DECADAL TRENDS IN ABUNDANCE, SIZE AND CONDITION OF ANTARCTIC TOOTHFISH IN MCMURDO SOUND, ANTARCTICA, 1972-2010

David G. Ainley[1], **Nadav Nur**[2], **Joseph T. Eastman**[3], **Grant Ballard**[2], **Claire L. Parkinson**[4], **Clive W. Evans**[5] and **Arthur L. DeVries**[6]

[1]H.T. Harvey & Associates, Los Gatos CA 95032

[2]PRBO Conservation Science, Petaluma CA 94954

[3]Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Athens, OH 45701

[4]Cryospheric Sciences Branch/Code 614.1, NASA Goddard Space Flight Center, Greenbelt, MD 20771

[5]School of Biological Sciences, University of Auckland, Auckland, NZ

[6]Department of Ecology, Ethology and Evolution, University of Illinois, Urbana, IL 61801

Abstract

We report analyses of a dataset spanning 38 years of near-annual fishing for Antarctic toothfish *Dissostichus mawsoni*, using a vertical setline through the fast ice of McMurdo Sound, Antarctica, 1972-2010. This constitutes one of the longest biological time series in the Southern Ocean, and certainly the longest for any fish. Fish total length, condition and catch per unit effort (CPUE) were derived from the >5500 fish caught. Contrary to expectation, length-frequency was dominated by fish in the upper half of the industrial catch. The discrepancy may be due to biases in the sampling capabilities of vertical (this study) versus benthic (horizontal) fishing gear (industry long lines), related to the fact that only large Antarctic toothfish (>100 cm TL) are neutrally buoyant and occur in the water column. Fish length and condition increased from the early 1970’s to the early 1990s and then decreased, related to sea ice cover, with lags of 8 months to 5 years, and may ultimately be related to the fishery (which targets large fish) and changes in the Southern Annular Mode through effects on toothfish’ main prey, Antarctic silverfish *Pleuragramma antarcticum*. CPUE was constant through 2001 and then decreased dramatically, likely related to the industrial fishery, which began in 1996 and which concentrates effort over the Ross Sea slope, where tagged McMurdo fish have been found. Due to limited prey choices and, therefore, close coupling among mesopredators of the Ross Sea, Antarctic toothfish included, the fishery may be altering the trophic structure of the Ross Sea.

Keywords Antarctic toothfish, Antarctic silverfish, climate change, change in fish condition, change in fish abundance, Ross Sea, Southern Annular Mode, Southern Ocean

Introduction

Unlike any other marine ecosystem in the world, the high latitude waters of the Southern Ocean contain a single lineage of teleost fishes that dominates fish diversity, abundance and biomass (Eastman 2005). Tectonic, oceanographic and climactic changes over the past few tens of millions of years eliminated previous fish faunas and provided an opportunity for this lineage of perciform notothenioids to radiate opportunistically and to fill most benthic and pelagic niches, despite the lack of a swim bladder. For example, the 2- meter-long Antarctic toothfish *Dissostichus mawsoni*, and the 15–25 cm-long forage species, Antarctic silverfish *Pleuragramma antarcticum*, are key piscine predator and prey in the ecosystem in spite of the incongruity of being closely related sister species/genera (Balushkin 2000). As adults Antarctic toothfish are an important component of the community of mesopredators (also including penguins, seals, and cetaceans) that inhabit the Ross Sea, Southern Ocean; and most of them, too, depend on silverfish (Ballard et al. 2011). To date, the Ross Sea is the least anthropogenically altered stretch of ocean remaining on Earth (Halpern *et al.* 2008) and, thus, the interactions of this group of mesopredators and their prey are of particular interest as a model for how cold-water, continental shelf food webs once operated elsewhere.

In this system, productivity is highest and trophic interactions most intense during summer. Most of the mesopredators are present over the Ross Sea (shelf and slope) only during summer, moving north with daylight and the pack ice during winter; a few —Antarctic toothfish, emperor penguin *Aptenodytes forsteri* and Weddell seal *Leptonychotes weddellii* — remain year round. All feed during summer primarily on three prey species over the shelf:

Antarctic silverfish and two species of krill: Antarctic krill *Euphausia superba* and crystal krill *E. crystallorophias* (Ballard *et al.* 2011, Smith *et al.* 2011). Over the southern shelf, the silverfish by its numbers and diet is thought to be the main predator of crystal krill and the toothfish to be the main predator of silverfish— as measured in McMurdo Sound, 71.2% by frequency of occurrence and 89.2 % by dry weight (Eastman 1985b, La Mesa *et al.* 2004), consistent with the generalization that fish are the most important predators in most marine ecosystems (Sheffer *et al.* 2005). Off the shelf, the diet of these mesopredators is much more diverse (Ainley *et al.* 1984, Fenaughty *et al.* 2003). Due to the reduced number of dietary items over the shelf, a tight trophic coupling has been observed among them, e.g. prey consumption of cetaceans negatively affects the foraging area and diet of penguins (Ainley *et al.* 2006), and the foraging of Weddell seals can negatively affect the prevalence of toothfish (Testa *et al.* 1985), although the consequences of this fish-seal interaction for local availability of silverfish remain unknown.

In this system, too, the apex predators are the Ross Sea killer whale *Orcinus [orca*]; thought to be a separate but yet-to-be-described species; Morin *et al.* 2010), which has been observed to feed substantially on toothfish (Ainley *et al.* 2009); and the larger killer whale "ecotype B" (*O. orca*), which feeds on seals and likely large penguins (Pitman and Ensor 2003, Ainley and Ballard 2011). Weddell seals also prey to a significant degree on toothfish (Ainley and Siniff 2009, and references therein; Kim et al. 2011), and along the Ross Sea shelf break and north, toothfish are fed upon by southern elephant seals *Mirounga leonina*, sperm whales *Physeter macrocephalus* and colossal squid *Mesonychoteuthis hamiltoni* (Yukhov 1970, Pinkerton *et al.* 2010, Ainley 2010, Smith *et al.* 2011).

To understand the trophodynamics of this system on the Ross Sea shelf requires detailed information on all of its predators and mesopredators. While much is known about the air-breathing members of the group, all of which have nowhere to hide from researchers, and indeed have been well researched in the Ross Sea since the mid-1900's, learning about toothfish life history and abundance has been a challenge. On the one hand, the morphology and physiology of Antarctic toothfish are among the best known of Southern Ocean species: it is one of just five neutrally buoyant nototheniids (Eastman and DeVries 1981), attaining this status at around 100 cm TL (Near *et al.* 2003), and ecologically dominates the Southern Ocean fish fauna in the sense that it is the major piscine predator (Eastman 1993). It has a suite of adaptations to allow presence at subzero temperatures including blood antifreeze (DeVries 1988, DeVries and Cheng 2005) and other adaptations (Eastman 1993); it grows rapidly when a subadult, then its growth rate slows, and it can live to 50 yrs. On the other hand, the ecology and population dynamics of Antarctic toothfish have remained obscure. From a fishery, the "legal" portion of which began in 1996-97 (hereafter we will identify austral summers by the initial year, 1996 in this case), we have learned about the geographic aspects of size-frequency distribution (Hanchet *et al.* 2008, 2010), confirmed growth rates (cf. DeVries and Eastman 1998, Horn 2002, Brooks *et al.* 2010) and gained insights into variation in condition (Fenaughty *et al.* 2008), age of recruitment (Parker and Grimes 2010) and diet of individuals in the deepest parts of the Ross Sea along its continental slope (Fenaughty *et al.* 2003). Otherwise, much remains to be learned about the Antarctic toothfish, unlike its only congener, the non-Antarctic Patagonian toothfish (*D. eleginoides*), about which much has been learned (Collins *et al.* 2010). Antarctic toothfish are thought to spawn during winter; no free eggs or larvae and rarely fish <50 cm have been collected in the Ross Sea region and the spawning frequency, fecundity and aspect of larval and juvenile life history are unknown. This information gap is the result of severe restrictions on scientific investigation resulting from this Antarctic species' "preferred habitat": deep, cold, sea ice covered ocean. Any data from the fishery are limited to just the 3-4 months of ice-free summer (Dec-March).

Toward learning more about this important Southern Ocean mesopredator, we present results of analysis on data collected from >5500 fish captured, measured, marked and released, during an extended effort led by A. DeVries almost annually in McMurdo Sound, southern Ross Sea, 1972-2010. The data set thus constitutes one of the longest biological time series available for the Southern Ocean, the only long one for a fish species, and one that persisted through a period that has seen interesting changes in the Ross Sea, in large part driven by climatic forces. The Southern Annular Mode midway in the period (i.e, about 1986) shifted to mostly positive leading to a marked increase in winds, sea ice extent and persistence of the coastal polynyas that strongly affect Ross Sea processes (Parkinson 2002, Zwally *et al.* 2002, Jacobs *et al.* 2002, Stammerjohn *et al.* 2008, Jacobs 2006, Russell *et al.* 2006). Several of the air breathing mesopredators are known to have responded through changes mediated by sea ice (Ainley *et al.* 2005). In addition, minke whales *Balaenoptera bonaerensis* were heavily hunted in the late 1970s-early 1980s, affecting penguin competitors, but since have recovered; Weddell seals in McMurdo Sound, too, were also severely hunted during that period but also appear to have mostly recovered (Ainley *et al.* 2007, Ainley 2010). In 1996, a toothfish fishery was inaugurated in the Ross Sea region, including to within ~60 km of McMurdo Sound (opposite side of Ross Island; FAO/CCAMLR Area 88), and this is now the largest fishery for toothfish south of the

Antarctic Polar Front (CCAMLR 2010). Therefore, in our analysis, given the close coupling observed among air breathing mesopredators, we hypothesized that we should see trends in toothfish condition, size and abundance that correlate with the above described environmental and anthropogenic changes. After examining trends over time, we explore the significance of environmental variables, especially those related to ice cover, to gain insight into the extent to which these factors could be explaining the observed temporal patterns in toothfish characteristics.

Methods

Fish capture

Scientific fishing occurred primarily from one site, about 4 km west of McMurdo Station, in the vicinity of 77^o 51’ S, 166^o 40’ E (Fig. 1); it was accessible from the Station by a ~10 min over-ice drive by tracked or wheeled vehicle. Note that most of the study period occurred before the age of GPS and the ability to precisely identify the location of the fish hut was limited. We know that the fishing site shifted slightly from year to year, e.g. to deal with pressure ridges, snow banks etc, and after 1999, to accommodate aircraft approach to the Sea Ice Runway. Both the runway and then the fish hut were repositioned anew each season, as noted. In 2000, the runway was shifted more than usual, this time northward, to be closer to and in view of McMurdo Station, forcing movement of the fishing site more west and south than usual. Nevertheless, all sites but one were within about a 2 km radius, with depth ranging 415 - 495 m. Moreover, all sites were within the area in which the survey by Testa *et al.* (1985) logged high catch rates of Antarctic toothfish and the area within which Weddell seals have been frequently seen with toothfish (Ainley and Siniff 2009), even to 2010. Beginning in 2008, the fishing was based out of Scott Base instead of McMurdo, requiring a longer drive by researchers.

