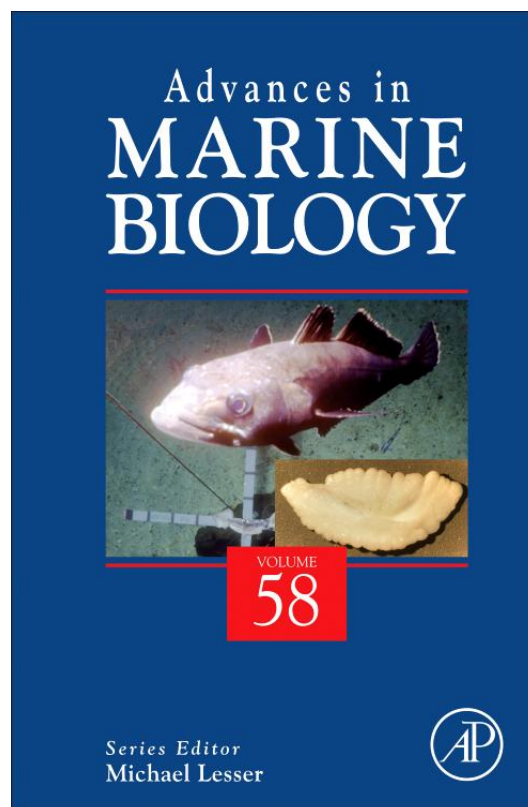


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THE PATAGONIAN TOOTHFISH: BIOLOGY, ECOLOGY AND FISHERY

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Abstract

Patagonian toothfish (*Dissostichus eleginoides*) is a large notothenioid fish that supports valuable fisheries throughout the Southern Ocean. *D. eleginoides* are found on the southern shelves and slopes of South America and around the sub-Antarctic islands of the Southern Ocean. Patagonian toothfish are a long-lived species (>50 years), which initially grow rapidly on the shallow shelf areas, before undertaking an ontogenetic migration into deeper water. Although they are active predators and scavengers, there is no evidence of large-scale geographic migrations, and studies using genetics, biochemistry, parasite fauna and tagging indicate a high degree of isolation between populations in the Indian Ocean, South Georgia and the Patagonian Shelf. Patagonian toothfish spawn in deep water (ca. 1000 m) during the austral winter, producing pelagic eggs and larvae. Larvae switch to a demersal habitat at around 100 mm (1-year-old) and inhabit relatively shallow water (<300 m) until 6–7 years of age, when they begin a gradual migration into deeper water. As juveniles in shallow water, toothfish are

primarily piscivorous, consuming the most abundant suitably sized local prey. With increasing size and habitat depth, the diet diversifies and includes more scavenging. Toothfish have weakly mineralised skeletons and a high fat content in muscle, which helps neutral buoyancy, but limits swimming capacity. Toothfish generally swim with labriform motion, but are capable of more rapid sub-carangiform swimming when startled. Toothfish were first caught as a by-catch (as juveniles) in shallow trawl fisheries, but following the development of deep water longlining, fisheries rapidly developed throughout the Southern Ocean. The initial rapid expansion of the fishery, which led to a peak of over 40,000 tonnes in reported landings in 1995, was accompanied by problems of bird by-catch and overexploitation as a consequence of illegal, unreported and unregulated fishing (IUU). These problems have now largely been addressed, but continued vigilance is required to ensure that the species is sustainably exploited and the ecosystem effects of the fisheries are minimised.

1. INTRODUCTION

Toothfish, named for the sharp teeth on their upper jaw, belong to the genus *Dissostichus* in the Family Nototheniidae (Antarctic cods) that are endemic to the southern hemisphere and dominate Antarctic fish assemblages (Gon and Heemstra, 1990; Kock, 1992). There are two species of toothfish; the Antarctic toothfish (*Dissostichus mawsoni*), which is found at high latitudes around Antarctica, and the Patagonian toothfish (*D. eleginoides*; Fig. 4.1), which occurs further north around sub-Antarctic islands



Figure 4.1 Photograph of a Patagonian toothfish (*Dissostichus eleginoides*) taken with a baited camera at 1000 m depth on the Patagonian Shelf.

such as South Georgia and around the southern tip of South America. There is, however, some overlap in their distribution in intermediate areas. Both species grow to large size, reaching lengths in excess of 2.3 m and weights greater than 200 kg, and are the target of valuable commercial fisheries.

Patagonian toothfish were first described in 1898 (Smitt, 1898), but interest in the species was limited until toothfish were caught as a by-catch in trawl fisheries off the South American coasts. The large size of Patagonian toothfish, coupled with high quality flesh, led to the development, in the mid 1980s, of a valuable longline fishery, targeting large adult Patagonian toothfish in deep water (> 500 m; Agnew, 2004). As with many new fisheries, the fishery developed ahead of the essential knowledge of the biology and ecology of the target species that is necessary to facilitate good management practices. Initially, the longline fishery caused extremely high incidental mortality to seabirds and while this problem has been largely overcome, there are still concerns about the sustainability of the various fisheries. In some areas, illegal, unreported or unregulated (IUU) fishing remains a major problem.

Here, we synthesise existing data on the biology, ecology and fishery for Patagonian toothfish, highlighting areas where the knowledge is lacking. We also review the management of stocks of this valuable species in different parts of its range. We have, where possible, attempted to avoid grey literature. However there is much valuable information in working group papers from the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). CCAMLR manages marine living resources south of the Antarctic Polar Front (APF) and, where necessary, we have cited this work.

2. TAXONOMY AND SYSTEMATICS

Order: Perciformes

Sub-order: Notothenioidei

Family: Nototheniidae

Genus: *Dissostichus* Norman, 1937

Species: *Dissostichus eleginoides* Smitt, 1898

The Notothenioidei are a suborder of the Perciformes that dominate the waters of the Southern Ocean. They are an acanthomorph clade of teleost fish that contain over 120 species (Eastman and Eakin, 2000; Eastman and McCune, 2000). Within this, the Family Nototheniidae is considered to be the most speciose and initially included the Eleginopinae, the Nototheniinae, the Trematominae and the Pleuragramminae (DeWitt *et al.*, 1990). On the basis of morphological and molecular data, the genus *Eleginops* was removed from the family (Balushkin, 2000; Bargelloni *et al.*, 1998, 2000; Near and Cheng, 2008; Near *et al.*, 2004; Sanchez *et al.*, 2007). *Eleginops* appears as the sister group to all of the nonbovichthid notothenioids, and

this is consistent with the fact that *Eleginops* is a sub-Antarctic, basal notothenioid lacking antifreeze proteins. The nototheniids, without *Eleginops*, are thus divided into three subfamilies based on De Witt *et al.* (1990) and Balushkin (2000). These are the Nototheniinae (*Notothenia*, *Paranotothenia*, *Gobionotothen*, *Lepidonotothen* and *Patagonotothen*), the Trematominae (*Trematomus* and *Pagothenia*) and the Pleuragramminae (De Witt *et al.*, 1990) or Pleuragrammatinae (Balushkin, 2000) (*Dissostichus*, *Pleuragramma*, *Aethotaxis* and *Gvodarus*).

Using molecular data (sequences of MLL, rhodopsin, cytochrome b and mitochondrial d-loop genes) Sanchez *et al.* (2007) confirmed Balushkin's Pleuragrammatinae and postulated that neutral buoyancy was gained from common ancestry as all of the species in this subfamily have this feature. However they pointed out that the anatomical features of neutral buoyancy are not the same in *Dissostichus*, *Pleuragramma* and *Aethotaxis* suggesting parallelisms in neutral buoyancy. Near and Cheng (2008) examined the phylogenetics of notothenioid fishes using both nuclear and mitochondrial gene sequences and found the clade containing neutrally buoyant notothenioids present in their mitochondrial dataset but not well resolved in their nuclear data. They found that, despite common notothenioid clades in both the nuclear and mitochondrial gene phylogenies, large differences exist in the phylogenies inferred from each of their two datasets with regard to the presence of particular clades and the overall phylogenetic resolution. They concluded that the absence of a monophyletic Nototheniidae and the neutrally buoyant clade in their nuclear gene tree was a result of a lack of phylogenetic resolution and not strong support of the paraphyly of these two groups.

The genus *Dissostichus* includes two species: the Antarctic toothfish *D. mawsoni* and the Patagonian toothfish *D. eleginoides*.

D. eleginoides was described by Fredrick Adam Smitt in 1898. Smitt (1898) failed to designate a holotype, but two syntypes were deposited at the Swedish Museum of Natural History (Naturhistoriska riksmuseet) (NRM 3235 (1), 3236 (1)). These specimens came from Puerto Torro (55° 24' S, 068° 17' W) on 11th December 1895 and from Lagotoaia on 10th February 1896.

The etymology of *Dissostichus* comes from the Greek disso, meaning double and stichus, meaning row or line referring to its two lateral lines, whilst *eleginoides* refers to its morphological affinities to the genus *Eleginops*.

Subsequently, Gill and Townsend (1901) reported the capture of a fish of nearly five feet in length from 1900 m by the *RV Albatross* in 1888 in the SE Pacific Ocean. Although the specimen was thrown overboard, a photograph was taken of it. The specimen was caught at dredge station 2788, off the Chonos Archipelago, Southern Chile (45° 35' S, 075° 55' W). The authors described it from the photograph as *Macrius amissus*, with the generic name a reference to its length and bulk, and the specific name reflecting the

geographic distance from its relatives as well as the loss of the type. When DeWitt saw the photograph, he was reminded of the illustrations of *D. eleginoides* published by F. A. Smitt in 1888, and after some comparison of the two, concluded that *Macrias amissus* was congeneric with Smitt's species. De Witt (1962) considered that it should be considered a distinct species, *D. amissus* (Gill and Townsend, 1901), differing from *D. eleginoides* and *D. mawsoni* in several ways. De Witt (1962) stated that *D. eleginoides* differed from *D. amissus* in having a longer lower lateral line, a longer head and snout, a larger eye and longer pectoral fin. Whereas *D. mawsoni* (Norman, 1937) differed from *D. amissus* in having a shorter lower lateral line, a larger eye, a longer pectoral fin and smaller, more numerous scales.

Using morphometric analyses, Oyarzun and Campos (1987) concluded that *D. amissus* is a junior synonym of *D. eleginoides* by Rule of Priority. They concluded that the characters used to distinguish between the species such as eye size, relative head length and the relative lengths of the lateral lines showed great variability and could not be used to separate the two. *D. eleginoides* differs from *D. mawsoni* by having several elongate scaleless areas on the dorsal side of its head and by having a longer lower lateral line (Gon and Heemstra, 1990).

3. DISTRIBUTION AND LIFE CYCLE

3.1. Determining distribution and abundance

A range of methods have been used to sample toothfish and determine distribution patterns. Initially, toothfish were caught as a by-catch in trawl fisheries (on the Patagonian shelf and around South Georgia) but, following the development of the longline fishery in Chile, longlining became the main fishing method especially in deeper water. Pots have also been trialled with varying success (Agnew *et al.*, 2001). Baited cameras have been used to examine distribution and to try to determine density (Collins *et al.*, 1999, 2006; Yau *et al.*, 2002).

Given the broad bathymetric range of toothfish, determination of abundance has proved problematic. Trawl surveys have been undertaken to depths of around 1000 m (e.g. Coggan *et al.*, 1996), but fishing deeper requires large amounts of trawl warp, is time consuming and in many areas the ground is too rough for trawl gear. Baited cameras were initially trialled on the South Georgia and Falkland Islands slopes (Collins *et al.*, 1999; Yau *et al.*, 1997, 2002), as a means to estimate abundance. With the baited camera systems, either the first arrival time of fish at the bait or the total number attracted from the estimated area of odour plume can be used to estimate abundance (Priede and Merrett, 1996). However, the initial results indicated that toothfish may be deterred from attending the bait by the

bright flashes of the camera every 60 s. A follow-up study, which used a video camera with low-illumination levels, had slightly better results (Collins *et al.*, 2006), but toothfish attended the bait only briefly, and with the camera alternating on and off, toothfish may have been missed, so a reliable estimate of abundance was not possible.

An alternative method to assess adult population size is a mark and recapture method, using external tags (see Section 4.2). Toothfish are extremely resilient and post-tagging survivorship is reported as high from both longlines and short-duration trawls (Agnew *et al.*, 2006a; Williams *et al.*, 2002). Tuck *et al.* (2003) used a modified (daily) Peterson mark and recapture method to assess the population size of toothfish at Macquarie Island. A length-dependent selectivity model was applied to take account of the movement of tagged fish to deeper water, which was unavailable to the trawl fishery. Mark and recapture methods have subsequently been used to determine adult population size in other areas such as South Georgia and the Ross Sea (Agnew *et al.*, 2006b).

3.2. Geographic distribution

Toothfish have a circum-sub-Antarctic distribution, being found on the southern Patagonian and Chilean shelves, and around sub-Antarctic islands (e.g. South Georgia and Shag Rocks, Crozet, Kerguelen, Heard, McDonald, Macquarie and Prince Edward islands), banks (e.g. Banzare Bank) and seamounts (e.g. Ob and Lena Seamounts) between latitudes 45° S and 62° S (Fig. 4.2) in the Southern Ocean (De Witt *et al.*, 1990). The distribution spans the Antarctic Polar Front (APF) and extends north to 35° S on the Patagonian Shelf in the Atlantic Ocean, to 30° S off Chile in the Pacific and to 40° S in the SW Indian Ocean (Abellan, 2005). In the Scotia Sea, the distribution extends from the Scotia Ridge (west of Shag Rocks) to South Georgia and the northern South Sandwich Islands, with the most southerly record in the Scotia Sea being from 61° S at King George Island in the South Orkneys (Arana and Vega, 1999). In the Ross Sea, Patagonian toothfish are common in the northern areas and have been recorded as far south as 75° 30' S (Hanchet *et al.*, 2004), with a catch of 14 large individuals taken on a longline from 1000 m at 71° 40' S (Stevenson *et al.*, 2008), which was attributed to unusual hydrographic conditions. There remain many places in the Southern Ocean that have not been sampled, so the known distribution may be extended.

A single specimen of toothfish was reported from the northern hemisphere (Moller *et al.*, 2003), which was suggested as evidence of long-distance migration. This record must be considered dubious, as the fish would have migrated at least 10,000 km, travelling at depths below the tropical waters.

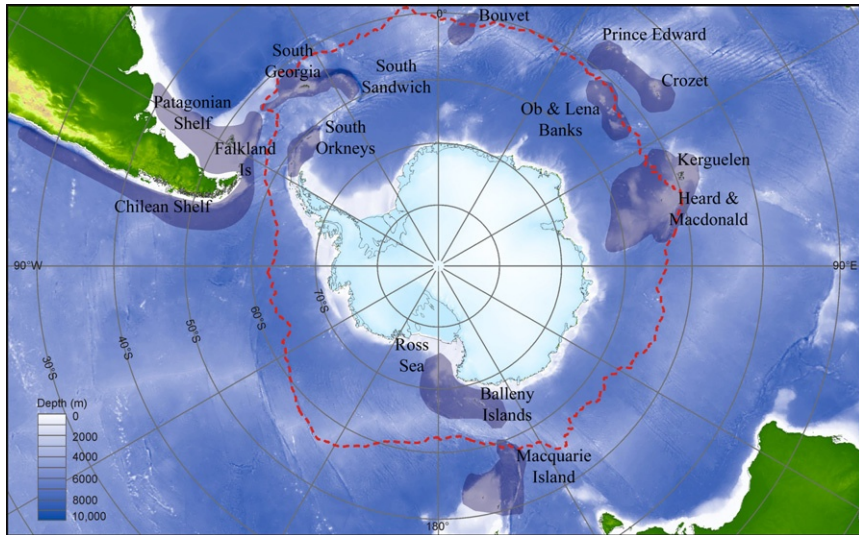


Figure 4.2 Polar projection of the southern hemisphere showing the known distribution of Patagonian toothfish (*Dissostichus eleginoides*). Polar Front indicated by the red dotted line.

Water temperature may be a key factor in limiting distribution. Unlike *D. mawsoni*, *D. eleginoides* lacks antifreeze and has at least a few glomeruli in its kidneys (Eastman, 1990), which led to the suggestion that toothfish were unlikely to occur in water cooler than 2 °C (Eastman, 1990). Collins *et al.* (2006) photographed Patagonian toothfish at depth in temperatures as low as 1.4 °C, but did not encounter toothfish when the temperature was less than this.

3.3. Life cycle and bathymetric distribution

Toothfish occupy a broad bathymetric range during their life cycle (Fig. 4.3). They are known to spawn in deep water during winter (June–September) (Agnew *et al.*, 1999; Evseenko *et al.*, 1995; Laptikhovskiy *et al.*, 2006) (see Section 6). Data on the distribution of eggs and larvae are scarce, but eggs (4.3–4.7 mm) have been found in the upper 500 m over deep water (Evseenko *et al.*, 1995) and are thought to hatch (at around 15 mm standard length (SL)) in October–December (Effremenko, 1979; Evseenko *et al.*, 1995; Kellermann, 1989; North, 2002; North and White, 1982). Larvae have been caught from around South Georgia (Efremenko, 1984; Evseenko *et al.*, 1995; North, 2002), Shag Rocks and Burdwood Bank (North, 2002). The majority of larvae have been reported from an area to the NW of South Georgia (North, 2002), but this is a heavily sampled

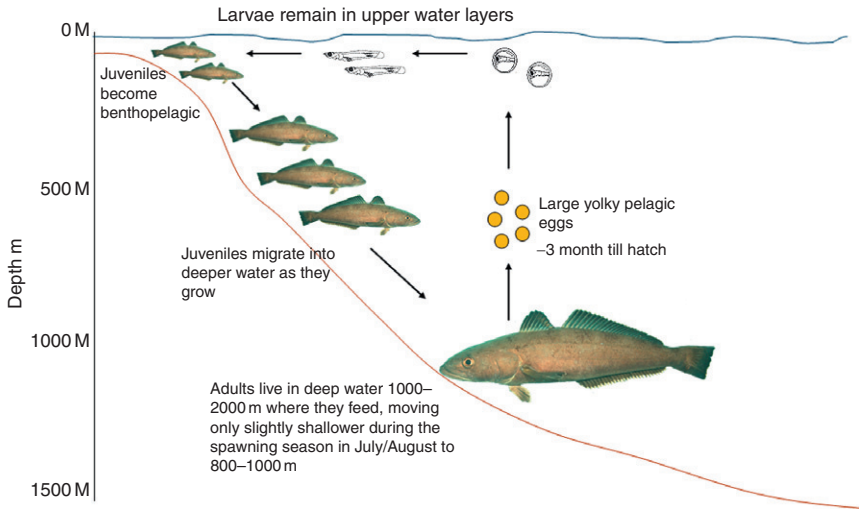


Figure 4.3 Schematic illustration of the life cycle of Patagonian toothfish (*Dissostichus eleginoides*).

location. Of the 43 larvae (18–63 mm SL) reported by North (2002), 40 were captured in the upper 250 m, 23 of which were in the upper 3 m at night.

When the pelagic larvae reach a threshold size, they become benthopelagic and are first caught in research bottom trawls in January at Shag Rocks at around 150 mm total length (TL) (age 1+) (Belchier and Collins, 2008), but smaller fish (80–93 mm TL) have been caught on the bottom near Crozet Islands during February (Duhamel, 1987). The otoliths of the latter fish had no visible growth increment and were thought to be 7–8 months old. The juvenile phase is typically spent in shallow waters and the recruitment of these juveniles may be concentrated over a limited spatial area. For instance, recruitment to the South Georgia population occurs primarily on the Shag Rocks shelf, to the NW of South Georgia (Collins *et al.*, 2007). Juveniles typically remain in shallow water for the next 4–5 years. On the Patagonian Shelf, the Isla de los Estados is the main area of recruitment (Woehler, unpublished), although small numbers of recruits occur across the southern Patagonian Shelf.

At a size of 500–700 mm TL, the juvenile toothfish disperse and gradually migrate down the slope, which may be associated with changes in both growth rate and diet. In general, adult toothfish occupy deep water (> 500 m), although large fish have been caught in shallow water, close inshore, at South Georgia (Collins *et al.*, 2007). Toothfish thus show the distinct bigger-deeper trend (Coggan *et al.*, 1996; Collins *et al.*, 2007; Laptikhovsky *et al.*, 2006; Lord *et al.*, 2006; Fig. 4.3) that is common in many deep-sea scavenging

fish (Collins *et al.*, 2005) and often associated with a switch from a predatory role to scavenging (see Section 7, Arkhipkin *et al.*, 2003).

The maximum depth for Patagonian toothfish is around 2500 m, but is likely to vary geographically, which may be linked to water temperature (see above). Using baited cameras, Collins *et al.* (2006) found toothfish as deep as 1600 m around South Georgia, but no fish were seen in deployments deeper than 1800 m. Toothfish have been caught down to 2122 m around the Falkland Islands (Laptikhovsky *et al.*, 2006).

3.4. Recruitment variability

Recruitment of juvenile toothfish, associated with the settlement of pelagic larvae, shows tremendous inter-annual variability. This is illustrated at South Georgia, where annual surveys showed a single cohort, first seen in 2003, dominating catches in subsequent years (Fig. 4.4), with little evidence of further recruitment until 2010 (Collins unpublished). The presence of dominant cohorts has also been detected in the fishery and through age determination from otoliths.

Recruitment variability at South Georgia appears to be linked to environmental variability (Belchier and Collins, 2008). Abundance of the 1+ juvenile toothfish cohort (13–15 month-old dependent on survey date) was found to vary inter-annually and to be inversely correlated with the sea surface temperatures (SST) experienced by adults prior to spawning. The mean length of 1+ toothfish attained after 13–15 months was higher in years of high juvenile abundance and was significantly inversely correlated with SST in the summer prior to adult spawning. Around the Falkland Islands, peaks in toothfish recruitment have also been identified, occurring approximately every 4 years (Laptikhovsky and Brickle, 2005).

4. POPULATION STRUCTURE, MOVEMENTS AND MIGRATION PATTERNS

Understanding the movements of toothfish at different temporal and spatial scales is essential to the management of this species. Although the Patagonian toothfish have a broad circum-Antarctic distribution, the bathymetric range of the juveniles and adults means that many island (adult) populations are potentially isolated from other populations by areas of deep ocean. Discrimination between different populations/stocks of Patagonian toothfish is an important part of the management process, as it is important to understand whether individual populations should be managed in isolation from other stocks. This has stimulated a range of studies that

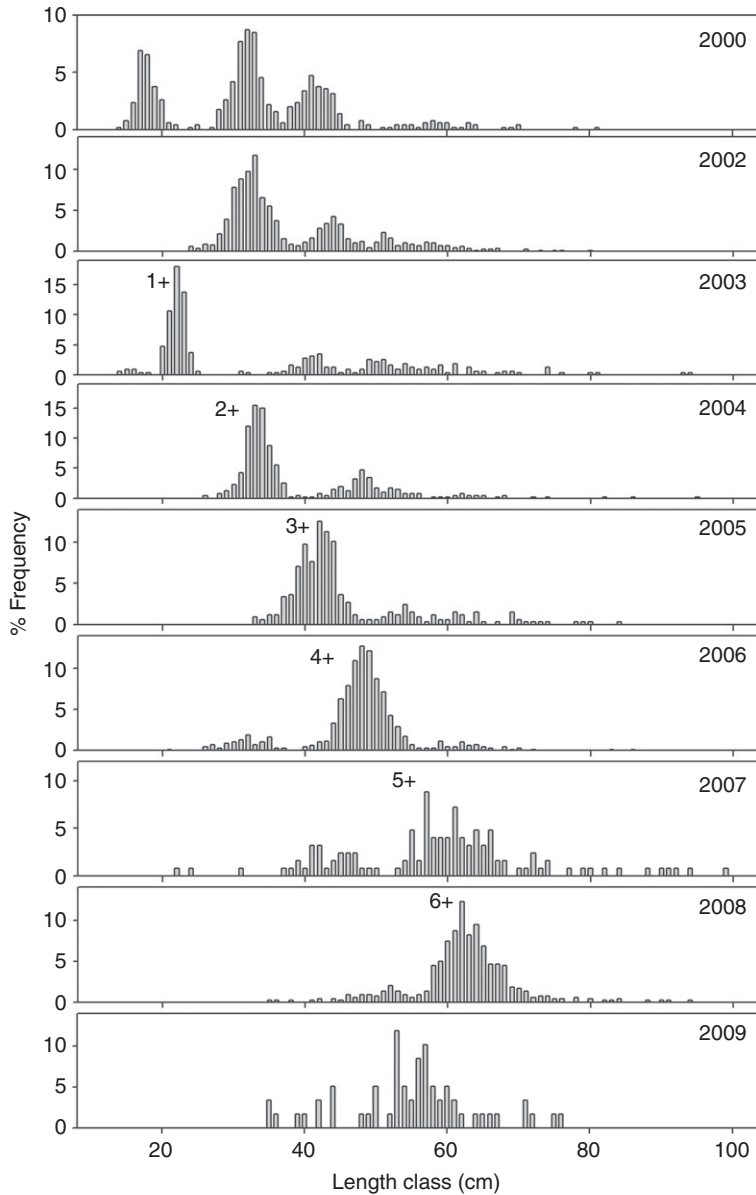


Figure 4.4 Length-frequencies of Patagonian toothfish (*Dissostichus eleginoides*) from trawl surveys (100–350 m) on the South Georgia and Shag Rocks shelves (modified from Belchier and Collins, 2008).

have investigated the degree of mixing between populations throughout the Southern Ocean and on the Patagonian Shelf. At a smaller scale, knowledge of the movements of larvae, juveniles and adults is key to understanding the life cycle.

