*Antarctic Science* page 1 of 7 *(2016)* © Antarctic Science Ltd 2016 doi:10.1017/S0954102016000584

# Changed prevalence, not absence, explains toothfish status in McMurdo Sound

**DAVID G. AINLEY[1], GRANT BALLARD[2], JOSEPH T. EASTMAN[3], CLIVE W. EVANS[4], NADAV NUR[2] and CLAIRE L. PARKINSON[5]**

[1]*H.T. Harvey & Associates Ecological Consultants, Los Gatos, CA 95032, USA*
[2]*Point Blue Conservation Science, Petaluma, CA 94954, USA*
[3]*Department Biomedical Sciences, Ohio University, Athens, OH 45701, USA*
[4]*School of Biological Sciences, University of Auckland, Auckland 1142, New Zealand*
[5]*Cryospheric Sciences Laboratory/Code 615, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA*
*dainley@penguinscience.com*

**Abstract:** We comment on the conjecture by Parker *et al*. (2016) that Antarctic toothfish recently returned to McMurdo Sound, arguing that this species never departed. Instead, as deduced from a 40-year fishing effort, toothfish water column prevalence became markedly reduced where bottom depths are <500 m, with research continuing to show their presence on the bottom or above the bottom where depths are deeper. We also counter arguments that toothfish departed, and remained absent, during and following a five-year presence of mega-icebergs residing near the opposite coast of Ross Island, the icebergs inhibiting or fomenting conditions that discouraged toothfish presence in the Sound. Available analyses reveal that toothfish movement into the Sound was probably not significantly affected, and additionally that neither changes in hydrography nor in primary productivity in the Sound would have been sufficient to impact toothfish presence through food web alteration. We hypothesize that the local effect of predation by seals and whales and the regional effect of a fishery targeting the largest toothfish (those neutrally buoyant and thus capable of occupying upper levels of the water column) has resulted in the remaining toothfish now being found predominantly closer to the bottom at greater depths.

Received 19 October 2015, accepted 5 October 2016

**Key words:** effects of fishing, effects of predation, iceberg B15/C16, neutral buoyancy, Ross Sea, Weddell seals

## Introduction

The ecology and natural history of the Antarctic toothfish (*Dissostichus mawsoni* Norman; hereafter, AnT) has been under investigation in McMurdo Sound and vicinity during the summer for the past 50 years of the modern era of Antarctic science. Information has been accumulated by direct observation of the fish by human divers, use of under-ice observation chambers or remotely operated vehicles (ROV; Kim *et al*. 2005, 2011 and references therein, Ponganis & Stockard 2007), observations of Weddell seals (*Leptonychotes weddellii* Lesson) catching the fish (Ainley & Siniff 2009 and references therein), or by the classical means of baited hook and line (Ainley *et al*. 2013, Cziko *et al*. 2014, Parker *et al*. 2016, unpublished data, P. Cziko, personal communication 2016). In regard to the hook and line method, it was found early in the period that if a fish was hooked by gear deployed on the bottom or within ~ 10 m of the bottom, and if the fish was not retrieved in a timely manner, i.e. < 24 h soak time, it would be attacked and consumed by scavenging amphipods (DeVries *In* Ainley *et al*. 2013). Therefore, what we here call the 'DeVries fishing array' was perfected to catch AnT for study (or tag and release) without being scavenged. In this approach, a vertical set line was deployed through a hole drilled through the McMurdo Sound fast ice 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' but not the bottom (Ainley *et al*. 2013, p. 346; see Fig. 1).

