman 2000; Law 2000; Conover 2000, 2007; Ashley et al. 2003). Longline gear, using large hooks, targets large and presumably old Antarctic toothfish that occur in deep, ice-free waters (see Fig. 3.2), while avoiding young fish (<4 years of age). Big fish, which are generally the fittest, are also the most aggressive foragers (Birkeland and Dayton 2005, and references therein) and thus the first to be caught (as shown in Hanchet et al. 2007, their Fig. 9). By targeting the largest fish for profit, the fishery effectively removes the best survivors (under natural conditions) and the most fecund members from the population. Such fishing reduces the average age and size of fish in the population, leading to an overall age truncation or juvenescence of the Antarctic toothfish stock (Brooks 2008; Longhurst 2010) (Fig. 3.7).

Furthermore, continuous removal of the oldest fish from the population, and alteration of the age distribution (juvenescence), risks "longevity overfishing," a form of overfishing that results from managing a long-lived species for biomass but not longevity (Beamish et al. 2006). CCAMLR's current management goal of reducing spawning toothfish biomass by 50% provides a typical example of a species being managed for these goals. Such management of long-lived species for biomass

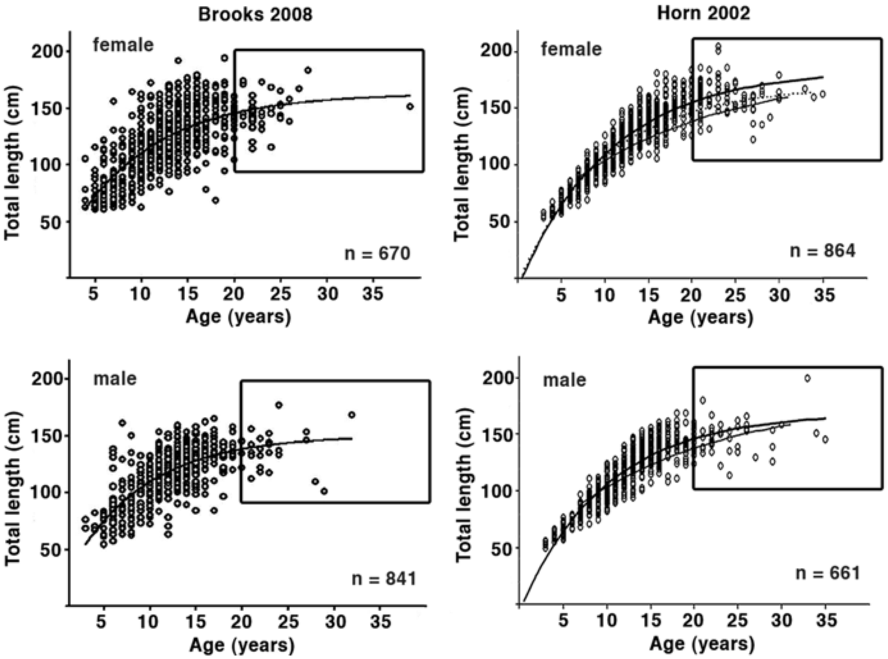


Fig. 3.7 Comparison of age structure, based on analysis of otoliths, in the complete 2003–2004 CCAMLR sample (Brooks 2008) with that from 1995 to 1999 (Horn 2002). Note truncation of age distribution with the passage of time

assumes that young fish have the same ecological function and productivity as older fish, an assumption that often is not supported by the literature (Beamish et al. 2006; Shust and Kozlov 2006). It also assumes that fecundity does not change with age (Longhurst 2010). Hence, by not including the population's age distribution and accounting for differences in productivity between age groups, the current management of the Antarctic toothfish is not truly precautionary, with the potential consequences reviewed below.