Various methods have been undertaken to examine connectivity between potential populations, including studies on genetics (Appleyard *et al.*, 2002, 2004; Rogers *et al.*, 2006; Shaw *et al.*, 2004), parasite fauna (Brickle *et al.*, 2005), biochemical markers in otoliths (Ashford and Jones, 2007; Ashford *et al.*, 2006) and tagging studies (Marlow *et al.*, 2003; Tuck *et al.*, 2003; Williams *et al.*, 2002), although tagging studies tend to be informative over shorter temporal and spatial scales.

4.1. Population structure

Genetic studies indicate that a high degree of isolation exists between Patagonian toothfish populations from different locations, with distinct populations identified in the southern Indian Ocean (comprising Heard, Crozet, Kerguelen, Prince Edward and Marion islands), the Atlantic Sector (South Georgia and the South Sandwich Islands) and the Patagonian Shelf (Appleyard *et al.*, 2002, 2004; Rogers *et al.*, 2006; Shaw *et al.*, 2004; Smith and McVeagh, 2000).

Using mitochondrial DNA and microsatellites, initially developed by Reilly and Ward (1999), Appleyard *et al.* (2002) found distinct differences in toothfish populations from Macquarie Island, Heard and McDonald Islands and South Georgia/Shag Rocks. Greater differentiation of mitochondrial DNA was detected and could be explained by either female philopatry or greater male dispersal. Subsequently, Appleyard *et al.* (2004) used the same approach to compare samples from populations at Crozet, Kerguelen, Prince Edward, Marion and Heard and McDonald islands, and found no evidence of genetic differentiation between these sites in the western Indian Ocean.

Genetic studies using mitochondrial DNA sequences (12S rRNA) have shown a distinct difference between toothfish populations on the Patagonian Shelf and those at South Georgia and on the North Scotia Ridge (Rogers *et al.*, 2006; Shaw *et al.*, 2004). Differences were attributed to the deep-ocean areas between the sites, which prevent adult migration, and the APF and sub-Antarctic Front and the associated high-velocity Antarctic Circumpolar Current, which limits larval dispersal. However, using microsatellites, Shaw *et al.* (2004) found much less distinct population structuring in the North Scotia Ridge samples and suggested that differences between mtDNA and nuclear DNA population patterns may reflect either genome population size effects or (putative) male-biased dispersal. Rogers *et al.* (2006) found that samples from south of the APF (South Georgia, Bouvet and Ob Seamount) had an identical 12S rRNA haplotype.

However, microsatellite genotype frequencies showed genetic differentiation between South Georgia samples and those obtained from around Bouvet Island and nearby seamounts. Large geographic distances and water depths in excess of 3000 m (below the bathymetric range of toothfish) separate these areas.

The composition of the parasite fauna of toothfish has also been used for stock discrimination and generally supports the genetic results. Drawing on previous studies, [Brickle \(2003\)](#) and [Brickle *et al.* \(2005\)](#) clearly demonstrated that parasites can be used to separate *D. eleginoides* populations from around the Southern Ocean and the Falkland Islands. They showed that there were significant differences between populations studied, with those around Heard Island and Macquarie Island showing some similarities. Based on infra-community structure, they also concluded that a number of individual toothfish had, relatively recently, migrated from Heard to Prince Edward Island.

[Oliva *et al.* \(2008\)](#) examined the metazoan parasites of *D. eleginoides* taken from 629 individuals caught in two localities in southern Chile (Lebu 36°S and Quellón 48°49'). They recovered 58,000 parasites from five taxa and concluded that their data did not support discrete stocks or provide evidence of any movement between the two localities.

Elemental signatures of otolith margins ([Ashford *et al.*, 2005b](#)) and nuclei ([Ashford *et al.*, 2006](#)), determined using an inductively coupled plasma mass spectrometer (ICP-MS), have also been used to distinguish Patagonian toothfish from different locations in the Southern Ocean. Otolith margin signatures of calcium, strontium, magnesium and barium showed differences between capture areas (Chile, Falklands, South Georgia, Kerguelen and Macquarie) and between years from the same location (South Georgia). Otolith nuclei showed clear differences between fish from South Georgia and the Patagonian Shelf, with a discontinuity at the APF.

Analysis of stable isotopes (δC^{13} , δO^{18}) in whole otoliths of *D. eleginoides* also demonstrated a distinct separation between stocks at South Georgia and those on the Patagonian Shelf ([Ashford and Jones, 2007](#)). Differences in O^{18} were attributed to ambient temperatures of water masses (Antarctic Intermediate water in the Patagonian shelf region; Circumpolar Deep Water in South Georgia), whilst differences in C^{13} were attributed to dietary differences.

In summary, the data from a range of sources indicate that separate toothfish stocks exist in the western Indian Ocean (Prince Edward, Marion, Crozet, Kerguelen, Heard and McDonald islands), Macquarie Island, the Atlantic sector (South Georgia and the South Sandwich Islands) and the Patagonian/Chilean shelf. Fish from Bouvet Island are similar to the South Georgia population. The relationship between the Ross Sea population and the Macquarie Island stock is not known.

4.2. Tagging studies and small-scale movements

Toothfish have been tagged with traditional T-bar (Agnew *et al.*, 2006b), dart, passive integrated transponder (PIT), data logging (Williams and Lamb, 2002) and more recently, pop-up archival tags (Brown *et al.*, unpublished). Tagging is an adaptable tool and has been utilised to examine geographic and bathymetric movements, growth, behaviour and to estimate population size but all methods can provide data on movements. Toothfish are relatively robust and, given the lack of a swim bladder, do not suffer serious decompression injuries when brought to the surface from depth (Agnew *et al.*, 2006a). Trawl, longline and pot-caught fish have been successfully tagged and recaptured. Trawl caught fish are best selected from short-duration trawls, when trauma injuries are less likely. Longline caught fish can suffer hook damage but survive well, providing animals in good condition are selected (Agnew *et al.*, 2006a). Pot-caught animals are generally in good condition, but potting is not always a commercially viable method of capture. Post-tagging survival is high and fish have been recaptured after 5 years at liberty (Agnew *et al.*, 2006b). Tagging is now widely used in assessing population sizes (Hillary *et al.*, 2006; Tuck *et al.*, 2003), but here, we limit our discussion to data on movements, with other uses of tagging data discussed elsewhere.

In general, tagging studies indicate that most sub-adult and adult fish remain within a relatively small area (Marlow *et al.*, 2003; Tuck *et al.*, 2003; Williams *et al.*, 2002), although small numbers of tagged fish have been recovered after moving considerable distances. Williams *et al.* (2002) tagged 5201 (400–1000 mm TL) trawl caught fish on the Heard Island fishing grounds, recapturing 738. Ninety-nine percent (734) of the fish were recaptured within 30 km of their release location after 1–3 years at liberty. However, three fish were caught on the Crozet Plateau having moved over 1850 km, and one was recaptured at Kerguelen, 390 km from the tagging location.

Marlow *et al.* (2003) reported on 37 recaptured fish from the early years of the South Georgia tagging programme. Of these recaptures, 28 (76%) were within 25 km of their release location. Two fish had moved 192 and 163 km in an E or SE direction from Shag Rocks towards South Georgia, consistent with their ontogenetic migration (see above; Collins *et al.*, 2007). Two other fish caught to the E and NE of South Georgia had moved in excess of 100 km in a NW direction. By 2005, over 8000 fish had been tagged in South Georgia, with 304 returns (excluding within year returns) and had moved an average of 27 km (Agnew *et al.*, 2006b). By 2009 over 25,000 fish had been tagged with over 2000 returns (CCAMLR, 2009). The population in the north of the South Sandwich Islands may be an extension of the South Georgia stock. A single fish tagged near the South Sandwich Islands was recaptured in the South Georgia fishery, approximately 740 km from the point of release (Roberts and Agnew, 2008).



5. AGE AND GROWTH

5.1. Estimating age and growth

Three principal methods have been applied to determining the age and growth of Patagonian toothfish; direct ageing from otoliths and scales (Horn, 2002; Hureau and Ozouf-Costaz, 1980), tagging studies (e.g. Marlow *et al.*, 2003; Williams *et al.*, 2002) and analysis of length–frequency data (e.g. Belchier and Collins, 2008). Although scales have been used, otolith age readings are the most widely used method of directly determining age and, when validated, provide key data for stock assessments. Length–frequency analysis is a less labour-intensive approach to indicate growth (e.g. Macdonald and Pitcher, 1979), but can be biased by sampling and does not necessarily indicate age.

5.2. Length-frequency data

Whilst growth parameters can be determined from analysis of length–frequency data (e.g. Collins *et al.*, 2008), in a long-lived species, such as toothfish, cohorts of adult fish are almost impossible to separate. The length–frequency data can, however, be informative about growth in the first few years when cohorts are more easily distinguished. It can also assist with the interpretation of the first few annuli of otoliths. From trawl surveys at Shag Rocks and South Georgia, a very strong toothfish cohort was first detected at modal size 220 mm TL in January 2003 (Fig. 4.4) and was tracked during surveys in the following years (Belchier and Collins, 2008; Collins *et al.*, 2007). Given that toothfish spawn in winter and larvae have been caught in January, it is highly likely that these were 1+ fish in 2003 (Belchier and Collins, 2008). The juvenile toothfish cohort grew by around 100 mm TL per year and was still present in the sampled population in 2008 (Fig. 4.4).

5.3. Direct ageing methods

The earliest age data were derived from a study undertaken by Zakharov and Frolkina (1976) on specimens caught at South Georgia, although little methodological detail was provided. Hureau and Ozouf-Costaz (1980) subsequently used both otoliths and scales to estimate the age of *D. eleginoides* caught at Kerguelen and Crozet islands, whilst Young *et al.* (1995) compared the utility of scales and otoliths for age determination of toothfish caught off southern Chile and found that scales gave significantly lower age estimates than otoliths in older fish. However, further work by Cassia (1998) on specimens caught at South Georgia found complete agreement between ages from scales and otoliths. A detailed comparison undertaken by Ashford *et al.* (2001) and lead–radium dating by Andrews

et al. (2010) both concluded that the use of scales was likely to lead to an underestimation of true age in *D. eleginoides*. Since 2000, all studies on age and growth of toothfish have relied on age estimates derived from the analysis of otoliths.

In 2001, a workshop on estimating age in Patagonian toothfish was held in the Centre for Quantitative Fisheries Ecology with 17 participants from several countries who were involved in ageing of toothfish. The aims were to consider toothfish otolith collection and preparation techniques as well as discuss quality control and validation.

5.4. Otolith preparation methods

Whilst different authors have advocated different methods for otolith preparation, most involve mounting the otolith in epoxy resin and then sectioning it transversely through the nucleus. In some cases, the otoliths are first baked whole for short periods at around 275 °C. Sections are then mounted on slides and examined with reflected light under a binocular microscope (Ashford *et al.*, 2002; Horn, 2002), although some readers prefer to use transmitted light (Brown and Belchier, unpublished) (see Fig. 4.5). Although interpretation of ring patterns in toothfish otoliths can be problematic (Horn, 2002), they often show clear banding patterns that reflect the somatic growth of the animal. Wide annuli are deposited during the first few years of life, a period of fast growth, before slowing at or following a change in habitat, which is manifested in a transition zone in the otoliths (Horn, 2002). Horn (2002) reported discrepancies between readers often caused by interpretation of the location of the first annulus (causing at least a 1 year error) and the presence of false rings between the first 3–5 years (leading to larger ageing errors).

5.5. Validation

The use of inaccurate ages has caused serious errors in the management and understanding of fish populations (Beamish and McFarlane, 1983) and can be particularly problematic in long-lived fish (Calliet and Andrews, 2008). Validation of the periodicity of increment formation is therefore essential before a particular method can be used to provide reliable age estimates of a species.

Validation that the formation of rings occurs annually in Patagonian toothfish has been attempted using nuclear bomb radiocarbon tracing (Kalish and Timmiss, 1998), marginal increment analysis (Horn, 2002), comparison with length–frequency data and by injecting calcium binding fluorescent dyes to mark otoliths of fish in tagging programmes (Krusic–Golub and Williams, 2004, 2005). Kalish and Timmiss (1998) used ‘bomb 14C’ methods on the otolith cores of *D. eleginoides*, which were

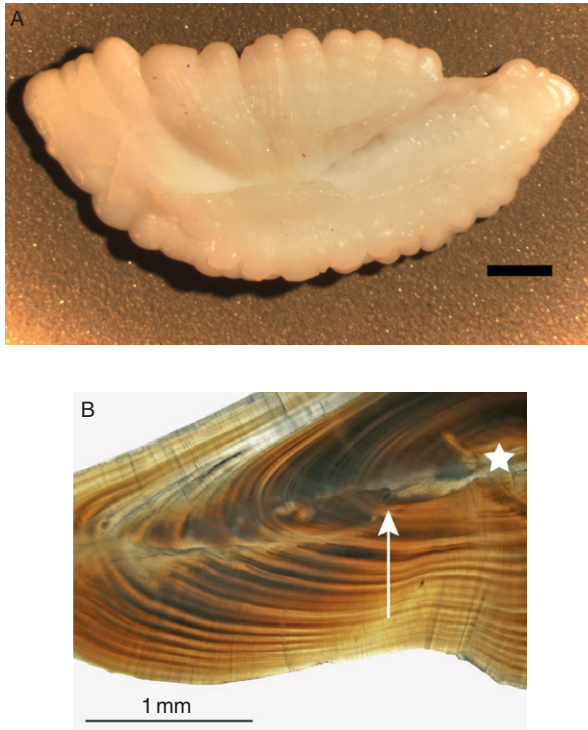


Figure 4.5 Patagonian toothfish (*Dissostichus eleginoides*) otoliths: (A) photograph of whole otolith; (B) photomicrograph of a thin transverse section of the dorsal section of an otolith of fish estimated to be 16 years old. The arrow indicates the position of first complete annulus and the star indicates the location of the otolith core. Scale bar = 1 mm.

elevated following nuclear testing in the 1960s, to calibrate growth ring counts, concluding that the counting of annual zones is probably accurate. [Andrews *et al.* \(2010\)](#) analysed the Pb/Ra of otoliths from South Georgia, Heard Island and Kerguelen, providing further confirmation of the annual deposition of growth increments. [Krusic-Golub *et al.* \(2005\)](#) used counts of daily micro-increments in otoliths of fish from Heard Island to validate the location of the first annulus and found that the average distance from the primordium to the outer edge of the first translucent zone was 0.630 mm.

[Krusic-Golub and Williams \(2004, 2005\)](#) examined otoliths from 142 strontium chloride injected and tagged fish (4–18 years old) from the Heard and McDonald Islands that were recaptured after 350–2571 days at liberty, to further validate the annual formation of growth rings. In most cases (88%), the number of rings after the strontium mark corresponded to the,

time at liberty, although this accuracy was reduced (52%) when the reader was unaware of the time at liberty. Errors were usually of 1 year.

Horn (2002) demonstrated that opaque zones were laid down at the otolith margins between September and February, with translucent zones laid down from February to June. All otoliths in June were found to have a translucent margin, indicating that one translucent zone was laid down annually. However in this study, there were only three samples from August and none from July or September, and the samples were aggregated over a number of years.

Ashford *et al.* (2002) and Belchier and Collins (2008) used the clear modal separation of length cohorts of juvenile toothfish caught in trawl surveys at South Georgia to provide further indirect validation of the otolith ageing methods. However, Ashford *et al.* (2002) interpreted the first year class (200 mm TL) as being 0+ fish, but these are almost certainly 1+.

5.6. Age and growth from otoliths

Otolith-based analyses of the age and growth of toothfish have now been conducted in all of the major fishery regions since 2000, including the Ross Sea, South Macquarie Ridge and Southern Campbell Plateau (Horn, 2002), South Georgia (Ashford *et al.*, 2002; Belchier, 2004) and the Kerguelen Plateau (Ashford *et al.*, 2005a).

In general, growth is initially fast, with juveniles growing in excess of 120 mm year⁻¹ (Belchier and Collins, 2008), but the growth pattern changes at ages of 4–8 years, probably associated with a change in habitat and the ontogenetic down-slope migration. Longevity varies between regions, but this may be related to sampling bias, as commercial fisheries may not sample larger, older fish in deep water. Horn (2002) reported that *D. eleginoides* from Macquarie Island and the northern Ross Sea reached 54 years of age. Toothfish are reported to reach 33 years on the Patagonian Shelf (Laptikhovskiy *et al.*, 2006), 36 years around Kerguelen Island (Ashford *et al.*, 2005a) and over 50 years of age at South Georgia (Belchier, 2004).

Growth typically follows the von Bertalanffy pattern, reaching an average asymptotic size and, in common with many teleost fish, growth rates (and von Bertalanffy parameters) vary regionally and between sexes (Table 4.1; Fig. 4.6). Females generally grow quicker and reach larger size than males (Horn, 2002). However, Aguayo (1992) and Young *et al.* (1992) found no sexual differences in growth for fish off southern South America, although females are known to attain a greater size than males in this region (see Moreno, 1998).

Regional differences in growth rate (Table 4.1; Fig. 4.6) may be attributed to differences in environmental conditions and prey availability between locations. However, the wide variation in growth parameters within and between locations suggests that sampling biases and to a lesser

Table 4.1 Von Bertalanffy growth parameters, derived from otolith increment counts, for Patagonian toothfish (*Dissostichus eleginoides*) from different locations and studies

Regions	Sex	L_{∞}	K	t_0	Author
Patagonian Shelf	Female	141.4	0.1500	-1.1000	Ashford <i>et al.</i> (2001)
	Male	120.7	0.1300	-1.5500	
South Georgia	Female	177.5	0.0820	0.3500	Aguayo (1992)
	Male	170.3	0.0860	-0.0150	
South Georgia	Combined	150	0.073	-0.792	Belchier (2004)
South Georgia	Combined	132	0.08	-0.3	CCAMLR 2009
Southern Chile	Female	209.7	0.0641	-1.1508	Young <i>et al.</i> (1992)
	Male	195.6	0.0742	-0.7205	
Heard Island	Female	74.4	0.4800	-0.4600	Ashford <i>et al.</i> (2001)
	Male	73.9	0.3100	-1.7100	
Kerguelen	Female	103.5	0.1100	-4.7000	Ashford <i>et al.</i> (2005a)
	Male	95.9	0.1200	-4.6000	
Macquarie	Female	205.3	0.0450	-1.5400	Kalish and Timmiss (1998)
	Male	138.4	0.0720	-1.3700	
Macquarie/NZ EEZ	Female	158.3	0.0850	-0.3500	Horn (2002)
	Male	134.3	0.1180	0.0800	

extent variability in otolith annuli interpretation have given rise to some of the observed differences. Ashford *et al.* (2005a) noted differences in the age composition of the catch of toothfish caught by different vessels fishing within the same region and noted that sampling effects, possibly caused by differences in fishing gear could generate biases in estimates of age structure. Unrealistically low estimates of asymptotic length and t_0 (Table 4.1) are most likely a result of bias from sampling only the fished population for the derivation of growth curves (Belchier, 2004). Candy *et al.* (2007) noted that poor fits of the von Bertalanffy model are in part a result of fishing gear selectivity, leading to under sampling of both the younger and older parts of the toothfish population.

5.7. Growth estimates from tagging

With the increase in tagging effort on many toothfish populations, it has been possible to obtain direct validation of otolith-derived growth models using mark recapture data. Such an approach has been undertaken for both Heard and McDonald Islands (HIMI) (Candy *et al.*, 2007) and South Georgia (Agnew *et al.*, 2006b; Marlow *et al.*, 2003). In both regions, growth in fish length observed during the time at liberty (i.e. between tagging and recapture) has been compared with a predicted growth increment based on the otolith-

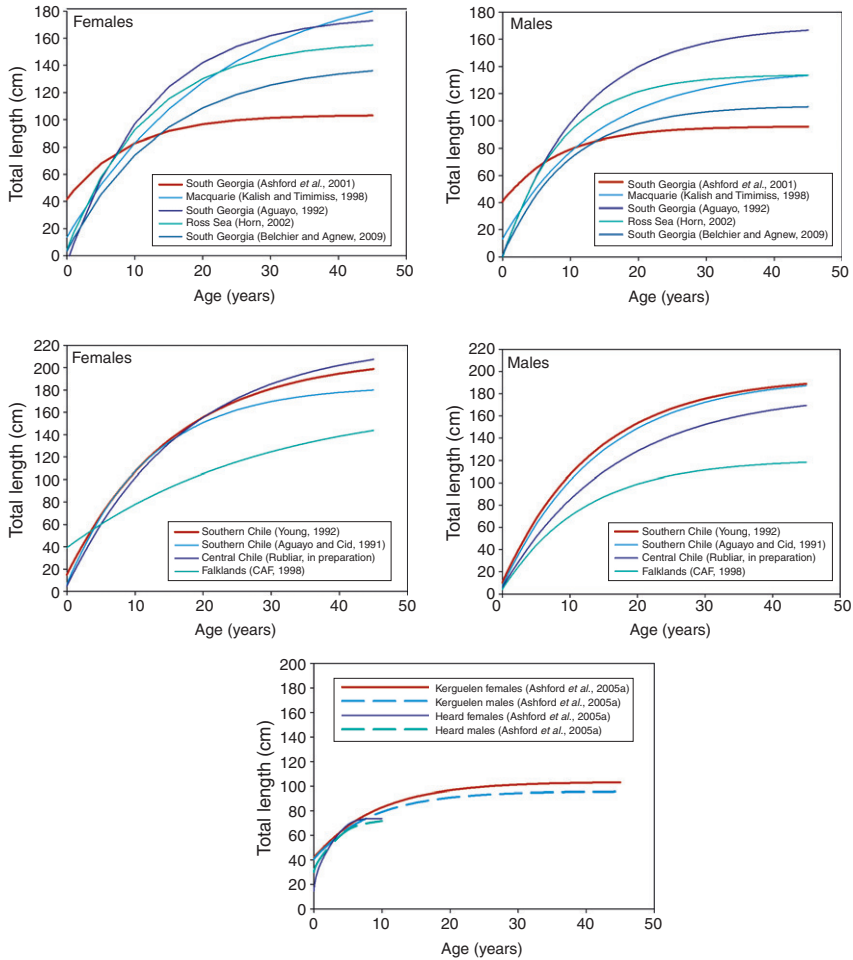


Figure 4.6 Comparison of von Bertalanffy growth curves of Patagonian toothfish (*Dissostichus eleginoides*), derived from otolith-based age studies in different geographic areas. CAF= Central Ageing Facility, Melbourne, Australia.

derived growth parameters. At both South Georgia (Agnew *et al.*, 2007) and HIMI (Candy *et al.*, 2007), there has been generally good agreement between estimates, but there is some evidence that otolith-derived growth parameters overestimate toothfish growth when compared to the mark recapture data. Candy *et al.* (2007) suggest that this may also be attributed to sampling bias. However, it is also likely that tagged fish experience some degree of growth retardation or ‘tag shock’ in which somatic growth is suppressed for an extended period (as much as a year) post-tagging. Growth retardation from

tagging has been well documented for other fish species (McFarlane and Beamish, 1990) and it is therefore advisable to exercise caution when estimating growth from mark-recaptured individuals.

