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# Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972–2011

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## Abstract

We report the analyses of a dataset spanning 39 years of near-annual fishing for *Dissostichus mawsoni* in McMurdo Sound, Antarctica, 1972–2011. Data on total length, condition and catch per unit effort (CPUE) were derived from the > 5500 fish caught, the large majority of which were measured, tagged and released. Contrary to expectation, the length frequency of the McMurdo Sound catch was dominated by fish in the upper two-thirds of the overall distribution exhibited in the industrial catch for the Ross Sea shelf. Fish length and condition increased from the early 1970s to the early 1990s and then decreased. Fish length positively correlated with Ross Sea ice extent in early spring, a relationship possibly caused by more ice encouraging larger fish to move farther south over the shelf and into the study area. Fish condition positively correlated with the amount of open water in the Ross Sea during the previous summer (Feb), perhaps reflecting greater availability of prey with the higher productivity that more open water brings. Decreasing fish size corresponds to the onset of the fishery, which targets the large individuals. CPUE was constant through 2001 and then decreased dramatically. We hypothesize that this decrease is related to the industrial fishery, which began in the 1996–97 austral summer, and concentrates effort over the ice-free Ross Sea continental slope. As a result of limited prey choices and close coupling among mesopredators of the region, Antarctic toothfish included, the fishery appears to be dramatically altering the trophic structure of the Ross Sea.

**Keywords** Antarctic toothfish, Antarctic silverfish, climate change, change in fish condition, change in fish abundance, sea-ice, Ross Sea, Southern Ocean

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## 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: the Notothenioidei (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 fishes to radiate opportunistically and to fill most benthic and pelagic niches, despite the lack of a swim bladder. For example the 2-m-long Antarctic toothfish (*Dissostichus mawsoni*, Nototheniidae) and the 15 to 25-cm-long forage species, Antarctic silverfish (*Pleuragramma antarcticum*, Nototheniidae), are key piscine predator and prey in Antarctic continental shelf ecosystems (Eastman 1993), despite 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). Over the continental slope, the main preys of toothfish are benthic grenadiers or rattails (*Macrourus* spp., Macrouridae). On the contrary, subadult and adult toothfish are important prey for Weddell seals (*Leptonychotes weddelli*, Phocidae), killer whales (*Orcinus orca*, Delphinidae) and sperm whales (*Physeter macrocephalus*, Physeteridae) as well as colossal squid (*Mesonychoteuthis hamiltoni*, Chranchiidae; Yukhov 1970; Pinkerton *et al.* 2010; Ainley 2010; Ainley and Siniff 2009; Ainley and Ballard 2012). The Ross Sea is the least anthropogenically altered stretch of ocean 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.

Understanding the trophodynamics of the Ross Sea shelf ecosystem requires detailed information on all of its predators and mesopredators, as it appears that their relationships are closely coupled. Indeed, prey consumption by cetaceans negatively affects the foraging area and diet of penguins (Ainley *et al.* 2006), the foraging of Weddell seals can negatively affect the prevalence of toothfish (Testa *et al.* 1985), and the foraging of most mesopredators, as well as silverfish, appears to reduce the abundance of krill (Ainley *et al.* 2006). Whereas much is known about the air-breathing members of the group, all of which have nowhere to hide from researchers, 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 fish 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 it 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 enable survival at subzero temperatures, including tissue antifreeze (DeVries 1988; DeVries and Cheng 2005) and other adaptations (Eastman 1993); it grows rapidly when a subadult (although this then slows); and it can live to 50 years. On the other hand, the ecology and population dynamics of Antarctic toothfish have remained obscure. From the 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.* 2011), and gained insights into variation in condition (Fenaughty *et al.* 2008), age of recruitment (Parker and Grimes 2010), and diet of individuals along the Ross Sea continental slope (Fenaughty *et al.* 2003). Otherwise, much remains to be learned about the Antarctic toothfish, unlike its only congener, the Patagonian toothfish (*D. eleginoides*, Nototheniidae), 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 aspects of larval and juvenile life history remain unknown (Parker and Grimes 2010). This information gap is in large part the result of the difficulty of scientific investigation in this species’ ‘preferred habitat’: deep, cold, ice-covered ocean. Any data from the fishery are limited to just the 3–4 months of ice-free summer (December–March).

In an effort to increase the understanding of this important Southern Ocean mesopredator, we present results of analysis of data collected from > 5500 fish captured, measured, marked and released, during an extended effort led by one of us (DeVries) almost annually in McMurdo Sound, southern Ross Sea, 1972–2011. The data set constitutes one of the longest biological time series available for the Southern Ocean, the only long time series for a fish species there, and one of the few studies of catch per unit effort (CPUE) and fish size that preceded the onset of a fishery. Fishing, inaugurated in 1996–97, occurs within ~60 km of the McMurdo Sound study site, and is now the largest fishery for toothfish south of the Antarctic Polar Front (CCAMLR 2010).

In addition, the data set persisted through a period that has seen interesting changes in the Ross Sea, in large part driven by climatic forces. The Southern Annular Mode, for example shifted from mostly negative early in the period to mostly positive, leading to a marked increase in winds, sea-ice extent and area, and persistence of the coastal polynyas that strongly affect Ross Sea processes (Jacobs *et al.* 2002; Parkinson 2002; Zwally *et al.* 2002; Jacobs 2006; Russell *et al.* 2006; Stammerjohn *et al.* 2008). In our analysis, we examine trends in toothfish condition, size and prevalence and report on correlations with the above-described environmental and anthropogenic changes.

## Methods

### Fish capture

Scientific fishing occurred primarily from one site, about 4 km west of McMurdo Station, in the vicinity of 77° 51′S, 166° 40′E (Fig. 1). The fishing site shifted slightly from year to year to deal with pres-

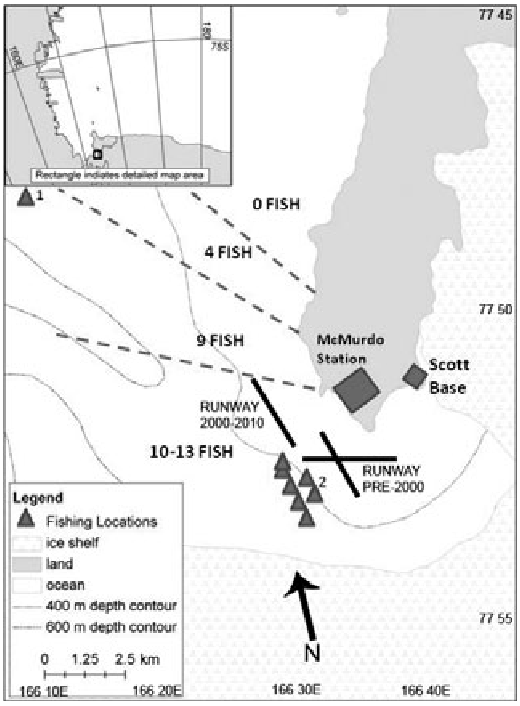

**Figure 1** Southern McMurdo Sound showing locations where the setline was positioned seasonally, 1972–2010. Numeral 1 indicates position of fishing site in 2009 and 2010, as well as the site of the 'Penguin Ranch', where Ponganis and Stockard (2007) recorded numerous seals capturing toothfish in 2003 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 runway (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 the top right corner of the map.