3.3.1 Evolutionary Consequences from Longevity Overfishing

Removing the largest and oldest individuals from the toothfish population in the Ross Sea region poses significant threats to the stock beyond ecological consequences. Age- and size-selective fishing may cause strong selection for slower growth and reproduction at a smaller size. Indeed, such selection has been shown to result in detectable changes in harvested species genotypes within months to years to decades, depending on the species generation time (Marteinsdottir and Steinarsson 1998; Thompson 1998; Browman 2000; Zimmer 2003; Hutchings 2005; Brander

2007; Allendorf and Hard 2009). For example, decreases in weight, length, and age at maturation have been observed in many commercially fished species (Law 2000; Conover 2000; Ashley et al. 2003; Conover et al. 2005), including heavily exploited stocks of deep-sea fish such as orange roughy (Smith et al. 1991; Kuparinen and Merilä 2007; Jørgensen et al. 2007) and Patagonian toothfish (Shust and Kozlov 2006). Paradoxically, age- and size-selective harvest reduces the prevalence of desired phenotypes (Conover 2007; Allendorf and Hard 2009), whereas in aquaculture and agriculture, breeders actively select for more productive phenotypes. Such unintended and "unnatural" selection (Allendorf and Hard 2009) through longevity overfishing not only causes smaller size distributions and earlier maturation but also leads to an exponential decline in the number of offspring produced and surviving until maturation (Berkeley et al. 2004a, b; Bobko and Berkeley 2004; Birkeland and Dayton 2005). Older fish are generally more experienced and successful spawners that also spawn for longer in a season. Therefore, selective harvesting of the most fecund individuals results in a reduction of the number and quality of larvae produced and a shortening of the reproductive season. In addition, this may in part reduce the larval survival window, a decrease in the average survival chance of larvae produced in response to intrinsic and seasonal environmental factors (Berkeley et al. 2004a, b; Bobko and Berkeley 2004; Birkeland and Dayton 2005).

For Antarctic toothfish, selection for slower growth and reproduction at a smaller size may have serious ecological repercussions, because only large, adult toothfish in good condition (>100–120 cm in size) are neutrally buoyant and can reside in surface waters without exerting muscular energy to hold position (addressed in more detail below) (Eastman and DeVries 1981, 1982; Near et al. 2003). Although Antarctic toothfish eggs have never been collected, recent models suggest that Antarctic toothfish eggs are released (or at least hatch) in surface waters where microplanktonic prey are abundant (Hanchet et al. 2008). Alternatively, spawning at depths of 1,500–2,000 m (where the longliners encounter adult fish in the nonspawning season) would force eggs or recently hatched larvae to undertake a long and precarious vertical ascent to reach surface waters where planktonic prey reside, assuming they could hatch at these depths. Hence, if fishery-induced selection causes Antarctic toothfish to spawn at a younger age when they are not large and buoyant enough to reach the surface waters without added energy expenditure, larval survival is likely to be greatly diminished, having grave implication for population sustainability (Munch et al. 2005; Greenberg 2010).

In extreme cases, harvest-induced unnatural selection can lead to irreversible loss of genetic heterogeneity (Birkeland and Dayton 2005; Allendorf and Hard 2009). For example, a recent study on Atlantic cod has shown that different genotypes of the species prefer different depth habitats, whereby "AA fish" prefer shallow water, "BB fish" are deep-water adapted, and "AB fish" are somewhat intermediate in their habitat choice (Árnason et al. 2009). As fishermen are targeting shallow waters, this fishery induces selection against the shallow-water-adapted fish, causing the AA genotype to rapidly disappear from the population (Árnason et al. 2009). In addition to the detrimental effects of the fishery-induced age truncation, this loss of the shallow-water-adapted genotype will likely contribute to the complete collapse of this fishery (Árnason et al. 2009).

Finally, the loss of genetic heterogeneity can seriously compromise the resilence of a species and its ability to respond to climate and other environmental changes. Studies have shown that juvenescent populations have unstable, nonlinear population dynamics that can result in extreme and unpredictable fluctuations (Hsieh et al. 2006; Anderson et al. 2008). Fish stocks that have a long-tailed age distribution can buffer environmental stochasticity to thus achieve stability, but with truncated age structure they become increasingly unstable because of changing demographic parameters (Anderson et al. 2008). Thus, these intrinsic consequences of fishery-induced juvenescence increase the likelihood of extirpation, without including the direct implications of harvesting (Anderson et al. 2008). The population sizes of Antarctic fishes have been shown to change considerably and suddenly; for example, *Champsocephalus gunnari* populations in the Scotia Sea region have marked fluctuations in numbers (Koch 1992).