Using a small hydro-winch with 3/32-inch wire and a 25 kg weight attached to the bottom end to keep the wire under tension (i.e., a vertical set line), a line was deployed through a hole drilled through the annual fast ice. A heated fish house was placed over the hole. Pulling the line, depending on number of fish caught, took 2-3 h. Initially 15-22 one-meter leaders with swiveled, stainless steel, long shank #10 hooks spaced 20-25 m apart were fished (thus sampling the lower ~300 m of water column, but not waters within 10-20 m of the bottom to avoid scavenging by benthic amphipods). Quickly it was found that most of the fish were caught in the lower half of the hook array. Thus leaders were shortened to 30 cm and hooks were spaced 3-5 m apart, starting 10 m from the bottom (thus the lower ~100m of water column was sampled but, again, not the bottom). For the first 3 years, live *Pagothenia borchgrevinki* were used for bait, but it was then found that dead bait worked just as well and so thereafter New Zealand yellow eyed mull*et Aldrichetta forsteri*, cut in half, was used. Sometimes the interval between deployments ran 12 h but the interval for the very large majority was 24 h sets. Some ran 48 h if poor weather prevented access to the fish house, but the fish caught were often exhausted after such prolonged time on hooks. Once this was realized, this long a soak time was avoided if possible. When the fishing became based out of Scott Base, this necessitated a much longer commute to the fish hut, and these sets often soaked for >45 h.

Captured fish not used for experiments were placed in a V-trough (with a seawater soaked cloth over their eyes), measured to the nearest cm; weighed to the nearest pound (converted to kg); tagged with a numbered “Floy” dart tag behind the 2nd ray of the 2nd dorsal fin and a tail locking tag; in many cases injected with tetracycline; and released. Tetracycline served as an otolith annuli marker in case the fish was recaptured. This procedure, lasting 3-5 min, was done on the floor of the heated fish hut so that the fish neither warmed nor froze. The open sea surface was 0.5 m below the level of the floor so that the fish could be gently lifted by their gill covers and returned to the water without abrading their skin and causing scale loss.

Small fish on the line for any length of time appeared to have been prone to attack by large fish, as those retrieved often had many parallel teeth marks on both sides of their body as well as many missing scales. This is consistent with reports of small toothfish found in the stomachs of larger ones taken in the industrial fishery (Petrov and Tartarnikov 2010). Because standard, stainless steel, long-shank hooks were used (not short-shank with the gap of the tip being less than that at the lower part of the curve, as in the industrial fishery; CCAMLR 2008), most of the fish >160 cm were likely lost, given that some hooks were straightened out or broken. Although Weddell seals cannot entirely be ruled out as taking the bait or hooked fish, it certainly cannot be other fish species because there are none that are anywhere near the size of the toothfish in McMurdo Sound. When we retrieved toothfish in the presence of Weddell seals sharing the fishing hole, the seals paid little attention, apparently not recognizing the toothfish as prey in that context. [NOTE: We were always sufficiently far from the ice edge that killer whales would not have access to the fishing holes and we did not fish when the killer whales were present in the ship's channel.] On the few occasions when a large treble or industrial-type hook was used, more of the larger specimens were caught. These hooks, however, left large wounds in the jaw likely leading to reduced survival. Therefore, their use was discontinued.

Data analysis

Fish metrics

Overall strategy. Our primary objectives with regard to analysis were two-fold: first to characterize change in fish metrics (length, condition, and capture rates) over the study period (1972-2010), and then to identify environmental variables influencing variation in these metrics among years and across decades. Analyses were conducted on trends in condition and length of toothfish (for condition, *n* = 5,403 individuals, and for length, *n* = 5,437, among the 5,587 caught among 27 yr of data), using both (1) mean condition index per year and (2) 50th, 75th, and 95th percentiles of total length (TL) in each year. (3) We confirmed the analysis of annual values of condition and length by analyzing trends with respect to the condition and length of individual fish. Finally (4), we assessed number of individuals caught per month and year as part of a "catch per unit effort" study (see "Catch per unit effort" below). Fish having partial data or measurements that clearly were wrongly recorded were excluded from the data.

We present results of toothfish length and condition in relation to variation among years, examining both linear and non-linear trends. To allow for non-linearity, we fit two types of models: (1) polynomials of second-order, and (2) results of "change-point" analyses using linear splines (Harrell 2001, pp. 18-19). In the latter case, two linear segments (each with its own slope) are joined at a specified “knot”. This allowed us to estimate and test for changes in (linear) trend. Both the second-order polynomial and the “two-joined-linear-segments” model have two degrees of freedom and thus are easily compared with respect to fit (e.g., by minimization of deviance). We also explored other simple models, such as cubic polynomial and “step-function” models (where there is a disjunct step-wise increase or decrease). The favored function fit to the data, and presented here, was the one that optimized AIC (Akaike Information Criterion).

Because the toothfish appears to prey primarily on silverfish over the shelf (see Introduction), especially those of approximately 4-5 years of age (Eastman, pers. obs., see below), and because La Mesa *et al.* (2010) noted an effect of the amount of open water on the production and survival of silverfish larvae, we considered environmental variables with lagged effects of 1 year (specifically, 8 mo) to 5 years. Therefore, we looked at the effect of ice cover and its persistence previous to the current (ice-covered) fishing season.

Condition. We calculated a Fulton-type condition factor (Anderson and Gutreuter 1983), scaled to center around 1.0, as an index of weight per unit length, an indirect estimate of fish girth (Davidson and Marshall 2010) and a proxy for body shape:

$$K = (W/TL^3) \times 10^2$$

where W = body weight in g and TL = total length in cm. Larger values for K indicate greater weight per unit length associated with a thicker body. We did not employ K as an indicator of body fat content. The resulting index varied from 0.577 to 2.99, with mean = 1.265 ± 0.149 SD.

Fenaughty *et al.* (2008) identified an important condition threshold, K_{ah}, which designates “axe-handle” fish that are in particularly poor physiological condition, K_{ah} = 1.01248. Therefore, in addition to changes in mean condition, we analyzed the proportion of individuals that each year was below this threshold. The term is derived from the long-thin body with a large head of emaciated fish. Higher *K* is generally associated with better physiological condition in wild fish.

Individual condition data came almost entirely (99.9%) from captures in four months: September, October, November, and December; 28.1% of captures were in October, 50.0% were in November. Since captures were essentially confined to four months, we have analyzed monthly variation in condition and length by treating month as a factor with four levels (i.e., as a categorical variable). Thus, in controlling for the effect of month, we make no assumptions about how the dependent variables change from month to month. The sample size of captures per year differed greatly (Table 1).

Mean condition index, *K*, was calculated for each year, as was the proportion of fish below the axe-handle threshold. Total length was considered to be both an index of body size and a proxy of approximate age (Horn 2002, Brooks *et al.* 2010). To assess changes in the frequency distribution of fish length, with specific attention to fish that were of greatest length (and thus of greater age), we analyzed three metrics: the 50th percentile (i.e., median), 75th percentile (i.e., upper quartile), and 95th percentile. The latter was chosen as a more statistically robust measure of “especially large” individuals than the simple maximum; the 95th percentile reflects a larger sample (in fact, in 20 of 27 yr, at least 5 individuals were ≥95th percentile).

Variation in the year-specific percentile values was compared to the percentile values for the entire study.

For analysis of annual change in condition, we weighted the mean value by the inverse of the standard error of mean condition. Similarly, for annual change in length, we weighted the 50th, 75th, and 95th percentiles for a given year by the inverse of the standard error of mean length for that year. Thus the weighting reflected the sample size as well as the individual-level variability in the metric for that year (e.g., the less variable, the greater the weight).

Catch per unit effort. To analyze patterns in toothfish catch rate, i.e., catch per unit effort (CPUE), we analyzed the number of fish caught divided by the most appropriate measure of capture effort. Among effort metrics evaluated, the metric most closely reflecting the number of fish caught per year was the total number of hooks set in each year. Comparing results among years, the number of hook-hours did not correlate with the numbers of fish caught, once we controlled for the number of hooks set per year. We also analyzed effort as a separate covariate, where the dependent variable was the number of individuals caught. Results were similar using either method (dividing number caught by effort or statistically controlling for effort); we only report the former because it is more widely used.

We conducted the abundance analysis in two ways: (1) captures per 10 hooks, natural log-transformed, and (2) proportional change in abundance from one year to the next. Note that the proportional change in abundance from year t, N_t, to abundance in year t+1, N_{t+1}, is equal to the antilog of $[\ln(N_{t+1})-\ln(N_t)]$. Hence, we present graphically the results of capture per 10 hooks in terms of ln-transformed capture rates.

Effort differed among months, and so did the capture rates with respect to month (see below; also Testa *et al*. 1985). We therefore analyzed between-year variation in captures per unit effort while controlling for month of capture, and present results that reflect the statistical adjustment with respect to month.

Furthermore, month of capture could confound observed patterns with respect to among-year variation in condition and length, given that monthly effort varied among years. To guard against such possible confounding, we repeated the analyses of condition and length, using individual observations instead, in relation to between-year patterns and with respect to the environmental variables. In all cases the pattern observed using annual measures of condition and length was confirmed as significant by the analyses of individuals, after controlling for month of capture.

Environmental variables

Sea Ice. Using satellite passive-microwave data for the Ross Sea sector from NASA Nimbus 7 satellite and the Defense Meteorological Satellite Program (e.g., Parkinson 2002, Zwally *et al.* 2002), ice area and ice extent were calculated daily or every other day for the period from January 1979 to December 2007, inclusive; no corresponding data were available prior to November 1978. Both ice variables to some degree measure the amount of open water over the shelf, one directly (area) and one indirectly (extent). Ice extent in the Ross Sea region varies with winter/spring wind strength and persistence, as does the extent of the coastal Ross Sea polynya (explained more fully in Ainley *et al.* 2005, 2010): more wind pushes the ice farther north, but also frees the coastal area of ice. It there is little wind, there is little water among ice floes and ice area is maximized.

Statistical analyses were primarily conducted on average monthly values of ice area and ice extent. The maximum and minimum values for the 12 monthly averages were determined for each year. The minimum was always in February, but the maximum could occur in August, September, October, or November. In addition, we determined daily maximum and minimum values. However, results were not improved using daily rather than monthly minimum or maximum values, and hence we show only results using the month-specific values, whether by specified calendar month, e.g., “September”, or with reference to maximum or minimum monthly value.

Analyses were also conducted on duration of the “ice season” or “open water season”: (1) duration (number of days) that ice area exceeded an upper threshold value (3,037,000 km^2) relative to the total number of days for which the metric was calculated for that year, and (2) duration (number of days) that ice area was below a lower threshold value (628,000 km^2) relative to the total number of days calculated for that year. The upper threshold was chosen to be the 95th percentile value of ice area in the year with the lowest maximum value (1986). The lower threshold was chosen to be the 5th percentile value of ice area in the year with the highest minimum value (2003). However, these measures of duration above an upper threshold or below a lower threshold were no better predictor variables with respect to toothfish metrics than were the maximum or minimum monthly averages of ice area or ice extent explained above. Thus, the results with respect to relative ice season duration are not shown.

Additional ice metrics analyzed included: timing (day of year) of minimum and maximum, the difference in ice area or ice extent between minimum and the following maximum, difference between the minimum and the previous maximum in terms of ice area or ice extent, the difference in days between the minimum and the maximum, and the rate of change (difference in ice area or extent between maximum and minimum divided by number of days between minimum and maximum). Again, none of these variables proved superior in predicting fish metrics and so results with respect to these variables also are not shown.

Other environmental variables. We examined the importance of several environmental variables that by influencing ocean characteristics may in turn directly or indirectly affect toothfish, as they have other Ross Sea mesopredators (Testa *et al*. 1992, Wilson *et al*. 2001, Ainley *et al.* 2005, Rotella *et al.* 2009). These other environmental variables were the Southern Oscillation Index (SOI), the Southern Annular Mode (SAM; also called Antarctic Oscillation Index), and a measure of the size of the Ross Sea Polynya. It is well known that the state of the sea ice in this part of the Southern Ocean is affected by the atmospheric processes embedded in SOI and SAM (Jacobs 2006, Stammerjohn *et al*. 2008).