sure ridges, snow banks, etc., and, after 1999, to accommodate aircraft approach to the Sea-Ice Runway. Nevertheless, all sites but one occurred within about a 2-km radius, with depth ranging 415–495 m. Moreover, all sites were within the area in which the broad-scale survey by Testa *et al.* (1985; Fig. 1) logged high catch rates of Antarctic toothfish and also within the area in which Weddell seals have been frequently seen with toothfish (Ainley and Siniff 2009), even to 2010.

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), a line was deployed through a hole drilled in the annual fast ice. A heated fish house was placed over the hole. In the first year, 10–15 one-meter leaders spaced 20–25 m apart with swiveled, stainless steel, #9 treble hooks were fished. Thus, the lower ~300 m of water column was sampled, but not 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 for all years thereafter, leaders were shortened to 30 cm (similar to that in the fishery; CCAMLR 2008) and 15–20 hooks were spaced 3–5 m apart, starting 10 m from the bottom, thus sampling the lower ~100 m of water column. In the first year, it was also found that the hooks left large wounds in the jaw, likely leading to reduced survival. Therefore, long-shanked #10 stainless hooks were used thereafter (similar to the fishery, which uses long-shanked #10; CCAMLR 2008).

For the first 3 years, live *Pagothenia borchgrevinki* (Nototheniidae) was used for bait, but it was then found that dead bait worked just as well. Thereafter, New Zealand yellow-eyed mullet (*Aldrichetta forsteri*, Mugilidae), cut in half, was used. Sometimes 12-h sets were made but the vast majority was 24-h sets; given that it took 2–3 h to retrieve and re-bait the line, therefore, 'soak' time was ~21 h on almost all deployments. Some sets 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, long soak times were avoided if possible (overall < 10% of sets were > 24 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 centimetre, weighed to the nearest pound (converted to kilogram), tagged with both 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 Tatarnikov 2010). Some 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 hooked fish because they take both small and large toothfish (Ainley and Siniff 2009; Kim *et al.* 2011), it certainly cannot be other fish species because there are none 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.)

### Data analysis

#### *Fish metrics*

*Overall strategy*. Our primary objectives with regard to analysis were twofold: first to characterize change in fish metrics (length, condition and capture rates) over the study period (1972–2011), and then to identify environmental variables that may be influencing variation in these metrics among years.

Analyses were conducted on variation in condition and length of toothfish (for condition, $n = 5404$ individuals, and for length, $n = 5438$, among the 5588 caught from year of data), using (1) 50th and 75th percentiles of total length (TL) in each year and (2) mean condition index ($K$) for each year. Although the median TL for a year provides a way to characterize the central tendency of the fish sample, an additional objective was to analyse variation (over time and with respect to environmental variables) specifically among larger fish, and therefore we analysed the upper quartile (75th percentile) value of TL. Total length was considered to be an index of both body size and approximate age (Horn 2002; Brooks *et al.* 2011). In addition, (3) analyses were repeated substituting mass index for condition index and thus eliminating any confounding because of length. (4) We analysed $K$ in relation to length. (5) We confirmed the analysis of annual values of condition and length by analysing trends with respect to the condition and length of individual fish. Finally, (6) we assessed the number of individuals caught per unit effort in relation to year as part of a 'catch per unit effort' study (see 'Catch per unit effort' below). Fish having measurements that clearly were wrongly recorded were excluded from the data.

Presented are results of toothfish length, condition and CPUE in relation to variation among years, examining both linear and non-linear trends. To allow for non-linearity, several types of models were fitted with respect to the explanatory variable of interest (either year or an environmental variable) and we chose the model that optimized Akaike Information Criterion (AIC). The models considered included a (1) linear model, (2) quadratic model, (3) cubic model and (4) quartic model. We also included transformations of the linear variable, specifically (5) inverse transformation, (6) natural log transformation and (7) quadratic transformation. The difference between (2) and (7) is that the former fits a true quadratic equation (i.e., includes linear and quadratic terms) and allows the dependent variable to attain an intermediate maximum or minimum, whereas the latter fits only a single monotonically increasing or decreasing trend, but allows for curvature of the trend (either upturned or downturned) (described in detail below). The final set of models examined variation with respect to year using (8) 'change-point' analyses with linear splines (Harrell 2001, pp. 18–19; Greene 2003). In this latter analysis, 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 of the fish metric in question over the course of the study period. Change-point analysis is an important tool because it allows us to identify and/or confirm a discrete change in trend during the study period. A quadratic equation also allows for a change in trend, but, in contrast to the linear spline change-point analysis, the former assumes that the trend over time is changing at a constant rate. We report the model among (1)–(8) that optimized AIC as well as competitive models (those within 2 AIC units). For change-point analysis, the location of the change point is the year X that optimizes AIC among all years considered, where X is constrained to be a year included in the data set analysed (i.e. to simplify the choice, only years with data were considered for a possible 'knot').

Being an exploratory analysis, we compared models with different change points to identify the change-point model with maximal explanatory power and then compared AIC for such a model with (1)–(7).

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 from months to 5 years. Therefore, we looked at the effect of ice cover and its persistence 8 months to 5 years before the current (ice-covered) fishing season (October–December). However, no lagged environmental variable proved significant in explaining variation in length, condition or CPUE.

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

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

where $W$ = body mass in g and $TL$ = total length in cm. Larger values for $K$ indicate greater mass 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, $K_{\mathrm{ah}}$, 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 analysed 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 (Fenaughty *et al.* 2008).

Individual condition data came almost entirely (99.9%) from captures in 4 months: September, October, November and December; 28.1% of captures were in October, 50.0% were in November. As captures were essentially confined to 4 months, we analysed monthly variation in condition and length by treating month as a factor with four levels (i.e. as a categorical variable, such that the five captures in August or January were combined with September or December respectively). Thus, in controlling for the effect of month, we make no assumptions about how the dependent variables change from month to month.