Significant environmental changes, including alteration of ocean temperature, salinity, and sea ice cover, have been detected in the Ross Sea during the past few decades (Jacobs et al. 2002; Parkinson 2002; Jacobs 2006). As such, Antarctic toothfish are put at risk not only by increasing fishing pressure but also by the species decreasing ability to adapt to drastic environmental changes, as caused by reductions in genetic diversity through fishery-induced juvenescence.

3.3.2 Ecological Consequences of Longevity Overfishing

Longevity overfishing of large predatory fish species has occurred in marine ecosystems throughout the world (Pauly et al. 1998; Baum et al. 2003; Myers and Worm 2003; Worm et al. 2005). Overwhelming evidence suggests that this form of overfishing has profound effects on community structure and diversity within the affected ecosystems consequent to the losses of "ecological services" of affected species. For example, stable isotope signatures in scales of the haddock (*Melanogrammus aeglefinus*) from Georges Bank (off Newfoundland), collected between 1929 and 1987, showed significant declines in $\delta^{15}N$, with the two most considerable declines occurring immediately after fishing efforts had increased dramatically (Wainwright et al. 1993). These authors surmised that the indicated change in haddock diet is related to the declining trophic structure and complexity of the ecosystems as the abundance of haddock and other large predator(s) decreased.

Another example of ecosystem collapse resulting from longevity overfishing was triggered by the removal of large sharks from waters off the east coast of North America. This change caused a trophic cascade when the shark's former prey species, the cownose ray *Rhinoptera bonasus*, exploded in numbers. Soon after, bay scallops (*Argopecten irradians*), the ray's primary prey species during migration, virtually disappeared (Myers et al. 2007). In yet another case, the removal of large Atlantic cod and other predatory fish from the Northwest Atlantic resulted in a dramatic increase of benthic macroinvertebrates, predominantly the northern snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*), which had been their prey (Myers and Worm 2003; Frank et al. 2005). This invertebrate explosion also affected other aspects of the ecosystem, such as the chemical composition of the waters as nutrient balances changed, as perhaps more detritus was being consumed. However, examples of trophic structure changes caused by longevity overfishing are not restricted to subpolar and temperate marine ecosystems. The removal of predatory fishes from reef ecosystems in Fiji and other tropical marine ecosystems facilitated an explosion of the crown-of-thorns starfish *Acanthaster planci*, which in turn decimated the coral organisms on which the starfish feed, and ultimately led to irreversible damage to the reefs themselves (Dulvy et al. 2004; Mumby et al. 2006, 2007; reviewed, also, in Longhurst 2010). These examples demonstrating trophic cascades caused by the overfishing of large piscine predators (see additional examples in Stevens et al. 2000; Baum and Worm 2009) begs the question: Will longevity overfishing of Antarctic toothfish have similar effects on the Ross Sea ecosystem?

The removal of toothfish, as one of the main predators of fish in the Ross Sea, risks several possible trophic cascades. These risks are presently speculation; however, they will likely be heightened by the ecosystem's simplified food web. One aspect of this simplified food web is that the Southern Ocean lacks the small, densely schooling fish species, such as herring, anchovies, or sardines, which in other ecosystems feed on phytoplankton. Instead, shorter-lived, swarming invertebrates, such as euphausiids, graze the phytoplankton in the Ross Sea. Euphausiids, in particular, *Euphausia crystallorophias*, are very important prey for many other predators in the Ross sea food web (Eastman 1993; Ainley et al. 2003; La Mesa et al. 2004). The loosely schooling Antarctic silverfish is one of the main predators of this euphausiid (reviewed in Ainley et al. 2006), and when euphausiids are seasonally depleted, this decreased availability leads to cannibalism in silverfish (Eastman 1985b). Because toothfish are the main predator of silverfish over the Ross Sea shelf, removing large toothfish should result in elevated abundance of silverfish, which would in turn reduce the abundance and density of euphausiids earlier in the season than occurs now. An earlier depletion of euphausiids could well have implications for other euphausiid predators, such as penguins, whose diet early in the summer is composed primarily of euphausiids (Ainley et al. 2003). For example, in recent years Adélie penguin populations in the Ross Sea have begun to increase dramatically (Lyver et al., unpublished data).