We used monthly SOI to calculate six metrics. The first three were: average annual SOI (January to December), the average for January to June, and the average for July to December. The other three were quadratic transformations of the corresponding SOI metric, designed to measure increasing effects of SOI associated with strong El Niño events, during which the SOI is strongly negative. The transformations were of the form $(SOI– c)^2$ where c = maximum (positive value) of the SOI metric (12-mo average or either of the 6-mo averages). (SOI – c) was thus always zero or negative and the stronger the El Niño the more negative was the value. Squaring (SOI – c) resulted in all non-negative values, with strong El Niño being associated with the largest positive values of the transformed metric and the strongest La Niña in the time series getting a score of zero (following the approach of Lee *et al.* 2007). In no case was a second-order polynomial (i.e., with 2 df) superior in terms of AIC to the respective quadratic transformation of SOI (i.e., with 1 df) when analyzing fish condition or length.

For all single-variable regression models, we report the regression coefficient (*b*, which is also commonly symbolized as β). Where more than one environmental variable was analyzed in the same model, we report the multiple regression coefficient (*b*) for the effect of a variable while controlling for all other variables in the model, symbolized. To aid in the comparison among variables (measured on very different scales, e.g., SOI and maximum ice area), we also present the standardized multiple regression coefficient (which we refer to as "*beta*"), which like a correlation coefficient, scales from -1 to +1 (Kutner *et al*. 2005).

SAM was represented by the value on 1 January each year (from http://www.antarctica.ac.uk/met/gjma/sam.html; Fig. 2) and is a proxy for strength of the Southern Ocean westerlies, which in turn affect the formation, extent and persistence of sea ice (Marshall *et al.* 2003, Russell *et al.* 2006, Stammerjohn *et al.* 2008). Using SAM values from 1 January, about 9 to 11 months before toothfish were captured as part of this study, means that a lag of -1 was used; lag of 0 means SAM is calculated in the same calendar year as applies to the sample of toothfish; lag of 1 means SAM is calculated between 1-plus years (21 to 23 months) before the toothfish sample was obtained, etc.

Among these environmental variables, we examined condition, length, and numbers caught per unit effort in relation to same-year values, as well as with lags of 1, 2, 3, 4, and 5 yr. One rationale for examining lags was that condition and numbers of toothfish could well reflect availability of their prey, i.e., Antarctic silverfish. For example, in McMurdo Sound toothfish consume silverfish that are 81–195 mm SL with modal values of 100–150 mm (Eastman and DeVries, unpublished data) and, on the basis of Hubold and Tomo's (1989) aging studies for Weddell Sea silverfish, these specimens are 4+ years old. Thus, we reasoned ice (or other environmental) conditions in a given year may influence availability of prey 1 to 5 years later.

Results

Characterization of the catch

Between 1972 and 2010, 5587 toothfish were caught, including 835 kept for experiments and/or whose survival was in doubt. The largest fish caught was 193 cm (92 kg) and the smallest was 81 cm (4.5 kg); individuals between 120 and 170 cm predominated, with very few <90-100 cm (Fig. 3).

Of the 4752 fish tagged and released in the study, 17 have been recaptured (0.4%) with the annual growth rate being 2.0 cm in TL and 1 kg in mass per year (DeVries, unpubl. data).

These growth rates are slightly below those reported from analyses of the industrial catch (cf. Horn 2002, Brooks *et al.* 2010). Most of the recaptures (12) occurred at the McMurdo fishing site, but one was recaptured by the Russian vessel, *Yantar*, and four have been reported by the New Zealand fleet (DeVries, unpubl. data). One tagged individual was recaptured >1300 km north of McMurdo Sound, indicating migration north of the Ross Sea, possibly for spawning (Hanchet *et al.* 2008, 2010). Most recaptured McMurdo fish were encountered again 4-5 yr after release, with the longest interval being 18 yr. The recapture rate in the fishery during the most recent years, 2004-2009, for a select number of boats and not including fish recaptured the same year, is 4.96% (CCAMLR 2010). The discrepancy between our low recapture rate and this one could well be due to 1) McMurdo Sound fish being more transient than those on the main fishing grounds (continental slope) and/or 2) the fact that recaptures of our fish by the fishery were under-reported, with many vessels other than those from NZ (just 4 of 15-20 permitted) reporting no recaptures at all (CCAMLR 2006). This would especially be true in early years of fishery, when no industry tagging program was in operation; and of course no data come from the Illegal, Unreported and Unregistered fleet. One of our tags was found on a vessel's processing room floor, indicating lack of vigilance.

Fish Length

Annual variation in total length, considered an approximate proxy for age, was analyzed with respect to three metrics: 50th, 75th (i.e., upper quartile), and 95th percentiles. In general, the overall pattern during the study period was similar for each of these metrics.

The most parsimonious model, favored by AIC, describing the pattern of change in length across years was a two-part spline with change point (i.e., “knot”) at 1992, with increasing TL to 1992 and decreasing TL subsequently (Table 2, Fig. 4). These models were superior to a single linear trend, quadratic polynomial, or cubic polynomial model, or other simple transformation, as determined by AIC, and they accounted well for the pattern observed, except for 1972 being an outlier with respect to the predicted pattern. In regard to the 75th percentile, for the linear trend 1972-1992, $b = 0.580$ (± 0.123 SE, $t = 4.7$, $P<0.0001$) and for the linear trend 1992-2010, $b = -0.526$ (± 0.242, $t = -2.2$, $P<0.04$). The change in trend was significant (Table 2). In regard to the 95th percentile, for the line segment 1972-1992, $b = 0.534$ (± 0.169, $t = 3.6$, $P = 0.004$) and for the line segment 1992-2010, $b = -0.662$ (± 0.331, $t = -2.0$, $P = 0.057$). The change in slope for the 95th percentile was also significant (Table 2). Finally, the 50th percentile (not shown) showed the same pattern, and was statistically significant with respect to analogous measures.

In order to assess whether or not the length statistics of the small sample of fish caught during 1991 and 1991 were mainly responsible for the observed 2-part trends, we also analyzed trends using individuals rather than years, analyzing with and without data from 1991 and 1992. Models included effect of calendar month (analyzed as categorical variable; Table 3). The 2-part spline model including 1991 and 1992, as expected, was highly significant (Table 3), as was the model excluding 1991 and 1992 data ($P <0.0001$, Table 3). The coefficient, b, for the 1972-1992 slope was 0.362 (SE = 0.041), and that for the 1972-1990 slope was 0.351 (SE = 0.041; in both cases, $P <0.0001$). Similarly, the coefficient, b, for the 1992-2010 slope was -0.291 (SE = 0.104) and that for the 1997-2010 slope was -0.272 (SE = 0.104; $P = 0.005$ and $P =$

009, respectively). Finally, the change in slope from the earlier period (up to 1992) to the later period (from 1992) was significant whether or not 1991 and 1992 were included (Table 3).

Fish Condition

Condition (*K*) of the Antarctic toothfish caught varied by month. *K* was relatively high in October and November, but lower in September and December (Fig. 5). Variation among months was significant ($F_{3,5394}$ = 4.09; *P* = 0.007); the pattern and significance of monthly variation in condition were very similar after controlling for annual variation (year as factor).

Across all years, there was no significant linear trend in toothfish condition (Fig. 6). Instead there was a trend for mean *K* to increase from 1972 to 1991 and/or 1992 and decrease subsequently. Mean *K* was higher for 1991 and 1992 than in any other year; nevertheless, an increasing trend is evident from 1972 to 1990. The pattern evident indicated that change point analysis, with either 1991 or 1992 being the knot, would be most appropriate. Adjusted R^2 was maximum and AIC was optimized when the change point was at 1992 rather than at 1991 (Table 2). For the line segment 1972-1992, *b* = 0.00358 (± 0.00094, *t* = 3.8, *P* = 0.001), and for the line segment 1992-2010, *b* = -0.00927 (± 0.00180, *t* = -5.2, *P* <0.001); the difference in slopes of the two lines was significant (Table 2).

AIC for a quadratic model for year was poorer than for the change-point analysis. More specifically, there is no evidence that the trend from 1972 to 1990 was anything but linear (linear trend through 1990: *P* <0.0001, quadratic term for that time period, *P* >0.2) and, therefore, the change-point analysis is preferred, with a change in trend either in 1991 or in 1992 (Figure 6).

In order to assess whether or not mean condition of the small sample of fish caught during 1991 and 1991 were mainly responsible for the observed trends in condition, we also analyzed trends using individuals rather than mean values, analyzing with and without data from 1991 and 1992. As with length, models included effect of calendar month (analyzed as categorical variable; Table 3). The 2-part spline model including 1991 and 1992, as expected, was highly significant (Table 3), as was the model excluding 1991 and 1992 data (Table 3). The coefficient, *b*, for the 1972-1992 slope was 0.00338 (S.E. = 0.00039), and that for the 1972-1990 slope was 0.00319 (S.E. = 0.00039 ;in both cases, P <0.0001). Similarly, the coefficient, *b*, for the 1992-2010 slope was -0.00938 (S.E. = 0.00099) and that for the 1997-2010 slope was -0.00910 (S.E. = 0.00099 ;P <0.001 in both cases). Finally, the change in slope from the earlier period (up to 1992) to the later period (from 1992) was significant whether or not 1991 and 1992 were included (Table 3).

Axe-handle fish. The proportion of axe-handle fish decreased during the period 1972 to 1992 from about 3 - 7% in the mid-1970's to 0 - 3% in the period 1987 to 1992, and then increased from 1992 on (Fig. 7). The one exception was 2010, in which there were no axe-handle fish, but only 7 total fish were caught that year. Among the set of models examined, the preferred model (as determined by AIC) was a two-part spline, with linear decrease up to 1992 (b = -0.00167 ± 0.00076, t = -2.19, P = 0.039), and a linear increase since (b = 0.00420 ± 0.00145, *t* = 2.90, *P* = 0.008). The linear trend in each time period was significant (see below) and the trends differ significantly from each other ($F_{1,24}$ = 8.68, *P* = 0.007).

Catch per Unit Effort

Catch rate varied by month within each season (Fig. 5). The lowest capture rate occurred in September (even lower in August but only two days of fishing were available), but it then increased dramatically in October. Rates for November and December remained high, though with a slight downward trend from November to December. There was no significant variation in catch rates among October, November, December ($P > 0.4$); but each of these differed from the September catch rate ($P < 0.001$).

In regard to annual trends, unlike condition and length, there was no peak in CPUE midway during the study period. Instead, captures were fairly stable through 2001 (Fig. 8), with a slight, non-significant decline in capture rate evident late in this period, equivalent to a decline in CPUE of 1.24% per year (back-transformed geometric mean SE = 1.76%: analysis of ln-transformed monthly capture rates, controlling for month of capture, slope not different from zero, $P > 0.4$). The pattern then changed dramatically, but unfortunately only 3 years of effort data were available after 2001. For those 3 years, captures per 10 hooks deployed, summarized per year, ranged 0 - 0.4 fish, compared to 1975-2001 when the range was 1.0 - 3.4 fish. Though the information is not included in our analyses, fishing was undertaken by another researcher (G. Hofmann) in the same localities in 2006 for 4 weeks: no fish were caught but effort data are not available.

Realizing that data were available for only 3 of the 9 years after 2001, and that these 3 years occurred at the end of this latter period, the best-fitting, most parsimonious model (optimizing AIC) indicated a step change to a different (and much lower) level of capture rate. This, however, must be viewed with caution with so few years since 2001. The pattern depicted is preferred by AIC when compared to the full set of competing models: (1) no change, (2) two linear segments joined at 1992, (3) two linear segments joined at 2001, (4) two linear segments joined at any year between 1992 and 2001, (5) two parallel lines with a step change occurring at or after 2001 (i.e., slope is non-zero but the same across all years; only the elevation changes at or after 2001), (6) inverse transformation of year, (7) year as a quadratic function, and (8) year as a cubic function. Nevertheless, with only three years of catch per unit effort available post-2001, it is not possible to adequately estimate the post-2001 trend. Essentially, all that can be said is that fishing success became dramatically reduced after 2001.