The resulting condition index, $K$, nevertheless demonstrated a significant association with length (see below; $P < 0.0001$ in each case for quadratic, cubic or quartic equations). In other words, in our sample, condition varied with TL in a non-linear fashion. Therefore, we developed a Mass Index, *MI*, such that *MI* was statistically independent of length. To do so, we fit a model of cube root of mass in relation to TL, $\mathrm{TL}^2$, $\mathrm{TL}^3$ and $\mathrm{TL}^4$. The model also controlled for variation in mass among the 4 months. Higher order terms of TL, i.e. $\mathrm{TL}^2$, $\mathrm{TL}^3$ and $\mathrm{TL}^4$, were included only if the latter was significant. We maintain that consideration of both condition and mass index enables us to better interpret temporal variation with respect to condition.

Mean $K$ and *MI* were calculated for each year, as was the proportion of fish below the axe-handle threshold. For analysis of annual variation in mean mass and condition indices, we weighted the mean value by the inverse of the standard error of the mean (either mass or condition; Kutner *et al.* 2004). Similarly, for annual variation in length, we weighted the 50th and 75th percentiles for a given year by the inverse of the standard error of mean length for that year. Weighted regression is appropriate where observations (in this case, mean values) display heteroskedasticity (Kutner *et al.* 2004), as was the case here. The weighting reflected the sample size as well as the individual-level variability in the metric for that year (e.g. the smaller the variance, the tighter the confidence interval around that mean, and the greater the weight). However, there were 3 years with very small sample size (i.e. $n \leq 7$): 1991, 2010 and 2011. Owing to the small sample size, we considered mean, median and 75th percentile values to be unreliable for those years. Therefore, analysis of annual values for mass and condition indices and length only used years for which the sample size was $\geq 17$ ($\overline{X} = 215.6$ per year).

*Catch per unit effort.* To analyse patterns in toothfish catch rate, i.e. CPUE, we analysed the number of fish caught in relation to the most appropriate measure of capture effort. Apparent effort varied with respect to the number of hooks set and the number of hours per hook (often approximately

24 h, but sometimes ~12 h or ~48 h; see above). Once the number of hooks was controlled for, the number of hours per hook was not significant; therefore, CPUE analysis was in relation to hooks set per session. We also analysed effort as a separate covariate, such that the dependent variable was the number of individuals caught. Statistical results were similar using either method (dividing number caught by effort or statistically controlling for effort); we only report the former, CPUE, because it is more widely used.

We conducted the abundance analysis in two ways: (i) captures per 10 hooks, natural log-transformed, analysed by individual fishing session ($n = 1229$) and (ii) captures per year per 10 hooks, ln-transformed, where captures and hooks were summed per year, with annual values being analysed ($n = 20$ years). Effort differed among months, and so did the capture rates with respect to month (see below; also Testa *et al.* 1985). We therefore analysed between-year variation in CPUE while controlling for month of capture, when analysing CPUE by individual fishing session. Time-series analysis was applied to analysis of annual values, as was the case for length and condition (see below).

*Time-series analysis.* We used time-series analysis to analyse variation in the annual values of length, condition and CPUE. For these variables, we modelled the relationship of the dependent variable to year (considered as linear or various non-linear models, as described above) including a first-order autoregression component ('AR1'; Chatfield 1989). Where the AR1 component was significant or marginally significant, we report results of such analyses. Where the AR1 component was not significant ($P > 0.1$), we re-ran the analyses without the AR1 component, and report those results.

We compare results of annual analyses with statistical analyses of individual fish (length, condition) or individual fishing session (CPUE). The analyses of individual fish or fishing session controlled for monthly variation (i.e. among calendar months) but did not control for autoregression. Concurrence of the two approaches (time-series analysis of annual values and analyses of individual fish or fishing sessions, controlling for calendar month) demonstrates the robustness of our conclusions.

In addition, *MI* was calculated on an annual basis and annual values controlled for monthly variation. As noted, results for *MI* and *K* were very similar.

*Environmental variables*

*Sea ice.* Using satellite passive microwave data for the Ross Sea sector from the NASA Nimbus 7 satellite and the Defense Meteorological Satellite Program (e.g., Parkinson 2002; Zwally *et al.* 2002), ice area (total areal coverage of ice, excluding water between ice floes; more specifically, the sum of the product of the area of each pixel of the satellite data times the ice concentration in that pixel) and ice extent (area of ice and the intervening water between ice floes; more specifically, the sum of the area of each pixel with ice concentration of at least 15%) 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. 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 month of maximum ice coverage varied from August to 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 or with reference to maximum or minimum monthly value. As maximum ice area/extent was usually observed in September and October, we also analysed the mean of the 2 months, 'September–October' ice extent and ice area.

*Southern oscillation.* We examined the importance of the Southern Oscillation (using the SO Index, SOI) which by influencing ocean characteristics may directly or indirectly affect toothfish, as is the case with other Ross Sea mesopredators (Testa *et al.* 1991, Wilson *et al.* 2001, Ainley *et al.* 2005; Rotella *et al.* 2009). Other studies have shown that the state of the sea-ice in this part of the Southern Ocean is affected by the atmospheric processes embedded in SOI (Jacobs 2006; Stammerjohn *et al.* 2008).

We used monthly SOI to calculate six metrics. The first three were average annual SOI (January–December), the average for January–June and the average for July–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 $(\text{SOI} - c)^2$ where $c$ = maximum (positive value) of the SOI metric (12-month average or either of the 6-month averages). $(\text{SOI} - c)$ was thus always zero or negative, and the stronger the El Niño, the more negative was the value. Squaring $(\text{SOI} - c)$ 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 analysing fish condition or length.

For all single-variable regression models, we report the regression coefficient ($\beta$). Where more than one environmental variable was analysed 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.

## Results

### Characterization of the catch

Between 1972 and 2011, 5588 toothfish were caught, including 835 kept for experiments and/or whose survival was in doubt (Appendix S1). The largest fish caught was 193 cm TL (92 kg in mass) and the smallest was 77.5 cm (4.5 kg); individuals between 120 and 170 cm predominated, with only 2.5% smaller than 100 cm (Fig. 2).

Of the 4752 fish tagged and released in the study, 17 have been recaptured (0.36%) 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.* 2011). 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 a 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 year after release, with the longest interval being 18 year. The fact that only a few recaptures have occurred > 7 year after initial tagging, over the 30 years of fishing, is puzzling given that capture and release procedures did not vary. 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 recapture rate and this one could well be due to (i) McMurdo Sound fish being more transient than those on the main fishing grounds (continental slope); (ii) 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); or (iii) the population of fish in McMurdo Sound was previously very large, thus diluting the probability of re-catching. It has only been in the last few years that there has been a vigorous industrial tag-recapture programme. Previously, there was no effort to look for tagged fish.