5.8. Larval and juvenile growth

Studies relating to the growth of larval and juvenile toothfish have been restricted to work on the South Georgia shelf. North (2002) estimated growth of larval and early juvenile toothfish at 0.8% SL d^{-1} from pelagic net samples taken from the north of South Georgia. This growth rate is around the mid-range of growth rates, of between 0.3% SL d^{-1} and 2% SL d^{-1} estimated for other larval notothenioids at South Georgia during summer (North, 1998). North (2002) observed annual growth of around 160 mm TL for the first year and noted that this was greater than predicted from the growth model. However, Belchier and Collins (2008) showed that there is considerable variability in the mean length attained by juvenile toothfish in their first year of growth at Shag Rocks. In this study, it was shown that mean fish length attained after 14 months can vary inter-annually by greater than 50 mm (TL). It is suggested that growth variability is related either directly or indirectly to environmental conditions. High growth rate was associated with strong cohorts, suggesting a positive correlation between juvenile growth and survivorship.

6. REPRODUCTION

Notothenioid reproduction is characterised by protracted gametogenesis and low fecundity, with most species not reaching maturity until at least 5 years -old (Kock and Kellermann, 1991). Information on Antarctic and sub-Antarctic fish suggest that spawning occurs in austral autumn and winter (Kock and Kellermann, 1991). There is limited information on the reproductive biology of *D. eleginoides* in the literature, but some work has been undertaken around the sub-Antarctic islands, on the Patagonian Shelf and off the coast of Chile.

6.1. Size at maturity

In Patagonian toothfish, maturity occurs at approximately half of their maximum length with some variation in 50% maturity values from different regions and studies (Table 4.2). Everson and Murray (1999) studied the size at sexual maturity of toothfish caught in the commercial fishery at South Georgia in 1996 and 1997 and found that there was evidence in 1997 that 25–43% of mature female *D. eleginoides* did not spawn. They noted that if

Table 4.2 Length at 50% ($L_{m_{50}}$) maturity for Patagonian toothfish (*Dissostichus eleginoides*) from different locations

Source	Area	$L_{m_{50}}$ (mm)	
		Male	Female
CCAMLR (1987)	South Georgia	577	1104
Moreno (1998)	South Georgia	670	860
Everson and Murray (1999)	South Georgia	785	982
Agnew <i>et al.</i> (1999)	South Georgia	750	1010
Laptikhovsky and Brickle (2005)	Patagonian Shelf	860	900
Prenski and Almeyda (2000)	Argentina	763	871
Moreno <i>et al.</i> (1997)	Chile	1050	1170
Young <i>et al.</i> (1999)	Chile		1287
Oyarzún <i>et al.</i> (2003)	Chile	780–940	1130–1170
Arana (2009)	Chile	810	890
Duhamel (1991)	Kerguelen	650	800
Lord <i>et al.</i> (2006)	Kerguelen	630	850

$L_{m_{50}}$ was calculated without taking this non-spawning into account, it would lead to an overestimation. Analysis of von Bertalanffy growth curves indicates that $L_{m_{50}}$ for toothfish is attained between the ages of 6 and 10 for males, and between 10 and 13 years for females. Skipped or incomplete spawning has been reported in numerous species of iteroparous fish (Rideout *et al.*, 2005), with non-spawning occurring due to either retaining or reabsorbing eggs or the fish remaining in a resting stage. Histological analysis is needed to determine the nature of this process in toothfish, and it is likely that in years with higher than average temperatures, a variable number of toothfish skip spawning which in turn will affect the strength of recruitment the following year (Brown and Brickle, unpublished data). This phenomenon has also been suggested by Arana (2009).

6.2. Fecundity

The Patagonian toothfish is the most fecund nototheniid, with absolute fecundities ranging from 48,900 to 528,900 on the Kerguelen plateau (Chikov and Mel'nikov, 1990) and between 56,940 and 567,490 in South Georgia (Nevinsky and Kozlov, 2002). The Chikov and Mel'nikov (1990) study indicated that there were two size groups in the measured oocytes in maturing fish caught between March and April. The first mode was between 0.1 and 1.1 mm (protoplasmic oocytes), with the second between 1.4 and 2.9 mm (trophoplasmic), indicating that the maturation of oocytes is

discontinuous and synchronous during vitellogenesis, which suggests single non-intermittent spawning. Larger vitellogenic oocytes were recorded to increase in volume quickly from a mean diameter of 1.53 mm in March to 1.9 mm in April (Chikov and Mel'nikov, 1990). Of the notothenioids studied to date, most spawn annually, with the vitellogenic process often taking 2 years (Everson, 1977; Kock and Kellermann, 1991; Shandikov and Faleeva, 1992). Therefore, it is probable that the two stocks of ova which are seen ripening at different stages in toothfish are for spawning in the current and following year. Chikov and Mel'nikov (1990) and Nevinsky and Kozlov (2002) investigated the relationship between fecundity and size (Fig. 4.7). The former's estimates are higher than those of the latter authors, which is probably due to the size range of individuals sampled. Chikov and Mel'nikov (1990) sampled individuals up to 1300 mm TL, whereas Nevinsky and Kozlov (2002) sampled toothfish up to 1600 mm TL.

6.3. Timing of spawning

Spawning in Patagonian toothfish generally occurs during the austral winter (June–September) period (Agnew *et al.*, 1999; Laptikhovsky *et al.*, 2006; Lord *et al.*, 2006; Arana, 2009). Laptikhovsky *et al.* (2006) analysed data collected by observers on longliners operating on the Patagonian Shelf and reported two spawning peaks for toothfish, a small peak in May and a major peak in July/August. Females were found to disperse over a greater depth range than males. They also found that males migrate to the spawning grounds on Burdwood Bank earlier than females and stay at a depth of 1500–2000 m until it is time to spawn at approximately 1000 m. Examination of maturity

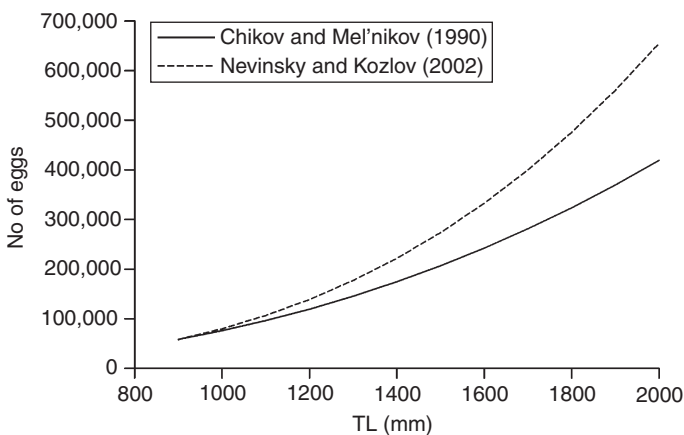


Figure 4.7 Relationship between fecundity and size in Patagonian toothfish (*Dissostichus eleginoides*).

data of toothfish caught around South Georgia and Shag Rocks revealed a large spawning event in late July/August, with a possible smaller spawning event in April/May, and fish were found to migrate up (females) and down (males) the slope to meet at the spawning grounds at around 800–1200 m (Agnew *et al.*, 1999). Lord *et al.* (2006) showed that toothfish spawning at Kerguelen occurs between late April/May and mid-July (for females) but begins later for males (end of May). Off the Chilean coast Arana (2009) found toothfish with developing gonads in June and July, mature gonads from July to September, and spent gonads from August to October.

Agnew *et al.* (1999) reported pre-spawning fish to be distributed all around the shelf slopes of South Georgia and Shag Rocks whereas both male and female spent fish were concentrated in the shallower waters to the northeast of Shag Rocks with very few spent fish being found around South Georgia. On the Patagonian Shelf, spawning only occurs to the south of the Falkland Islands. (Laptikhovskiy and Brickle, 2005; Laptikhovskiy *et al.*, 2006). In the Pacific, spawning is not found north of 50°S and this coupled with the hypothesised reduced migratory capabilities of toothfish, might explain the progressive decline in yields north of 47°S (Arana, 2009). It is likely that toothfish north of the Polar Front are at the edge of their range, thus explaining the southerly location of the spawning grounds in the Pacific and Atlantic Oceans (Brown and Brickle, unpublished data).

6.4. Eggs and larvae

Once hydrated and spawned, the eggs are 4.4–4.5 mm in diameter with a rough chorion and large perivitelline space and a homogeneous yolk (Evseenko *et al.*, 1995).

A number of authors have described various sizes of toothfish from embryo (Evseenko *et al.*, 1995; Kellermann, 1989), to larvae 11–28 mm (Ciechomski and Weiss, 1976; Evseenko *et al.*, 1995; Kellermann, 1989) to larvae/early juveniles 18–63 mm (Effremenko, 1979; North, 2002). Pigmentation consists of a band on the posterior post-anal section, single pigment spots below the pectoral fin, melanophores along the abdominal region and occipital melanophores on the brain (Kellermann, 1989). Well-developed canine teeth are present on the lower jaw once larvae reach 20–22 mm SL. The pigmentation remains unchanged during larval development, except for the formation of a ventral row of melanophores appearing from the posterior pigment band to the anus (Kellermann, 1989).

Larvae are thought to occur from November onwards and are in the region of 14 mm at hatching (Kock and Kellermann, 1991). North (2002), using this size at hatching and early larval growth rates, predicted that larvae caught around South Georgia hatch between November and mid December, suggesting a 3.5-month period of embryogenesis. This is rapid in comparison to other notothenioids; 4–6 months in

Nototheniops nudifrons (Kellermann, 1990) and up to 5 months in *Notothenia coriiceps* (Everson, 1977; White *et al.*, 1982).

7. TROPHIC ECOLOGY

7.1. Toothfish diet

Korovina *et al.* (1991) described the digestive tract of toothfish as consisting of a large stomach, six to seven pyloric caeca and a digestive tract comprising 87% of the standard body length. A strongly developed muscular membrane in the midgut wall (94% of wall thickness) is present, a morphological adaptation which allows toothfish to consume large quantities of prey.

The diet of adult and juvenile toothfish has been studied using conventional stomach contents analysis on trawl, longline and pot-caught fish (Table 4.3), and using biomarkers such as stable isotopes and fatty acids (Stowasser, BAS unpublished). There are clear ontogenetic changes in the diet of toothfish, associated with the down-slope migration and general switch to scavenging as size increases. The diet of larval toothfish has not been studied.

The diet of juvenile toothfish (<750 mm TL) has largely been determined from trawl caught specimens, which are primarily piscivorous, usually taking the most abundant small fish in their area (Barrera-Oro *et al.*, 2005; Collins *et al.*, 2007). Zhivov and Krivoruchko (1990) did, however, find that smaller juveniles (250–400 mm TL) at South Georgia and Shag Rocks fed mainly on hyperiid amphipods and euphausiids.

On the Patagonian Shelf, juveniles take a diverse fish fauna, including *Patagonotothen ramsayi* and juveniles of other nototheniid species (Arkhipkin *et al.*, 2003); however, with increasing size (and depth of occurrence), the diet changes to include deeper-dwelling and larger species such as hoki (*Macruronus magellanicus*) and southern blue whiting (*Micromesistius australis*). Garcia de la Rosa *et al.* (1997) also found the diet of juveniles to be dominated by fish with cephalopods also taken.

In four summer seasons, Collins *et al.* (2007) found that the diet of juveniles at Shag Rocks was dominated by the abundant yellow-finned notothen (*Patagonotothen guntheri*), which made up 90% of the diet, whereas at South Georgia, where *P. guntheri* is absent, other nototheniids were the primary prey. In contrast, during March–April 1996, Barrera-Oro *et al.* (2005) did not find any *Patagonotothen guntheri* in the diet, with *Lepidonotothen squamifrons* the most abundant prey species at Shag Rocks; however, almost 49% of the fish were not identified to species. Some pelagic prey species have been reported to be taken, including myctophids and Antarctic krill (Collins *et al.*, 2007; Garcia de la Rosa *et al.*, 1997).

The diet of large, adult toothfish has been studied from both longline and pot-caught fish. In general, adult toothfish are opportunistic carnivores,

Table 4.3 Diet of Patagonian toothfish (*Dissostichus eleginoides*)

Location	Depth range (numbers sampled)	Gear and size range	Diet summary	Main Prey Species	Source
South Georgia, 1985–1986	200–400 m (244)	Trawl	Fish (74 %F); crustaceans (15 %F); cephalopods (5 %F)	Unidentified fish (51 %F); <i>Electrona carlsbergi</i> (9 %F); crabs (5 %F); squid (5 %F)	Zhivov and Krivoruchko (1990)
	400–600 m (217)	Trawl	Fish (56 %F); crustaceans (24 %F); cephalopods (12 %F)	Unidentified fish (28 %F); <i>E. carlsbergi</i> (10 %F); lobsters (24 %F); squid (10 %F)	
Shag Rocks	600–1000 m (249)	Trawl	Fish (77 %F); crustaceans (14 %F); cephalopods (7 %F)	Unidentified fish (47 %F); <i>Patagonotothen guntheri</i> (10 %F); krill (4.8 %F)	Barrera-Oro <i>et al.</i> (2005)
	1000–1400 m (160)	Trawl	Fish (44 %F); crustaceans (42 %F); cephalopods (12 %F)	Unidentified fish (43 %F); crabs (12.5 %F); squid (10 %F)	
South Georgia and Shag Rocks		Trawl; < 750 mm TL.	Fish (70 %F)	Unidentified fish (49 %F); <i>L. squamifrons</i> , <i>Champscephalus gunnari</i> and <i>Chaenocephalus aceratus</i>	
Shag Rocks, Jan (2003–2006)	100–400 m (636)	Trawl; < 750 mm TL	Fish (98 %M); crustaceans (2 %M)	<i>P. guntheri</i> (85 %M); <i>Gymnoscopelus nicholsi</i> (4 %M); <i>Euphausia superba</i> (2 %M)	Collins <i>et al.</i> (2007)

South Georgia, Jan (2003–2006)	100–400 m (159)	Trawl; < 750 mm TL	Fish (89 %M); crustaceans (10 %M)	<i>Trematomus hansonii</i> (23 %M); <i>Lepidonotothen larseni</i> (22 %M); <i>C. gunnari</i> (13 %M); <i>E. superba</i> (8 %M)	
South Georgia and Shag Rocks, Dec 87–Jan 88	50–500 m (50)	Trawl	Fish (96 %F)	<i>Muraenolepis</i> sp., <i>Paraechaenichthys georgianus</i> and <i>L. larseni</i>	McKenna (1991)
South Georgia and Shag Rocks, March–May 2000	200–1650 m (2268)	Pot; 600–1200 mm TL	Crustaceans (48 %N); fish (34 %N); cephalopods (8 %N)	80% of fish unidentified; <i>P. guntheri</i> ; myctophids; <i>Nauticaris</i> sp.; <i>Paralomis</i> sp.; <i>Thymops birsteini</i> ; <i>E. superba</i> ; <i>Kondakovia longimana</i> ; <i>Pareledone turqueti</i> ; <i>Gonatus antarcticus</i>	Pilling <i>et al.</i> (2001); Xavier <i>et al.</i> (2002)
Shag Rocks, May–August 2000	300–600 m (122)	Longline	Fish (51 %F); crustacean (16 %F); cephalopod (9 %F)	<i>Macrourus</i> sp., <i>Muraenolepis</i> spp., nototheniids, channichthyids	Pilling <i>et al.</i> (2001)
South Georgia and Shag Rocks, February 1994	300 m (129)	Trawl; 180–900 mm TL	Fish (86 %F); krill (20 %F)	<i>E. superba</i> ; <i>Champsoccephalus gunnari</i> ; <i>Gobionotothen gibberifrons</i> ; <i>Pseudochaenichthys georgianus</i> ; <i>Notototheniops nudifrons</i>	Garcia de la Rosa <i>et al.</i> (1997)

(continued)

Table 4.3 (continued)

Location	Depth range (numbers sampled)	Gear and size range	Diet summary	Main Prey Species	Source
South Georgia and Shag Rocks, March–April 1995	1050–1530 m (226)	Longline	Fish (60 %F); squid (14 %F); crustaceans (22 %F)	<i>P. guntheri</i> ; myctophids; <i>Antimora rostrata</i> ; <i>Macrourus holotrachys</i> ; <i>Bathyraco</i> sp., <i>Chionodraco</i> sp., <i>Lycodapus</i> spp., <i>Pachycara brachycephalus</i> , <i>K. longimana</i>	
Macquarie Island, summer 1995/96, 1996/97; 1997/98;	500–1290 m (462)	Trawl; 310–1490 mm TL	Fish (58 %M); squid (32 %M); crustaceans (10 %M)	<i>Bathylagus</i> sp. (14 %M); <i>Gonatus antarcticus</i> (16 %M); macrourids; nototheniids and myctophids	Goldsworthy <i>et al.</i> (2002)
Argentine Shelf	<650 m (135)	Shelf. 290–950 mm TL	Fish (95 %F); cephalopods (7 %F)	<i>Patagonotothen ramsayi</i> (26 %F), <i>Micromesistius australis</i> ; <i>Ilucoetes fimbriatus</i> ; <i>Merluccius hubsi</i> ; <i>Macruronus magellanicus</i> ; <i>Illex argentinus</i> and <i>Loligo gahi</i>	Garcia de la Rosa <i>et al.</i> (1997)

Falkland Islands, Apr 1999–Aug 2002	< 500 m (135)	< 400 mm TL	Fish (75% F); cephalopods (21% F)	<i>P. ramsayi</i> (24 %F); juvenile nototheniids (20 %F); unidentified fish (24 %F); <i>Loligo</i> <i>gahi</i> (24 %F)	Arkhipkin <i>et al.</i> (2003)
	< 500 m (366)	400–600 mm TL	Fish (73 %F); cephalopods (22 %F)	<i>P. ramsayi</i> (28 %F); juvenile nototheniids (5 %F); unidentified fish (34 %F); <i>L. gahi</i> (21 %F)	
	< 500 m (109)	> 600 mm TL	Fish (90% F); cephalopods (7.3 %F)	<i>M. magellanicus</i> (20.2 % F); <i>M. australis</i> (18 % F); unidentified fish (31 %F); <i>Moroteuthis</i> <i>ingens</i> (6 %F)	
	500–1000 m (62)	400–1600 mm TL	Fish (72% F); crustaceans (15 %F); cephalopods (6 %F)	<i>A. rostrata</i> (29 %F); unidentified fish (32 %F); <i>AcanthePHYra</i> <i>pelagica</i> (15 %F); <i>M. ingens</i> (5 %F)	
	> 1000 m (63)	500–1900 mm TL	Fish (61 %F); crustaceans (43 %F); cephalopods (5 %F)	<i>A. rostrata</i> (11 %F); unidentified fish (37 %F); <i>A. pelagica</i> (41 %F); <i>M.</i> <i>holotrachys</i> (6 %F); unidentified cephalopods (5 %F)	

(continued)

Table 4.3 (continued)

Location	Depth range (numbers sampled)	Gear and size range	Diet summary	Main Prey Species	Source
Central and Southern Chile, Oct 2001–Oct 2002	> 500 m (203)	Artisanal fishery; 570–1610 mm TL	Fish (96% IRI)	Macrouridae (22% <i>F</i>); Ophidiidae (16% <i>F</i>); unidentified fish (37 % <i>F</i>); Onychoteuthidae (5 % <i>F</i>)	Murillo <i>et al.</i> (2008)
Kerguelen	(748)		Fish (90 % <i>F</i>)	<i>C. gunnari</i> (25 % <i>F</i>) and <i>L. squamifrons</i> (12 % <i>F</i>), myctophids (27 % <i>F</i>)	Duhamel (1981)
Crozet	(31)		Fish (36 % <i>F</i>); crustaceans (37 % <i>F</i>); cephalopods (8 % <i>F</i>)	Nototheniids, myctophids and amphipods	Duhamel and Pletikovic (1983)

%*F* = percent frequency of occurrence; %*M* = percent by mass; %*N* = percent numbers.

feeding on suitably sized locally abundant prey, including a variety of demersal and pelagic fish, crustaceans and cephalopods. Evidence from baited cameras (Collins *et al.*, 1999, 2006) and longline captures indicate the propensity to scavenge food, but the importance of scavenging is not known and may vary spatially, temporally and ontogenetically.

Studies of adult diet have been undertaken at South Georgia, the Patagonian Shelf and around Kerguelen. From a study at South Georgia, Pilling *et al.* (2001) showed that the proportion of empty stomachs was generally higher in longline caught animals than pot-caught animals, which the authors attributed to an increase in stress-induced regurgitation in line caught fish. However, there was also a distinct difference in diet between fish caught by the two methods, with decapod prawns of the genus *Nauticaris* found in pot-caught toothfish stomachs. It is possible that the prawns were attracted to the baited traps and were consumed inside the traps by the toothfish, which would bias the results of the pot-caught fish. Pilling *et al.* (2001) also found an increase in *Nauticaris* sp. and cephalopods with size (and depth), with a decrease in the importance of fish. The fish they identified in the diet included myctophids, nototheniids, *Muraenolepis* sp., morid cods and grenadiers. The cephalopod component of the prey from the Pilling *et al.* (2001) study was also reported in more detail by Xavier *et al.* (2002). Garcia de la Rosa *et al.* (1997) also examined the diet of adult toothfish at South Georgia and found fish (mostly unidentified), isopods and the squid *Kondakovia longimana* as the main prey, with lithodid crabs also taken.

Less information is available for toothfish diet in the Indian Ocean sector, but on the Kerguelen shelf, the diet was also dominated by fish, with the principal prey being myctophids and the notothenioids *Champscephalus gunnari* and *Lepidonotothen squamifrons* (Duhamel, 1981). A relatively small study at Crozet (74 stomachs) found the main prey (% occurrence) to be amphipods, with nototheniid and myctophids fish also important (Duhamel and Pletikotic, 1983).

Many diet studies have focussed on a single season (summer), and diet may change seasonally, but data on seasonal changes is limited. Arkhipkin *et al.* (2003) reported that toothfish (400–600 mm TL) exhibited seasonal variations in their diet on the Patagonian Shelf. They concluded that seasonal changes in diet reflected the seasonal variations in prey abundance on the shelf. *Patagonotothen ramsayi* was abundant in the diet throughout the year, whereas *Loligo gahi* only appeared from February to October during its offshore seasonal migrations. During November to January, *Loligo gahi* migrate inshore to spawn and subsequently disappeared from toothfish diet. Instead, toothfish consumed southern blue whiting (*Micromesistius australis*), which spread out over the shelf after spawning to the south west of the Falkland Islands.

7.2. Feeding rates

Tarverdiyeva (1972) calculated daily rations for *D. eleginoides* as 5.1% of its wet body weight per day (at temperatures of 1.2–1.3 °C). In studies of diet of toothfish at South Georgia, Collins *et al.* (2007) found over 75% of stomachs examined contained food, with the contents averaging around 2% body weight. Trawls were only undertaken during daylight, but there was no relationship between fullness and time of day.

7.3. Foraging behaviour

A combination of dietary data, baited cameras and data-logging tags indicate that toothfish forage in the mesopelagic realm as well as on the seafloor. Pelagic prey make up a significant part of the diet, and evidence from data-logging tags shows that toothfish spend some of their time off the seafloor (Williams and Lamb, 2002), perhaps foraging or utilising currents for transport. Scavenging is also important, and baited camera work has shown that large toothfish approach squid or mackerel bait from down current, presumably using olfaction to detect odour plumes from carcasses or bait (Collins *et al.*, 1999, 2006). Toothfish appear cautious and circle the bait before attempting to consume it, but this may be a response to the light, as footage from baited video cameras shows them repeatedly circling the illuminated area, before venturing in to grab the bait (Collins *et al.*, 2006). The bait was attached by wire to a graduated cross and toothfish were seen pulling the bait off with a jerky motion, before swallowing the squid (bait) whole. In one case, a toothfish ‘barrel rolled’ through three complete turns to remove the bait from the cross (Collins *et al.*, 2006).

Live fish kept in captivity have been noted to take pieces of food (fish muscle) from the bottom of the tank and midwater as it floats down, and swallow it whole. They initially are seen to ‘smell’ the food. Smaller fish (<600 mm) were more aggressive during feeding, attempting to take food from other fish in the tank. On numerous occasions, if two fish had a hold of a large piece of bait, fish were recorded to ‘barrel roll’ to break the food (Howes, Falkland Fisheries Department personal communication).