Influence of environmental variables on fish metrics

Fish Length. Exploratory analyses of the effects of the full set of candidate ice variables (see Methods) on our three TL metrics revealed four of particular interest: minimum ice area, minimum ice extent, maximum ice area, and maximum ice extent. Each of these was analyzed with respect to lags of 0 - 5 yr, yielding 24 ice variables (= 4 variables x 6 lags). For 95th percentile length, none of the 24 ice variables was significant. For 75th percentile length two variables were significant: maximum ice area with 4-yr lag and maximum ice area with 5-yr lag (Fig. 9); for 4-yr-lag, weighted regression, b = -0.0000084 (± 0.0000039, t = -2.15, P = 0.048;

Table 4). We do not show results for 5-yr-lag because this relationship, though significant (*b* = -0.0000089 ± 0.0000041, *P* = 0.049), is driven entirely by results from 1991 and 1992.

Comparison of correlation coefficients between 75th percentile length and each of the two ice variables (maximum ice area with 4-yr lag vs 5-yr lag) is instructive, with and without 1991 and 1992. For the 5-yr lag, the correlation coefficient with respect to 75th percentile length was r =-0.499, including the 2 years, but r = -0.050 without those 2 years. For the 4-yr lag, the correlation coefficient with respect to 75th percentile length was r = -0.486 including the 2 years, but only dropped to r = -0.404, excluding the two years. Thus, the relationship between 75th percentile length and maximum ice area, with 4-yr-lag, does not hinge on these 2 years having unusually large upper quartile values.

Median length (50% percentile) also demonstrated a significant relationship to maximum ice area 4 years previously (Table 4; Fig. 9), and one that was stronger than that shown for upper quartile length (for median length: correlation coefficient, *r* = -0.608, *P* < 0.01; compared to *r* = -0.486 for upper quartile length and the same ice variable). This relationship is robust with respect to values for any individual year. Whereas 1991 is an influential observation, 1992 in this case is not (median length in 1992 = 136, compared to median length for entire sample = 134). Excluding 1991 still yields a relationship that is close to significant (*P* = 0.075).

Fish Condition. Two distinct ice variables provided the best statistical predictors of changes in *K*: minimum ice area (always in February) of the current year (8-10 mo prior to fishing season) and maximum ice extent 3 yr previously (Fig. 10). While minimum ice area could also be a proxy for amount of open water, understanding maximum ice extent is far more complex, owing to the fact that large scale ice extent is a function largely of wind strength and persistence in the Ross Sea sector. Stronger winds (greater ice extent) also usually mean that the coastal polynyas are more prevalent (though not always, depending on temperature), a subject we shall return to in the Discussion. Regardless, these two variables (minimum ice area, maximum ice extent 3 yr previous) were relatively uncorrelated with each other ($r = 0.324$). There were several other variables (such as length of ice season) that provided good predictive ability for explaining change in condition, though not quite as high, but also highly correlated with the two primary variables. Thus, as noted in Methods, we keep those results in mind but do not report them.

The relationship between toothfish condition and minimum ice area 8 - 10 mo earlier was non-linear: mean *K* declined with increasing minimum ice area (less open water than usual), but in an accelerating (down-turned) fashion. In a weighted regression, mean *K* in relation to minimum ice area, the relationship best reflected a quadratic transformation of minimum ice area (predictor variable = (minimum ice – c)^2 where c = smallest minimum ice area observed in any year = 131,448 in 1979) and was significant: $b = -2.39 \times 10^{-13}$ ($\pm 1.07 \times 10^{-13}$, $t = -2.23$, $P = 0.039$; Table 4).

When analyzing the data at the individual level, the effect of minimum ice area (quadratic transformed) on condition, while controlling for calendar month of capture, was also significant, $b = -1.52 \times 10^{-13}$ ($\pm 4.08 \times 10^{-14}$, $t = -3.73$, $P = 0.0002$). Furthermore, even excluding the influential year 2003 (greatest minimum ice area and lowest mean condition index in the data set), the result of analyzing individual fish condition demonstrated a significant negative effect of minimum ice area (quadratic transformed), $b = -1.14 \times 10^{-13}$ ($\pm 4.24 \times 10^{-14}$, $t = -2.69$, $P = 0.007$). Minimum ice area was a better predictor (as determined by AIC) of mean condition than was date of minimum or minimum ice extent.

The second primary ice variable to account for annual variation in mean condition was maximum ice extent 3 years earlier (Fig. 10); other lags showed no significant relationship, (0, 1, 2, 4, or 5). Maximum ice extent was a better predictor than was ice extent in any specific month (e.g., October). In this case the relationship was linear. In a weighted regression, mean K in relation to maximum ice extent with 3-yr-lag was: $b = -7.18 \times 10^{-8}$ ($\pm 3.19 \times 10^{-8}$, $t = -2.23$, $P = 0.04$; Table 3).

There was no significant relationship ($P > 0.15$) between proportion axe-handle fish and minimum ice area in the same year nor between proportion axe-handle fish and maximum ice extent 3 years previously, the two variables that correlated strongly with mean condition. However, there was a significant relationship between the proportion of axe-handle fish and maximum ice area 4 years previously, the same variable that predicted 50th percentile and 75th percentile length (Fig. 7). With increasing maximum ice area, the proportion of axe-handle fish increased 4 years later (adj $r^2 = 0.2698$, $F_{1,15} = 6.91$, $P = 0.019$).

Change in Catch Rate (CPUE). There was no evidence that any environmental variable (ice variables, whether lagged or not, or SOI variables) affected toothfish CPUE (ln-transformed) or annual changes in toothfish CPUE. Furthermore, there is no significant or AIC-justified association between CPUE (or changes in CPUE) and any of the ice variables, lagged or not, during the pre-crash period, 1972 to 2001. As noted, despite environmental variability, there was little change in capture rates from one year to the next up to 2001 (Figure 8).

Relationships to the Southern Oscillation. No significant relationship existed between SOI and the three types of fish metrics analyzed. This is not to say that SOI is unimportant, only that the effect of SOI is not direct. Instead, SOI during the months July-December is strongly associated with maximum ice area in the same year (this reaffirms previous analyses, i.e., Wilson *et al*. 2001); b = 108,700 (± 2400, t = 4.52, P = 0.0001; Fig. 11). A linear relationship between the two variables is best supported and confirmed by AIC (Table 3).

Because maximum ice area reflected SOI in July to December and maximum ice area predicted 75th percentile length of toothfish 4 years later (see above), there was consequently a modest, non-significant, negative correlation between SOI in July-December and 75th percentile length 4 years later ($r = -0.255$, $P > 0.2$; Table 4). However, once we accounted for the effect of maximum ice area on length (with 4-yr-lag), the effect of SOI in July-December on 75th percentile length 4 years later was even less significant and reversed sign (partial regression coefficient, $b = 0.585 \pm 0.721$, $t = 0.81$, $P > 0.4$; standardized partial regression coefficient *beta* = 0.225.), while the effect of maximum ice area on length 4 years later remained, even while controlling for SOI in July-December (partial regression coefficient, $b = -0.0000107 \pm 0.00000485$, $t = -2.21$, $P = 0.044$; standardized partial regression coefficient *beta* = -0.613).

Results were very similar to that found for 75th percentile length analyzing either 50th or 95th percentile length in relation to the same two independent variables: SOI (July-Dec) with a 4-year lag and maximum ice area with a 4-year lag. The effect of maximum ice area was significant, controlling for SOI, while the effect of SOI was not.

It was also the case that SOI influenced maximum ice extent and thus exerted an indirect effect on mean condition. However, just as with 75th percentile length, there was no direct effect of SOI on condition 3 years later, once we controlled for maximum ice extent (partial regression coefficient $b = 0.0063 \pm 0.0082$, $t = 0.73$, $P > 0.4$, standardized partial regression coefficient $beta = +0.217$). Note that SOI in the current year was not correlated with mean condition or any of the length metrics, nor was SOI associated with minimum ice area in the current year.

Relationships to Southern Annular Mode. There was little evidence of a direct effect of SAM (measured on a continuous scale) on toothfish length or condition, whether lagged or not. The regression of mean condition or the three percentiles of length on SAM was not significant in every case, with lags of 1 to 5 years.

However, the sign of SAM changed from predominantly negative prior to 1976, to increasingly positive from 1976 to the early 1990s, and then to mostly positive thereafter; during the period from 1972 (first year of this study) to 1992, 12 out of 21 years were ≤ 0, whereas from 1993 to 2011, 15 out of 19 years were positive (LRS = 5.60, df = 1, $P = 0.018$; Fig. 2). In accord with the increasing windiness as a result of positive SAM, sea ice extent (and related aspects of sea ice) changed as well (Fig. 11). During the more “negative” period of SAM (1972 to 1992), condition and length both increased. During the (mostly) “positive” period of SAM (1993 to 2011), condition and length both declined significantly.

While there was no relationship between condition or the length metrics and SAM as a quantitative variable, 75th percentile length was significantly greater in years in which SAM was positive 4 years earlier as compared with years in which SAM was negative (≤0) 4 years earlier: 145.85 (± 1.17; n = 14 years) vs. 142.14 (± 1.20; n = 13 years; *P* = 0.036; results of weighted regression). Results were even stronger comparing 50th percentile lengths. The median fish length 4 years after a year with positive SAM was 136.39 (SE = 1.21) compared to median fish length of 131.84 (SE = 1.13) 4 years after a year with SAM of 0 or less (*P* = 0.011).

Discussion

In this study we found that (1) the length-frequency of the McMurdo Sound catch was dominated by fish >100 cm and in the upper two-thirds of the overall distribution exhibited in the industrial toothfish catch; (2) McMurdo Sound fish length and condition increased from the early 1970’s to the early 1990s and then decreased, the proportion of “axe handle” fish (poor condition) in the catch changing inversely with mean fish condition; (3) fish length and condition decreased with increasing sea ice cover and/or inversely with the extent of open water, lagged by 8 mo to 5 yr; and (4) catch per unit effort, controlling for within-season variability, was constant through 2001 and then decreased dramatically. Below, we propose and discuss hypotheses explaining these patterns.

Toothfish length-frequency

Models to estimate stock size based entirely on what can be gleaned from the industrial catch, as is the case for the Ross Sea region toothfish fishery (CCAMLR 2005-2010), assume that after making certain statistical assumptions and corrections, e.g., by virtue of mark-recapture data, models are sufficient to inform the management strategy. One main assumption is that the size-age distribution in the catch, with adjustment, is representative of the full population. The disparity in the size distribution in the McMurdo Sound catch compared to the fishery catch is therefore of concern. The McMurdo Sound catch, ranging from 81-193 cm with a broad mode at 120-170 cm, reasonably mirrors the upper two-thirds of the commercial catch, i.e. "…50 to 180 cm….In all seasons, there was a broad mode of adult fish at about 120–170 cm…" (CCAMLR 2010, p. 6); ~15-20% of the industrial catch overall appears to be of fish <100 cm, and in years when there are more of these smaller fish the conclusion is that the fishery centered more over the Ross Sea shelf than in other years (CCAMLR 2010). In fact, with very few fish <100 cm (2.5%) in the McMurdo Sound catch, this disparity is even more apparent when compared to the size-frequency distributions in Hanchet *et al*. (2010). In the latter, only fish captured by the fishery over the shelf are displayed and >50% are <100 cm, with the fishery expending significant effort over the shelf (though less than on the slope) including waters close to the scientific fishing location (i.e., on the opposite side of Ross Island (Hanchet *et al*. 2008).