The picture of AnT prevalence that emerged from this long history of research, in our opinion, was that, at least under heavy ice cover, the species existed as a 'cloud' of fish (AnT are not schooling). The cloud can extend upward from the bottom, generally ~ 100 m thick, although at times, especially during that part of the day when summer sunlight was diminished, it can reach within 12 m of the surface, even where the bottom depth is > 500 m (Fuiman *et al*. 2002). In times of brighter light levels, the top of the AnT cloud can descend deeper, as indicated by the observation that seals had to dive to 300 m from the surface to find them (Fuiman *et al*. 2002). Large AnT can move in the water column without undue swimming effort because once they begin to accumulate significant lipid in their tissues, generally upon surpassing ~ 100 cm in total length (TL), they become increasingly neutrally buoyant (Near *et al*. 2003). Smaller AnT generally remain close to or on the substrate hiding

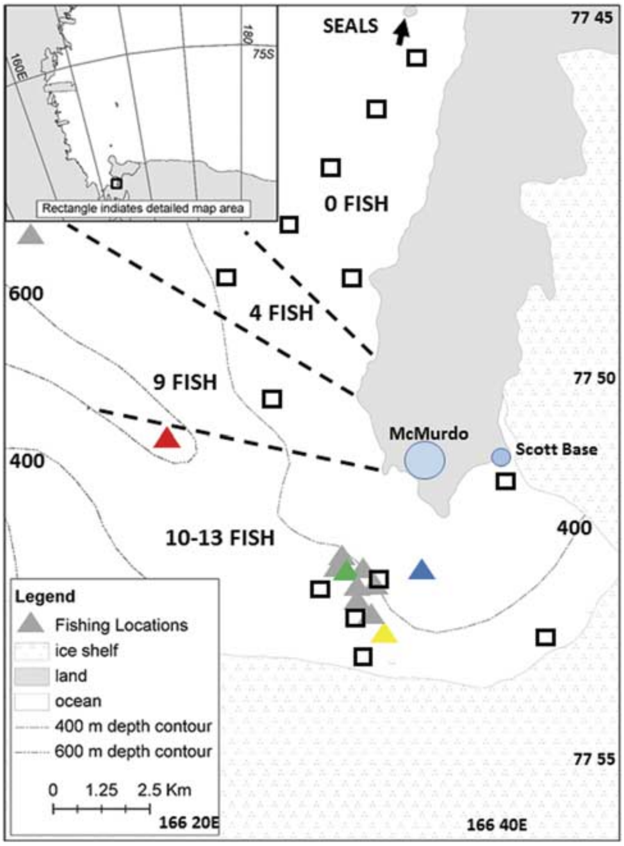


**Fig. 1.** Updated from Ainley *et al.* (2013), approximate sites of scientific fishing. Squares are those of Testa *et al.* (1985), with average catch per set within the areas bounded by dashed lines. Triangles by colour: grey = sites of DeVries 1972–2011 (site clusters 1 and 2), green = Cziko *et al.* (2014) 2012, and Parker *et al.* (2016): blue = no fish caught, yellow = four fish caught and red = 19 fish caught. During the fishing season, Weddell seals concentrate from Turtle Rock (arrow) northward, with a few near Scott Base. McMurdo Ice Shelf only approximate, as edge changes regularly.

among the forest of sessile invertebrates there (e.g. Eastman & Barry 2002, Eastman *et al.* 2013 fig. 1e). As of yet, it is not known what proportion of AnT exist at any given time in the cloud or on the bottom or how long their residence time in it might be, though the age-size-condition structure of the AnT in the cloud, and the availability of prey, would be involved in that determination. At depths above the bottom, i.e. in the water column, AnT in the cloud would be pursuing their principal, energetically valuable prey, the Antarctic silverfish (*Pleuragramma antarctica* Boulenger; Eastman 1985a, 1985b, La Mesa *et al.* 2004, Lenky *et al.* 2012), which also exhibits a diel vertical migration (Fuiman *et al.* 2002, Robison 2003, O'Driscoll *et al.* 2011). Otherwise, available evidence suggests that a major factor that can affect AnT distribution in the water column, besides buoyancy and prey pursuit, is predation, especially by Weddell seals (Ainley & Siniff 2009). This is shown by past research results indicating toothfish presence as long as vertical set lines were deployed where the bottom was > 300 m and not within foraging range of a high concentration of Weddell seals (Testa *et al.* 1985, who fished using the DeVries array at 17 fishing holes spaced around south-eastern McMurdo Sound; Fig. 1). However, changes in these patterns occurred in *c.* 2000 (Ainley *et al.* 2013), and herein we discuss this change.