7.4. Predators of toothfish

Data on toothfish predators are rather limited. In shallow water, reported predators of juveniles include penguins (Brown and Klages, 1987; Goldsworthy *et al.*, 2001), fur (Green *et al.*, 1989; Reid and Arnould, 1996) and elephant seals (Green *et al.*, 1989; Reid and Nevitt, 1998; Slip, 1995), but with increased size and habitat depth, the range of potential predators is likely to decline (Table 4.4). From extensive studies undertaken at South Georgia,

Table 4.4 Predators of Patagonian toothfish

Potential predator	Maximum depth	Comments	Sources
Southern elephant seal <i>Mirounga leonina</i>	Dive to >2000 m.	Reported to consume toothfish, but importance in diet not established; potentially a significant predator	Slip (1995); Reid and Nevitt (1998)
Antarctic fur seal <i>Arctocephalus gazella</i>	Dive to 300 m	Toothfish otoliths occasionally in scats at South Georgia and Heard Island; unlikely to be a significant predator	Green <i>et al.</i> (1989), Reid (1995); Reid and Arnould (1996)
Weddell seal <i>Leptonychotes weddelli</i>	Dive to 450 m	Know to take <i>D. mausoni</i> in Weddell Sea; small South Georgia population may take <i>D. eleginoides</i>	Calhaem and Christoffel (1969); Testa <i>et al.</i> (1985); Plotz (1986); Lake <i>et al.</i> (2003)
Hooker's sea-lions <i>Phocartos hookeri</i>	Dive to 500 m	Toothfish otoliths reported in 42% of scats	McMahon <i>et al.</i> (1999)
Sperm whale <i>Physeter macrocephalus</i>	Dive in excess of 2000 m	Known to consume toothfish; take toothfish from longlines; population size at South Georgia is unknown	Korabelnikov (1959); Clarke (1980); Abe and Iwami (1989); Watkins <i>et al.</i> (1993); Ashford <i>et al.</i> (1996); Purves <i>et al.</i> (2004); Kock <i>et al.</i> (2006)
Killer whale <i>Orcinus orca</i>	Dive to 200 m	Take toothfish off longlines, but do not dive deep enough to catch adults	Ashford <i>et al.</i> (1996); Purves <i>et al.</i> (2004); Kock <i>et al.</i> (2006)
King penguin <i>Aptenodytes patagonicus</i>	Dive to 300 m	Piscivorous, but pelagic feeders generally taking small fish (myctophids) and squid; no toothfish reported in diet at South Georgia, but reported in diet at Crozet ($n = 2$, 4.3% occurrence)	Kooyman <i>et al.</i> (1992); Cherel <i>et al.</i> (1996); Olsson and North (1997)
Gentoo penguin <i>Pygoscelis papua</i>	Dive to 150 m	Not known to take toothfish in South Georgia area, but toothfish recorded in diet at Macquarie Islands (0.1–1.2% occurrence) and Kerguelen (2.5% occurrence). Juvenile toothfish noted in diet around the Falkland Islands	Adams and Klages (1989); Robinson and Hindell (1996); Goldsworthy <i>et al.</i> (2001); Lescroel <i>et al.</i> (2004); Putz <i>et al.</i> (2001)

(continued)

Table 4.4 (continued)

Potential predator	Maximum depth	Comments	Sources
Macaroni penguin <i>Eudyptes chrysolophus</i>	Dive to 120 m	Single incidence of toothfish in diet at Marion Islands, never recorded at South Georgia	Brown and Klages (1987)
Magellanic penguin <i>Spheniscus magellanicus</i>	Dive to 150 m	Juvenile toothfish noted in diet around the Falkland Islands	Putz <i>et al.</i> (2001)
Rockhopper penguin <i>Eudyptes chrysocome</i>	Dive to 150 m	Juvenile toothfish noted in diet around the Falkland Islands	Putz <i>et al.</i> (2001)
Black-browed albatross <i>Thalassarche melanophris</i>	Surface feeders	Toothfish in stomachs probably from hooks and/ or discards from fishing vessels	Cherel <i>et al.</i> (2000, 2002)
Grey-headed albatross <i>Thalassarche chrysostoma</i>	Surface feeders	Toothfish in stomachs probably from hooks and/ or discards from fishing vessels	Cherel <i>et al.</i> (2002); Xavier <i>et al.</i> (2003)
White chinned petrels <i>Procellaria aequinoctialis</i>	Dive to 10 m	Toothfish in stomachs probably from hooks and/ or discards from fishing vessels	Catard <i>et al.</i> (2000)
Patagonian toothfish <i>Dissostichus eleginoides</i>	2500 m	Some cannibalism likely, with large fish taking smaller cohorts, but will be limited by the size–depth distribution pattern	Arkhipkin <i>et al.</i> (2003)
Kingclip <i>Genypterus blacodes</i>	100–700 m	Occasionally predate on small juvenile toothfish on Falklands Shelf	Nyegaard <i>et al.</i> (2004)
Sleeper sharks <i>Somniosus</i> sp.	2000 m	Toothfish recorded in stomachs, but may be net feeding and scavenging on discarded heads	Cherel and Duhamel (2004)
Giant Antarctic squid <i>Mesonychoteuthis hamiltoni</i>	Unknown	Reach large size (> 100 kg); incidentally caught on longline hooks targeting toothfish. Possible predator, abundance unknown	Collins and Rodhouse (2006); Collins (unpublished)

toothfish are rarely taken by fur seals or penguins and only are occasionally taken by these species elsewhere (see Table 4.4).

The most important predators of adult toothfish are likely to be large, deep-diving vertebrates, such as sperm whales and elephant seals, which have the capacity to dive to the depths which toothfish inhabit. Toothfish have been recorded in sperm whale stomachs (Abe and Iwami, 1989; Clarke, 1980; Korabelnikov, 1959) and, although generally considered squid eaters, they are potentially important toothfish predators. The population size of sperm whales in the Southern Ocean is not, however, known, so the impact is difficult to assess. Elephant seals, particularly males, also have the ability to dive to the depths that adult toothfish occur and toothfish have occasionally been identified in their diet (Reid and Nevitt, 1998; Slip *et al.*, 1994). Sperm and killer whales are both known to take toothfish from longlines during hauling (Ashford *et al.*, 1996; Kock *et al.*, 2006; Purves *et al.*, 2004), but adult toothfish habitat is beyond the normal diving capabilities of killer whales. Antarctic toothfish are known in the diets of Weddell seals (Ainley and Siniff, 2009), and the distribution of Weddell seals overlaps with Patagonian toothfish in some places (e.g. South Georgia), making them a potential predator.

Little is known about the ecology of *Mesonychoteuthis hamiltoni*, but these large squid are probably capable of catching and consuming large toothfish, and are occasionally caught on longline hooks at South Georgia (Collins, unpublished data).

Albatross and white-chinned petrels are known to take toothfish (Catard *et al.*, 2000; Cherel *et al.*, 2000, 2002), but these are, almost certainly, fish that escape from hooks or are discards from fishing vessels. A wandering albatross has been witnessed swallowing whole a recently tagged 550 mm TL toothfish (Collins, personal observation).

7.5. Accumulation of mercury in toothfish tissue

As toothfish are large, relatively slow growing predatory or scavenging fish and occupy a similar top trophic level to large tunas, swordfish and sharks there has been some concern that their tissues may also accumulate high levels of mercury (Hg) that could be detrimental to human health when consumed. A preliminary study of 18 fish by Mendez *et al.* (2001) showed that mercury levels ranged between 0.12 and 0.73 mg kg⁻¹ with some samples having levels above the EU and Australian limit for mercury in fish of 0.5 mg kg⁻¹. A subsequent study on juveniles caught at Macquarie Island (McArthur *et al.*, 2003) also found mercury levels close to the recommended maximum and concluded that levels of mercury would increase as fish grew larger. A recent study by Guynn and Peterson (2008) demonstrated a clear increase in mercury concentrations in fish muscle with increasing size but also noted that there were distinct regional differences in

overall levels of mercury found in toothfish tissue. Mercury levels found in fish caught in regions north of the APF (Chilean waters and the Prince Edward Islands) had far higher levels of mercury than those detected in fish caught at South Georgia to the south of the APF.

8. PARASITES

8.1. Parasite fauna and host specificity

Sixty-two species of parasite have been reported from Patagonian toothfish from different areas of the host's distribution (Brickle, 2003; Brickle *et al.*, 2005, 2006; Gaevskaya *et al.*, 1990; Hamilton, 1995; Oliva *et al.*, 2008; Parukhin and Lyadov, 1982; Rodriguez and George-Nascimento, 1996) (Table 4.5; Fig. 4.8). Comparisons of these results have demonstrated major differences in the parasite fauna of *D. eleginoides* from different locations across their range (Brickle, 2003; Brickle *et al.*, 2005; Gaevskaya *et al.*, 1990).

Thirteen oioxenic species, comprising two microsporideans, four myxozoans, three digeneans, three monogeneans and one acanthocephalan, have been reported solely from *D. eleginoides* (Gaevskaya *et al.*, 1990; Brickle, 2003). However, considering that the knowledge of the ichthyoparasite fauna of the sub-Antarctic and Antarctic is poor in comparison to other regions, it is possible that some of these species may be reported from other fish species in the future.

Four parasitic species found in *D. eleginoides* are specific to the Nototheniidae and are thus stenoxenic (Brickle, 2003). These include one nematode, one digenean, one monogenean and one acanthocephalan. The nematode *Hysterothylacium nototheniae* was reported from the Ob and Lena Banks, the acanthocephalan *Metacanthocephalus rennicki* was only reported from the Lena Bank and the monogenean *Pseudobenedeniella branchialis* occurred in South Georgia.

Forty-three of the parasites reported from *D. eleginoides* are considered generalists (eurixenic), which infect fish other than the nototheniids (Brickle *et al.*, 2005; Gaevskaya *et al.*, 1990; Oliva *et al.*, 2008; Rodriguez and George-Nascimento, 1996). Six of these species, appear to be specific to the perciform suborder Notothenioidea. The latter include *Dichelyne* (*Cucullanellus*) *fraseri*, *Lecithophyllum champsocephali*, *Lepidapedon taeniatum*, *Lepidapedon garrardi*, *Heterosentis heteracanthus* and *Eubrachiella antarctica*.

Clesthobothrium crassiceps is considered one of two accidental infections for *D. eleginoides*. Specimens were found to infect *D. eleginoides* from the Patagonian Shelf (Brickle, 2003) and in a single fish caught at South Georgia (Gaevskaya *et al.*, 1990). *Clesthobothrium crassiceps* is stenoxenic and usually found in *Merluccius* spp. (Esch and Fernandez, 1993), so it is little surprising

Table 4.5 Geographical distribution of parasites infecting *Dissostichus eleginoides* from around the Southern Ocean

		Type	Geographic range								
			C	PS	SG	OB	LB	PE	HI	MI	RS
Microsporidia	Microsporidean sp. 1	O			■						
	Microsporidean sp. 2	O		■							
Myxozoa	<i>Neoparvicapsula subtile</i>	O		■							
	<i>Sphaerospora dissostichi</i>	O		■							
	<i>Ceratomyxa dissostichi</i>	O		■							
	<i>Alatospora</i> sp.	O		■	■			■	■	■	■
Digenea	<i>Brachyphallus crenatus</i> (adult)	E	■								
	<i>Derogenes varicus</i> (adult)	E	■	■				■	■	■	
	Digenean sp. 1 (adult)	O							■		
	<i>Elytrophalloides oatesi</i> (adult)	E		■	■	■		■	■		
	<i>Glomericirrus macrouri</i> (adult)	E		■				■	■	■	■
	<i>Gonocerca crassa</i> (adult)	E		■							
	<i>Gonocerca phycidis</i> (adult)	E	■	■	■	■		■	■	■	
	<i>Gonocerca taeniata</i> (adult)	E		■							
	<i>Helicometra antarcticae</i> (Dadult)	E									■
	<i>Hirundinella ventricosa</i> (larva)	Acc		■							
	<i>Lecithaster australis</i> (adult)	E		■							
	<i>Lecithaster macrocotyle</i> (adult)	E			■				■		
	<i>Lecithochirium genypteri</i> (adult)	E	■	■							
	<i>Lecithochirium</i> sp. (adult)	O								■	
	<i>Lecithophyllum champscephali</i> (adult)	E						■	■	■	
<i>Lepidapedon garrardi</i> (adult)	E			■							
<i>Lepidapedon taeniatum</i> (adult)	E		■	■							

(continued)

Table 4.5 (continued)

		Type	Geographic range								
			C	PS	SG	OB	LB	PE	HI	MI	RS
Monogenea	<i>Neolepidapedon magnatestis</i> (adult)	S	■	■	■		■	■			■
	<i>Neolepidapedon</i> sp. (adult)	O									
	<i>Neolibouria georgiensis</i> (adult)	E		■	■						■
	<i>Stenakron glacialis</i> (adult)	E						■			
	<i>Neopavlovskioides georgianus</i> (adult)	O		■	■	■	■	■	■	■	■
	<i>Neopavlovskioides dissostichi</i> (adult)	O		■							
	<i>Pseudobenedenia dissostichi</i> (adult)	O		■	■						
Nematoda	<i>Pseudobenedeniella branchialis</i> (adult)	S			■						
	<i>Anisakis</i> Type 1 (larva)	E	■								
	<i>Anisakis</i> Type 2 (larva)	E	■								
	<i>Anisakis simplex</i> (larva)	E		■	■	■	■				
	<i>Anisakis</i> spp. (larva)	E	■	■	■			■	■	■	■
	<i>Acarophis nototheniae</i> (adult)	E		■	■			■	■	■	
	<i>Capillaria</i> sp. (adult)	E			■	■		■		■	
	<i>Contracecum osculatum</i> (larva)	E		■							
	<i>Contracecum</i> sp. (Nematode, larva)	E			■	■	■	■	■		
	<i>Dichelyne (Cucullanellus) fraseri</i> (adult)	E		■	■	■	■	■	■	■	
	<i>Hysterothylacium</i> sp. (adult/larva)	E	■		■			■	■	■	■
	<i>Hysterothylacium aduncum</i> (adult/larva)	E		■	■						
	<i>Hysterothylacium nototheniae</i> (adult/larva)	S		■		■	■				
<i>Pseudoterranova decipiens</i> (adult)	E		■	■		■	■	■	■	■	

Cestoda	<i>Clestophrium crassiceps</i> (larva)	Acc	■	■								
	<i>Grillotia erinaceus</i> (adult)	E		■	■				■			
	<i>Hepatoxylon trichiuri</i> (adult)	E	■	■			■	■	■			
	<i>Lacistorhynchus tenuis</i> (larva)	E		■								
	<i>Phyllobothrium</i> sp.(lava)	E							■			
	Pseudophyllidean cercoides (larva)	E	■	■	■				■	■		
Acanthocephala	Tetraphyllidean cercoides (larva)	E		■	■	■	■	■		■	■	
	<i>Aspersentis megarhynchus</i> (adult)	E				■		■				
	<i>Corynosoma arctcephali</i> (larva)	E				■			■	■	■	
	<i>Corynosoma bullosum</i> (larva)	E	■	■	■				■	■	■	
	<i>Corynosoma hamanni</i> (larva)	E		■		■	■					
	<i>Corynosoma pseudohamanni</i> (larva)	E		■								
	<i>Echinorhynchus longiproboscis</i> (adult)	E		■								
	<i>Echinorhynchus petrotschenkoi</i> (adult)	E		■	■				■		■	
	<i>Heteracanthocephalus dissostichi</i> (adult)	O		■		■						
	<i>Heterosentis heteracanthus</i> (adult)	E				■						
	<i>Metacanthocephalus rennicki</i> (adult)	S						■				
	Copepoda	<i>Eubrachiella antarctica</i> (adult)	E		■	■			■	■	■	

C = Chile; PS = Patagonian Shelf; SG = South Georgia; OB = Ob Bank; LB = Lena Bank; PE = Prince Edward Islands; HI = Heard Island; MI = Macquarie Island; RS = Ross Sea. Types of parasite: O = oioxenic (*D. eleginoides* only); S = stenoxenic (Nototheniidae only); E = eurixenic (wider range); Acc = accidental infection.

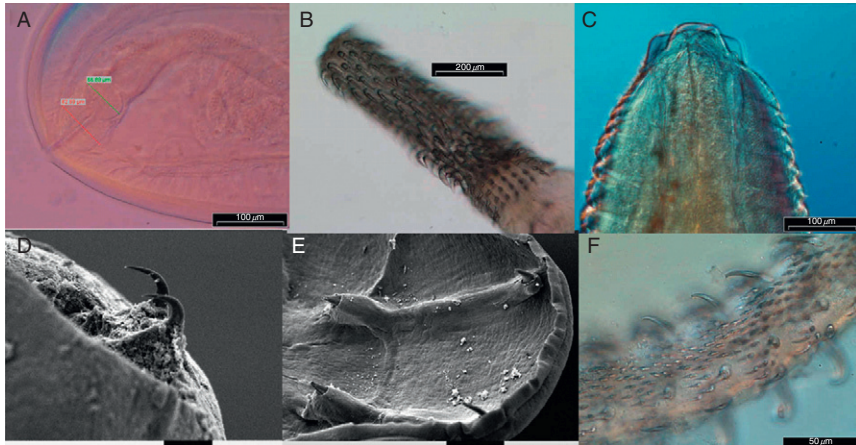


Figure 4.8 Parasites of Patagonian toothfish (*Dissostichus eleginoides*): (A) *Echinorhynchus longiproboscis* vagina and sphincter (Acanthocephala), (B) *Corynosoma arctocephali* proboscis (Acanthocephala), (C) *Pseudoterranova decipiens* (Nematoda), (D) *Neopavlovskioides georgianus* opisthohaptor (scale = 40 μm ; Monogenea), (E) *Pseudobenedenia dissostichi* opisthohaptor (scale = 300 μm ; Monogenea), (F) *Grillotia erinaceus*.

that this parasite was reported from South Georgia (Gaevskaya *et al.*, 1990). Since merluccids are not reported from south of the APF, the only plausible explanations are that either a merluccid species strayed from the Patagonian Shelf or the *D. eleginoides* in question migrated from the Patagonian Shelf. The other accidental infection was a single *Hirudinella ventricosa*, a parasite of tunas, recovered from a toothfish on the Patagonian Shelf.

8.2. Geographical differences in parasite fauna

Distinct geographic variability has been identified in the parasite fauna of Patagonian toothfish (Brickle *et al.*, 2005; Gaevskaya *et al.*, 1990; Parukhin and Lyadov, 1982). Gaevskaya *et al.* (1990) reviewed work conducted between 1972 and 1983 from the Patagonian Shelf region, South Georgia, and the Ob and Lena Banks. Thirty-eight parasite species were found in these fish, including myxosporideans (1 species), monogenean trematodes (3), cestodes (5), nematodes (8), acanthocephalans (7), copepods (1) and digenean trematodes (13).

Gaevskaya *et al.* (1990) found that the characteristic feature of the parasite fauna of *D. eleginoides* was the predominance of helminths, with 92% of them having complex life cycles. They attributed this to the predatory behaviour of the host and examined the parasite fauna of prey species in the Patagonian area, to establish the origin of many of the

incidental parasite species found in the host. They suggested that the cestode *Clestobothrium crassiceps* infects *D. eleginoides* through the ingestion of infected hake (*Merluccius* spp.), the trematode *Gonocerca taeniata* through southern blue whiting (*Micromesistius australis australis*), the trematodes *Lepidapedon taeniata* and *Glomericirrus macrouri* through grenadiers (Macrouridae), the trematodes *Neolebouria georgiensis* and *Lecithaster australis* from fish of the family Nototheniidae, and acanthocephalans of the genus *Corynosoma* through amphipods, isopods and fish of the family Nototheniidae. Many of these parasites were found sporadically with low intensities.

In the Ob and Lena Banks, Patagonian toothfish appear to obtain the vast majority of their parasites from their principal prey species, *Nototheniops larsoni* (Gaevskaya *et al.*, 1990), notably *Hysterothylacium nototheniae*, *Cucullanellus fraseri* and *Corynosoma hammani* together with other parasites characteristic of nototheniid fish. In the South Georgia area, where the main prey of toothfish are nototheniid fish, Gaevskaya *et al.* (1990) identified three trematodes (*Neolebouria georgiensis*, *Lepidapedon antarcticus*, *Elytrophalloides oatesi*), two nematodes (*Ascarophis nototheniae* and *Cucullanellus fraseri*) and two acanthocephalans (*Echinorhynchus georgianus* (= *E. petrotschenkoii*) and *Corynosoma bullosum*). In general, the parasite fauna of *D. eleginoides* is determined to a significant degree by the ichthyoparasite fauna of the area it inhabits (Gaevskaya *et al.*, 1990) and is richer in the west of its range than in the east, which indicates that the centre of origin of *D. eleginoides* was the Patagonian Shelf (Gaevskaya *et al.*, 1990).

Brickle *et al.* (2005) reported 32 parasite taxa, including 10 species being reported from *D. eleginoides* for the first time, from six locations around the sub-Antarctic (Shag Rocks, South Georgia, Prince Edward Island, Heard Island, Macquarie Island and the Ross Sea). Juvenile toothfish from the Shag Rocks area had a lower species diversity than samples collected from the other areas, with the exception of the Ross Sea, and Brickle *et al.* (2005) suggested that larger fish provide more internal and external space for infection and can support higher infection rates because they consume more infected prey.

Brickle *et al.* (2005) found that some parasite species appeared to be specific to certain localities. The heaviest infections of larval tetraphyllideans occurred in immature fish around Shag Rocks, which may be related to their diet. Microsporidean species and *Neolebouria antarctica* infected adult toothfish only at South Georgia. Gaevskaya *et al.* (1990) also found *Neolebouria georgiana* (= *N. antarctica*) around South Georgia and not around the Ob and Lena Banks. *Stenakron* sp. and *Aspersentis megarhynchus* were found only around Prince Edward Island at relatively high prevalences. *Lecithophyllum champsocephali* was restricted to Heard, Macquarie and Prince Edward Islands. Sørensen's similarity index illustrated that the parasite faunas of *D. eleginoides* were similar around the sub-Antarctic but showed

greater differences with the Ross Sea. The greatest similarities were between Prince Edward, Heard and Macquarie Island.

8.3. Ontogenetic changes in parasite fauna

Brickle *et al.* (2005) demonstrated that fish size (but not sex) was a significant determinant of the parasite fauna of juvenile Patagonian toothfish from Shag Rocks. There were significant decreases in the abundance and prevalence of tetraphyllidean (Cestoda) plerocercoides with increasing host length, whilst the larval acanthocephalan *Corynosoma bullosum*, the copepod *Eubrachiella antarctica*, the monogenean *Pseudobenedenia dissostichi* and the nematode *Hysterothylacium* sp. increased. The reduction in tetraphyllideans was attributed to the reduction in the euphausiids, intermediate hosts for tetraphyllidean cestodes, in the toothfish diet. Increases in *Corynosoma* were likely due to the presence of intermediate amphipod hosts in the diet, whilst other increases were associated with increased potential attachment areas.

The nematode *Anisakis* sp. did not show a significant increase in abundance with fish length but did show a pattern of increasing prevalence with increasing fish length. *Anisakis* spp. use euphausiids as their first intermediate hosts and squid and fish as second intermediate hosts. Their larvae can be passed onto other fish and squid without further moults; these squid and fish, therefore, act as paratenic hosts. Adult *Anisakis* spp. are parasites of pinnipeds and cetaceans. *D. eleginoides* will accumulate increasing numbers of *Anisakis* spp. by feeding on infected euphausiids and, later, by feeding on fish. The digenean *Gonocerca physidis* and the monogenean *Neopavlovskioides georgianus* did not show significant correlations of abundance with increasing host length. Although *Neopavlovskioides georgianus* showed a pattern of increasing prevalence with length, it is likely that older/larger toothfish are more suitable hosts for this parasite, and this is highlighted by the high range of intensities encountered in adult fish around the sub-Antarctic.

In a detailed study of the parasites of the Falkand Islands' toothfish population (11,362 parasites from 27 taxa), Brickle *et al.* (2006) found correlations between abundance of certain parasitic taxa and increasing host length. They also detected differences in the parasite community with season and depth of capture.

9. PHYSIOLOGY

There is a considerable body of literature on the physiological adaptations that have evolved within the Nototheniidae (see Farrell and Steffensen, 2005; Kock, 1992 for reviews). The majority of these studies have focussed on species living at the highest and coldest latitudes where

issues of freezing resistance and cold adaptation are the most acute. Studies on the physiology of sub-Antarctic and temperate notothenioids, including *D. eleginoides*, are more limited. However, aspects of the physiology of the congener *D. mawsoni* have been studied in greater detail allowing inferences to be made about many, but not all, physiological adaptations to the environment of *D. eleginoides*.