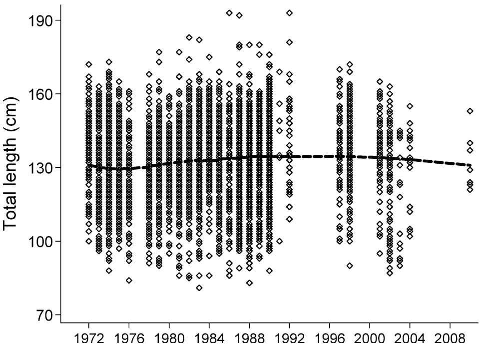

**Figure 2** Length-frequency of Antarctic toothfish caught in southern McMurdo Sound, 1972–2010 (single 77-cm fish caught in 2011 not shown). Dashed line is the locally weighted regression (lowess, using running-line least squares) of length on year.

### Fish length

The overall pattern of annual variation during the study period was similar for both metrics of fish length (median and upper quartile; Table 1). The first-order autoregressive component (AR1) was significant ($P = 0.05$) for year when analysing 75th percentile length; therefore, we report results that include the AR1 component for both median and upper quartile TL.

The most parsimonious model, favored by AIC, describing the pattern of change in median TL across years was an increasing but decelerating trend (Table 2, Fig. 3). An increase in median TL is apparent well beyond 1992 and the trend con-

**Table 1** Statistical summary of preferred models for fish metric annual trends; result of weighted regression model of annual values.

| Variable | df | Estimate | SE | *P* value | Footnotes |
|---|---|---|---|---|---|
| (A) Median Length (cm, $n$ = 25) | | | | | 1 |
| Quadratic-transform of year | 1 | −0.00762 | 0.00371 | 0.040 | |
| Intercept | 1 | 137.29 | 2.39 | <0.0001 | |
| AR1 | 1 | 0.236 | 0.224 | 0.29 | |
| (B) 75th percentile length (cm, $n$ = 25) | | | | | 1 |
| Year linear | 1 | −1.398 | 0.720 | 0.052 | 2 |
| Year quadratic | 1 | 0.157 | 0.0674 | 0.020 | |
| Year cubic | 1 | −0.00367 | 0.00164 | 0.025 | |
| Intercept | 1 | 143.53 | 1.99 | <0.0001 | |
| AR1 | 1 | 0.449 | 0.227 | 0.050 | |
| (C) Mean condition index (unitless, $n$ = 25) | | | | | 3 |
| Year to 1992 | 1 | 0.00364 | 0.00089 | 0.0005 | 4 |
| Year from 1992 | 1 | −0.01024 | 0.00181 | <0.0001 | 4 |
| Intercept | 1 | −5.94 | 1.77 | 0.003 | |
| (D) Catch per unit effort (ln[fish per 10 hooks], $n$ = 21) | | | | | 1 |
| Year to 1997 | 1 | −0.0048 | 0.0029 | 0.098 | 5 |
| Year from 1997 | 1 | −0.1926 | 0.0054 | <0.0001 | 5 |
| Intercept | 1 | 10.14 | 5.75 | 0.078 | |
| AR1 | 1 | −0.710 | 0.025 | <0.0001 | |

[1] Autoregressive (first-order) component included for length analysis.
[2] Year coded as 1972 = 0.
[3] No first-order autoregression ($P > 0.1$).
[4] Difference in slopes: $F(1,22) = 31.92$, $P < 0.0001$.
[5] Difference in slopes: $\chi^2(1) = 580.65$, $P < 0.0001$.

tinues until at least 2000. The trend may have ceased by 2001–2004, but results are very variable. Too few fish were caught after 2004 to allow for analysis. Median TL after the peak in 2001 (140 cm) were all lower (77–139 cm in 2002–2004).

The pattern is less ambiguous for the 75th percentile of TL (Tables 1 and 2: Fig. 3). Here the best model was cubic: an initial decline in the early-mid 1970s was followed by an increase from the late 1970s until at least 1992. There were no data for 1993–1996, but the cubic equation indicates a peak in 1995 followed by a decline in recent years. Thus, at least for the segment of the population represented by larger fish, there has been a recent decline. Both median and 75th percentile TL increased from the late 1970s to the early 1990s.

To help identify and confirm the pattern observed for annual values of length summarized above, we analysed TL of individual fish ($n = 5423$ from the same set of years) and compared the quadratic transformation and quadratic and cubic models. The cubic equation was strongly preferred to the quadratic transformation (Delta AIC = 14.53) and the cubic term was significant ($\beta = -0.00127 \pm 0.000457$, $P = 0.0053$). Thus, both analysis of the upper quartile length and that of length of individual fish argue for a recent decline, from the mid-1990s to 2004. In other words, the upper quartile of length has shown a more pronounced decline in the past decade than has the median length.

There was no relationship of median or 75th percentile length to SOI, with or without lags ($P > 0.1$). Neither was mean condition related to SOI, with or without lags ($P > 0.1$).

## Fish condition

### *Condition index (K)*

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. 4). Variation among months was significant ($F(3, 5385) = 3.51$, $P = 0.015$); the

**Table 2** Comparison of models, Akaike Information Criterion (AIC) values; only those within 2 AIC units of best model shown, but for A and D only the top 5 models are shown. A, C and G analysed as time series (AR1); the others are not.