A recently published paper, titled 'Have Antarctic toothfish returned to McMurdo Sound?' (Parker *et al.* 2016), reported results of a pilot study on AnT. This paper, based on using the DeVries array at three sites, reported 23 AnT caught (bottom depths >500 m at the two sites where fish were caught; Fig. 1) during 11 days in November 2014 (hereafter, 'Parker dataset'). Also included in this report were results of a vessel-based survey using benthic longlines deployed at similar or deeper depths in northern McMurdo Sound. The paper by Parker *et al.* (2016) was written as a comment on conclusions drawn from analysis of a 39-year time series of mark–recapture fishing in southern McMurdo Sound (Fig. 1), using the DeVries array, where >5500 fish were caught in October–December 1972–2011 at a closely spaced cluster of sites where bottom depths were <500 m ('DeVries dataset', Ainley *et al.* 2013). Additional effort has been expended since then at the same site (Cziko *et al.* 2014; Fig. 1). In the DeVries dataset, TL, abundance (as assessed by catch-per-unit effort (CPUE)), and body condition of fish caught showed a marked decrease, beginning in the late 1990s for condition and after 2001 for CPUE, reflecting fewer large, neutrally buoyant fish in the water column at the depths fished. In the absence of any detectable relationships of CPUE variability to environmental factors, Ainley *et al.* (2013) hypothesized that the recent trends in the DeVries catch might have been related to a commercial AnT fishery that had been initiated in the Ross Sea in 1997, reaching maximum landings by 2004. The fishery, which has targeted the largest fish, mostly occurs along the Ross Sea continental slope but has spent appreciable effort as well in waters immediately bordering McMurdo Sound, at least since 2004. For example, while perhaps not representing the entire catch, depending on year, there were 1000–7000 fish, from 26–206 hauls in Food and Agriculture Organization Areas 88.1 J and L, that were measured to characterize the fishery, as well as additional catch (3000–6000 fish sampled) in Area 88.1 M, fished through 2008 (SC-CAMLR 2013, p. 6). The latter area includes McMurdo Sound.

Findings from the DeVries dataset were presented to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Working Group on Fish Stock Assessment (WG-FSA) in 2012 (Ainley *et al.* 2012). The WG-FSA concluded, and Parker *et al.* (2016) agreed, that the fishery could not be involved in affecting the McMurdo Sound trends, but surmised that the patterns evident in the DeVries dataset were the result of temporary environmental factors. Despite a further WG-FSA conclusion that the DeVries dataset, owing to its small spatial scale, could not have reflected the overall state of the toothfish stock in Area 88.1 (SC-CAMLR 2012, p. 318), this group subsequently reported that recent trends in the commercial catch regarding AnT body condition, as measured by Fulton's Condition Index (*K*; Nash *et al.* 2006), matched trends in the DeVries dataset (p. 318, 346). Moreover, as WG-FSA subsequently noted, consistent with later trends in the DeVries dataset, that the modal length of toothfish caught in the major fishing grounds (Ross Sea slope) has shown a marked decrease in large fish (SC-CAMLR 2013, p. 5–6).