There are at least two factors that could explain the discrepancy. First, owing to lack of buoyancy in fish <100 cm (Eastman and Sidell 2002, Near *et al.* 2003), the vertical setline failed to attract many of the smaller fish that remain on the bottom (Eastman and Barry 2002, Near *et al.* 2003), whereas the industrial longlines, deployed along the bottom, caught these fish in greater proportion. Second, the discrepancy could be due to the fact that large fish ate most of the smaller fish caught on the vertical set line. However, of the stomachs inspected in the McMurdo catch (*n* = 58), evidence for cannibalism was absent (Eastman 1985a, b; La Mesa *et al.* 2004). That large toothfish, at least under ice cover, reside high in the water column, as indicated by the catch we report herein, is a fact confirmed by crittercams placed on Weddell seals as well as on a number of occasions by ROVs (to within 12 m of the surface: Fuiman *et al.* 2002, Kim *et al.* 2011); that small toothfish do occur in McMurdo Sound is indicated by the catch of Weddell seals, who take the entire size range (cf. Ponganis and Stockard 2007, Ainley and Siniff 2009). In any case, it would appear that assumptions made in CCAMLR's fishery models about the representativeness of age-size structure as revealed by longlines need to be reconsidered.

In the context of the discrepancy between vertical and horizontal-bottom sampling it is interesting to consider why this species is one of the few neutrally buoyant Southern Ocean fish. The most parsimonious explanation is probably historical. Given the eradication of the previous taxonomically diverse Eocene fauna, the modern notothenioids diversified into a developing ecosystem with vacant water-column niches. As inferred from molecular sequence data, these niches were filled first by the neutrally buoyant clade about 24 million years ago (Near 2004). The water column contained few fishes and underexploited resources were available—the Antarctic toothfish diversified coincident with silverfish in response to this unusual situation. The questions remain: Is neutral buoyancy the means to exploit the high prevalence of silverfish (another neutrally buoyant species), the means to escape cannibalism, or both (Pinkerton *et al.* 2007)? Is the lack of any water-column species in the diet of longline-caught fish (Fenaughty *et al.* 2003) a reflection of benthic longlines catching mainly fish that reside on or near the bottom? Why, supposedly, are toothfish only found mostly on the bottom in ice-free waters? Regardless, it appears that the clear ontogenetic shift in Antarctic toothfish from dwelling on the bottom as small fish to somewhere in the water column as large fish, at least in ice covered waters, is a major aspect of this species' natural history (DeVries and Eastman 1981, Near *et al.* 2003), with further implication of whether or not removing large fish results in the increase of small fish (through competitive release), i.e. the basis for modern fishery theory (cf. Constable *et al.* 2000, Longhurst 2010). In the hypothetical life history scenario proposed by Hanchet *et al.* (2008) no mention is made of the ontogenetic shift in buoyancy and its implications, other than to say that as fish mature they occupy waters having deeper bathymetry. The assumption is made that this species is entirely bottom dwelling (except perhaps larvae).

One further interesting question that arises from the size-frequency of McMurdo Sound fish compared to that of the industrial catch revolves around the age-related fecundity of this species. All large McMurdo Sound fish are sexually mature, but in gonadal resting stage; some females showed signs of previous spawning (Eastman and DeVries 2000). If the industrial catch underestimates the prevalence of large fish over the shelf, it would seem that estimates of age/size at maturity, which is based on the size-frequency seen in the industrial catch, needs to be revised once more (recently it was doubled from ~8 to ~16 y; Parker and Grimes 2010).

Trends in toothfish length and condition

Both total length and condition of toothfish in the McMurdo Sound catch increased from the mid 1970s to the early 1990s, and then switched to gradually decrease. Because of the low sample size for 1991 and 1992, and the lack of any data during 1993-1996, it is difficult to say when length and condition trends actually leveled off in the early to mid-1990's before decreasing. However, in the period up to and including 1990 there was no indication of leveling off. Instead, a linear trend was evident in condition and length from 1972 to 1990. Whether or not the decreasing trend is represented in the industrial catch, which only began (legally) in 1996 (CCAMLR refers this as the 1997 fishing season), we do not know. Seemingly this would be difficult to ascertain in a sampling regime that is not only non-random but is geared to catch the largest fish as fast as possible before the season closes (Constable *et al*. 2000, Brooks 2008).

Regardless, it appears that growth rate in this species is not a constant but is subjected to environmental and potentially anthropogenic factors. According to fishery theory, as fish (especially large ones) are removed from the stock, fish size and condition should show a positive growth as smaller fish are released from competition. This is rarely demonstrated (Longhurst 2010) and is not evident in the McMurdo Sound data. What then are the factors that could account for the observed increases and then decreases in length and condition? If change in length is a function both of food availability and age, was there 1) a release from predation during the 1970-80s, thus allowing older fish to remain in the population longer, and/or 2) more favorable foraging related to competitive release or climatic factors that influenced silverfish?

Release from predation. The southern Ross Sea was the scene for a number of “heroic” expeditions during the early half of the 1900s, and they all took large numbers of Weddell seals for human and dog food. The southern Ross Sea seal population was thought to have recovered by the 1960s (Stirling 1971), but then the NZ Antarctic Programme began to kill 50-100 seals annually to feed sled dogs and by the time this ended in the mid-1980s, the population, at least as measured in McMurdo Sound was halved, from 3000 to 1500 seals. Then over the next decade, it slowly recovered (partially) to ~2000+, where it has remained ever since (summarized in Ainley 2010). Given that Weddell seals eat a significant number of Antarctic toothfish (Ainley and Siniff 2009, and references therein; Kim *et al.* 2011), this marked decrease in Weddell seals in the southern Ross Sea is consistent with a lessening of predation pressure on Antarctic toothfish. Certainly, the lag that would occur between these two long-lived, late maturing species, predator versus prey, would be large. Added to this is the fact that another toothfish predator, sperm whales (admittedly at the periphery of their range), owing mainly to contraction of range as whalers depleted the stocks in the warmer parts of the Pacific during 1700-mid 1900s, even now are a shadow of their former numbers in the Ross Sea sector (Whitehead 2000). Their numbers in the Ross Sea sector also may well have begun to recover in recent decades as they have elsewhere (see for instance, Whitehead *et al.* 1997, Branch and Butterworth 2001). The same is true for southern elephant seals, still another toothfish predator, which disappeared from the Ross Sea during the 1980s, their foraging range contracting as the Macquarie Island breeding population became severely reduced (summarized in Ainley 2010).

More favorable foraging related to competitive release or climatic factors. The industrial take of minke whales during the 1970s-early 1980s (~20,000 taken from Ross Sea region), which appears to have resulted in the population increase of trophically competing Adélie Penguins at the time (Ainley *et al.* 2007), also could have benefited Antarctic toothfish, both the whales (and penguins) and the toothfish being significant predators of Antarctic silverfish (Ballard *et al*. 2011). Furthermore, the time of the switch in toothfish length and condition trends from positive to negative corresponds to when the minke whale population was deemed to have reached recovery (roughly 1986-1990; Branch 2006, Ainley 2010).

There is also the possibility that the shifting climate of the Ross Sea region has affected (is affecting) the abundance of Antarctic silverfish, a subject about which we know even less. According to La Mesa *et al*. (2010), the prevalence of larval silverfish in the western Ross Sea was an order of magnitude higher in the 1999-2000 austral summer, when the Ross Sea polynyas opened early and large, compared to the austral summers of 1997-98 and 2003-04; with more open water, earlier, primary production is increased and, hypothetically, silverfish survival is enhanced owing to increased food. Silverfish spawn during the winter and their eggs can be found among the frazil ice associated with heavy pack or fast ice (Vacchi *et al*. 2004). Perhaps this is a protective strategy, and more ice at this time is beneficial, but once the eggs hatch the larvae need to forage on microbial organisms. In any case, though most of the silverfish contained in toothfish stomachs in McMurdo Sound during late spring are 100–150 mm SL (Eastman and DeVries, unpublished data) and on the order of 4+ years old (Hubold and Tomo 1989), we did find that toothfish condition is positively affected by extensive open water, and hence water open to insolation, during mid-summer. We also found the effect of a 3-yr-lag in ice extent on toothfish condition, and note that Ross Sea primary productivity cycles on a 2-4 year period owing to a combination of nutrient and sea ice factors (Peloquin and Smith 2007). Consistent with the 4 yr and older age classes of silverfish that toothfish eat in mid-summer, we also found a negative relationship between toothfish length and maximum sea ice area 4-5 years earlier. Greater ice area means less open water. That's not to say that we understand the interconnections, but these few factors and relationships would seem to implicate the availability (and possibly condition) of silverfish as being important to toothfish growth and condition. Obviously, we need to learn considerably more, not just about toothfish, but about silverfish as well, if we are to understand toothfish. Making what we can of the trends in axe handle fish, we note the consistency between the decreasing trend in prevalence while toothfish length and mean condition were increasing during the first half of the study period, as opposed to the increased prevalence of axe handles as length and condition began to decrease.

Another factor to consider is the Southern Annular Mode, a major driver of climate in the Southern Ocean (Thompson and Solomon 2002, Stammerjohn *et al*. 2008). During the period when toothfish length and condition were increasing, beginning in the mid 1970s SAM was increasingly becoming less negative and more positive until becoming almost entirely positive starting at the inflection point of both toothfish length and condition. Therefore, owing to increased windiness blowing south to north (as well as westerly winds in the north increasing Ekman transport), sea ice extent was expanding, early appearance of coastal polynyas was becoming more reliable, and the sea ice season was lengthening (Parkinson 2002, Stammerjohn *et al.* 2008). It would seem that more reliably present coastal polynyas in the Ross Sea would favor silverfish production, but the decreasing annual period of open water would not. Other than the correspondence in the inflection points of length and condition and the onset of continually positive SAM, we again emphasize that we don't understand much about this predator-prey system, toothfish and silverfish. The correspondence in trends between those changes in trend and SAM, though, is noteworthy and deserving of closer study.

That the Southern Oscillation Index had no direct correlation to variation in any Antarctic toothfish parameters is perhaps not surprising. In the Patagonian toothfish, SOI correlates to egg and larval prevalence through its influence on ocean temperature but by the time fish recruit into the breeding population, the SOI signal has become obscured (Belchier and Collins 2008). Certainly many factors come into play between spawning and recruitment in a fish that matures 15 years later. Other, shorter-lived ground fish in the Scotia Sea have exhibited correlations to SOI, but as those authors note, these fish feed heavily on krill, a species known to track closely SOI changes to its ocean environment. Antarctic toothfish, as far as anyone knows, do not feed readily on krill; but then no one knows what toothfish eat during winter along the Ross Sea slope where krill and krill predators are abundant (Ballard *et al*. 2011).

Change in toothfish prevalence

Monthly Pattern in CPUE. The within-year pattern of apparent toothfish abundance (catch rate) was interesting but somewhat resists explanation given the lack of other information. The pattern shown in the 27 years of data was similar in form but with a lesser decrease in catch rate after November than reported by Testa *et al*. (1985). In fact, the pattern apparent in our data was similar to one of the three years in the Testa *et al*. study; the other two showed a more extreme decrease for December. To explain the temporal pattern, one might be tempted to invoke some sort of migratory movement on the scale of shorebirds visiting the Arctic tundra to breed but then vacating it before food becomes unavailable, or for that matter the annual invasion and evacuation of the Ross Sea by Adélie penguins (Ballard *et al*. 2010). After all, McMurdo Sound tagged fish have been recaptured well to the north of McMurdo Sound, as noted (see Hanchet *et al*. 2008); southward movement into the southern Ross Sea by industry-tagged fish (along the slope) has been detected as well (Hanchet *et al*. 2010). On the other hand, toothfish could also seasonally change their position in the water column to be more vulnerable to our setline array. From personal experience with other fish species (ocean salmon), if you are not fishing at the depth where they occur you won't catch them, and their depth can change dramatically and day-to-day (D. Ainley, 100s of hours of pers. obs.). Therefore, we are inclined to explain the early spring increase in our catch rate on the basis of shifting position in the water column due to food availability. In early spring (August, September) with the sun first rising on 20th August, there would be no reason for silverfish, and therefore toothfish, to be very high above the bottom (where our hooks are located) given a phytoplankton concentration close to zero (indicated by visibility ~80 m; Barry 1988). Any prey for silverfish would be on or near the bottom and, indeed, crystal krill are known to feed on benthic detritus during winter (Nicol *et al*. 2004, Deibel and Daly 2007). Therefore, perhaps all toothfish, along with their prey, are found at or near the bottom at that time, and not inclined to find our baits. A couple of months later, when the plankton blooms begin and which are sufficiently dense to alter the 1% light level from 54 m to just a few meters deep (visibility to <6 m; Barry 1988, Arrigo *et al*. 1998), there is ample reason for zooplankton and fish to occupy the water column. Then, the depth of toothfish tracks that of silverfish in as noted in McMurdo Sound (Fuiman *et al.* 2002).