| | K | Log likelihood | Delta AIC | AIC |
|---|---|---|---|---|
| (A) Median length – year | | | | |
| Year – quadratic-transform | 4 | −59.023 | 0 | 126.05 |
| Year – linear | 4 | −59.305 | 0.56 | 126.61 |
| Spline – change point 1997 | 5 | −58.354 | 0.66 | 126.71 |
| Year – Inverse-Transform | 4 | −59.541 | 1.23 | 127.28 |
| Year – cubic equation | 6 | −57.685 | 1.32 | 127.37 |
| (B) Median length – environmental variables | | | | |
| Cubic September–October ice extent | 4 | −40.286 | 0 | 88.57 |
| Cubic September–October ice area | 4 | −41.124 | 1.68 | 90.25 |
| September–October ice extent – quadratic-transform | 2 | −43.126 | 1.68 | 90.25 |
| (C) 75th Percentile length – year | | | | |
| Year – cubic equation | 6 | −51.887 | 0 | 115.77 |
| No other model within 2 units | | | | |
| (D) 75th percentile length – environmental variables | | | | |
| September–October ice extent – quadratic-transform | 2 | −39.287 | 0 | 82.57 |
| September–October ice area – quadratic-Transform | 2 | −39.668 | 0.77 | 83.34 |
| September–October ice extent – inverse-transform | 2 | −39.858 | 1.15 | 83.72 |
| Quadratic September–October ice extent | 3 | −38.935 | 1.3 | 83.87 |
| September–October ice extent – log-transform | 2 | −40.056 | 1.54 | 84.11 |
| (E) Mean condition – year | | | | |
| Spline – change point 1992 | 4 | 60.542 | 0 | −115.08 |
| No other model within 2 units | | | | |
| (F) Mean condition – environmental variables | | | | |
| Minimum ice area – inverse-transform | 2 | 40.693 | 0 | −77.39 |
| No other model within 2 units | | | | |
| (G) CPUE – year | | | | |
| Spline – change point 1997 | 5 | −95.854 | 0 | 201.71 |
| Spline – change point 2001 | 5 | −96.435 | 1.16 | 202.87 |

K, number of parameters.

pattern and significance of monthly variation in condition were very similar after controlling for annual variation ('year' treated as a factor). There was no significant autocorrelation ($P > 0.1$) from one year to the next for mean condition and therefore, subsequent analyses did not include an autoregressive component.

Across all years, there was no significant linear trend in toothfish condition (Fig. 5). Instead, there was a trend for mean *K* to increase from 1972 to 1992 and decrease subsequently. Mean *K* was higher for 1992 than in any other year; nevertheless, an increasing trend is evident from 1972 to 1990 ($\beta = 0.00329 \pm 0.00080$, $P < 0.001$). We compared a change-point model with a 'knot' at 1992 with the set of models enumerated in the Methods section (i.e. linear, transformations of linear variable and polynomial models), as well as knots at other years in the data set. The model optimizing AIC had the change point at 1992. Not only were trends significant for each time period (up to 1992, from 1992 to 2004), but the linear trends also differed significantly from each other (see Tables 1 and 2). We confirmed that the result was not driven by 1992, which appears to be an outlier, by re-analysing the change-point model without data from 1992. Linear trends before and after 1992 were as significant without 1992 data as they were with 1992 data ($P = 0.001$ up to 1992 and $P < 0.001$ from 1992 respectively, with or without 1992), and the change in trend was similarly significant with or without 1992 ($P < 0.0001$).

We confirmed the pattern identified for annual variation in mean condition by analysing condition indices of individual fish. These analyses also included effect of calendar month (analysed as categorical variable). The two-part spline model demonstrated significant increase in condition up to 1992 ($\beta = 0.00342 \pm 0.00039$, $P < 0.0001$), significant decrease since 1992 ($\beta = -0.00992 \pm 0.00103$, $P < 0.0001$) and a significant change in slope between the two periods ($P < 0.0001$). Furthermore, the change-point model displayed superior AIC results compared to a quadratic, cubic or quartic model (delta AIC = 3.38, 3.55 and 4.88 respectively).

### *Mass index*

The relationship of *MI* to year was very similar to the pattern shown for the condition index, *K*, suggesting that month of capture and length did not

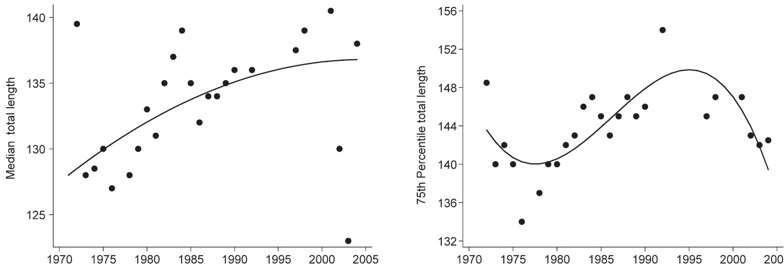

**Figure 3** Change in TL in relation to year, 1972–2004, with models determined by Akaike Information Criterion (AIC) (Table 2): left, median length, shown as quadratic transformation of year; right, upper quartile length, shown as cubic polynomial of year. Too few fish were caught after 2004 to include in these analyses.

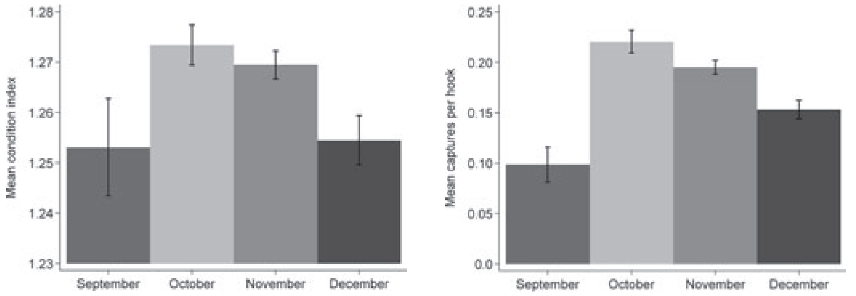

**Figure 4** Monthly trends in McMurdo Sound fish caught, 1972–2011 ($n > 5500$): left, mean toothfish condition and standard error; right, mean catch per unit effort and standard error.

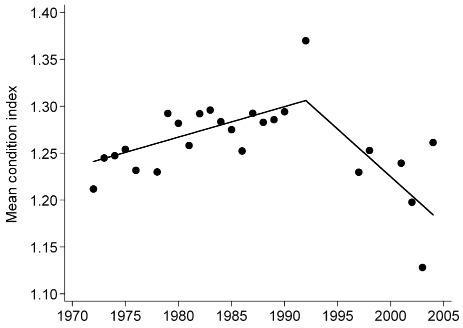

**Figure 5** Mean condition in relation to year: shown is a change-point model with the knot at 1992, which provides best fit (Akaike Information Criterion, AIC; see Table 2).

confound the relationship between condition index and year reported above.

*Axe-handle fish*

The proportion of axe-handle fish decreased during the early-mid part of the study, up to and including 1992. However, after that the proportion has increased (Fig. 6). The preferred fit to the data was a fourth-order polynomial. The fourth-order polynomial fits better than a quadratic because the former allows for an asymmetric function. The fit of the fourth-order polynomial was highly significant: $F_{(4,20)} = 4.88$, $P = 0.007$, $R^2_{\text{adj}} = 0.393$.