However, there are issues regarding Fulton's Condition Index. In particular, when comparing individual fish, there is a potential for its values to be confounded by gender and breeding status. If the changes in *K* were affected by a shift in sex ratio in the two datasets (e.g. Blackwell *et al.* 2000), then using *K* would not be appropriate as an assessment of condition. If sex ratio and breeding status differed over time, the change in *K* in McMurdo Sound fish might well reflect the recent decreased prevalence of female toothfish in the stock (as judged from fishery catch; SC-CAMLR 2014, p. 19–20). However, Fenaughty (2006) showed no significant difference of *K* between sexes of fish sampled in the southern Ross Sea region (south of 70°S), and concluded that *K* was thus an appropriate metric to measure toothfish condition among fish over the shelf and slope. Indeed, the fish in Fenaughty's sample were mostly not reproductively active, similar to fish caught in McMurdo Sound (Ainley *et al.* 2013, Parker *et al.* 2016; see also Eastman & DeVries 2000). Therefore, no gender-based differences in fish shape would alter *K* of Ross Sea shelf-caught fish, as confirmed by Fenaughty *et al.* (2008).

While we agree with Parker *et al.* (2016) that it is scientifically valuable to monitor AnT prevalence in McMurdo Sound using the single-site for a long-term set line effort (but see Discussion), or better some sort of stratified sampling of multiple sites, we have some concerns about the conclusions reached by Parker *et al.*: i) the implication that AnT had earlier left McMurdo Sound, as implied by the title of the paper and their fig. 3, and ii) their agreement with WG-FSA (SC-CAMLR 2012, p. 319) that later trends in the DeVries dataset may have been the result of temporary alteration of McMurdo Sound hydrography and sea ice owing to the presence, 2001–05, of mega-icebergs in place against the opposite, north-eastern shore of Ross Island. Given restrictions against our attendance at WG-FSA proceedings to argue against the mega-iceberg hypothesis, we here do so in

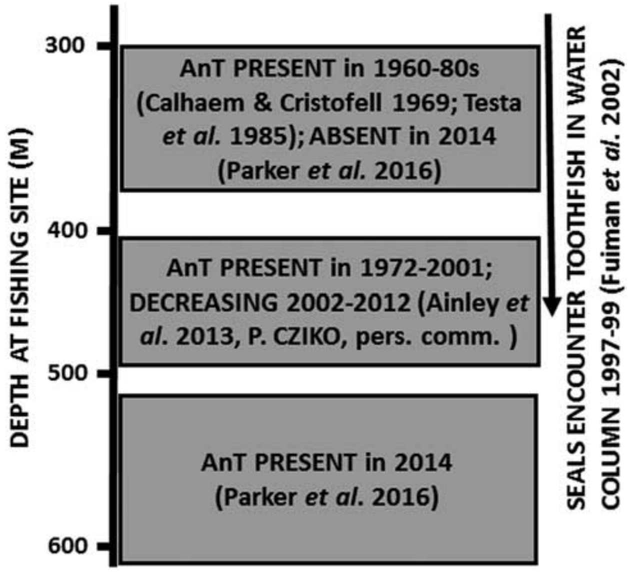


**Fig. 2.** Schematic summarizing results of research on prevalence of Antarctic toothfish (AnT) by depth of fishing site in McMurdo Sound (see Fig. 1); for comparison, the arrow indicates the depth range in the water column of toothfish and silverfish, as encountered by Weddell seals fitted with critter-cams, 1997–99, prior to the decreased fish prevalence noted in Ainley *et al.* (2013; arrow indicates the maximum depth of the seal diving), at a study site where bottom depth was 570 m and toothfish were observed within 12 m of the surface (Fuiman *et al.* 2002).

*Antarctic Science*, appreciating the open discussion allowing additional facts and viewpoints to be presented.