9.1. Buoyancy

The majority of notothenioids are benthic and are heavier than sea water, with all species lacking a swim bladder (Eastman and Devries, 1982). However, in several species, including those of the genus *Dissostichus*, a range of adaptations and mechanisms have evolved to achieve neutral buoyancy, which conserves muscular energy and enables exploitation of the pelagic realm (Eastman and Sidell, 2002; Near *et al.*, 2003; Oyarzun *et al.*, 1988). To compensate for the lack of a swim bladder, *Dissostichus* spp., in common with other members of the clade of neutrally buoyant notothenioids, have much diminished mineralisation of the skeleton (Eastman, 1990). The ash content of the skeleton is only around 6% of the overall body weight. Cartilage is also substituted for bone in some areas such as the skull, pectoral girdle and caudal skeleton. Furthermore, the scales, which also contain heavy bone salts, have an unmineralised portion at their posterior margin (Eastman, 1990; Oyarzun *et al.*, 1988).

Large lipid deposits, consisting mainly of triglycerols and a small number of wax esters, also contribute to the buoyancy of *D. eleginoides*. These lipids have a specific gravity less than sea water (0.93) and therefore provide considerable static lift. In a study of specimens caught in the Chilean fishery, Oyarzun *et al.* (1988), found that white muscle from the dorsal areas of the body may contain >25% lipid and may rise considerably (>46%) in regions close to the centres of mass and buoyancy such as the origin of the pectoral fin and regions ventral to the pelvic fins. A thick layer of subcutaneous lipid may account for nearly 5% of the overall body weight but decreases towards the caudal zone. In *Dissostichus* species, lipid is stored in typical adipose cells and is therefore likely to be available for metabolism and hence act as an energy reserve. The loss of subcutaneous and intra-muscular lipid stores through metabolism without replacement can lead to an 'axe handle' morphology in *D. mawsoni* with animals having an associated low condition factor. Emaciation in these fish is most likely caused by the mobilisation of lipid reserves for migration and reproduction and may lead to fluctuations in buoyancy throughout the life of the animal (Fenaughty *et al.*, 2008). The vertebrae of *D. eleginoides* are also known to contain lipid-filled cavities; however, it is not thought that the relatively small liver is an organ for buoyancy. The large pectoral fins of *Dissostichus* species are also thought to

provide lift during forward propulsion assisting the ability to maintain position within the water column.

Near *et al.* (2003) demonstrated that *D. mawsoni* experience a distinct ontogenetic change in buoyancy with juveniles heavier than water (non-buoyant) and with adults becoming neutrally buoyant at a mean length of around 810 mm (TL). It is suggested that this could be associated with a change in habitat use, with juveniles exploiting benthic habitats and adults foraging within the entire water column over deeper water. Although directed studies have not been carried out, it is likely that such an ontogenetic change in buoyancy occurs in *D. eleginoides* associated with a marked change in distribution and trophic ecology with size/age (Belchier and Collins, 2008; Collins *et al.*, 2007). However, in juvenile *D. eleginoides*, there is little evidence of benthic feeding, as juveniles are known to forage above the seabed and feed predominantly on pelagic and semi-pelagic fish species (Collins *et al.*, 2007). The ontogenetic change in buoyancy may be a result of a change in prey availability with a need to conserve energy as toothfish move to greater depths where prey are more scarce.

9.2. Antifreeze glycopeptides

The evolutionary development of antifreeze compounds has been essential for fish survival in many of the colder, higher latitude habitats of the Southern Ocean and has enabled the radiation of many notothenioids into these environments. A major physiological-biochemical adaptation has been the ability to synthesise macromolecular antifreeze substances for circulation in the body fluids. These antifreezes prevent notothenioids freezing when they come into direct contact with ice. However, *D. eleginoides*, which generally live in water temperatures of 2–11 °C, lack antifreeze within their body fluids. The congener *D. mawsoni* possesses eight antifreeze glycopeptides (AFGPs), which are synthesised in the liver. Ghigliotti *et al.* (2007) noted that whilst *D. mawsoni* has high levels of circulatory AFGPs and an associated high level of AFGP genes, *D. eleginoides* has barely detectable AFGP sequences in its DNA. The authors suggest that despite their close phylogenetic kinship, the evolution of these species in disparate thermal regimes means that they show some distinct genetic and biological characteristics.

9.3. Vision

Whilst there have been no studies to date on the optical physiology of *D. eleginoides*, an extensive comparative study of the ocular morphology of Antarctic notothenioids included a detailed examination of the morphology of the eye of *D. mawsoni* (Eastman, 1988). As the two congeners show much similarity in behaviour, morphology and ecology, it is likely that the

adaptations to eye morphology observed in *D. mawsoni* are also present in *D. eleginoides*. In a study of the gross and microscopical anatomy of 18 species found in the sea ice zone in McMurdo Sound, Antarctica, *D. mawsoni* was shown to possess by far the lowest number of cones and the highest ratio of rods/cones in the retina of all species examined. The rod-dominated retina of *Dissostichus* is especially sensitive and well suited to respond to dim light levels at depth. The huge reduction in the number of cones is typical of deep-water species and serves to increase the sensitivity of the retina whilst reducing the visual acuity. It is not certain whether juvenile *Dissostichus* have the same eye morphology as adults or whether there is a change in eye development during the ontogenetic movement into deeper water. It is clear that adult toothfish can migrate vertically throughout the water column and have often been caught in relatively shallow depths (<40 m) close to the shore. [Collins et al. \(1999, 2006\)](#) noted the sensitivity of toothfish to flashes and lights associated with underwater photography, including the ability to rapidly change colour, which clearly indicates a highly developed visual system.

10. BEHAVIOUR

10.1. Methods of studying behaviour

Data on Patagonian toothfish behaviour come from three main sources, observations of captive animals, baited camera systems (conventional 35 mm and video) and from data-logging tags ([Williams and Lamb, 2002](#)) that have been attached to toothfish.

10.2. Baited camera systems

Adult toothfish are readily attracted to bait, which makes them susceptible to baited longlines, but also enables them to be studied using baited cameras. Baited cameras have been used to investigate the abundance and behaviour of toothfish on the Patagonian Shelf ([Collins et al., 1999](#)) and on the shelf around South Georgia and Shag Rocks ([Collins et al., 2006](#); [Yau et al., 2002](#)). The baited camera work was undertaken using autonomous lander systems ([Priede and Bagley, 2000](#)) that were dropped to the seafloor, ballasted with scrap metal and remained on the seafloor for periods of a few hours to weeks. Initial work on toothfish utilised a high-resolution 35 mm camera with powerful flash lights (200 J), but the data suggested that the lights discourage the toothfish from attending the bait, and the number of encounters was small ([Collins et al., 1999](#); [Yau et al., 2002](#)). Later work utilised a low-light video camera and many more toothfish encounters were recorded ([Collins et al., 2006](#); [Yau et al., 2002](#)).

10.3. General behaviour patterns

Toothfish appeared to be solitary and generally avoided one another. Any accidental contact between conspecifics resulted in sudden departure in different directions; similarly, unintended contact with the stone crabs (Lithodidae) also led to the rapid departure of the toothfish. Unlike other deep-water scavengers, toothfish did not accumulate at the bait, instead fish took a piece of bait and rapidly departed. No attempts were made to approach the bait when large numbers of stone crabs were clustered around it (Collins *et al.*, 1999, 2006).

10.4. Swimming form and speeds

Observations from baited video cameras (Collins *et al.*, 2006) and captive animals (Brown, unpublished) show that labriform swimming (sculling with the large pectoral fins) is the principal means of locomotion in Patagonian toothfish. This gentle sculling with the pectoral fins produces relatively slow cruising speeds with a mean of 0.17 m s^{-1} or approximately 0.22 BL s^{-1} (Collins *et al.*, 2006; Yau *et al.*, 2002). The pectoral fins are also used in a gliding motion, particularly when toothfish swim close to the seafloor. Subcarangiform swimming (using the caudal trunk and fin) was also observed typically during turning or rapid acceleration. The maximum swimming speed recorded was 2.23 m s^{-1} for an individual of 0.72 cm TL (3.1 BL s^{-1}) when the fish was in 'panic flight' (Yau *et al.*, 2002).

Using tagging data, Agnew *et al.* (2006a) reported an average distance moved by toothfish around South Georgia, at 10 km year^{-1} indicating little large-scale movements. *D. mawsoni* and *D. eleginoides* are comprised of a large percent of white muscle (51% of the body weight in *D. mawsoni* (Eastman and Devries, 1981)), resulting in most of their movement being dominated by small periods of rapid movements, and their reduced amount of red muscle, for slow sustained swimming, explains their strong site fidelity.

From archival data storage tags deployed on toothfish around Heard Island (Williams and Lamb, 2002), toothfish of 710–820 mm TL were recorded making daily movements both upwards and downwards, of between 20 and 130 m (mainly $< 60 \text{ m}$). They concluded that this behaviour was in response to several factors, including environmental parameters (day and lunar phase), behaviour of prey species and bottom topography.

11. FISHERY

11.1. History of the fishery

Patagonian toothfish were first investigated as a fisheries resource in Chile in the 1950s (Guerrero and Arana, 2009; Moreno, 1991), with exploratory trawling limited to shallow depths. Toothfish were subsequently caught as a by-catch in

trawl fisheries around Kerguelen Island, on the Patagonian Shelf and around South Georgia in the early 1980s. Development of longline gear capable of operating in deep water, targeting the large adult fish, led to the targeted fishery in Chilean waters, which began in the mid-1980s and quickly spread to other areas such as the Patagonian Shelf, South Georgia and Kerguelen. The high price commanded by toothfish (currently US\$15 per kg) led to a rapid expansion in the catches, with new fishing grounds identified and targeted. The FAO reported that landings increased from less than 5000 tonnes in 1983 to 40,000 tonnes in 1992 (Fig. 4.9), although these figures include only the legal catches within the CCAMLR area and national territorial waters.

At South Georgia (UK Overseas Territory), the longline fishery began with Soviet Union vessels in late 1988, which were later joined by Chilean, Bulgarian and Ukrainian vessels. In 1993/1994, CCAMLR designated the South Georgia region as a special area for protection and scientific study and undertook a depletion experiment to determine stock size. The depletion experiment was not successful (Parkes *et al.*, 1996), but the presence of observers on board demonstrated the severity of the seabird by-catch problem and led to the fishery being limited to the winter months from 1998 (Agnew, 2004). Since 1999, the season has been restricted to the period from May 1st until August 31st, with opportunities for a season extension of 2 weeks into September and at the end of April for vessels that were fully compliant with management measures the previous year (CCAMLR, 2009). In recent years, the total allowable catch (TAC) in the South Georgia fishery has been around

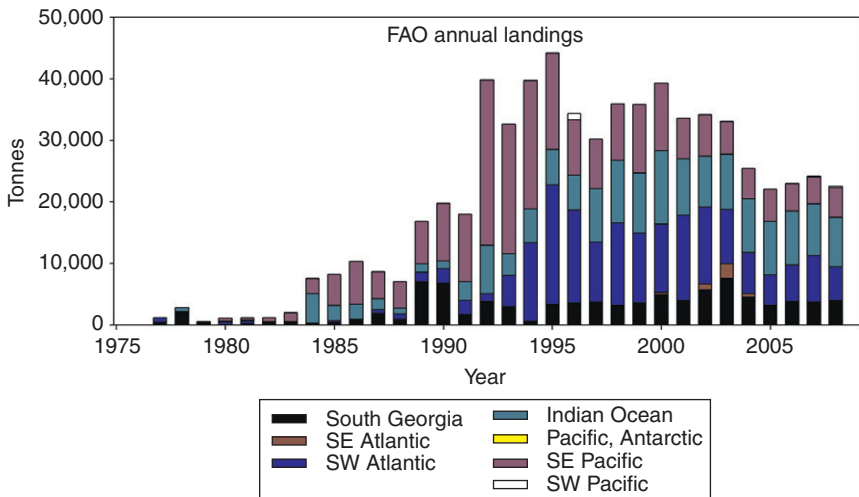


Figure 4.9 Annual landings of Patagonian toothfish (*Dissostichus eleginoides*) from different regions. Data based on FAO figures. Note that this only includes reported landings.

3000 tonnes. A small fishery also operates around the northern area of the South Sandwich Islands (Roberts and Agnew, 2008), with the TAC currently 41 tonnes (CCAMLR, 2009).

In the southern Indian Ocean, a targeted trawl fishery began on the western Kerguelen shelf (French exclusive economic zone (EEZ)) in 1984/1985, when former USSR trawlers found and began to exploit large concentrations of toothfish (Lord *et al.*, 2006). Longlining started in the Kerguelen fishery in 1991, and since 2001/2002, the fishery has been exclusively longliners (Lord *et al.*, 2006). The Kerguelen fishery operates year round, although catch rates are lower in winter, and since 1994, the legal catches have been around 5000 tonnes per year. The Heard and McDonald Islands (HIMI) shelf (Australian EEZ) is contiguous with the Kerguelen shelf and is probably the same population of toothfish. Apart from some Polish research fishing in the 1970s, there was little known exploitation on the HIMI shelf (Williams and de la Mare, 1995) until trawl fisheries developed for toothfish and icefish in 1996. The fishery was opened up to longlining in 2002/2003 and is currently exploited by both trawlers and longliners, with a catch limit of around 2500 tonnes.

At Crozet Island (French EEZ), 900 miles west of the Kerguelen Plateau, the longline fishery began in 1996/1997, with reported catches of up to 1200 tonnes, but the fishery suffered from considerable illegal fishing activity from 1995 to 2002. Current legitimate catches are less than 1000 tonnes per year.

The Prince Edward Islands (South African EEZ) fishery, which spans the edge of the CCAMLR zone, began in 1996/1997 as a seasonal fishery (May 1st–August 31st), but the fishery suffered from high levels of illegal catches, with an estimated 21,000 tonnes illegally taken in 1997 (Brandao *et al.*, 2002). In an attempt to counter the illegal fishing, the fishery was opened year round in 1998, in the hope that the presence of legal operators would deter the illegal vessels (Brandao *et al.*, 2002), but catch rates and legal catches declined sharply. The TAC in 2002/2003 was set at 400 tonnes and recent estimates of IUU are zero, with legal catches of around 200 tonnes per year.

Elsewhere in CCAMLR waters, toothfish fishing has occurred on isolated banks and seamounts, such as Banzarre Bank and the Ob and Lena Seamounts. The fisheries in these areas were rapidly overexploited and stocks remain depleted (McKinlay *et al.*, 2008).

The Macquarie Island (Australian EEZ) fishery began in late 1994 in the Aurora Trough and spread to the Macquarie Ridge 2 years later when toothfish aggregations were detected. Initially, catches were over 1000 tonnes per year, but the fishery was closed (except for research fishing) from 1999 to 2003, when it resumed with a reduced TAC (Phillips *et al.*, 2009). Although trawling has been the main method of fishing since 1994, a 3-year longline trial began in August 2007, primarily on the Macquarie Ridge north and south of the island. Current quotas are around 300 tonnes

from the Aurora Ridge, with 100 tonnes from Macquarie Ridge (Phillips *et al.*, 2009).

Toothfish were initially taken as by-catch in trawl fisheries on the Patagonian Shelf, with longline fisheries subsequently established in Argentine and Falkland Island waters. The Argentinian fishery started in the 1990s with the highest catches in 1995 (18,225 tonnes); however, catches have declined since then (Wohler, unpublished data). Based on advice from the National Institute of Fishing Research and Development (INIDEP), new management practices have been enforced by the Fishing Authority since 2000. These include catch documentation scheme (CDS), larger hook sizes, minimum fish size, minimum fishing depths and establishment of a protected juvenile area.

The Falklands longline fishery began in 1992 as an experimental fishery and became an established fishery in 1994 (Laptikhovsky and Brickle, 2005). Catches peaked in the first year of the directed fishery (2733 tonnes in 1994) and subsequently stabilised to a level of 1200–1800 tonnes (currently, 1200 tonnes).

The Chilean fishery is divided into two zones. The north zone, between Chile's northern limit (18° 21' S) and 47° S, is reserved exclusively for artisanal fishing, whereas in the south zone (47° S to 57° S), the resource is exploited through industrial fishing activities (Guerrero and Arana, 2009). The only gear permitted is the demersal longline, although pots have been trialled (Guerrero and Arana, 2009). The Chilean fishery has also been instrumental in developing new gears, such as the trotline and cachalotera system (Moreno *et al.*, 2006, 2008, see below).

Areas in the high seas (outside of national jurisdiction) have also been exploited, notably the Scotia Ridge between Shag Rocks and the Falklands. In these areas, catches have not been limited and stocks quickly depleted.

11.2. Fishing methods and gears

The principal method of catching adult toothfish is demersal longlining (see Figs. 4.10 and 4.11), in which a longline of baited hooks are deployed close to the seafloor at depths up to 2000 m. Surface buoys indicate the presence of lines, and vessels typically recover lines after a 'soak-time' of 24–48 h. Bait is usually squid or sardine. Longline vessels are generally small vessels (30–80 m; Fig. 4.10). There are three principal types of longlining: the Spanish (double-line) system, autoline and more recently, the trotline system (Fig. 4.11), which often includes cetacean exclusion nets (umbrellas or cachaloteras). In all cases, lines are deployed from the stern of the vessel and recovered via a hauling hatch on the starboard side.

The Spanish or double-line system (Fig. 4.11A) uses a strong main- or mother-line attached at each end to an anchor and buoy line. The fishing line is attached to the main line by a series of connecting ropes. The hooks



Figure 4.10 The fishery for Patagonian toothfish (*Dissostichus eleginoides*): (A) photograph of an autoliner; (B) aerial photograph of a Spanish double-line longliner, note the hauling area on the starboard side; (C) toothfish being gaffed; (D) circle-type (left) and J-type hooks used in the South Georgia fishery.

are attached to the fishing line with monofilament snoods, with each section of the fishing line comprising around 25 hooks, with around 7000 hooks per line and with vessels deploying 2–3 lines per day. Weights (6–10 kg) are attached between each section of hooks to sink the line and keep it on the seafloor. The hooks are baited by hand, which is relatively labour intensive.

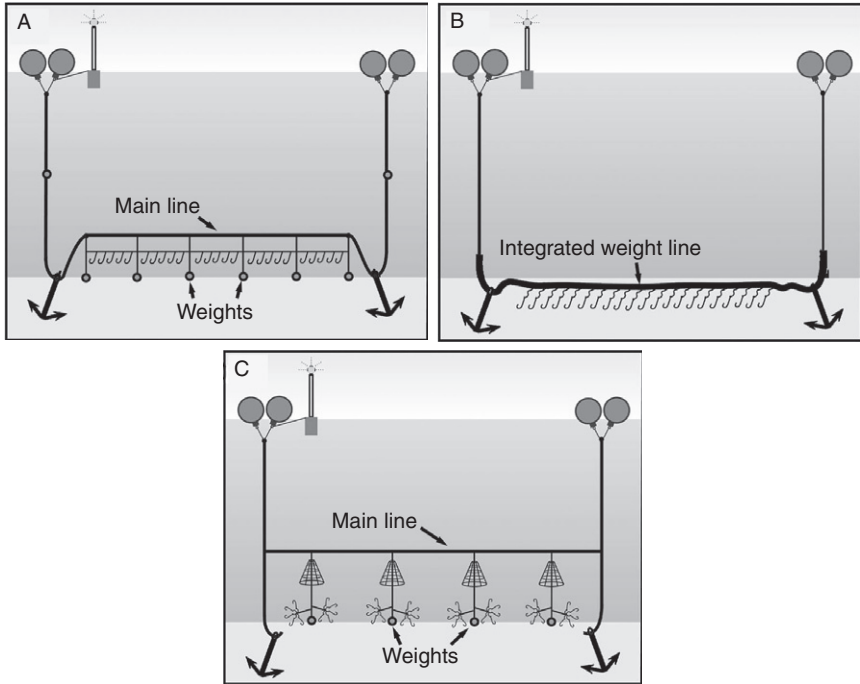


Figure 4.11 Illustration of the three methods of longlining: (A) Spanish double-line system, (B) autoline system and (C) trotline with net sleeves.

The autoline system (Fig. 4.11B) has a single weighted line (polypropylene line with integrated weight, around 50 gm^{-1}), from which hooks are attached via swivels and multifilament snoods. The line is divided into magazines, each consisting of 1000–1500 hooks, and although the length of lines and hence the number of hooks varies, typically an autoliner will be able to deploy 30,000 baited hooks per day. Hooks on auto-lines are automatically baited.

Trotlines (Fig. 4.11C) were initially developed in the Chilean artisanal fishery (Moreno *et al.*, 2008) and are a modification of the Spanish system, in which the hook line is replaced by a series of vertical branch lines, placed at $\sim 40 \text{ m}$ intervals. Each of the vertical branch lines supports clumps of 8–20 short hook lines and, at its extremity, a bag of weights. In the Falklands, there is one clump of 8 hooks per branch line with a single 6 kg weight at the bottom (Brown *et al.*, 2010). The clumping of the hooks near the weights allows the baited hooks to sink rapidly to avoid seabirds, but the method also allows for the use of net sleeves, umbrellas or cachaloteras to reduce depredation by whales (see below). Each branch line can have a buoyant net or sleeve attached that is able slide up and down the line.

During the set, this sleeve remains at the upper end of the branch line, but when the thick main line is hauled, the movement of the vertical branch line through the water causes the sleeve to slide down the line covering the hooks and any captured fish.

Pots were initially trialled as a method of reducing seabird mortality (see below) and also to stop depredation by sperm and killer whales. The traps (Fig. 4.12) used are typically a truncated conical shape, with a circular base of around 1.5 m, an upper part of 0.9 m diameter and 0.9 m high and made of steel and mesh panels (120 mm for the body and 38 mm for the mouth). Pot fishing is used in the fishery on the Patagonian Shelf and southern Chile, but has not proved successful at South Georgia, where catch rates were substantially lower than longlines (Agnew *et al.*, 2001; Guerrero and Arana, 2009).

There has been considerable regional variability in the success of different fishing methods, which is probably a consequence of bottom topography, current speeds and, possibly, toothfish behaviour. The autoline system has not been successful in the Falklands, but works well in other areas such as South Georgia and Heard Island. With the trotline system, catches (g/hook) are usually less at high toothfish density, probably because it is rare for each clump of hooks (8–20) to catch more than two fish. In the Falklands the catch per unit effort (CPUE) has been reported to be up to ten times higher with umbrella lines than Spanish longlines (in the same area); however, this is not a linear relationship, with Spanish lines performing better in areas of high local abundance of toothfish (Brown *et al.*, 2010). The Falklands fishery initially used the Spanish system, but has recently switched to using trotlines with cachaloteras.



Figure 4.12 A typical pot used to catch toothfish in the Falkland Islands Patagonian toothfish (*Dissostichus eleginoides*) fishery.

Gill nets have also been used to catch toothfish, but are banned throughout CCAMLR waters, as they have the potential to 'ghost fish' if the gear is not recovered. Gill nets are, however, used by illegal, unreported and unregulated (IUU) vessels (see below) that fish in the Southern Ocean. Bottom trawling is used to target toothfish on the shelf-slope at Heard Island. However, bottom-trawling is less discriminate than longlining, with a greater by-catch and is also likely to cause considerably more damage to seafloor habitats.

Different types and sizes of hooks have been used to catch toothfish. The commonest types are the 'circle' and 'j' hooks (Fig. 4.11D). The type and size of hook can influence the size and quantity of both target and non-target species. Bait is usually sardine and/or squid. Sardine, being an oily fish, produce good odour; however, as they have softer flesh than squid, the sardine generally do not last as long on the hooks, as they are consumed by amphipods. A combination of the two types of bait is considered to produce the best catch rates by many fishermen.

11.3. Illegal, unreported and unregulated (IUU) fishing

IUU fishing has been a major problem in toothfish fisheries throughout the southern hemisphere (Baird, 2006; Lack, 2008; Lack and Sant, 2001). The high value of the catch and difficulties of enforcing regulations in such a large and inhospitable ocean led to the development of significant illegal fishing in the early 1990s. This undoubtedly had a detrimental effect on the toothfish stocks and, since IUU vessels are unlikely to follow mitigation measures, on by-catch of seabirds (as described later) and non-target species.