*Relation of condition to length*

Because of the marked change in the trend of $K$ with year up to 1992 and from 1992 on, we analysed condition index in relation to length separately in the two time periods: 1972–1992 and from 1992 (Fig. 7). The relationship of condi-

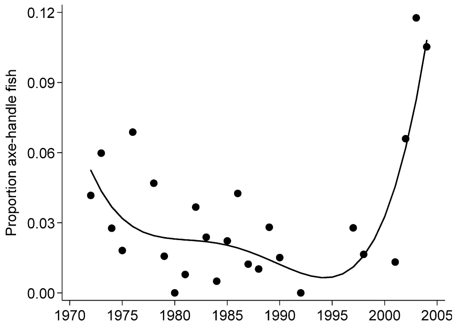

**Figure 6** Change in prevalence of axe-handle fish in the McMurdo Sound toothfish catch, 1972–2004; preferred model (by Akaike Information Criterion, AIC) is fourth-order polynomial.

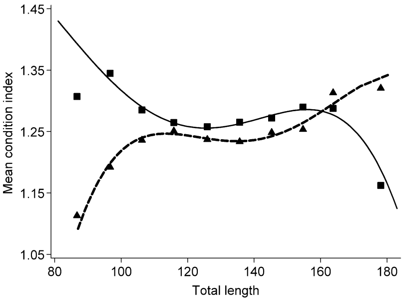

**Figure 7** Condition index in relation to TL for the period prior to 1992 and from 1992. Curves shown are polynomial equations of best fit. Curve for 1992 and earlier (solid line, squares), fourth-order polynomial model: $n = 4847$, $F(4, 4842) = 19.72$, $P < 0.0001$. Linear, quadratic, cubic and quartic coefficients (with SE) are -0.00630 (0.00467), −3.72e-05 (1.41e-04), 2.64e-06 (1.76e-06) and −1.90e-08 (7.80e-09) respectively. After 1992 (dashed line), fourth-order polynomial model, $n = 556$, $F(4, 551) = 3.68$, $P = 0.006$. Linear, quadratic, cubic and quartic coefficients (with SE) are 0.0279 (0.0112), −7.63e-04 (3.28e-04), 8.48e-06 (3.89e-06) and −3.19e-08 (1.62e-09) respectively. Symbols show mean values for 10 evenly spaced groups. Analysis was carried out on individuals; grouped data shown for illustrative purposes only.

tion to length differed strongly and significantly during the two time periods (see figure caption for statistics). During the early period, there was a negative trend overall between condition and length, especially among the smallest fish and very large fish. After 1992, the relationship was overall positive with an increase in condition as length increased from 80 to about 115 cm, and a second increase observed from about 155–180 cm. Thus, not only did trends over time with respect to condition differ between the two time periods, but the relationship of condition to length also differed in the two time periods.

## Catch per unit effort

Catch rate varied by month within each season (Fig. 4). The lowest capture rate occurred in September, but it then increased dramatically in October. Rates for November and December remained high. There was no significant variation in catch rates among October, November and December ($P > 0.4$); but each of these differed from the September catch rate ($P < 0.001$). We analysed CPUE in two ways: by fishing session ($n = 1229$) and by year, in the latter case, summing captures and effort for each year. Results were similar in either case; here, we present results for annual variation in CPUE. The by-year analysis incorporated an autoregressive component. However, the by-session analysis adjusted capture rates by month.

Unlike condition and length, there was no peak in CPUE midway during the study period. Instead, captures were fairly stable through at least 1997, possibly to 2001 (Fig. 8), followed by a steep decline in the most recent years. The best model was a two-part spline with a change point in 1997 (Table 2). As is evident, the slope up until 1997 was nearly flat; sometime between 1997 and 2001, the onset of a decline is evident. The subsequent decline relative to 1997 is significant (Table 1) and is significantly different from the slope from 1975 to 1997. Note that the change-point model was superior to all others examined: linear, transformation of a linear variable and polynomial models (Table 2).

## Influence of environmental variables on fish metrics

### *Fish length*

Exploratory analyses of the effects of the full set of candidate ice variables on our two TL metrics revealed six of particular interest: minimum ice area, minimum ice extent, maximum ice area, maximum ice extent, ice extent in 'early spring' (September–October) and ice area in September–October. Although maximum ice extent often occurred in September or October, September–October ice extent and maximum ice extent were not especially highly correlated ($r = +0.843$). Each

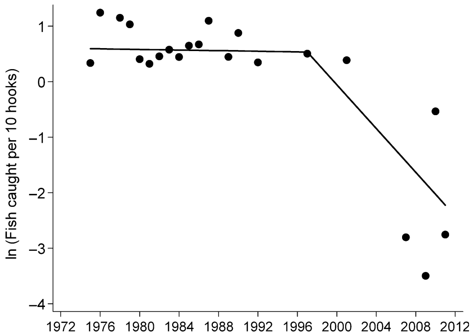

**Figure 8** CPUE in relation to year, analysed with the change point in 1997. CPUE analysed as ln(Fish caught per 10 hooks); results of weighted regression shown (see text).

of these was analysed with respect to lags of 0–5 years, yielding 36 ice variables (i.e. six variables × six lags).

*Median TL* demonstrated a significant relationship to September–October ice extent ($P = 0.003$; Table 3). The relationship best supported by AIC was cubic with an overall upward trend (Fig. 9, Table 2). An inverse relationship (asymptotically increasing and then leveling off with increasing ice extent) was also significant, but the AIC was not as good. Whereas it is evident that median length was low when September–October ice extent was low, it is less clear that median length increased for September–October ice extent beyond 3 900 000 km$^2$.

**Table 3** Statistical summary of preferred models for fish metrics and environmental variables; results of weighted regression model of annual values. Ice area and extent measured in thousands of km$^2$.

| Variable | df | Estimate | SE | *P* value |
|---|---|---|---|---|
| (A) Median length (cm, *n* = 25) | | | | |
| September–October ice extent – linear | 1 | 3.15 | 1.380 | 0.038 |
| September–October ice extent – quadratic | 1 | 7.71E-04 | 3.43E-04 | 0.040 |
| September–October ice extent – cubic | 1 | 6.28E-08 | 2.83E-08 | 0.042 |
| Intercept | 1 | −4141 | 1848 | 0.041 |
| (B) 75th percentile Length (cm, *n* = 25) | | | | |
| Quadratic-Transform of September–October ice extent | 1 | −4.93E-06 | 1.27E-06 | 0.001 |
| Intercept | 1 | 147.7 | 0.921 | <0.0001 |
| (C) Mean condition index (unitless, *n* = 25) | | | | |
| Inverse-transform minimum ice area | 1 | 0.150 | 0.049 | 0.007 |
| Intercept | 1 | 1.312 | 0.015 | <0.0001 |

The pattern for *75th percentile TL* was roughly similar to that observed for median length: the environmental variable that best predicted 75th percentile length was September–October ice extent, but the best fit was a quadratic transformation of September–October ice extent, upper quartile length increasing but in a decelerating fashion (Fig. 9, Table 3). The linear effect of September–October ice extent on 75th percentile length was significant ($P = 0.003$), but nonetheless a quadratic transformation was superior to the linear model ($P = 0.001$; Tables 2 and 3). No lagged ice variables were as good predictors as was September–October ice extent in the year of capture, and none were significant.