## Review of evidence

Parker *et al.* (2016) suggest that the pattern shown in Ainley *et al.* (2013) for AnT in McMurdo Sound may have been the consequence of the temporary presence of mega-icebergs that caused shifts in environmental conditions resulting in an absence of AnT in the region. Contrary to implications of the title (and abstract) of Parker *et al.*, neither Ainley *et al.* (2012, 2013) nor other researchers with datasets from the vicinity have reported an absence, other than that of large AnT, in McMurdo Sound. Indeed, after CPUE decreased towards the end of the DeVries dataset, observations of Weddell seals taking small AnT continued (e.g. Ponganis & Stockard 2007, Kim *et al.* 2005, 2011) and AnT continued to be caught by scientists, especially using benthic gear (Cziko *et al.* 2014 and P. Cziko, personal communication 2016, also see http://antarcticsun.usap.gov/science/contentHandler.cfm?id=2866). Results presented in SC-CAMLR (2014) do not show a disappearance in numbers or shift in mean CPUE in the fishery, but rather a change in the modal size and condition of the fish caught. In accordance with effects observed elsewhere in the Ross Sea, we therefore contend that what has changed in McMurdo Sound is not the presence of AnT *per se* but the prevalence of large, neutrally buoyant fish and changes in where these can now be found (Figs 1 & 2).

What has changed is that the AnT cloud, which once ascended the McMurdo Sound slopes from its maximum depths of >700 m, apparently no longer does so above ~ 500 m, although small, negatively buoyant fish are still found on the bottom at shallower depths. The DeVries study, fished at sites where bottom depths were 415–495 m (also Cziko *et al.* 2014 and P. Cziko, personal communication 2016; Fig. 1), provides values of fish size and condition at that depth. The Parker dataset also originates predominantly from a vertical set line, with the exception of two sets using horizontal line. It was fished at sites at which bottom depths either were appreciably shallower or deeper than the DeVries effort (see Figs 1 & 2): 324 m (site 1), 505 m (site 2) or 607 m (site 3). In both datasets, the fish were caught on those hooks that were in the lower ~100 m of the line. This mismatch in bottom depth at the sites fished is critical, and should be understood within the context of the AnT cloud. That is, in order to properly understand the results of Parker *et al.* (their fig. 3), the size and condition of the AnT caught should be evaluated against some expectation of where DeVries' fishing (and also that of Testa *et al.* 1985), as well as Fuiman's seals, found them in earlier years, and what condition they could be expected to have attained given their length. However, they report no catch at the shallower site (though Testa *et al.* 1985, and seals, had found them at sites having such depths in early years; see Figs 1 & 2), and the fish caught at the deeper sites, though in the water column, were deeper than those caught in the DeVries effort.

We contend that the results of Parker *et al.* support the hypothesis presented in Ainley *et al.* (2013) that the fishery may be affecting the distribution and abundance of large, neutrally buoyant fish in McMurdo Sound, in accord with the changes in fish size shown by SC-CAMLR (2014). Any impacts of the fishery will be evident when contrasted against the expectations resulting from the above-mentioned factors driving habitat selection by the large AnT. Individual vessels target the habitat in which the largest fish occur in order to quickly fill their holds before sea ice formation or attainment of the Total Allowable Catch closes the fishery season. The selective removal of large fish by the fishery would result in a reduction of the neutrally buoyant fish capable of moving throughout the water column, which is the trend detected in the DeVries dataset (cf. Fuiman *et al.* 2002). The fish in the Parker dataset were all > 100 cm TL, but caught only at depths greater than those of the DeVries dataset, and their body condition index, *K* (mean 1.218 ± 0.0239 standard error (SE), range 0.999–1.444, 5% > 1.4), was at the lower end of the range in the DeVries catch (mean 1.267 ± 0.0020 SE, range 0.578–2.992, 15% > 1.4; Table I). We deem this worthy of noting, as well as recognizing that differences in sample size could be playing a role. That being said, most of the AnT stomachs reported in Parker *et al.* were empty, consistent with the fishes' lower condition, their stomach fullness being quite unlike AnT caught higher in the water column in former years (see Eastman 1985a, 1985b).