If there is a diminution of catch rate after November/December (perhaps in a few years; Testa *et al*. 1985), we hypothesize that this is related to a true decrease in toothfish abundance (especially large fish) owing to predation, which increases severely at that time as Weddell seals attempt to recover from breeding (beginning in late November), as a new cohort of seals begin to forage in the foodweb (late November), and as Ross Sea killer whales appear (early December; Ainley and Siniff 2009, Ainley *et al*. 2009). Dearborn (1965) and Calhaem and Christoffel (1969) reported toothfish eaten abundantly by seals as late as January in McMurdo Sound. Moreover, industrial vessels have been quite successful as well in January (Hanchet *et al*. 2010). Thus, the fish are present. Testa *et al*. (1985) showed that predation affects the spatial extent of toothfish abundance, so why not the temporal extent as well?

Indeed, according to Everson (1970), the movements and annual cycles of nototheniids in the Scotia Sea appear to have evolved to avoid predation by top predators. This brings us back to the question of why it seems that as encountered by the fishery, in ice-free waters, Antarctic toothfish are found on the bottom? Sperm whales and elephant seals (summer, ice-free visitors only) are known to dive to 2400 and 3000 m, respectively, Weddell seals to 700 m, and fish-eating killer whales to 350 m (Ballard et al. 2011); of course average foraging depths are proportionately much shallower. The fishery targets the fish in waters 1000-2000 m. Living at that depth would be out of range for at least two of these predators. In shallower waters, the smaller fish, being also cryptically colored, appear to hide within the “forest” of benthic invertebrates (Eastman and Barry 2002). Of interest, in trophic studies that looked at fish caught in deep waters along the Ross Sea slope and over sea mounts to the north, 59-64% had empty or essentially empty (food “trace”) stomachs (Fenaughty *et al.* 2002). In contrast, surface waters over the slope are teaming with foraging predators, gorging on krill and fish (Ballard *et al.* 2011), and over the shelf in ice covered waters only 10% of toothfish stomachs have been found empty (Eastman 1985b). It would appear that the toothfish in the deep depths are biding their time, awaiting the return of sea ice cover and the seasonal departure of some of their predators. At this time they could be particularly vulnerable to baited hooks.

Decadal Pattern in CPUE. In regard to longer-term change in catch rate, no factor that we used in our analyses could explain the drop off in the CPUE of toothfish in McMurdo Sound beginning after 2001. One could hypothesize that the mega icebergs that blocked McMurdo Sound 2001-2005 were responsible (Arrigo *et al*. 2002), and one of the explanations favored by Hanchet *et al*. (2010, discussing a preliminary report of the McMurdo Sound data set), but other than a temporary effect, no other mesopredator was affected by the icebergs in a long-lasting manner (beyond 2005). In fact, Weddell seal numbers and pup production immediately returned to pre-iceberg levels (Siniff *et al*. 2008), Adélie penguin breeding population in the southwestern Ross Sea increased during this period and through to the present, and the prevalence of emperor penguins in McMurdo Sound increased by an order of magnitude (Landcare Research NZ, unpubl. data; Ainley pers. obs.). All of these species appear to have a broadly similar diet during summer in waters of the southern shelf as do toothfish, principally through high consumption rates of silverfish (cf. La Mesa *et al*. 2004, Ballard *et al*. 2011). The fishing site did not change sufficiently to explain the trend either (see Hanchet *et al*. 2010).

Coincident with the decrease in the CPUE of toothfish, toothfish length (and condition) decreased as well. We can only conclude that the industrial fishery, which targets the largest fish, is reducing their prevalence in the southwestern Ross Sea. Could it also be reducing the prevalence of "high quality" individuals (ones that grow faster and mature quickly and are in better condition), as other fisheries do when targeting the largest, oldest fish (Longhurst 2010, Ainley *et al*. 2011)? Apparently this is happening in the heavily fished Patagonian toothfish of the Scotia Sea, although detected over a longer time period (Shust and Kozlov 2006). Given the inability of the industrial fishery to catch many large Antarctic toothfish over the Ross Sea shelf (Hanchet *et al*. 2008, 2010), fishery biologists dependent on CCAMLR data would not be aware of this decreasing prevalence of large fish. Indeed, Hanchet *et al*. (2010) state that trends are unlikely to be found in the industrial catch data owing to the high variability in catch rates and characteristics of individual vessels.

A change in the representation of large fish in the southern Ross Sea, indicative of the entire stock, would not be ecologically neutral (Longhurst 2010, Ainley *et al*. 2011 and references therein). How to detect this change is a challenge. Such a change was involved in the crash of Atlantic cod *Gadus morhua*, where the diminishment of the inshore portion of the stock occurred well before any signal was evident in the larger offshore stocks and prior to the eventual total collapse of the fishery (Longhurst 2010, and references therein). In accord with the decreasing numbers of large fish, the Ross Sea killer whale prevalence in the southwestern Ross Sea continues to decrease (Ainley *et al*. 2009, unpubl. data), a pattern played out by the now endangered large-fish-eating, resident killer whales in waters of western Canada and Puget Sound (Ford *et al*. 2010). The killer whale social structure depends on the existence of large fish. The increase in penguin populations would be consistent as well with decreased competition with toothfish for silverfish prey.

Recommendations

We could suggest that this toothfish fishery in the Ross Sea be closed until the natural history of Antarctic toothfish, and its silverfish prey, is much better understood, given the observation of recent declines in condition, size, and CPUE for the Antarctic toothfish of McMurdo Sound, the only monitoring conducted independent of the fishery. An easier option to implement, given that New Zealand has taken 55% of the toothfish from the Ross Sea area (Ainley *et al*. 2011) and that the United States imports 40% of the total world catch of “Chilean sea bass” (including Ross Sea fish; US Dept of State website), is for NZ and US fishery agencies to immediately reconstitute the scientific fishing program described herein as it was up to 2001 (annual, entire season), as well as initiate other research, e.g. monitoring of dependent species, that would be independent of the unexplained biases in the industrial sampling. Besides McMurdo Sound, vertical longlines could be deployed in an analagous fashion through the seasonally long-lasting fast ice of Terra Nova Bay as well as Edisto-Moubray bays farther north along the Ross Sea coast. Doing so would be consistent for an agency, CCAMLR (Commisison for the Conservation of Antarctic Marine Living Resources), that has made its name as setting the pace in ecosystem-based and precautionary management and which has a formal monitoring program (CCAMLR Ecosystem Monitoring Program; CEMP) from which management of fisheries is supposed to become effectively informed (Constable *et al*. 2000, Croxall and Nicol 2004, Constable 2011). Trends in the "unofficial CEMP" based on changes in numbers of fish-eating killer whales, seals and penguins underway in the southern Ross Sea, by scientists engaged in pure rather than fishery-directed research, is pointing to the need for meaningful action.

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Table 1 Summary of data used to calculate changes in fish length, condition and catch per unit effort (based on hooks deployed). If the field "total hooks fished" is blank, then no effort data were available for that year. Other aspects of "standardizing" the effort, include: vessel = same each year (fish hut); vessel operator = same (DeVries); fish measurer = same (DeVries); gear = same (vertical set line, number of hooks varied, as indicated); location = same, i.e. within 2 km radius off Cape Armitage, except in a couple of years as noted in Fig 1; depth = 415-495 m in all years.

Year	Dates	24 h fishing periods	N fish caught (measured)	Total hooks fished	Fish per hook
1972	9/15-12/13	90	96 (96)		
1973	9/11-12/6	86	184 (184)		
1974	9/8-12/19	105	470 (470)		
1975	9/16-12/29	105	346 (331)	2525	0.137
1976	12/1-1/2	33	167 (160)	485	0.344
1977			-		
1978	10/15-12/21	67	349 (341)	1113	0.314
1979	10/18-12/11	55	261 (255)	938	0.278
1980	10/20-12/15	57	202 (184)	1373	0.147
1981	10/13-12/20	69	268 (255)	1986	0.135
1982	10/12-12/22	71	499 (218)	2939	0.170
1983	10/13-12/20	69	553 (546)	3155	0.175
1984	10/1-12/8	69	205 (200)	1338	0.153
1985	10/15-12/20	67	318 (315)	1690	0.188
1986	11/2-12/30	58	151 (141)	783	0.193
1987	10/11-12/10	60	412 (407)	1388	0.297
1988	9/4-12/11	98	294 (294)		
1989	9/7-12/6	90	182 (178)	1185	0.154
1990	8/31-12/8	100	283 (265)	1190	0.238
1991	11/19-11/30	11	7 (7)		
1992	9/9-11/18	70	32 (31)	231	0.139
1993			-		
1994			-		
1995			-		
1996			-		
1997	10/11-12/14	64	72 (72)	442	0.163
1998	10/9-12/9	61	243 (243)		
1999			-		
2000			-		
2001	11/14-12/11	27	76 (76)	499	0.144
2002	10/18-12/15	59	91 (91)		
2003	10/3-12/22	80	17 (17)		
2004	10/11-12/22	74	19 (19)		

2005	1/10-1/14	5	0		
2006	*	*	*		
2007	10/18-11/30	73	2 (0)	660	0.003
2008			-		
2009	12/1-12/20	20	0	117	0.000
2010	10/26-12/3	38	10 (7)	162	0.043

* Another researcher (G. Hofmann, pers. comm.) at site off Cape Armitage (same location as most others shown in Fig 1) in late Nov 2001, 10 24-h sets (15 hooks/set), caught 71 fish (included in the 2001 total); in late Nov 2006, approximately same site, 7 24-h sets (12 hooks/set), caught 0 fish.

Table 2 Weighted regression analysis of percentile total length (A, B) and mean condition index, *K* (C); shown are statistics for the two-part spline model and for the difference in slope 1972 to 1992 and from 1992 to 2010 (N = number of years analyzed).

	N	Df	F	*P*	Adj r^2
A) TL 75th percentile					
2-part spline model	27	2, 24	11.07	0.004	0.436
Test of difference in slope		1, 24	11.75	0.002	
B) TL 95th percentile					
2-part spline model	27	2, 24	5.09	0.014	0.24
Test of difference in slope		1, 24	7.32	0.012	
C) Mean condition, K					
2-part spline model	27	2, 24	13.77	0.001	0.496
Test of difference in slope		1, 24	27.07	0.0001	

Table 3 Regression analysis of total length (A, B) and condition index, *K* (C, D) using individuals (N) and comparing data sets with (A, C) and without (B, D) 1991 and 1992. Shown are results of models for 2-part spline (estimated slope up to1992 plus estimated slope since1992, with knot at 1992) and for the difference in the two slopes. All models included month of capture (df = 3, for September, October, November, and December).