In the Ross Sea ecosystem, the majority of fish species, principally notothenioids, are benthic, preying on invertebrates (Eastman 1993; La Mesa et al. 2004). The best examples are the plunderfishes, *Pogonophryne* (Artedidraconidae). Including 19 species, they are the most speciose notothenioid genus (Eakin et al. 2009), and are well represented in the Ross Sea at depths ranging from 300 to 2,500 m. Occasionally they are taken as by-catch by toothfish longliners and can be an intermittent prey species of toothfish (Arana and Vega 1999; Prutko 2004). Given that these are cold-water fish, they grow slowly and reach maturity at an older age (Eastman 1993). They are also extremely sedentary and territorial (Olaso et al. 2000; Lombarte et al. 2003). These characteristics impart even greater sensitivity to perturbation than that imparted by slow growth and maturation, because population turnover and productivity following extraction would be very slow.

In shallower waters, species of *Trematomus*, also nototheniids, are ecologically important, and one species in particular, *Trematomus bernacchii*, is the principal predator of the Antarctic scallop *Adamussium colbecki* (Vacchi et al. 2000). As notothenioids have weakly ossified jaws and their teeth are small and weakly attached (Eastman 1993), *T. bernacchii* preys extensively on the soft scallop larvae, which in turn explains spatial variation in scallop abundance (Chiantore et al. 2000, 2001). Where scallops are dense they play an important role by filtering and cleaning a significant amount of the particulate content of the water column (Chiantore et al. 1998). Given that *T. bernacchii* has not been identified specifically as a prey of Antarctic toothfish, although unidentified *Trematomus* have (Prutko 2004; La Mesa et al. 2004), the example mentioned earlier involving sharks and scallops may foreshadow possible similar outcomes in the Ross Sea if large predatory toothfish are removed.

Overwhelming evidence from overfishing in other marine ecosystems suggests that ecosystem function is at risk when large predatory fish are removed. Thus, its quite plausible that longevity overfishing of Antarctic toothfish could cause profound changes to the Ross Sea ecosystem.

3.4 Management Solution for Antarctic Toothfish

To move away from longevity overfishing of the Antarctic toothfish in the Ross Sea and toward “wise use,” managers must employ precautionary measures in the Total Allowable Catch. According to Allendorf and Hard (2009; p. 9988), “Fisheries and wildlife managers have yet to adopt management strategies that guard against rapid evolutionary response to exploitation. Managers have focused on demographic parameters that affect population abundance and growth rates because their primary goal is sustainable yield in the short-term. However, recognition is growing [as we have detailed above] that evolution under exploitation can reduce population growth and viability and ultimately might reduce yield” (Hutchings 2000; Law 2000; Milner et al. 2006).

In other fisheries that target long-lived fish (e.g., sturgeon, *Acipenser transmontanus*), successful management has been achieved by employing “slotted size limits,” which utilizes gear that removes only middle-aged fish and avoids the youngest and oldest (Oregon Fish and Wildlife 2010). Such selectivity by gear type is not possible with longlines (except by change in hook size?) and it is likely not possible given the competition among vessels to fill their holds before the TAC is reached. But because toothfish seem to utilize different habitats during various stages of their life history, it would be possible to achieve “slotted size limits” through spatial management. While this would be complicated by their purported spawning migrations, various parts of the Ross Sea shelf, slope, and associated ridges and seamounts could be closed, perhaps via a Marine Protected Area to ensure the largest individuals are spared.

To ensure that the Ross Sea remains a functioning ecosystem, it is imperative that old, large toothfish are allowed to exist in relatively high abundance. To protect toothfish and this ecosystem for the long term, it is necessary to include major portions of the Ross Sea shelf and slope, as well as some of the seamounts to the north, in a network of marine protected areas (MPAs). Low-level fishing could then be allowed at the edges of these MPSs while keeping the majority of the toothfish population, with a natural age distribution, intact. Many examples of how such MPAs have succeeded in the management of fish stocks are available (Sumaila et al. 2000; Lubchenco et al. 2003), along with examples that failed owing to poor or unenforced management (Longhurst 2010). Currently, longline fishing throughout the entire Antarctic toothfish range extracts the oldest, largest, and likely most fecund fish (see above; Brooks 2008; Brooks and Ashford 2008) (Fig. 3.7). As we argued in this chapter, we believe that these old age classes of Antarctic toothfish need to be restored within this population to avoid irreversible evolutionary and ecological consequences, heightened in an age and area of rapid and profound climate change (Jacobs 2006; Trathan and Agnew 2010).

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