**Table I.** Details of the fish caught by Parker *et al.* (2016) in McMurdo Sound during spring 2014, including calculation of the Fulton Fish Condition Index (*K*) (see Fenaughty 2006, Fenaughty *et al.* 2008).

| ID | Total length (cm) | Mass (g) | Index |
|---|---|---|---|
| 42191 | 140 | 30 600 | 1.1152 |
| 42209 | 155 | 39 100 | 1.0500 |
| 42210 | 142 | 33 300 | 1.1630 |
| 42211 | 136 | 30 400 | 1.2085 |
| 42212 | 123 | 26 800 | 1.4402 |
| 42213 | 144 | 39 700 | 1.3295 |
| 42220 | 124 | 22 400 | 1.1749 |
| 42223 | 138 | 36 700 | 1.3965 |
| 42228 | 139 | 26 800 | 0.9979 |
| 42230 | 154 | 49 000 | 1.3416 |
| 42237 | 108 | 15 600 | 1.2384 |
| 42238 | 134 | 27 700 | 1.1512 |
| 42257 | 125 | 23 100 | 1.1827 |
| 42280 | 129 | 26 500 | 1.2345 |
| 42285 | 143 | 35 000 | 1.1969 |
| 42287 | 133 | 28 800 | 1.2242 |
| 42294 | 130 | 24 700 | 1.1243 |
| 42315 | 145 | 36 900 | 1.2104 |
| 42320 | 149 | 42 100 | 1.2727 |
| 42357 | 130 | 28 900 | 1.3154 |

## Alternative explanations

How may we answer Parker *et al.*'s (2016) question contained in their title? WG-FSA has maintained that the commercial fishery was not involved, in part arguing that it has been too geographically distant to be generating the trends reported in the DeVries dataset (SC-CAMLR 2012, 319). Instead, WG-FSA surmised that environmental conditions brought about by the mega-icebergs were responsible. Parker *et al.* (2016) considered the WG-FSA position, and in accord with their title, offered reasons why AnT may indeed have 'returned'. We review here counter arguments to the WG-FSA/Parker *et al.* (2016) positions, noting as explained above that AnT never left McMurdo Sound, though large ones that occupied the cloud above the bottom became less prevalent.

### *First, regarding the contention of the remoteness of the fishery in relation to DeVries fishing sites in the vicinity of Ross Island*

This, we maintain, is without basis since AnT have been fished commercially in waters immediately adjacent to

Ross Island from the fishery's inception (e.g. SC-CAMLR 2012, p. 347; see above), and various WG-FSA studies have also shown movement of tagged fish between the shelf and slope (the main area of the fishery).

*Second, regarding the contention that mega-icebergs in 2001–05 discouraged movement of Antarctic toothfish into McMurdo Sound*

The icebergs had a draft of ~ 250 m, and, as they were perched on a pinnacle of the Beaufort Caldera, there was > 500 m of water beneath them in which AnT could have moved (see MacAyeal *et al.* 2008). Significantly, Kim *et al.* (2011), using video from a ROV, reported AnT beneath the McMurdo Ice Shelf (ice shelves being the source of mega-icebergs in the Ross Sea) 35 km in from the ice shelf edge.

*Third, regarding the contention that mega-icebergs altered the hydrography in such a way as to discourage Antarctic toothfish from entering McMurdo Sound*

Parker *et al.* (2016), and WG-FSA earlier, relied on the relevant and timely study by Robinson & Williams (2012), who reported the disruption of surface circulation in McMurdo Sound during the icebergs' presence, adjacent to the north-east coast of Ross Island. However, with bottom depths up to 1000 m and iceberg draft only ~ 250 m, the icebergs would not have presented a significant barrier and any facilitation of AnT movement by subsurface current flow (used to some degree by AnT; Hanchet *et al.* 2008) would not have been seriously compromised. Moreover, Robinson & Williams (2012) only investigated hydrography in the eastern third of McMurdo Sound, but not the mixed circulation of the middle Sound nor the opposing circulation in the west that emanates from beneath the McMurdo Ice Shelf (Barry & Dayton 1988). In these western waters, AnT have been observed recently (Kim *et al.* 2011 and references therein).