### *Fish condition*

The best environmental predictor of *K* was minimum ice area (always in February) of the year of capture (8–10 months prior to the fishing season; Fig. 10). The relationship was non-linear: mean *K* declined with increasing minimum ice area (less open water than usual), but in an accelerating (downturned) fashion. In a weighted regression, the relationship best reflected an inverse transformation of minimum ice area (Tables 2 and 3).

In an analysis at the individual level, the effect of minimum ice area (inverse transformed) on condition, while controlling for calendar month of

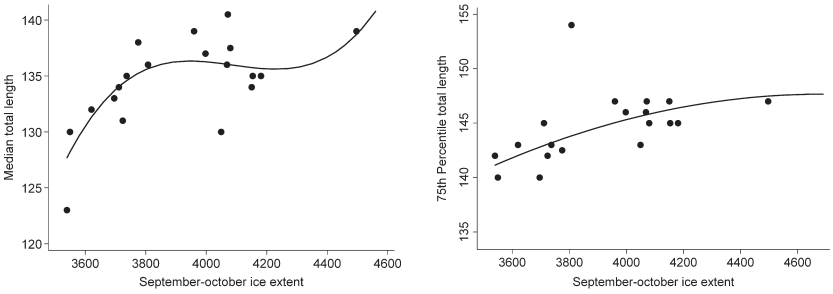

**Figure 9** TL length in relation to September–October Ice Extent (in thousand km$^2$): left, median length (cubic model); right, 75th percentile (quadratic model).

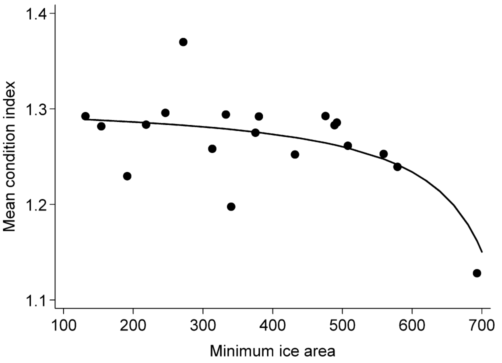

**Figure 10** Mean condition index in relation to minimum ice area (thousands of km$^2$). Model favoured by Akaike Information Criterion (AIC) is shown as an inverse transformation of minimum ice area (see Table 3 for statistics).

capture, was also significant ($\beta = 0.118 \pm 0.027$, $t(3802) = 4.60$, $P < 0.0001$, $n = 3807$). Most importantly, even if data from 2003 (a year with unusually low condition index) are omitted, there is still a significant ($P = 0.005$) relationship with minimum ice area, inverse-transformed ($\beta = 0.0855 \pm 0.0301$). Minimum ice area was a better predictor (as determined by AIC) of mean condition than was date of minimum ice area or minimum ice extent. No lagged ice variables were significant in relation to mean condition.

*Change in CPUE*

There was no evidence that any environmental variable (ice variables, whether lagged or not, or SOI variables) was significantly associated with annual variation in toothfish CPUE (ln-transformed). As noted, despite environmental variability, there was little change in capture rates from one year to the next, up to 2001 (Fig. 8).

## Discussion

In this McMurdo Sound study, we found that (i) 97% of the catch was composed of individuals > 100 cm, which means that these fish were larger than the average fish caught by the industrial fishery; (ii) median fish length increased from fish that were 126–130cm TL in the early 1970s to ones that were 135–140cm 35 years later, with the trend decelerating to near stability in 1998–2001 (smaller fish were caught thereafter, but they were too few in number to include in this analysis); (iii) the largest fish, above the 75th percentile, however, began to decrease in TL sharply after the mid-1990s; (iv) fish condition (index) improved slightly to the early 1990s and then worsened sharply thereafter, a pattern accompanied by a sharp increase in the proportion of 'axe-handle' fish (fat depleted) in later years; (v) bigger fish had lower condition index than smaller fish during the early period, but during the later period, bigger fish were generally in better condition than smaller ones; and (vi) finally, after being stable for over 25 years, CPUE decreased sharply after 2000.

### Toothfish length frequency

The Ross Sea region toothfish fishery management strategy is based on models to estimate stock size formulated entirely on what can be gleaned from the industrial catch (CCAMLR 2005, 2006, 2008, 2010). One main assumption is that the statistically adjusted size-age distribution in the catch is representative of the full population. The disparity in the size distribution in the McMurdo Sound catch compared with that in the fishery catch is therefore problematic. The McMurdo Sound catch, ranging 81–193 cm with most fish > 100cm and a broad mode at 120–170 cm, approximately reflects the upper two-thirds of the commercial catch, which ranges '…50–180 cm….In all seasons, there was a broad mode of adult fish at about 120–170 cm…' (CCAMLR 2010, p. 6). About 15–20% of the industrial catch overall is composed of fish < 100 cm (compared to 2.5% in this study). In years when there were more smaller fish, Commission for the Conservation of Antarctic Marine Living Resources [CCAMLR (2010)] concluded that the fishery was centred more over the Ross Sea shelf than in other years. Given that our fishing site is on the shelf, this conclusion about the preponderance of small fish is not supported by our findings. The disparity is even more apparent when compared to the size-frequency distributions in another study that included only fish captured by the fishery over the shelf, including near McMurdo Sound, where >50% were <100 cm (Hanchet *et al.* 2008).

There are at least two factors that could explain the discrepancy. Firstly, owing to lack of buoyancy in fish <100 cm (Eastman and Sidell 2002; Near *et al.* 2003), our vertical setlines 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 (although baits float up about a metre), caught these fish in greater proportion. Secondly, the discrepancy could be due to the fact that large fish ate most of the smaller fish caught on the vertical setlines. However, evidence for cannibalism was absent in the stomachs inspected in the McMurdo catch (*n* = 58; Eastman 1985a,b; La Mesa *et al.* 2004). Our finding that large toothfish reside high in the water column is confirmed by Crittercams placed on Weddell seals as well as ROVs (Fuiman *et al.* 2002; Kim *et al.* 2011); that small toothfish do occur in McMurdo Sound is indicated by the catch of Weddell seals, which take the entire size range (cf. Ponganis and Stockard 2007; Ainley and Siniff 2009; Kim *et al.* 2011). In summary, assumptions made in CCAMLR's fishery models about the representativeness of age-size structure as revealed by long lines need to be reconsidered.