	N	Df	F	*P*	Adj R^2
A) Total Length, all years					
full model (includes month)	5437	5, 5431	30.15	0.0001	0.0261
2-part spline component		2, 5431	41.42	0.0001	
Test of difference in slope		1, 5431	25.89	0.0001	
B) Total Length, without 1991 & 1992					
full model (includes month)	5399	5, 5393	29.34	0.0001	0.0256
2-part spline component		2, 5393	38.48	0.0001	
Test of difference in slope		1, 5393	23.25	0.0001	
C) Condition, all years					
full model (includes month)	5403	5, 5397	24.66	0.0001	0.0214
2-part spline component		2, 5397	55.94	0.0001	
Test of difference in slope		1, 5397	108.61	0.0001	
D) Condition, without 1991 & 1992					
full model (includes month)	5365	5, 5359	22.98	0.0001	0.0201
2-part spline component		2, 5359	50.66	0.0001	
Test of difference in slope		1, 5359	99.46	0.0001	

Table 4 Summary of statistics for regression analyses with respect to fish length (75th and 50th percentiles) and mean condition in relation to environmental variables, and relationship between SOI and Max ice. N = number of years analyzed.

	N	df	F	*P*	Adj r^2
TL 75th percentile-Max ice area 4 yr lag	17	1, 16	4.63	0.048	0.1849
TL 50th percentile-Max ice area 4 yr lag	17	1, 16	8.78	0.009	0.3273
Condition – Min ice area 8 mo lag	20	1, 19	4.99	0.039	0.1734
Condition – Max ice extent 3 yr lag	18	1, 17	4.98	0.040	0.1895
TL 75th percentile – SOI (July-Dec) 4 yr lag	25	1, 24	1.59	0.219	0.0242
SOI – Max ice area same year	29	1, 28	20.5	0.0001	0.4101

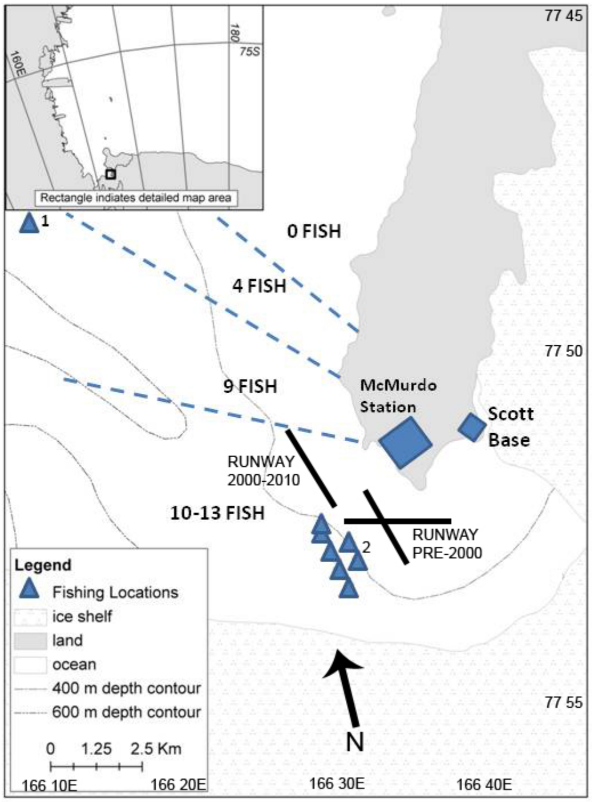

Figure 1 Southern McMurdo Sound showing locations where the set line was positioned seasonally, 1972-2010. Numeral 1 indicates position of fishing site in 2009 and 2010, as well as site of “Penguin Ranch”, where Ponganis and Stockard (2007) recorded numerous seals capturing toothfish in 2003 and 2004; numeral 2 is alongside positions where fishing was otherwise conducted; movement of sites in part forced by shifting location of the sea ice runways (only the two most common runway positions shown). The dashed lines separate zones of fishing success attained by Testa *et al.* (1985; fish per day) as a function of distance from the major Weddell seal breeding location, which is in top right corner of map.

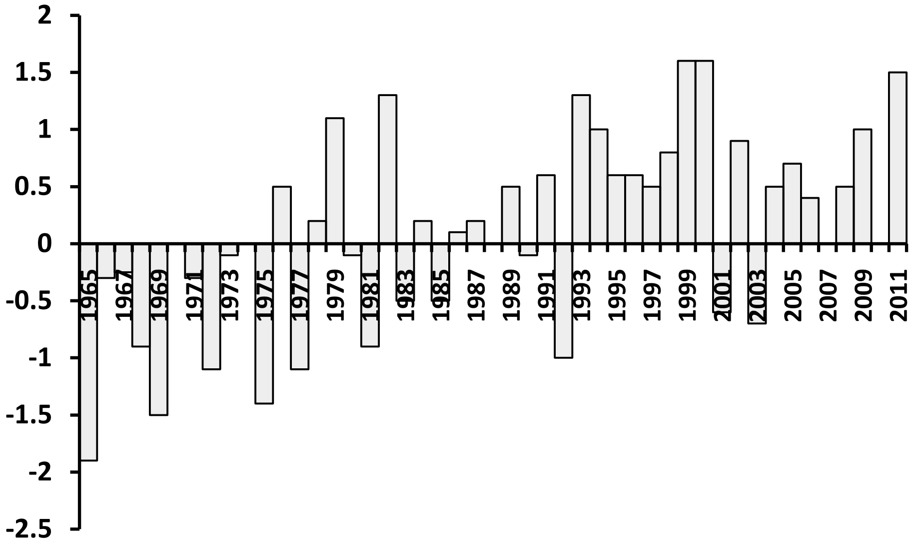

Figure 2 Variation in Southern Annular Mode, 1965 – 2011, values on 1 Jan each year (data from http://www.antarctica.ac.uk/met/gjma/sam.html).

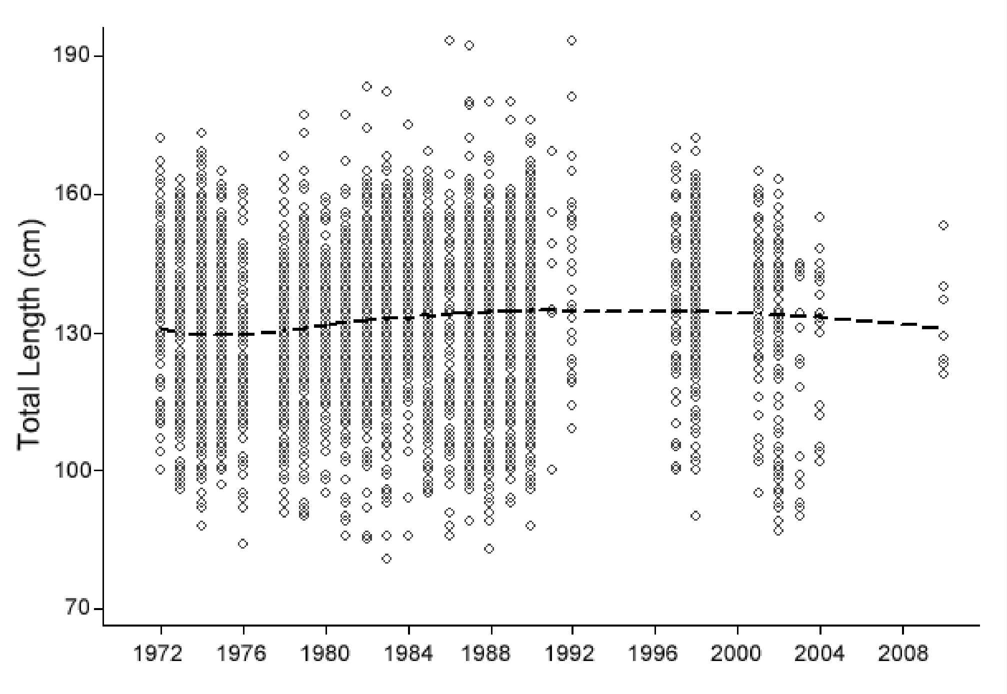

Figure 3 Length-frequency of Antarctic toothfish caught in southern McMurdo Sound, 1972-2010. Dashed line is the locally weighted regression (lowess, using running-line least squares) of length on year.

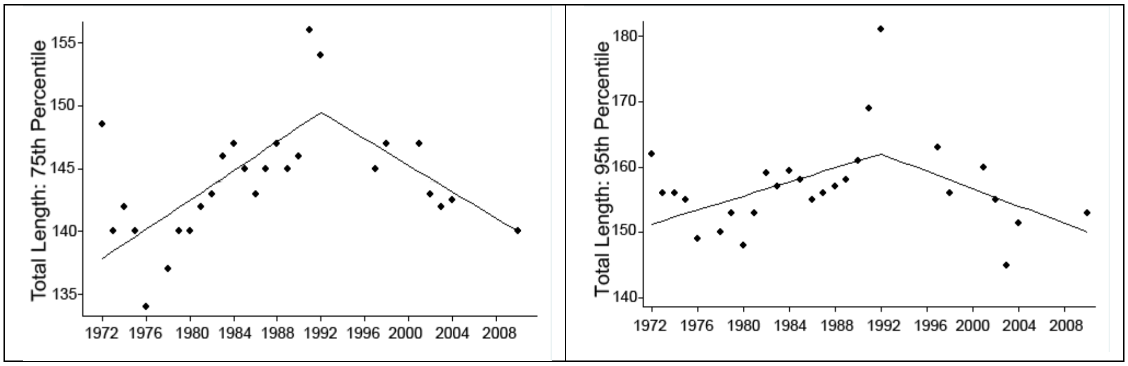

Figure 4 Left, change in fish length in the McMurdo Sound catch, expressed as the 75th percentile of length; right, change in fish length in the McMurdo Sound catch, expressed as the 95th percentile of length, 1972-2010.

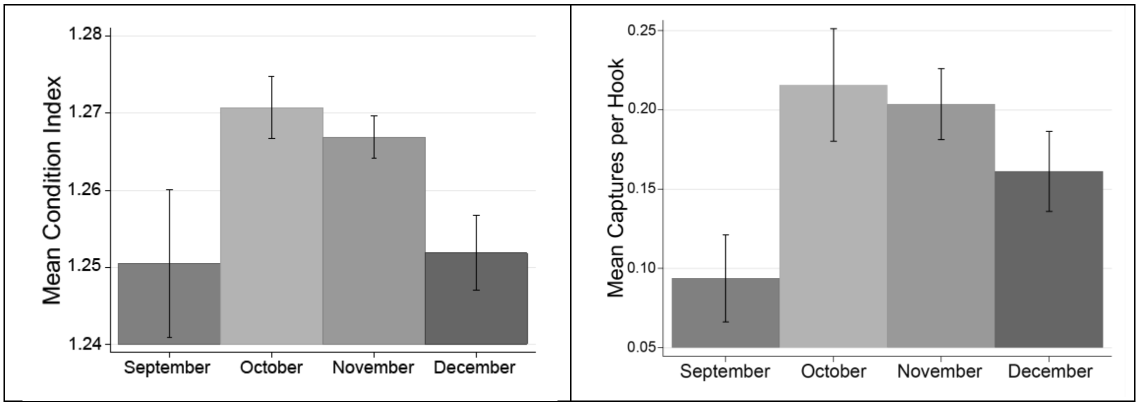

Figure 5 Left, mean toothfish condition and standard error among fish caught in McMurdo Sound, monthly, 1972-2010 (n >5500 fish); right, mean catch per unit effort and standard error by month over the period 1975-2010.