In CCAMLR waters, IUU fishing started in 1992 around South Georgia (Agnew and Kirkwood, 2005). Following a series of arrests by U.K. authorities in that area, IUU operations moved to the Indian Ocean sector in 1996 and 1997 after the identification of large areas there where toothfish could potentially be caught. Since then, most activity has been concentrated on fishing grounds around Prince Edward and Marion Islands (South Africa), Crozet and Kerguelen Islands (France), Heard Island (Australia) and on oceanic banks in high seas areas such as the Banzare Bank.

CCAMLR and its member states have introduced a number of measures designed to reduce the level of IUU. These include the CDS (Agnew, 2000), satellite-derived tamperproof vessel monitoring systems (VMS) and rigorous patrolling, with high-profile arrests and prosecutions. Vessels fishing in CCAMLR waters must also carry an international observer and provide regular catch reports. The CDS, which was adopted in 2000, applies to both species of *Dissostichus* and is designed to demonstrate if toothfish were caught in compliance with conservation measures by tracking landings and trade. If a consignment of toothfish does not have the necessary documentation, it is assumed to be IUU. Under the VMS, every

vessel licensed by CCAMLR members to fish in the Convention Area is required to have a VMS, monitored by the flag State and forwarded to the CCAMLR Secretariat. This information can then be used to corroborate toothfish landings in the CDS. Some CCAMLR member states have taken additional steps in the fisheries that they manage in their territory. For instance, in the South Georgia fishery, which has been certified as sustainably managed by the Marine Stewardship Council, all toothfish products are weighed and verified at the end of the season. This ensures that licensed vessels do not exceed their allocated quota.

CCAMLR estimate the amount of toothfish taken by IUU vessels and include this data in stock assessments (CCAMLR, 2009), but Lack (2008) analysed trade data and suggested that CCAMLR may underestimate IUU catches by up to 50%. In 2002, a proposal to list toothfish on Appendix II of the Convention on International Trade in Endangered Species (CITES) was subsequently withdrawn, recognising that the CCAMLR CDS already monitors trade in toothfish.

Not all Patagonian toothfish fisheries are in the CCAMLR area (e.g. Chile, Argentina, Falklands, Crozet, Macquarie Island), and in these areas, domestic legislation and enforcement are relied upon to address IUU fishing.

11.4. By-catch issues

Although more selective than trawling, longlining still generates a by-catch. The principal by-catch species are grenadier (Macrouridae), morid cods such as *Antimora rostrata* (Moridae) and skates (Rajidae). By-catch levels vary between regions and depths, and also between fishing methods and with hook type and size and bait. At South Georgia, the by-catch of grenadiers is considerably greater with the autoline system than the Spanish double-line system. Species that possess a swim bladder (e.g. macrouids, morids) suffer severe decompression trauma when brought to the surface and will not survive if returned. Survival of species that lack a swim bladder can be high and in CCAMLR fisheries vessels are required to release (some with tags) all skate that are in good condition when caught. Longlines also capture and damage benthic invertebrates and the need to protect Vulnerable Marine Ecosystems (VMEs), such as those associated with cold-water corals, is a high priority within CCAMLR and other fisheries (Martin-Smith, 2009; Sharp *et al.*, 2009).

11.5. Interactions with seabirds

Interactions with seabirds are a problem with many longline fisheries (Brothers, 1991). Scavenging seabirds, including many albatross and petrel species, are attracted to baited hooks when they are deployed and, when they dive for the bait, they become hooked, sink with the lines and drown.

This has been a major problem within the majority of Patagonian toothfish fisheries in the Southern Ocean (Ashford *et al.*, 1994, 1995; Delord *et al.*, 2005, 2010; Moreno *et al.*, 1996; Nel *et al.*, 2002; Reid *et al.*, 2004; Williams and Capdeville, 1996), many of which operate in important foraging areas for threatened albatross and petrel species (Fig. 4.13). In the late 1980s, large numbers of seabirds were killed, but not quantified.

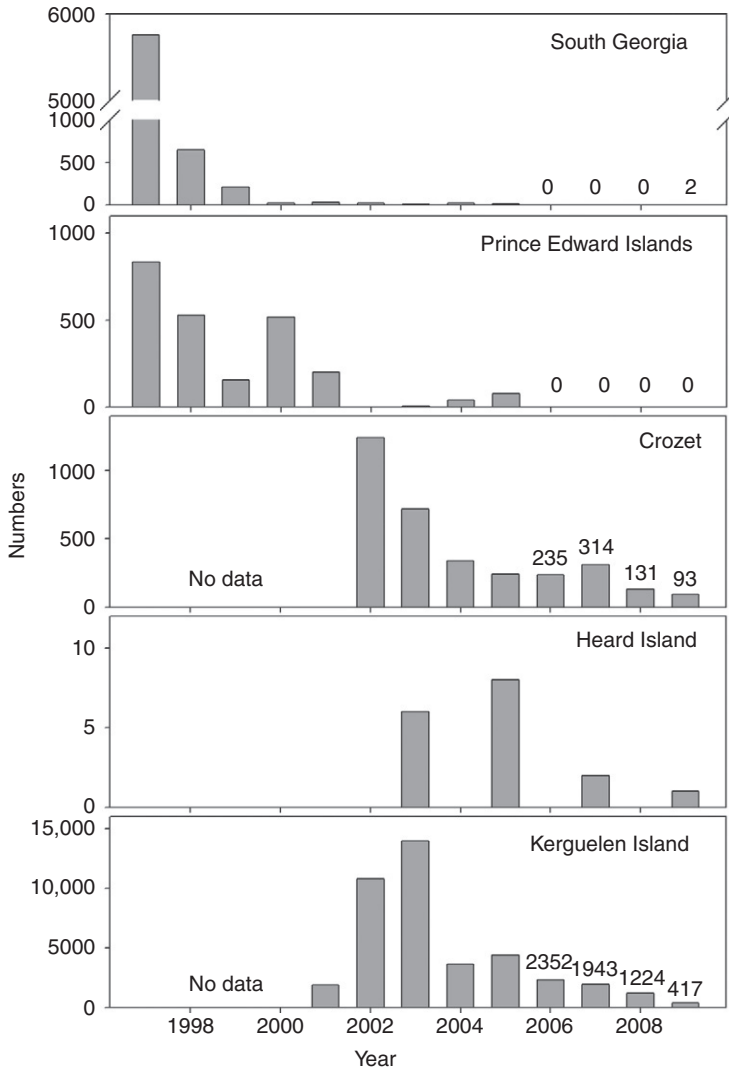


Figure 4.13 Numbers of seabirds reported killed in fisheries for Patagonian toothfish (*Dissostichus eleginoides*) at Kerguelen, Heard and Macdonald, Crozet, Prince Edward Island and South Georgia.

In 1992, CCAMLR responded to the seabird mortality issue and adopted a suite of mitigation measures, including the use of streamer lines, night setting and controls on offal discharge. The ad hoc working group on incidental mortality associated with longline fishing (IMALF) was then established in 1993 to monitor the problem and develop further mitigation. The CCAMLR Scientific Observer Scheme, which was also adopted in 1992, ensured 100% observer coverage on toothfish vessels, to monitor mitigation and by-catch. Additional mitigation measures included line-weighting schemes (Agnew *et al.*, 2000; Robertson *et al.*, 2000, 2007; Wienecke and Robertson, 2004) to ensure that hooks sink rapidly, the use of streamer or Tori lines during shooting (Fig. 4.14A) and the 'Brickle Curtain' (seven weighted vertically hung lines which form a curtain; Fig. 4.14B) to keep birds from the hauling area.

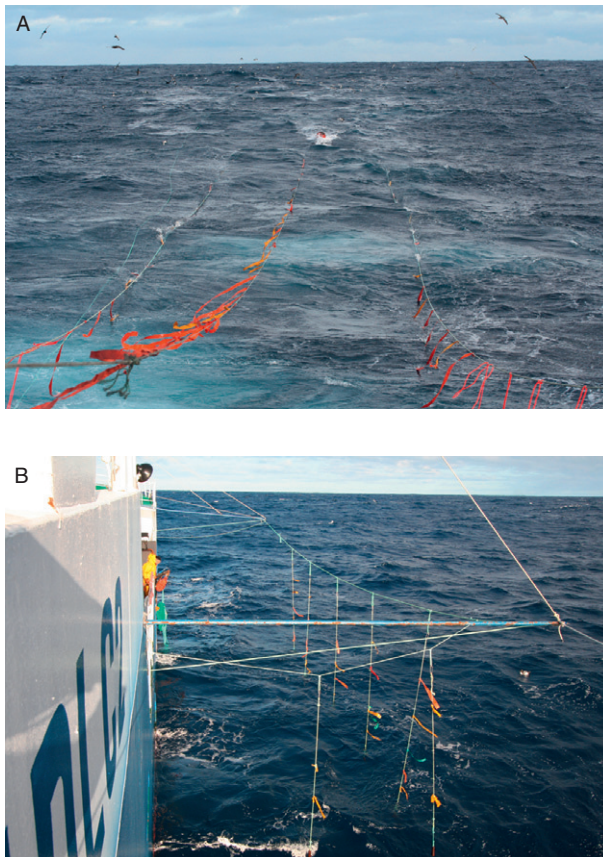


Figure 4.14 Seabird mitigation methods in action on a longliner; (A) streamer or Tori lines; (B) Brickle curtain around hauling area.

Further restrictions were introduced on fisheries under CCAMLR management, including the closure of the South Georgia fishery during the summer months, when species such as white-chinned petrel are particularly susceptible to capture. The mitigation measures implemented by CCAMLR had the desired effect, with the bird by-catch now close to zero (Fig. 4.13) in areas that CCAMLR is the competent authority (CCAMLR, 2009). Although the EEZ of the French territories of Kerguelen and Crozet fall in or partially in the CCAMLR zone, the French authorities manage the fisheries outside of the CCAMLR framework, and the reduction in seabird mortality has been considerably slower, with considerable numbers of birds still killed in the Kerguelen and Crozet fisheries (Delord *et al.*, 2010). The main species effected are white-chinned petrels (*Procellaria aequinoctialis*) and grey petrels (*Procellaria cinerea*), with between 7766 and 10,542 birds estimated to have been killed between September 2003 and August 2006 (Delord *et al.*, 2010). This level of mortality has now been reduced as some of the CCAMLR mitigation measures have been adopted (CCAMLR, 2009; Fig. 4.13).

The mitigation measures developed by CCAMLR have gradually been introduced in national EEZs. In the early days of the Falkland Islands fishery, large numbers of seabirds were killed, but mitigation has been introduced, and by 2001, a suite of mitigation was in place and by-catch was reduced (Otley *et al.*, 2007). However, 134 seabirds were estimated to have been killed in 2003/2004 (Otley *et al.*, 2007). With the introduction of the umbrella system, correct line-weighting regimes and the use of well-designed streamer lines and the 'Brickie Curtain', seabird mortality was eliminated during the 2007/2008 and 2008/2009 seasons (Brown *et al.*, 2010).

In the Chilean fishery, the introduction of trotlines has dramatically reduced the number of seabirds killed (Moreno *et al.*, 2006, 2008). In 2002, 1542 birds were killed, compared to zero in 2006. The difference is attributed to the greater sinking rate of the trotline system, in which the hooks are clumped with weights. A further problem is that of hook ingestion by scavenging birds, particularly wandering albatross, which occurs when hooks are not removed from discarded by-catch and offal (Phillips *et al.*, 2010). The discarding of baited hooks or of hooks in by-catch species is prohibited in many fisheries. However the increased use of trotlines has been implicated as the reason for a recent increase in hooks in wandering albatross regurgitates (Phillips *et al.*, 2010), with a greater number being cut off and discarded when they become tangled with the net-sleeves during hauling.

11.6. Interactions with marine mammals

Interactions between marine mammals and fisheries can take the form of competition for resources, incidental by-catch and depredation of fish from fishing gear. Incidental mortality is not a significant problem in Patagonian

toothfish fisheries, although there have been very occasional reports of sperm whales drowning following entanglement in Spanish-double line gear (CCAMLR, 2009). Competition has been considered in the trophic ecology section, so here, the focus is on the issue of depredation.

Marine mammal depredation of line caught fish is a problem throughout the world (Visser, 2000; Yano and Dahlheim, 1995) but has become particularly acute in the high value Patagonian toothfish fishery in recent years. Depredation by killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) was first reported by observers at South Georgia in 1994 (Ashford *et al.*, 1996) but has since been reported in other fisheries (Nolan *et al.*, 2000), and recent years have seen the problem increase (Ashford *et al.*, 1996; Kock *et al.*, 2006; Nolan *et al.*, 2000; Purves *et al.*, 2004). Depredation is apparent from heads and lips that are left on the line by the cetaceans and, at times, the majority of the catch on a line could be lost to depredation. Depredation from sperm whales and killer whales are rather different. Killer whales operate in pods of 3–15 animals, whilst sperm whales are often solitary. Sperm whales are natural predators of toothfish and can take toothfish from lines at depth, whereas killer whales only dive to 300 m and tend to strip fish from lines close to the surface (Fig. 4.15).

Quantifying the lost catch is not straightforward. One approach is to look at catch rates in the presence and absence of both killer and sperm whales. Since sperm whales are natural predators on toothfish, they tend to be abundant in areas where toothfish are abundant, and in some areas, there is no evidence of a reduction in catch rates in the presence of sperm whales (Brown *et al.*, 2010; Hucke-Gaete *et al.*, 2004; Purves *et al.*, 2004).



Figure 4.15 Killer whale (*Orcinus orca*) with a Patagonian toothfish (*Dissostichus eleginoides*) depredated from a line. Photo-courtesy of Manuel Sampedro Garcia (FV CFL Gambler).

However, when killer whales are present, catches can be greatly reduced, and if the vessel does not stop hauling, whole lines may be stripped. In Crozet, the CPUE dropped 22% in the presence of killer whales, 12% in the presence of sperm whales and 42.5% when both were present (Roche *et al.*, 2007). Overall, the level of depredation at Kerguelen (3%) is considerably lower than at Crozet (33%), which is attributed to the lower abundance of killer whales at Kerguelen (Roche *et al.*, 2007).

Fishing vessels have responded to the cetacean problem in a number of ways. Fishing with pots prevents both sperm and killer whales from taking the catch, but pot-catch rates are considerably lower than those of longlines. The use of net sleeves or cachaloteras is effective against sperm whales; however, killer whales are learning to bypass the nets and there is evidence of predation by killer whales on umbrella lines (Brown *et al.*, in press). A common practice in response to the presence of killer whales is to stop hauling and buoy the line off, so that the fish are beyond the diving range of the orcas. The vessel will then move to another location at speed and attempt to lose the killer whales, or pass them to another vessel. Acoustic deterrents have been used to mediate the problem of killer whales (Jefferson *et al.*, 1996; Morton and Symonds, 2002), but whales can quickly become accustomed to such devices.

Antarctic fur seals have also been implicated in depredation at Kerguelen (Roche *et al.*, 2007) and occasionally at South Georgia. At South Georgia, depredation by fur seals increased during the 2009 season, when the abundance of Antarctic krill, the primary prey of fur seals, was exceptionally low.

12. STOCK ASSESSMENT

A number of methods, have been used to carry out stock assessments for Patagonian toothfish fisheries around the Southern Ocean, the Patagonian Shelf and Chilean waters.

Initially, there were insufficient data to assess the fisheries using conventional stock assessment techniques. As Patagonian toothfish are long lived and slow growing, a reasonable catch and effort dataset combined with a suite of life history parameters is required for any age or length-based assessment methods, and it takes several years to build up these datasets. Early attempts at assessing fisheries used Leslie stock depletion models. Parkes *et al.* (1996) used the Leslie depletion model to examine local patterns in CPUE of toothfish in longline fisheries around South Georgia and off the Pacific coasts of Chile. They found that 54 out of 107 CPUE series showed a negative trend with cumulative catch, which was less than would be expected by chance according to binomial theory; however, only 18 of these datasets showed a significant negative trend. They concluded that depletion models were not a suitable method for estimating local abundance, and the authors

cited fish behaviour and the actions of fishermen as complicating factors that made the use of regression models inappropriate. In the same year, [des Clers *et al.* \(1996\)](#) applied a modified DeLury depletion model to toothfish CPUE in the Falkland Islands longline fishery but also failed to produce reliable results, concluding that the model's assumptions were not valid and that there was a likely extensive migratory behaviour in the Patagonian toothfish.

The rapid expansion of the toothfish fishery in the Southern Ocean in the late 1980s and early 90s was a major concern, which was compounded by the lack of data for traditional stock assessment methods. Also, adult populations were inaccessible to trawl surveys and therefore could not be estimated by traditional swept area methods ([Constable *et al.*, 2000](#)). To take into account this lack of data and the fact that the fishery was already in progress, CCAMLR developed two approaches for management, a generalised yield model (GYM) for stock assessment ([Constable and de la Mare, 1996](#)) and regulations restricting the development of new fisheries. The GYM was built on the approaches already developed for a krill yield model. As data from the longline fishery were insufficient and fishery independent surveys could not access the adult population, there was no estimate of initial biomass (B_0). These problems were overcome by using absolute estimates of recruits (using CMIX, [de la Mare, 1994](#)) and projecting those forward using simulations. This allowed for recorded catches to be discounted from the population, and consequently, a long-term yield could be assessed in tonnes rather than as a proportion of B_0 . In South Georgia, a relatively large number of bottom trawl survey data were available allowing the estimation of recruitment of 4-year-old toothfish. This approach was used to assess the South Georgia stock from 1995 to 2004, when it was replaced by an integrated approach using mark-recapture data.

Mark and recapture methods have been used to assess toothfish population sizes in Macquarie Island ([Tuck *et al.*, 2003](#)) and South Georgia ([Agnew *et al.*, 2006a](#)) fisheries. Essentially, exact time of release and recapture data are used in a stock assessment model that unifies a semi-parametric approach with the Petersen method. A maximum likelihood approach is used to estimate the available abundance of toothfish (fishable abundance, which is different to total or spawning biomass).

An attempt at estimating adult toothfish densities using baited cameras was conducted by [Yau *et al.* \(2001\)](#) in the Falkland Islands and South Georgia. They used an autonomous camera system (see [Section 10](#)) and attempted to calculate toothfish density based on mean first arrival time, as demonstrated by [Priede and Merrett \(1996\)](#). [Yau *et al.* \(2001\)](#) data gave estimates of 0.4 and 1.32 toothfish per km² for South Georgia and the Falkland Islands, respectively. However, the behaviour of the toothfish differed from other scavenging species to which the method had previously been applied, leaving considerable uncertainty about the results.

Since 2004, many of the major fisheries for *Dissostichus* spp. in the CCAMLR convention area have used fully integrated age-structured stock assessments with differing complexities and features that can deal with a large variety of age- and length-structured data. CASAL (Bull *et al.*, 2005) (C++ algorithmic stock assessment laboratory) is an integrated assessment method that can be used to implement either an age- or length-structured model, with options to structure the population by sex, maturity and/or growth path. CASAL can be used for a single stock or fishery or for multiple stocks, areas and fishing methods. The data can be taken from a number of different sources, including catch-at-age or catch-at-size data from commercial fishing, survey and other biomass indices, survey catch-at-age or catch-at-size data and tag release and recapture data. Estimations can be by least squares, maximum likelihood or Bayesian methods. CASAL can generate point estimates of the parameters of interest and can calculate likelihood or posterior profiles, generating Bayesian posterior distributions using Monte Carlo Markov chain methodologies. It can also project stock status into the future using deterministic or stochastic recruitment and can generate a number of yield measures commonly used in stock assessments. CASAL is now used in the assessment of both the Antarctic (Dunn and Hanchet, 2007; Dunn *et al.*, 2004) and Patagonian (Agnew *et al.*, 2007; Candy and Constable, 2008; Hillary *et al.*, 2006) toothfish. This method differs from the GYM in that many parameters can be estimated within the model, including B_0 , rather than having to estimate the parameters individually.

CCAMLR advocates an ecosystem approach to managing fisheries and all CCAMLR toothfish assessments are highly precautionary. Within CASAL, the historic stock dynamics are projected 35 years into the future under a variety of plausible scenarios. A constant catch projection allows the calculation of a long-term yield that satisfies the CCAMLR decision rules. The yield is chosen such that the probability of spawning stock biomass (SSB) dropping below 20% of its median pre-exploitation level during the 35-year projection is not greater than 10% and that the median escapement in the SSB at the end of the projection is not less than 50%.

Age-structured production models (ASPMs) have been used for the assessment of a number of marine resources, including for Patagonian toothfish stocks. Its first application to toothfish was by Gasiukov and Dorovskikh (2000). ASPMs have an advantage over biomass-based (aggregated) production models because they allow for a delay in the reduction of spawning stock biomass (SSB) and thus year class strength as a result of fishing (Brandao *et al.*, 2002). Brandao *et al.* (2002) used a simple ASPM for the assessment of the toothfish resource within the Prince Edward Islands EEZ, which provided a robust indication that the SSB had been depleted to a few percent of its original level, and their projections suggested that the annual TAC should be reduced to 400 tonnes.

Payne *et al.* (2005) used an ASPM based on Brandao *et al.*'s (2002) work to assess the Patagonian toothfish population in the Falkland Islands. They used two models, one with a Beverton-Holt stock recruitment relationship and another using trawler CPUE to estimate yearly recruitment. The models were fitted to standardised longliner CPUE and catch-at-length data. The two models produced estimates showing similar declines in biomass as the fishery progressed, but the initial and final biomasses varied slightly between models. The models provided estimates of the current biomass at between 38% and 46% of its pre-exploitation level and maximum sustainable yields (MSY) of between 912 and 3000 tonnes. There was a poor fit to CPUE between 1994 and 1996 which Payne *et al.* (2005) attributed to IUU catches or changes in catchability and/or mortality. During this time (mid 90s), there was considerable IUU activity in the SW Atlantic, and when their model was adjusted to allow an estimated level of extra catch, the fit improved and 5000 tonnes of extra catch was estimated. The ASPM was adapted further by Paya and Brickle (2008) to include updated von Bertalanffy and natural mortality parameters. Further developments in the Paya and Brickle (2008) model included a model to allow both longline and trotline (with cachalotera) CPUE series to be used.

13. CONCLUDING REMARKS

The initial rapid development of Patagonian toothfish fisheries in the Southern Oceans took place without the requisite knowledge of the biology of the target species or any assessment of the ecosystem impacts of the fisheries. Sustainable management of these fisheries has also been hampered by their remote locations, which have limited both research opportunities and surveillance. Consequently in many areas stocks were rapidly depleted and large numbers of seabirds killed. Knowledge of the biology and ecology of toothfish has expanded considerably in the last decade, with significant advances in stock discrimination; assessments of population size through tagging; growth rates and in trophic ecology. Significant gaps still remain in our knowledge of toothfish. There is still uncertainty about the distribution of Patagonian toothfish, with many parts of the Southern Ocean remaining unexplored. Whilst genetic and other studies have revealed segregation of stocks there are still important questions about linkages between populations in proximate locations. The larval phase of toothfish is poorly known, and whilst links between recruitment and oceanography have been identified the functional relationship is not established. A better knowledge of the larval phase will be key to understanding the potential consequences of climate change, since change is more likely to be manifested in surface temperatures and currents than in the deeper water occupied by adults.

Fisheries have adapted rapidly and methodology radically changed to limit the negative effects on the ecosystem, but further changes are likely to counter the depredation problem. Finally, stock assessments will continue to be refined by increased knowledge of population parameters and improved estimates of stock size from methods such as tagging. Continued vigilant management and surveillance is essential for the long-term sustainability of the valuable Patagonian toothfish fisheries.