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 (Eastman and DeVries 1981; Near *et al.* 2003). 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 eggs, larvae and fry).

Size-related fecundity of this species is also important to consider in the context of fishery management. All large McMurdo Sound fish are sexually mature, but in a 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, estimates of age/size at maturity, which is based on the size frequency seen in the industrial catch, need to be revised once more (recently it was doubled: Parker and Grimes 2010).

## Trends in toothfish length and condition

Despite reductions in TL of the largest McMurdo Sound fish, median length increased rapidly early in the study and then levelled off near the end. Seemingly, the loss of the relatively few largest fish was statistically compensated for by the increase in median length among the majority of fish. Mean condition of fish, however, dropped sharply after the mid-1990s, and there was an increased incidence of 'axe-handle' fish. Given that the industrial fishery is geared to catch the largest fish as fast as possible before the season closes (Constable *et al.* 2000; Brooks and Ashford 2008), this could explain the disappearance of the very large fish, a pattern duplicated in the maximum size of fish that Weddell seals once caught (Kim *et al.* 2011). Loss of fish quality also results when these most aggressive and thus largest fish are removed from a stock (summarized in Ainley *et al.* 2012).

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, although this is rarely demonstrated (Longhurst 2010). The fact that a rapid increase in median length predated the fishery in our study raises questions as to what factors could account for the observed increases (and then decreases) in length and condition? If change in fish length is a function both of food availability and age, (i) was there a release from predation during the 1970–80s, thus allowing older fish to remain in the population longer, and/or (ii) was there more favourable foraging related to competitive release, and/or (iii) were the characteristics of a few year classes being measured during much of the study no longer the case owing to changes related to climatic factors?

### *Release from predation*

The southern Ross Sea was the scene for a number of 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. Population numbers slowly recovered (partially) over the next decade to about 2000+ animals, 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 would contribute to a lessened predation pressure on Antarctic toothfish. In addition, another toothfish predator, sperm whales (admittedly at the periphery of their range) are a shadow of their former numbers in the Ross Sea sector (Whitehead 2000) owing mainly to contraction of range as whalers depleted the stocks in the warmer parts of the Pacific between 1700 and the mid-1900s. The same is true for southern elephant seals (*Mirounga leonina* Phocidae), 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 favourable foraging related to competitive release*
The industrial take of minke whales during the 1970s and early 1980s (~20 000 taken from the 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 over the shelf (Eastman 1985a; Ballard *et al.* 2011).

*Climatic factors*
The growth of toothfish in the data set indicated the possibility that just a few strong year classes, available near the onset of the study, were being measured over the course of the study. The ocean environment changed dramatically over the period when a rapid increase in fish length was detected, owing to the Southern Annular Mode (SAM), a major driver of climate in the Southern Ocean (Thompson and Solomon 2002; Stammerjohn *et al.* 2008). Beginning in the mid-1970s, the Antarctic Oscillation Index, which represents SAM, switched from a decade or more of being negative to a state of being mostly positive as a result of wind patterns altered by the Antarctic Ozone Hole and a warming middle latitude ocean (references above). As a consequence of increased wind forcing from south to north in the Ross Sea region (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). Adélie penguins responded positively to these changes (Ainley *et al.* 2005), and perhaps toothfish did too. The fact that changes in certain toothfish metrics correlated with sea-ice variables offers some basis for a connection existing to the decadal SAM patterns. Unfortunately, SAM changed to positive too early in the McMurdo Sound time series to be helpful in resolving this question and we do not know anything about what factors affect spawning success and egg/larval survival.

### 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 was similar in form to that reported by Testa *et al.* (1985), but with a lesser decrease in catch rate after November. To explain the temporal pattern, one might be tempted to invoke some sort of seasonal occurrence related to migratory movement. 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 contrary, toothfish could also seasonally change their position in the water column to be more vulnerable to our setline array. 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, 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 (McMurdo Sound toothfish are also known to feed on benthic mysids; Eastman 1985a). A couple of months later, when the plankton blooms begin and 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. As a result, the depth of toothfish tracks that of silverfish 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), this could be related to a true decrease in toothfish abundance (especially large fish) owing to predation, which increases severely at that time. Weddell seals, upon becoming free of breeding and pupping, attempt to recover (beginning in late November); a new cohort of seals begins to forage in the food web (late November); and 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 are 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 deep. 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 coloured, 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.* 2003). 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*

With 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 in 2001–2005 were responsible (Arrigo *et al.* 2002), and this is one of the explanations favoured by Hanchet *et al.* (2010, discussing a preliminary report of the McMurdo Sound data set). However, 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 populations 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).

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), as other fisheries do when targeting the largest, oldest fish (Longhurst 2010; Ainley *et al.* 2012)? 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.* 2012 and references therein). How to detect this change is a challenge. Such a change was involved in the crash of Atlantic cod (*Gadus morhua*, Gadidae), 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; Ainley and Ballard 2012), 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 there depends on the existence of large fish.

### Recommendations

Given the observation of recent marked declines in condition, size and CPUE for the Antarctic toothfish of McMurdo Sound, the only monitoring conducted independent of the fishery, we suggest that the toothfish fishery in the Ross Sea be closed until the natural history of Antarctic toothfish, and its silverfish prey, is much better understood. An easier option to implement, given that New Zealand has taken 55% of the toothfish from the Ross Sea area (Ainley *et al.* 2012) and that the USA imports 40% of the total world catch of 'Chilean sea bass' (including Ross Sea fish; US Department of State website), is for NZ and US fishery agencies to immediately reconstitute the scientific fishing programme described herein as it was up to 2001 (annual, entire season). In addition, other research should be initiated, including monitoring of dependent species, that would be independent of the unexplained biases in the scientific versus industrial sampling. Of course, management would be adjusted depending on results of this effort. Besides McMurdo Sound, vertical longlines could be deployed in an analogous 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 within the scope of an agency, CCAMLR, that has made its name as setting the pace in ecosystem-based and precautionary management and that has a formal monitoring programme (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 highlight the need for meaningful action.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1**. Summary of data used to calculate changes in fish length, condition and catch per unit effort (based on hooks deployed).