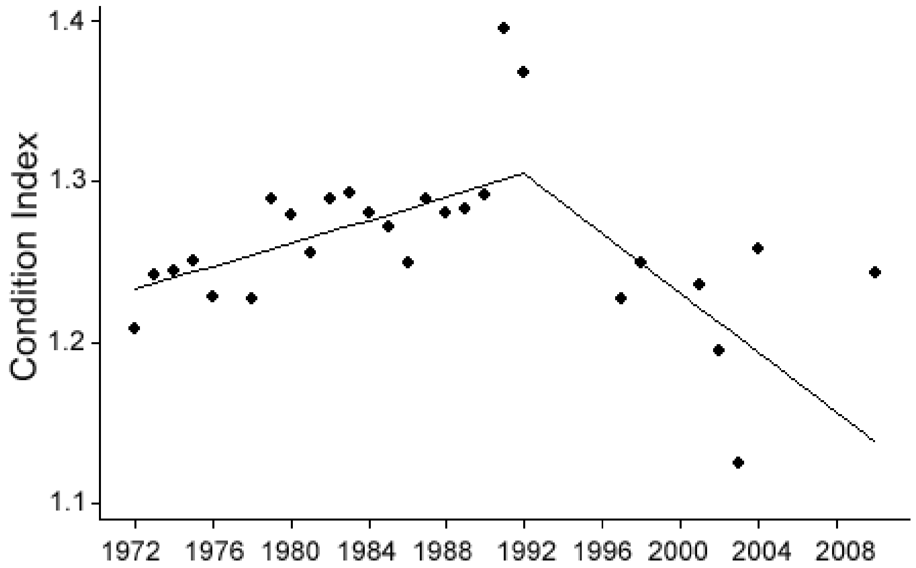

Figure 6 Trends in mean fish condition, K, among fish caught in McMurdo Sound, 1972-2010

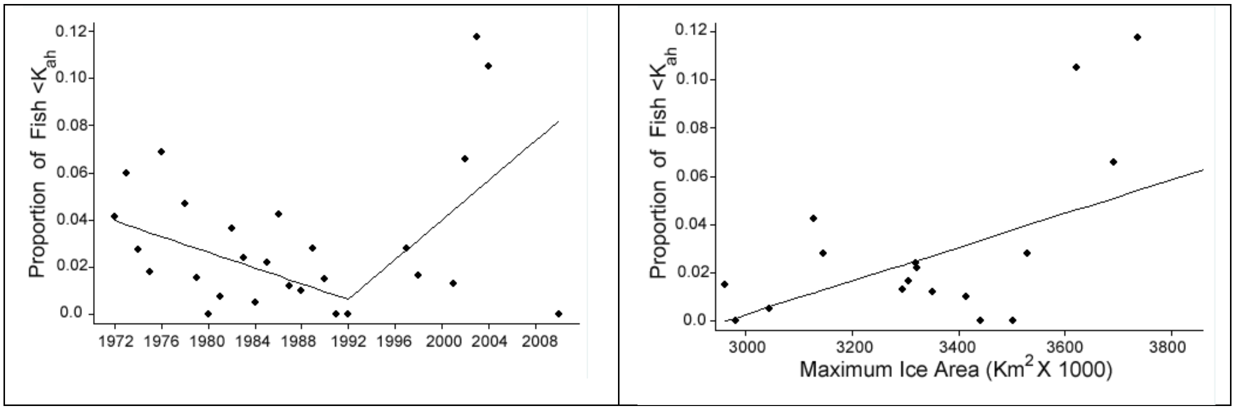

Figure 7 Left, change in prevalence of axe handle fish in the McMurdo Sound toothfish catch, 1972-2010; right, relationship between proportion of axe handle fish in the catch and maximum ice area 4 years earlier.

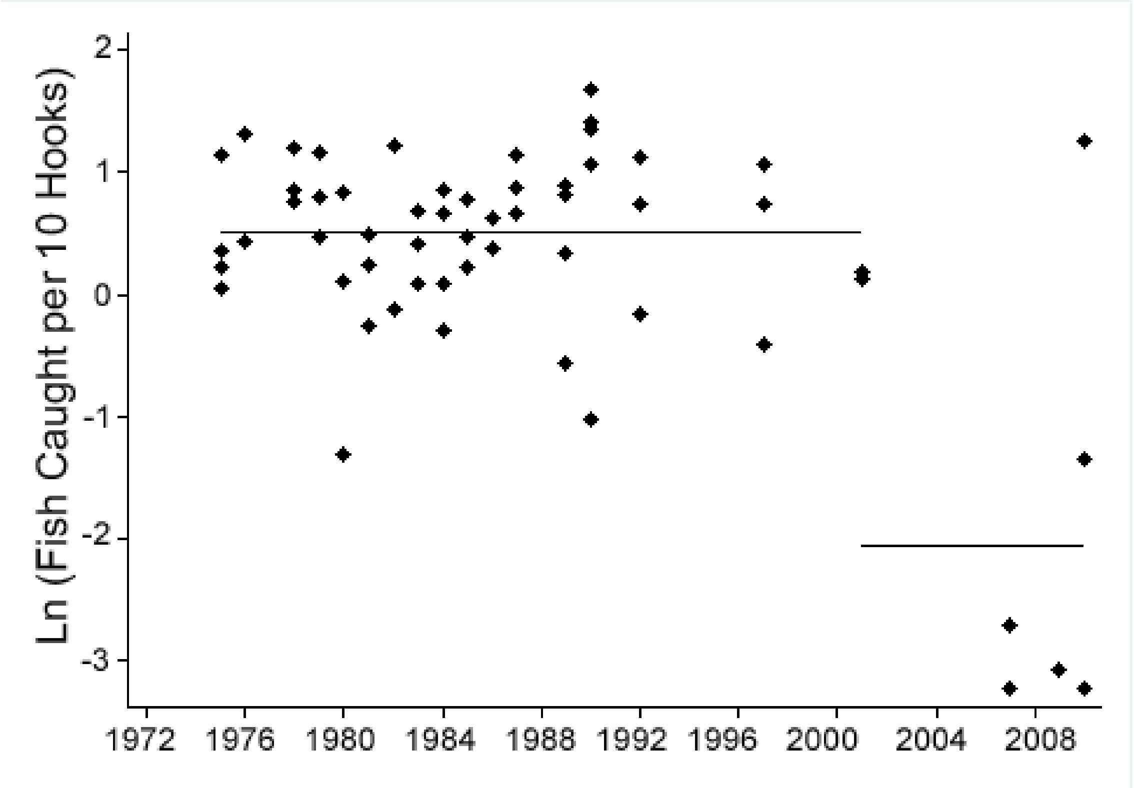

Figure 8 Annual variation in fish captures (ln-transformed) per 10 hooks set in McMurdo Sound, 1972-2010. Monthly variation in capture rates, after adjusting for month of capture, as well as best-supported model for annual variation (stair-step), are shown.

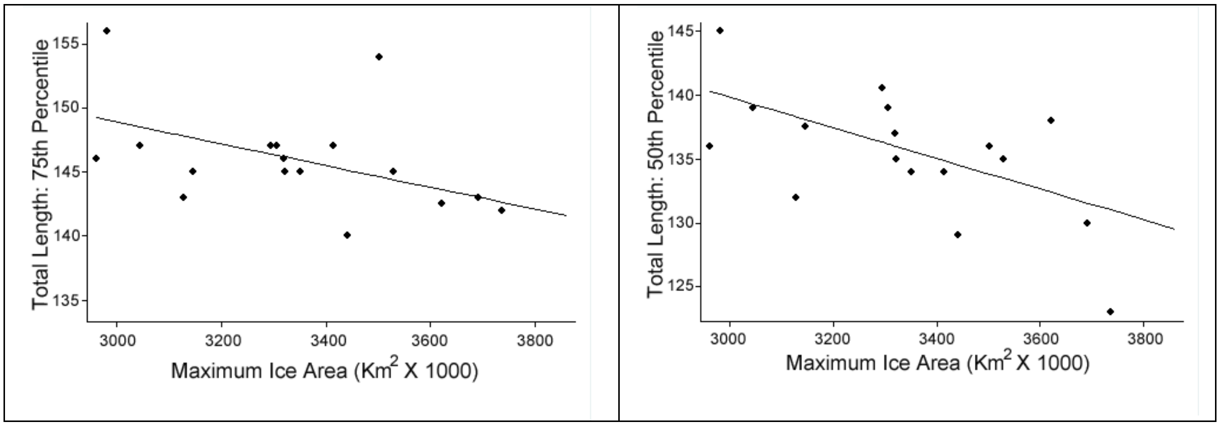

Figure 9 Fish length as affected by maximum ice area, 4 years previous, for both 75th and 50th percentile.

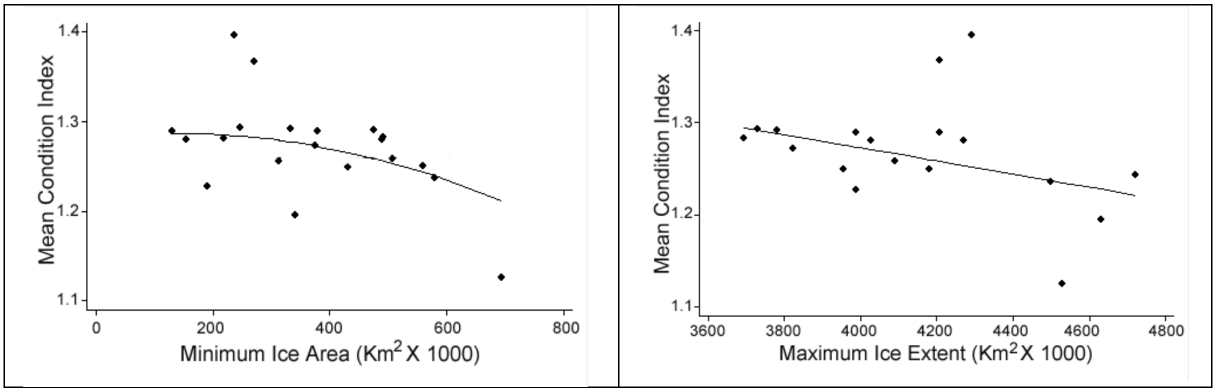

Figure 10 Left, mean condition index in relation to minimum ice area 8-10 months previously, 1979-2007; right, fish condition as affected by ice extent three years previously, 1979-2007.

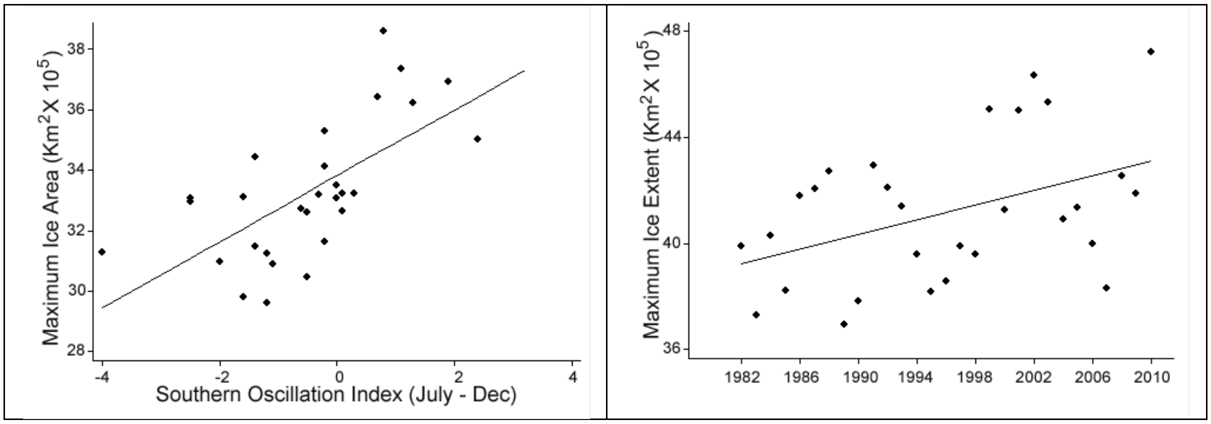

Figure 11 Left, relationship between maximum ice area and SOI during July-December of same year; right, trend in maximum ice extent 3 years previously during the study period (consistent with Zwally *et al*. 2002, though a longer time series).