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REFERENCES

- Abe, T., and Iwami, T. (1989). Notes on fishes from the stomachs of whales taken in the Antarctic II. On *Dissostichus* and *Ceratius*, with an appendix (Japanese names of important Antarctic fishes). *Proc. NIPR Symp. Polar Biol.* **2**, 78–82.
- Abellan, L. J. L. (2005). Patagonian toothfish in international waters of the southwest Indian Ocean (Statistical Area 51). *CCAMLR Sci.* **12**, 207–214.
- Adams, N. J., and Klages, N. T. (1989). Temporal variation in the diet of the gentoo penguin *Pygoscelis papua* at Sub-Antarctic Marion Island. *Colonial Waterbirds* **12**, 30–36.
- Agnew, D. J. (2000). The illegal and unregulated fishery for toothfish in the Southern Ocean, and the CCAMLR catch documentation scheme. *Marine Policy* **24**, 361–374.
- Agnew, D. J. (2004). *Fishing South: History and Management of South Georgia Fisheries*. The Penna Press, St Albans, 128pp.
- Agnew, D. A., and Kirkwood, G. P. (2005). A statistical method for estimating the level of IUU fishing: Application to CCAMLR sub-area 48.3. *CCAMLR Sci.* **12**, 119–141.
- Agnew, D., Heaps, L., Jones, C., Watson, A., Berkiet, K., and Pearce, J. (1999). Depth distribution and spawning pattern of *Dissostichus eleginoides* at South Georgia. *CCAMLR Sci.* **6**, 19–36.
- Agnew, D. J., Black, A. D., Croxall, J. P., and Parkes, G. B. (2000). Experimental evaluation of the effectiveness of weighting regimes in reducing seabird by-catch in the longline toothfish fishery around South Georgia. *CCAMLR Sci.* **7**, 119–131.
- Agnew, D. J., Daw, T. M., Pilling, G. M., and Purves, M. G. (2001). Fishing for toothfish using pots: Results of trials undertaken around South Georgia, March–May 2000. *CCAMLR Sci.* **8**, 93–105.
- Agnew, D. J., Clark, J. M., McCarthy, P. A., Unwin, M., Ward, M., Jones, L., Breedt, G., Du Plessis, S., Van Heerden, J., and Moreno, G. (2006a). A study of Patagonian toothfish (*Dissostichus eleginoides*) post tagging survivorship in Subarea 48.3. *CCAMLR Sci.* **13**, 279–289.
- Agnew, D. J., Kirkwood, G. P., Pearce, J., and Clark, J. (2006b). Investigation of bias in the mark-recapture estimate of toothfish population size at South Georgia. *CCAMLR Sci.* **13**, 47–63.

- Agnew, D. A., Hillary, R. M., and Pearce, J. (2007). Preliminary stock assessment of the South Georgia toothfish stock. CCAMLR WG-FSA 07/29.
- Aguayo, M., and Cid, L. (1991). Recopilación, proceso y análisis de los antecedentes biológico-pesqueros en la pesca exploratoria de bacalao de profundidad realizada por el B/P /Friosur V/. Instituto Fomento Pesquero, Chile. Informe Interno, 63 pp.
- Aguayo, M. (1992). Preliminary analysis of the growth of *Dissostichus eleginoides* from the austral zone of Chile and South Georgia. CCAMLR WG-FSA 92/30.
- Ainley, D., and Siniff, D. B. (2009). The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. *Antarct. Sci.* **21**, 317–327.
- Andrews, A. H., Brooks, C. M., Ashford, J. R., Krusic-Golub, K., Duhamel, G., Belchier, M., Lundstrom, C., and Cailliet, G. M. (2010). Lead-radium dating of Patagonian toothfish (*Dissostichus eleginoides*) reveals spatial variation in ageing bias on the Kerguelen Plateau. *Mar. Freshw. Res.* (in press).
- Appleyard, S. A., Ward, R. D., and Williams, R. (2002). Population structure of the Patagonian toothfish around Heard, McDonald and Macquarie Islands. *Antarct. Sci.* **14**, 364–373.
- Appleyard, S. A., Williams, R., and Ward, R. D. (2004). Population genetic structure of Patagonian toothfish in the West Indian Ocean sector of the Southern Ocean. *CCAMLR Sci.* **11**, 21–32.
- Arana, P. (2009). Reproductive aspects of the Patagonian toothfish (*Dissostichus eleginoides*) off southern Chile. *Latin Am. J. Aqua. Res.* **37**, 381–394.
- Arana, P. M., and Vega, R. (1999). Exploratory fishing for *Dissostichus* spp in the Antarctic region (sub-Areas 48.1, 48.2 and 88.3). *CCAMLR Sci.* **6**, 1–17.
- Arkhipkin, A., Brickle, P., and Laptikhovsky, V. (2003). Variation in the diet of the Patagonian toothfish with size, depth and season around the Falkland Islands. *J. Fish Biol.* **63**, 428–441.
- Ashford, J., and Jones, C. (2007). Oxygen and carbon stable isotopes in otoliths record spatial isolation of Patagonian toothfish (*Dissostichus eleginoides*). *Geochim. Cosmochim. Acta* **71**, 87–94.
- Ashford, J. R., Croxall, J. P., Rubilar, P. S., and Moreno, C. A. (1994). Seabird interactions with long-lining operations for *Dissostichus eleginoides* at the South Sandwich Islands and South Georgia. *CCAMLR Sci.* **1**, 143–153.
- Ashford, J. R., Croxall, J. P., Rubilar, P. S., and Moreno, C. A. (1995). Seabird interactions with longlining operations for *Dissostichus eleginoides* around South Georgia, April to May 1994. *CCAMLR Sci.* **2**, 111–121.
- Ashford, J. R., Rubilar, P. S., and Martin, A. R. (1996). Interactions between cetaceans and longline fishery operations around South Georgia. *Mar. Mamm. Sci.* **12**, 452–457.
- Ashford, J. R., Wischniowski, S., Jones, C., Bobko, S., and Everson, I. (2001). A comparison between otoliths and scales for use in estimating the age of *Dissostichus eleginoides* from South Georgia. *CCAMLR Sci.* **8**, 75–92.
- Ashford, J., Jones, C., Bobko, S., and Everson, I. (2002). Length-at-age in juvenile Patagonian toothfish (*Dissostichus eleginoides*). *CCAMLR Sci.* **9**, 1–10.
- Ashford, J., Duhamel, G., Jones, C., and Bobko, S. (2005a). Age, growth and mortality of Patagonian toothfish (*Dissostichus eleginoides*) caught off Kerguelen. *CCAMLR Sci.* **12**, 29–41.
- Ashford, J. R., Jones, C. M., Hofmann, E., Everson, I., Moreno, C., Duhamel, G., and Williams, R. (2005b). Can otolith elemental signatures record the capture site of Patagonian toothfish (*Dissostichus eleginoides*), a fully marine fish in the Southern Ocean? *Can. J. Fish. Aquat. Sci.* **62**, 2832–2840.
- Ashford, J. R., Arkhipkin, A. I., and Jones, C. M. (2006). Can the chemistry of otolith nuclei determine population structure of Patagonian toothfish *Dissostichus eleginoides*? *J. Fish Biol.* **69**, 708–721.

- Baird, R. J. (2006). Aspects of illegal, unreported and unregulated fishing in the Southern Ocean Springer, Netherlands.
- Balushkin, A. V. (2000). Morphology, classification, and evolution of notothenioid fishes of the Southern Ocean (Notothenioidei, Perciformes). *J. Ichthyol.* **40**, (Supplement), 74–109.
- Bargelloni, L., Marcato, S., and Patarnello, T. (1998). Antarctic fish hemoglobins: Evidence for adaptive evolution at subzero temperature. *Proc. Natl. Acad. Sci. USA* **95**, 8670–8675.
- Bargelloni, L., Marcato, S., Zane, L., and Patarnello, T. (2000). Mitochondrial phylogeny of notothenioids: A molecular approach to Antarctic fish evolution and biogeography. *Syst. Biol.* **49**, 114–129.
- Barrera-Oro, E. R., Casaux, R. J., and Marschoff, E. R. (2005). Dietary composition of juvenile *Dissostichus eleginoides* (Pisces, Nototheniidae) around Shag Rocks and South Georgia, Antarctica. *Polar Biol.* **28**, 637–641.
- Beamish, R. J., and McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112**, 735–743.
- Belchier, M. (2004). The age structure and growth rate of Patagonian toothfish (*Dissostichus eleginoides*) at South Georgia. CCAMLR WG-FSA 04/86.
- Belchier, M., and Collins, M. A. (2008). Recruitment and body size in relation to temperature in juvenile Patagonian toothfish (*Dissostichus eleginoides*) at South Georgia. *Mar. Biol.* **155**, 493–503.
- Belchier, M., and Agnew, D. A. (2009). Adding catch at age survey data to the 48.3 toothfish CASAL assessment. CCAMLR WG-SAM 09/13.
- Brandao, A., Butterworth, D. S., Watkins, B. P., and Miller, D. G. M. (2002). A first attempt at an assessment of the Patagonian toothfish (*Dissostichus eleginoides*) resource in the Prince Edward Islands EEZ. *CCAMLR Sci.* **9**, 11–32.
- Brickle, P. (2003). The parasite ecology of the Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898). Aberdeen University, (Ph.D. Thesis, 211 pp.).
- Brickle, P., MacKenzie, K., and Pike, A. (2005). Parasites of the Patagonian toothfish, *Dissostichus eleginoides* Smitt 1898, in different parts of the sub-Antarctic. *Polar Biol.* **28**, 663–671.
- Brickle, P., MacKenzie, K., and Pike, A. (2006). Variations in the parasite fauna of the Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898), with length, season, and depth of habitat around the Falkland Islands. *J. Parasitol.* **92**, 282–291.
- Brothers, N. (1991). Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biol. Conserv.* **55**, 255–268.
- Brown, C. R., and Klages, N. T. (1987). Seasonal and annual variation in diets of macaroni (*Eudyptes chrysolophus chrysolophus*) and southern rockhopper (*E. chrysocome chrysocome*) penguins at sub-Antarctic Marion Island. *J. Zool.* **212**, 7–28.
- Brown J., Brickle P., Hearne S., and French G. (2010). An experimental investigation of the ‘umbrella’ and ‘Spanish’ system of longline fishing for the Patagonian toothfish (*Dissostichus eleginoides*) in the Falkland Islands: Implications for stock assessment and seabird by-catch. *Fish. Res.* Doi:10.1016/j.fishres.2010.09.013.
- Bull, B., Francis, R. I. C. C., Dunn, A., McKenzie, A., Gilbert, D. J., and Smith, M. W. (2005). CASAL User Manual v2.07–2005/07/06 NIWA.
- Calhaem, I., and Christoffel, D. A. (1969). Some observations of the feeding habits of a Weddell seal, and measurements of its prey, *Dissostichus mawsoni*, at McMurdo Sound, Antarctica. *N. Z. J. Mar. Freshw. Res.* **3**, 181–190.
- Calliet, G. M., and Andrews, A. H. (2008). Age-validated longevity of fishes: Its importance for sustainable fisheries. In “Fisheries for Global Welfare and Environment” (K. Tsukamoto, T. Kawamura, T. Takeuchi, T. D. Beard and M. J. Kaiser, eds), 5th World Fisheries Congress 2008. pp. 103–120. Terrapub.

- Candy, S. G., and Constable, A. (2008). An integrated stock assessment for the Patagonian toothfish (*Dissostichus eleginoides*) for the Heard and Macdonald Islands using CASAL. *CCAMLR Sci.* **15**, 1–34.
- Candy, S. G., Constable, A. J., Lamb, T., and Williams, R. (2007). A von Bertalanffy growth model for toothfish at Heard Island fitted to length-at-age data and compared to observed growth from mark-recapture studies. *CCAMLR Sci.* **14**, 43–66.
- Cassia, M. C. (1998). Comparison of age readings from scales and otoliths of the Patagonian toothfish (*Dissostichus eleginoides*) from South Georgia. *CCAMLR Sci.* **5**, 191–203.
- Catard, A., Weimerskirch, H., and Cherel, Y. (2000). Exploitation of distant Antarctic waters and close shelf-break waters by white-chinned petrels rearing chicks. *Mar. Ecol. Prog. Ser.* **194**, 249–261.
- CCAMLR (1987). Scientific Committee Report, Hobart.
- CCAMLR (2009). Scientific Committee Report, Annex 5: Report of the Working Group on Fish Stock Assessment, Hobart, 133pp.
- Cherel, Y., Ridoux, V., and Rodhouse, P. G. (1996). Fish and squid in the diet of king penguin chicks, *Aptenodytes patagonicus*, during winter at sub-antarctic Crozet Islands. *Mar. Biol.* **126**, 559–570.
- Cherel, Y., and Duhamel, G. (2004). Antarctic jaws: cephalopod prey of sharks in Kerguelen waters. *Deep-Sea Res.* **151**, 17–31.
- Cherel, Y., Weimerskirch, H., and Trouve, C. (2000). Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Mar. Ecol. Prog. Ser.* **207**, 183–199.
- Cherel, Y., Weimerskirch, H., and Trouve, C. (2002). Dietary evidence for spatial foraging segregation in sympatric albatrosses (*Diomedea* spp.) rearing chicks at Iles Nuageuses, Kerguelen. *Mar. Biol.* **141**, 1117–1129.
- Chikov, V. N., and Mel'nikov, Y. S. (1990). On the question of fecundity of the Patagonian toothfish, *Dissostichus eleginoides*, in the region of the Kerguelen Islands. *Voprosy ikhtologii* **30**, 864–866.
- Ciechomski, J. D., and Weiss, G. (1976). Desarrollo y distribución de postlarvas del robalo *Eleginops maclovinus* (Valenciennes, 1830) Dollo 1904, de la merluza negra *Dissostichus eleginoides* Smitt 1898 y de la nototenia *Notothenia* spp. (Pisces, Nototheniidae). *Physis* **35**, 115–125.
- Clarke, M. R. (1980). Cephalopods in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discov. Rep.* **37**, 1–324.
- Coggan, R. A., Nolan, C. P., and George, M. J. A. (1996). Exploratory deep-sea fishing in the Falkland Islands, south-western Atlantic. *J. Fish Biol.* **49**, 298–310.
- Collins, M. A., and Rodhouse, P. G. (2006). Southern Ocean cephalopods. *Adv. Mar. Biol.* **50**, 191–265.
- Collins, M. A., Yau, C., Nolan, C. P., Bagley, P. M., and Priede, I. G. (1999). Behavioural observations on the scavenging fauna of the Patagonian slope. *J. Mar. Biol. Assoc. UK* **79**, 963–970.
- Collins, M. A., Bailey, D. M., Ruxton, G., and Priede, I. G. (2005). Trends in body size across an environmental gradient: A differential response in scavenging and non-scavenging demersal deep-sea fish. *Proc. R. Soc. Lond. B* **272**, 2051–2057.
- Collins, M. A., Everson, I., Paterson, R., Bagley, P. M., Yau, C., Belchier, M., and Hawkins, S. (2006). *In situ* observations of the scavenging fauna of the South Georgia slope. In "Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries Part 2: Conference poster papers and workshop papers" (R. Shotton, ed.), pp. 45–53. FAO, Rome.
- Collins, M. A., Ross, K. A., Belchier, M., and Reid, K. (2007). Distribution and diet of juvenile Patagonian toothfish on the South Georgia and Shag Rocks shelves (Southern Ocean). *Mar. Biol.* **152**, 135–147.

- Collins, M. A., Shreeve, R. S., Fielding, S., and Thurston, M. H. (2008). Distribution, growth, diet and foraging behaviour of the yellow-fin notothen *Patagonotothen guntheri* on the Shag Rocks shelf (Southern Ocean). *J. Fish Biol.* **72**, 271–286.
- Constable, A., and de la Mare, W. K. (1996). A generalised model for evaluating yield and the long term status of fish stocks under conditions of uncertainty. *CCAMLR Sci.* **3**, 54–60.
- Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I., and Miller, D. (2000). Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.* **57**, 778–791.
- de la Mare, W. K. (1994). Estimating confidence intervals for fish stock abundance estimates from trawl surveys. *CCAMLR Sci.* **1**, 203–207.
- De Witt, H. H. (1962). On the probable identity of *Macrias amissus*, a deep-water notothenioid fish from the Chilean coast. *Copeia* **3**, 659–687.
- De Witt, H. H., Heemstra, P. C., and Gon, O. (1990). Nototheniidae. In “Fishes of the Southern Ocean” (O. Gon and P. C. Heemstra, eds), pp. 279–331. J. L. B. Smith Institute of Ichthyology, Grahamstown.
- Delord, K., Gasco, N., Weimerskirch, H., Barbraud, C., and Micol, T. (2005). Seabird mortality in the Patagonian toothfish longline fishery around Crozet and Kerguelen Islands, 2001–2003. *CCAMLR Sci.* **12**, 53–80.
- Delord, K., Gasco, N., Barbraud, C., and Weimerskirch, H. (2010). Multivariate effects on seabird bycatch in the legal Patagonian toothfish longline fishery around Crozet and Kerguelen Islands. *Pol. Biol.* **33**, 367–378.
- Des Clers, S., Nolan, C. P., Baranowski, R., and Pompert, J. (1996). Preliminary stock assessment of the Patagonian toothfish longline fishery around the Falkland Islands. *J. Fish Biol.* **49**, 145–156.
- Duhamel, G. (1981). Caractéristiques biologiques des principales espèces de poissons du plateau continental des Iles Kerguelen. *Cybiurn* **5**, 19–32.
- Duhamel G. (1987). Ichthyofaune des secteurs indien occidental et atlantique oriental de l’océan austral: biogéographie, cycles biologiques et dynamique des populations. Ph. D. Thesis (Université P. et M. Curies, Paris), 687 pp.
- Duhamel, G. (1991). Biology and harvesting of *Dissostichus eleginoides* around Kerguelen Islands (Division 58.5.1). *CCAMLR WG-FSA* 91/7.
- Duhamel, G., and Pletkovic, M. (1983). Données biologiques sur les Nototheniidae des Iles Crozet. *Cybiurn* **7**, 43–57.
- Dunn A., Hanchet S.M. (2007). Assessment models for Antarctic toothfish (*Dissostichus mausoni*) in the Ross Sea including data from the 2006/07 season. *CCAMLR WG-FSA* 07/37.
- Dunn A., Gilbert D.J., Hanchet S.M., Bull B. (2004). Development of an Antarctic toothfish (*Dissostichus mausoni*) stock model for CCAMLR Subareas 88.1 for the years 1997/98 to 2003/04. *CCAMLR WG-FSA* 04/36.
- Eastman, J. T. (1988). Ocular morphology in Antarctic notothenioid fishes. *J. Morphol.* **196**, 283–306.
- Eastman, J. T. (1990). The biology and physiological ecology of notothenioid fishes. In “Fishes of the Southern Ocean” (O. Gon and P. C. Heemstra, eds), pp. 34–51. J.L.B. Smith Institute of Ichthyology, Grahamstown.
- Eastman, J. T., and Devries, A. L. (1981). Buoyancy adaptations in a swim-bladderless Antarctic fish. *J. Morphol.* **167**, 91–102.
- Eastman, J. T., and Devries, A. L. (1982). Buoyancy studies of Notothenioid fishes in Mcmurdo Sound, Antarctica. *Copeia* **6**, 385–393.
- Eastman, J. T., and McCune, A. R. (2000). Fishes on the Antarctic continental shelf: Evolution of a marine species flock? *J. Fish Biol.* **57**, 84–102.

- Eastman, J. T., and Eakin, R. R. (2000). An updated species list for notothenioid fish (Perciformes; Notothenioidei), with comments on Antarctic species. *Arch. Fish. Mar. Res.* **48**, 11–20.
- Eastman, J. T., and Sidell, B. D. (2002). Measurements of buoyancy for some Antarctic notothenioid fishes from the South Shetland Islands. *Polar Biol.* **25**, 753–760.
- Effremenko, V. N. (1979). The larvae of six species of the family Nototheniidae from the Scotia Sea. *J. Ichthyol.* **19**, 95–104.
- Efremenko, V. N. (1984). Larvae of the family Nototheniidae from the Scotia Sea. *J. Ichthyol.* **24**, 34–43.
- Esch, G. W., and Fernandez, J. C. (1993). A functional biology of parasitism: Ecological and evolutionary implications, p. 352. Chapman and Hall, London.
- Everson, I. (1977). Reproduction in *Notothenia neglecta* Nybelin. *Br. Antarct. Surv. Bull.* **23**, 81–92.
- Everson, I., and Murray, A. W. A. (1999). Size at sexual maturity of Patagonian toothfish. *CCAMLR Sci.* **6**, 37–46.
- Evsenko, S. A., Kock, K. H., and Nevinsky, M. M. (1995). Early life history of the Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898 in the Atlantic Sector of the Southern Ocean. *Antarct. Sci.* **7**, 221–226.
- Farrell, A. P., and Steffensen, J. F. (2005). *The Physiology of Polar Fishes*. Elsevier Academic Press, San Diego, 408 pp.
- Fenaughty, J. M., Eastman, J. T., and Sidell, B. D. (2008). Biological implications of low condition factor “axe handle” specimens of the Antarctic toothfish, *Dissostichus mawsoni*, from the Ross Sea. *Antarct. Sci.* **20**, 537–551.
- Gaevskaya, A. B., Kovaljova, A. A., and Paraukhin, A. M. (1990). Peculiarities and formation of parasitofauna of the Patagonian toothfish *Dissostichus eleginoides*. *Biologiya Morya (Mar. Biol.)* **4**, 23–28, (In Russian).
- García de la Rosa, S. B., Sanchez, F., and Figueroa, D. (1997). Comparative feeding ecology of Patagonian toothfish (*Dissostichus eleginoides*) in the South-western Atlantic. *CCAMLR Sci.* **4**, 105–124.
- Gasiukov P., Dorovskikh R. (2000). Results of *D. eleginoides* stock assessment for Subarea 48.3 using a dynamic age-structured production model. CCAMLR WG-FSA 00/46.
- Ghigliotti, L., Mazzei, F., Ozouf-Costaz, C., Bonillo, C., Williams, R., Cheng, C. H. C., and Pisano, E. (2007). The two giant sister species of the Southern Ocean, *Dissostichus eleginoides* and *Dissostichus mawsoni*, differ in karyotype and chromosomal pattern of ribosomal RNA genes. *Polar Biol.* **30**, 625–634.
- Gill, N. A., and Townsend, S. E. (1901). The largest deep-sea fish. *Science* **14**.
- Goldsworthy, S. D., He, X., Tuck, G. N., Lewis, M., and Williams, R. (2001). Trophic interactions between the Patagonian toothfish, its fishery, and seals and seabirds around Macquarie Island. *Mar. Ecol. Prog. Ser.* **218**, 283–302.
- Goldsworthy, S. D., Lewis, M., Williams, R., He, X., Young, J. W., and van den Hoff, J. (2002). Diet of Patagonian toothfish (*Dissostichus eleginoides*) around Macquarie Island, South Pacific Ocean. *Mar. Freshw. Res.* **53**, 49–57.
- Gon, O., and Heemstra, P. C. (1990). *Fishes of the Southern Ocean*. J.L.B. Smith Institute of Ichthyology, Grahamstown.
- Green, K., Burton, H. R., and Williams, R. (1989). The diet of Antarctic fur seals *Arctocephalus gazella* (Peters) during the breeding season at Heard Island. *Antarct. Sci.* **1**, 317–324.
- Guerrero, A., and Arana, P. (2009). Fishing yields and size structures of Patagonian toothfish (*Dissostichus eleginoides*) caught with pots and longlines off far southern Chile. *Latin Am. J. Aqua. Res.* **37**, 361–370.

- Guyann, K. D., and Peterson, M. S. (2008). Mercury concentrations in the Patagonian toothfish, *Dissostichus eleginoides* Smitt 1898, among three distinct stocks. *Pol. Biol.* **31**, 269–274.
- Hamilton, H. F. (1995). A preliminary parasite survey of the Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898) from the Falkland Islands with a view to differentiation of stocks in the Antarctic Aberdeen University, (M.Sc. Thesis).
- Hanchet, S. M., Stevensen, M. L., Phillips, N. L., and Horn, P. L. (2004). A characterisation of the toothfish fishery in sub-areas 88.1 and 88.2 from 1997/98 to 2003/04. CCAMLR WG-FSA **04/20**.
- Hillary, R. M., Kirkwood, G. P., and Agnew, D. J. (2006). An assessment of toothfish in Subarea 48.3 using CASAL. *CCAMLR Sci.* **13**, 65–95.
- Horn, P. L. (2002). Age and growth of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mausoni*) in waters from the New Zealand subantarctic to the Ross Sea, Antarctica. *Fish. Res.* **56**, 275–287.
- Hucke-Gaete, R., Moreno, C. A., and Arata, J. (2004). Operational interactions of sperm whales and killer whales with the Patagonian toothfish industrial fishery off southern Chile. *CCAMLR Sci.* **11**, 127–140.
- Hureau, J. C., and Ozouf-Costaz, C. (1980). Age determination and growth of *Dissostichus eleginoides* Smitt, 1898 from Kerguelen and Crozet. *Cybiium* **3**, 23–32.
- Jefferson, T. A., Stacey, P. J., and Baird, R. W. (1996). Acoustic methods of reducing or eliminating marine mammals-fisheries interactions: do they work? *Ocean Coast. Manag.* **31**, 41–70.
- Kalish J.M., and Timmiss T.A. (1998). Determination of Patagonian toothfish *Dissostichus eleginoides* age, growth and population characteristics based on otoliths. CCAMLR WG-FSA 98/40.
- Kellermann, A. (1989). Catalogue of early life stages of Antarctic notothenioid fish. In "Identification Key and Catalogue of Larval Antarctic Fishes" (A. Kellermann, ed.), BIOMASS Scientific Series. pp. 45–136.
- Kellermann, A. (1990). Catalogue of early life stages of Antarctic notothenioid fishes. *Berichte Polarforschung* **67**, 45–136.
- Kock, K. H. (1992). Antarctic fish and fisheries Cambridge University Press, 359 pp.
- Kock, K. H., and Kellermann, A. (1991). Reproduction in Antarctic notothenioid fish. *Antarct. Sci.* **3**, 125–150.
- Kock, K. H., Purves, M. G., and Duhamel, G. (2006). Interactions between cetacean and fisheries in the Southern Ocean. *Polar Biol.* **29**, 379–388.
- Kooyman, G. L., Cherel, Y., Le Maho, Y., Croxall, J. P., Thorson, P. H., Ridoux, V., and Kooyman, C. A. (1992). Diving behaviour and energetics during foraging cycles in king penguins. *Ecol. Monogr.* **62**, 143–163.
- Korabelnikov, L. V. (1959). The diet of sperm whales in the Antarctic seas. *Priroda* **3**, 103–104.
- Korovina, V. M., Neyelov, A. V., and Bondarenko, Y. P. (1991). The anatomy and histology of the intestine of the Patagonian toothfish (*Dissostichus eleginoides* Smitt). *Voprosy ikhtiologii* **44**, 218–224.
- Krusic-Golub K., and Williams R. (2004). Progress towards validation of ageing of *Dissostichus eleginoides* using otoliths. CCAMLR WG-FSA 04/67.
- Krusic-Golub K., and Williams R. (2005). Age validation of Patagonian toothfish (*Dissostichus eleginoides*) from Heard and Macquarie islands. CCAMLR WG-FSA 05/60.
- Krusic-Golub K., Green C., and Williams R. (2005). First increment validation of Patagonian toothfish (*Dissostichus eleginoides*) from Heard Island. CCAMLR WG-FSA 05/61.
- Lack, M. (2008). Continuing CCAMLR's Fight against IUU Fishing for Toothfish. WWF Australia and TRAFFIC International, Sydney, 50 pp.
- Lack, M., and Sant, G. (2001). Patagonian toothfish: Are conservation and trade measures working? *TRAFFIC Bull.* **19**, 15–32.

- Lake, S., Burton, H., and van den Hoff, J. (2003). Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. *Mar. Ecol. Prog. Ser.* **254**, 293–305.
- Laptikhovsky, V., and Brickle, P. (2005). The Patagonian toothfish fishery in Falkland islands' waters. *Fish. Res.* **74**, 11–23.
- Laptikhovsky, V., Arkhipkin, A., and Brickle, P. (2006). Distribution and reproduction of the Patagonian toothfish *Dissostichus eleginoides* Smitt around the Falkland Islands. *J. Fish Biol.* **68**, 849–861.
- Lescroel, A., Ridoux, V., and Bost, C. A. (2004). Spatial and temporal variation in the diet of gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands. *Polar Biol.* **27**, 206–216.
- Lord, C., Duhamel, G., and Pruvost, P. (2006). The patagonian toothfish (*Dissostichus eleginoides*) fishery in the Kerguelen Islands (Indian Ocean sector of the Southern Ocean). *CCAMLR Sci.* **13**, 1–25.
- Macdonald, P. D. M., and Pitcher, T. J. (1979). Age groups from size frequency data: A versatile and efficient method of analyzing distribution mixtures. *J. Fish. Res. Board Can.* **36**, 987–1001.
- Marlow, T. R., Agnew, D. J., Purves, M. G., and Everson, I. (2003). Movement and growth of tagged *Dissostichus eleginoides* around South Georgia and Shag Rocks (Subarea 48.3). *CCAMLR Sci.* **10**, 101–111.
- Martin-Smith, K. (2009). A risk-management framework for avoiding significant adverse impacts of bottom fishing gear on Vulnerable Marine Ecosystems. *CCAMLR Sci.* **16**, 177–193.
- Mendez, E., Giudice, H., Pereira, A., Inocente, G., and Medina, D. (2001). Preliminary report on the total mercury content of Patagonian toothfish (*Dissostichus eleginoides*). *J. Food Comp. Anal.* **14**, 547–549.
- McArthur, T., Butler, E. C. V., and Jackson, G. D. (2003). Mercury in the marine food chain in the Southern Ocean at Macquarie Island: an analysis of a top predator, Patagonian toothfish (*Dissostichus eleginoides*) and a mid-trophic species, the warty squid (*Moroteuthis ingens*). *Pol. Biol.* **27**, 1–5.
- McFarlane, G. A., and Beamish, R. J. (1990). Effect of an external tag on growth of sablefish (*Anoplopoma fimbria*), and consequences to mortality and age at maturity. *Can. J. Fish. Aqua. Sci.* **47**, 1551–1557.
- McKenna, J. E. (1991). Trophic relationships within the Antarctic demersal fish community of South Georgia Island. *Fish. Bull.* **89**, 643–654.
- McKinlay, J. P., Welsford, D. C., Constable, A. J., and Nowara, G. B. (2008). An assessment of the exploratory fishery for *Dissostichus* spp. on Banzare Bank (CCAMLR Division 58.4.3b) based on fine-scale catch and effort data. *CCAMLR Sci.* **15**, 55–78.
- McMahon, C. R., Holley, D., and Robinson, S. (1999). The diet of itinerant male Hooker's sea lions, *Phocartos hookeri*, at sub-Antarctic Macquarie Island. *Wildl. Res.* **26**, 839–846.
- Moller, P. R., Nielsen, J. G., and Fossen, I. (2003). Patagonian toothfish found off Greenland – This catch is evidence of transequatorial migration by a cold-water Antarctic fish. *Nature* **421**, 599.
- Moreno, C. (1991). Hook selectivity in the longline fishery of *Dissostichus eleginoides* (Notothentidae) off the Chilean coast. *CCAMLR Sel. Sci. Pap.* **8**, 107–119.
- Moreno C. (1998). Do the males of *Dissostichus eleginoides* grow faster, or only mature before females? CCAMLR WG-FSA 98/17.
- Moreno, C., Rubilar, P. S., Marschoff, E. R., and Benzaquen, L. (1996). Factors affecting the incidental mortality of seabirds in the *Dissostichus eleginoides* fishery in the southwest Atlantic (Subarea 48.3, 1995 season). *CCAMLR Sci.* **3**, 79–91.
- Moreno, C. A., Rubilar, P. S., and Zuleta, A. (1997). Ficha técnica del bacalao de profundidad *Dissostichus eleginoides* Smitt, 1898. CCAMLR WG-FSA 97/42.

- Moreno, C., Arata, J., Rubilar, P. S., Hucke-Gaete, R., and Robertson, G. (2006). Artisanal longline fisheries in southern Chile: Lessons to be learned to avoid incidental seabird mortality. *Biol. Conserv.* **127**, 27–36.
- Moreno, C., Castro, R., Mujica, L. J., and Reyes, P. (2008). Significant conservation benefits obtained from the use of a new fishing gear in the Chilean Patagonian toothfish fishery. *CCAMLR Sci.* **15**, 78–79.
- Morton, A. B., and Symonds, H. K. (2002). Displacement of *Orcinus orca* (L) by high amplitude sound in British Columbia, Canada. *ICES J. Mar. Sci.* **59**, 71–80.
- Murillo, C., Oyarzun, C., and Fernandez, I. (2008). Latitudinal and temporal variation in the diet of *Dissostichus eleginoides* Smitt, 1898 (Perciformes: Nototheniidae) in deep environments of the south and center coast of Chile. *Gayana* **72**, 94–101.
- Near, T. J., and Cheng, C. H. C. (2008). Phylogenetics of notothenioid fishes (Teleostei: Acanthomorpha): Inferences from mitochondrial and nuclear gene sequences. *Mol. Phylogenet. Evol.* **47**, 832–840.
- Near, T. J., Russo, S. E., Jones, C. D., and Devries, A. L. (2003). Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (Perciformes: Nototheniidae). *Polar Biol.* **26**, 124–128.
- Near, T. J., Pesavento, J. J., and Cheng, C. H. C. (2004). Phylogenetic investigations of Antarctic notothenioid fishes (Perciformes: Notothenioidae) using complete gene sequences of the mitochondrial encoded 16S rRNA. *Mol. Phylogenet. Evol.* **32**, 881–891.
- Nel, D. C., Ryan, P. G., and Watkins, B. P. (2002). Seabird mortality in the Patagonian toothfish longline fishery around the Prince Edward Islands, 1996–2000. *Antarct. Sci.* **14**, 151–161.
- Nevinsky, M. M., and Kozlov, A. N. (2002). The fecundity of the Patagonian toothfish *Dissostichus eleginoides* around South Georgia Island (South Atlantic). *J. Ichthyol.* **42**, 571–573.
- Nolan, C. P., Liddle, G. M., and Elliot, J. (2000). Interactions between killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) with a longline fishing vessel. *Mar. Mamm. Sci.* **16**, 658–664.
- North, A. W. (1998). Growth of young fish during winter and summer at South Georgia, Antarctica. *Polar Biol.* **19**, 198–205.
- Norman, J. R. (1937). Coast Fishes Part II. The Patagonian region. *Discov. Rep.* **16**, 1–150.
- North, A. W. (2002). Larval and juvenile distribution and growth of Patagonian toothfish around South Georgia. *Antarct. Sci.* **14**, 25–31.
- North, A. W., and White, M. G. (1982). Key to postlarvae from the Scotia Sea, Antarctica. *Cybius* **6**, 13–32.
- Nyegaard, M., Arkhipkin, A., and Brickle, P. (2004). Variation in the diet of *Genypterus blacodes* (Ophidiidae) around the Falkland Islands. *J. Fish Biol.* **65**, 666–682.
- Oliva, M. E., Fernandez, I., Oyarzun, C., and Murillo, C. (2008). Metazoan parasites of the stomach of *Dissostichus eleginoides* Smitt 1898 (Pisces: Notothenidae) from southern Chile: A tool for stock discrimination? *Fish. Res.* **91**, 119–122.
- Olsson, O., and North, A. W. (1997). Diet of the king penguin *Aptenodytes patagonicus* during three summers at South Georgia. *Ibis* **139**, 504–512.
- Otley, H., Reid, T. A., and Pompert, J. (2007). Trends in seabird and Patagonian toothfish *Dissostichus eleginoides* longliner interactions in Falkland Island waters, 2002/03 and 2003/04. *Mar. Ornithol.* **35**, 47–55.
- Oyarzun, C., and Campos, P. W. (1987). *Dissostichus eleginoides* Smitt, 1898; consideraciones sobre su determinación taxonómica e implicancias biogeográficas (Pisces, Perciformes, Nototheniidae). *Rev. Biol. Mar. Valparaíso* **23**, 173–192.
- Oyarzun, C., Campos, P. W., and Valeria, H. R. (1988). Adaptaciones para la flotabilidad en *Dissostichus eleginoides* Smitt, 1898 (Pisces, Perciformes, Nototheniidae). *Investigaciones Pesqueras* **52**, 455–466.

- Oyarzún, C., Gacitúa, S., Araya, M., Cubillos, L., Salamanca, M., Pino, C., Galleguillos, R., Aedo, G., and Lamilla, J. (2003). Asignación de edades y crecimiento de bacalao de profundidad. *Informe Final, Proyecto FIP 2001-17* 130.
- Parkes, G., Moreno, C. A., Pilling, G., and Young, Z. (1996). Use of the Leslie stock depletion model for the assessment of local abundance of Patagonian toothfish (*Dissostichus eleginoides*). *CCAMLR Sci.* **3**, 55–77.
- Parukhin, A. M., and Lyadov, V. N. (1982). Helminth fauna of food Nototheniidae fishes from Kerguelen region. *Ekologiya Morya, Kiev* **10**, 49–57 (in russian).
- Paya, I., and Brickle, P. (2008). Stock Assessment and Total Allowable Catch of Toothfish (*Dissostichus eleginoides*). Falkland Islands Government Fisheries Department Scientific Report.
- Payne, A. G., Agnew, D. J., and Brandao, A. (2005). Preliminary assessment of the Falklands Patagonian toothfish (*Dissostichus eleginoides*) population: Use of recruitment indices and the estimation of unreported catches. *Fish. Res.* **76**, 344–358.
- Phillips K.L., Rodgers M., and Ansell E. (2009). Macquarie Island toothfish fishery. In “Fishery status reports 2007: status of fish stocks managed by the Australian Government” (D. T. Wilson, R. Curtotti, G. A. Begg, and K. L. Phillips, eds), pp. 359–365. Bureau of Rural Sciences, Canberra.
- Phillips, R. A., Ridley, C., Reid, K., Pugh, P. J. A., Tuck, G. N., and Harrison, N. (2010). Ingestion of fishing gear and entanglements of seabirds: Monitoring and implications for management. *Biol. Cons.* **143**, 501–512.
- Pilling, G. M., Purves, M. G., Daw, T. M., Agnew, D. A., and Xavier, J. C. (2001). The stomach contents of Patagonian toothfish around South Georgia (South Atlantic). *J. Fish Biol.* **59**, 1370–1384.
- Plotz, J. (1986). Summer diet of Weddell seals (*Leptonychotes weddelli*) in the eastern and southern Weddell Sea, Antarctica. *Polar Biol.* **6**, 97–102.
- Prenski, L. B., and Almeyda, S. M. (2000). Some biological aspects relevant to patagonian toothfish (*Dissostichus eleginoides*) exploitation in the argentine exclusive economic zone and adjacent ocean sector. *Frente Marítimo* **18**, 103–124.
- Priede, I. G., and Bagley, P. M. (2000). *In situ* studies on deep-sea demersal fishes using autonomous unmanned lander platforms. *Oceanog. Mar. Biol. Ann. Rev.* **38**, 357–392.
- Priede, I. G., and Merrett, N. R. (1996). Estimation of abundance of abyssal demersal fishes; a comparison of data from trawls and baited cameras. *J. Fish Biol.* **49**, 207–216.
- Purves, M. G., Agnew, D. J., Balguerías, E., Moreno, C. A., and Watkins, B. (2004). Killer whale (*Orcinus orca*) and sperm whale (*Physeter macrocephalus*) interactions with longline vessels in the Patagonian toothfish fishery at South Georgia, South Atlantic. *CCAMLR Sci.* **11**, 111–126.
- Putz, K., Ingham, R. J., Smith, J. G., and Croxall, J. P. (2001). Population trends, breeding success and diet composition of gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rockhopper *Eudyptes chrysocome* penguins in the Falkland Islands. *Polar Biol.* **24**, 793–807.
- Reid, K. (1995). The diet of Antarctic fur seals (*Arctocephalus gazella* Peters 1875) during winter at South Georgia. *Antarctic Sci.* **7**, 241–249.
- Reid, K., and Arnould, J. P. Y. (1996). The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol.* **16**, 105–114.
- Reid, K., and Nevitt, G. A. (1998). Observation of southern elephant seal, *Mirounga leonina*, feeding at sea near South Georgia. *Mar. Mamm. Sci.* **14**, 637–640.
- Reid, T. A., Sullivan, B. J., Pompert, J., Enticott, J. W., and Black, A. D. (2004). Seabird mortality associated with Patagonian Toothfish (*Dissostichus eleginoides*) longliners in Falkland Islands waters. *Emu* **104**, 317–325.
- Reilly, A., and Ward, R. D. (1999). Microsatellite loci to determine population structure of the Patagonian toothfish *Dissostichus eleginoides*. *Mol. Ecol.* **8**, 1753–1754.

- Rideout, R. M., Rose, G. A., and Burton, M. P. M. (2005). Skipped spawning in female iteroparous fishes. *Fish Fish.* **6**, 50–72.
- Roberts, J., and Agnew, D. A. (2008). Proposal for an extension to the mark recapture experiment to estimate toothfish population size in Subarea 48.4. *CCAMLR WG-FSA* 08/46.
- Robertson, G. (2000). Effect of line sink rate on albatross mortality in the Patagonian toothfish longline fishery. *CCAMLR Sci.* **7**, 133–150.
- Robertson, G., Moreno, C. A., Crujeiras, J., Wienecke, B., Gandini, P., McPherson, G., and Pon, J. P. S. (2007). An experimental assessment of factors affecting the sink rates of Spanish-rig longlines to minimize impacts on seabirds. *Aqua. Conserv. Mar. Freshw. Ecosyst.* **17**, S102–S121.
- Robinson, S. A., and Hindell, M. A. (1996). Foraging ecology of gentoo penguins *Pygoscelis papua* at Macquarie Island during the period of chick care. *Ibis* **138**, 722–731.
- Roche, C., Guinet, C., Gasco, N., and Duhamel, G. (2007). Marine mammals and demersal longline fishery interactions in Crozet and Kerguelen exclusive economic zones: An assessment of depredation levels. *CCAMLR Sci.* **14**, 67–82.
- Rodriguez, L., and George-Nascimento, M. (1996). The Metazoan parasite fauna of the Patagonian toothfish *Dissostichus eleginoides* Smitt, 1898 (Pisces: Nototheniidae) of central Chile: Taxonomic, ecological and zoogeographic aspects. *Rev. Chil. Hist. Natl.* **69**, 21–33.
- Rogers, A. D., Morley, S., Fitzcharles, E., Jarvis, K., and Belchier, M. (2006). Genetic structure of Patagonian toothfish (*Dissostichus eleginoides*) populations on the Patagonian Shelf and Atlantic and western Indian Ocean Sectors of the Southern Ocean. *Mar. Biol.* **149**, 915–924.
- Sanchez, S., Dettai, A., Bonillo, C., OzoufCostaz, C., Detrich, H. W., and Lecointre, G. (2007). Molecular and morphological phylogenies of the Antarctic teleostean family Nototheniidae, with emphasis on the Trematominae. *Polar Biol.* **30**, 155–166.
- Shandikov, G. A., and Faleeva, T. I. (1992). Features of gametogenesis and sexual cycles of six notothenioid fishes from East Antarctica. *Polar Biol.* **11**, 615–621.
- Shaw, P. W., Arkhipkin, A. I., and 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. *Mol. Ecol.* **13**, 3293–3303.
- Sharp, B. R., Parker, S. J., and Smith, N. (2009). An impact assessment framework for bottom fishing methods in the CCAMLR convention area. *CCAMLR Sci.* **16**, 195–210.
- Slip, D. J. (1995). The diet of southern elephant seals (*Mirounga leonina*) from Heard-Island. *Can. J. Zool.* **73**, 1519–1528.
- Slip, D. J., Hindell, M. A., and Burton, H. R. (1994). Diving behaviour of southern elephant seals from Macquarie Island: An overview. In “Elephant seals: Population Ecology, Behaviour and Physiology” (B. G. Le Boeuf and R. M. Laws, eds), pp. 253–270. University of California Press, Berkeley.
- Smith, P., and McVeagh, M. (2000). Allozyme and microsatellite DNA markers of toothfish population structure in the Southern Ocean. *J. Fish Biol.* **57**, 72–83.
- Smitt FA (1898). Poissons de l'expédition scientifique a la terra de feu. Bihang till Kongl Svenska Vetenskaps-Akademiens Handlingar Brand 24 IV, 1–80.
- Stevenson, M. L., Hanchet, S. M., and Dunn, A. (2008). A characterisation of the toothfish fishery in Subareas 88.1 and 88.2 from 1997/98 to 2007/08. *CCAMLR WG-FSA* 08/22.
- Tarverdiyeva, M. I. (1972). Daily food consumption and feeding patterns of the South Georgia cod (*Notothenia rossii marmorata*) and the Patagonian toothfish (*Dissostichus eleginoides*) (Fam. Nototheniidae) in the South Georgia area. *J. Ichthyol.* **12**, 684.
- Testa, J. W., Siniff, D. B., Ross, M. J., and Winter, J. D. (1985). Weddell seal-Antarctic cod interactions in McMurdo Sound, Antarctica. In “Antarctic Nutrient Cycles and Food

- Webs" (W. R. Siegfried, P. R. Condy and R. M. Laws, eds), pp. 561–565. Springer-Verlag, Berlin.
- Tuck, G. N., de la Mare, W. K., Hearn, W. S., Williams, R., Smith, A. D. M., He, X., and Constable, A. (2003). An exact time of release and recapture stock assessment model with an application to Macquarie Island Patagonian toothfish (*Dissostichus eleginoides*). *Fish. Res.* **63**, 179–191.
- Visser, I. N. (2000). Killer whale (*Orcinus orca*) interactions with longline fisheries in New Zealand waters. *Aqua. Mamm.* **26**, 241–252.
- Watkins, W. A., Daher, M. A., Frstrup, K. M., Howald, T. J., and Disciara, G. N. (1993). Sperm whales tagged with transponders and tracked underwater by sonar. *Mar. Mamm. Sci.* **9**, 55–67.
- White, M. G., North, A. W., Twelves, E. L., and Jones, S. (1982). Early development of *Notothenia neglecta* from the Scotia Sea, Antarctica. *Cybiurn* **6**, 43–51.
- Wienecke, B., and Robertson, G. (2004). Validation of sink rates of longlines measured using two different methods. *CCAMLR Sci.* **11**, 179–187.
- Williams, R., and Capdeville, D. (1996). Seabird interactions with trawl and longline fisheries for *Dissostichus eleginoides* and *Champscephalus gunnari*. *CCAMLR Sci.* **3**, 93–99.
- Williams, R., and de la Mare, W. K. (1995). Fish distribution and biomass in the Heard Island zone (Division 58.5.2). *CCAMLR Sci.* **2**, 1–20.
- Williams R., Lamb T. (2002). Behaviour of *Dissostichus eleginoides* fitted with archival tags at Heard Island: preliminary results. *CCAMLR WG-FSA 02/60*.
- Williams, R., Tuck, G. N., Constable, A. J., and Lamb, T. (2002). Movement, growth and available abundance to the fishery of *Dissostichus eleginoides* Smitt, 1898 at Heard Island, derived from tagging experiments. *CCAMLR Sci.* **9**, 33–48.
- Xavier, J. C., Rodhouse, P. G., Purves, M. G., Daw, T. M., Arata, J., and Pilling, G. M. (2002). Distribution of cephalopods recorded in the diet of the Patagonian toothfish (*Dissostichus eleginoides*) around South Georgia. *Polar Biol.* **25**, 323–330.
- Xavier, J. C., Croxall, J. P., Trathan, P. N., and Wood, A. G. (2003). Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Mar. Biol.* **143**, 221–232.
- Yano, K., and Dahlheim, M. E. (1995). Killer whale, *Orcinus orca*, depredation on longline catches of bottom fish in the southeastern Bering Sea and adjacent waters. *Fish. Bull.* **93**, 355–372.
- Yau, C., Collins, M. A., Bagley, P. M., Everson, I., Nolan, C. P., and Priede, I. G. (2001). Estimating the abundance of Patagonian toothfish *Dissostichus eleginoides* using baited cameras: a preliminary study. *Fish. Res.* **51**, 403–412.
- Yau, C., Collins, M. A., Bagley, P. M., Everson, I., and Priede, I. G. (2002). Scavenging by megabenthos and demersal fish on the South Georgia slope. *Antarct. Sci.* **14**, 16–24.
- Young, Z., Gili, R., and Cid, L. (1995). Prospección de bacalao de profundidad entre las latitudes 43° y 47°S. *Informe Técnico IFOP*, 1–47.
- Young, Z., Oliva, J., Olivares, A., and Dias, E. (1999). Aspectos reproductivos del recurso bacalao de profundidad en la I a X Regiones. Informe Final Proyecto *FIP*, 97–16, 51pp.
- Young Z., Zuleta A., Robotham H., Aguayo M., and Cid L. (1992). Evaluación del stock de bacalao de profundidad entre las latitudes 47° y 57° S. Informe Técnico IFOP-SUB-PESCA, 1–63.
- Zakharov, G., and Frolkina, Z. (1976). Some data on the distribution and biology of Patagonian toothfish occurring in the southwest Atlantic. *Tr. Atlant NIRO* **65**, 143–150, (in Russian).
- Zhivov, V. V., and Krivoruchko, V. M. (1990). On the biology of the Patagonian toothfish, *Dissostichus eleginoides*, of the Antarctic part of the Atlantic. *J. Ichthyol.* **30**, 142–146.