*Fourth, regarding the contention that extensive sea ice reduced sunlight during some years in the 2001–05 period, lowering primary production sufficiently to reduce availability of Antarctic toothfish prey*

Such speculation assumes carry-over effects into 2011 (and 2012, when P. Cziko (personal communication 2016) reported continued low water column AnT CPUE at sites where bottom depths were < 500 m). Note that the microbial community of the sea ice contributes only ~ 12% of productivity (Saenz & Arrigo 2014), with the remainder advected in from the Ross Sea (Barry & Dayton 1988). Therefore, changes in food web structure owing to reducing primary productivity within the sea ice microbial community in McMurdo Sound would have had little effect on the water column food web. Moreover, Dugger *et al.* (2014) found that variable productivity in the southern Ross Sea (which includes McMurdo Sound) during the iceberg presence did not affect the breeding success of a trophic competitor of AnT, the Adélie penguin (*Pygoscelis adeliae* Hombron & Jacquinot). The penguins continued to forage intensively on silverfish, diving typically to depths of 50–80 m in pursuit (see Ainley *et al.* 2015b, Saenz *et al.*, personal communication 2015 for foraging studies in McMurdo Sound). In addition, the breeding populations of this penguin species in and bordering McMurdo Sound grew immensely during the iceberg presence (with the exception of the tiny and regularly ice-bound Cape Royds colony; Lyver *et al.* 2014), indicating no food limitation. Other research has indicated that euphausiids and Antarctic silverfish (the shared penguin/AnT prey; cf. Eastman 1985a, 1985b, Ainley *et al.* 2003) in the southern Ross Sea are not closely coupled with phytoplankton abundance (cf. Smith *et al.* 2014, Ainley *et al.* 2015b).

*Our interpretation of factors affecting changed Antarctic toothfish prevalence*

In contrast to Parker *et al.* (2016) following on from WG-FSA, we hypothesize that predator effects (including that of humans) may be an important factor in the observed trends in AnT prevalence, i.e. the recession in depth of the top of the AnT cloud. Within McMurdo Sound and adjacent habitat under ice shelves (Kim *et al.* 2011), if the upper water column prevalence of the AnT has been reduced by commercial fishing pressure (targeting the larger fish), this would facilitate the possibility that the area's high concentrations of AnT predators, killer whales (*Orcinus orca* L.) and Weddell seals, could contribute to altering AnT prevalence further (within the diving range of these mammals). Owing to the large size and energy density of toothfish (Lenky *et al.* 2012), they are sought by these predators, and fewer AnT might well increase interspecific competition for them, thus decreasing prevalence in easier-to-reach depths. This hypothesis is supported by the observation that depths > 500 m (Fig. 2; the part of the water column to which AnT appear to be currently relegated) are below the usual maximum diving depth of fish-eating killer whales (Reisinger *et al.* 2015; although they very occasionally reach 700 m in McMurdo Sound (R. Pitman, personal communication 2015)). The depth of 500 m is below the usual Weddell seal diving range as well, with deeper dives testing breath-holding capacity and reducing the seals' prey searching ability within respective dives (as well as those of the killer whales), thus increasing foraging effort (Castellini *et al.* 1992). Notably, while there is evidence that Antarctic silverfish depth distribution includes the benthopelagic realm (Causse *et al*. 2011, Hanchet *et al*. 2013), a depth of ≥ 500 m is also below the usual depth of these fish (< 400 m; Fuiman *et al*. 2002, O'Driscoll *et al*. 2011; see Fig. 2), which are the main prey of AnT (and the shallow-diving Adélie penguins) in McMurdo Sound. Having to feed on less energy-rich prey, perhaps helps to explain the poor condition of the fish caught by Parker *et al*.

It is not unusual for notothenioid fish to change their use of space as a strategy to reduce predation risk from mammal predators, even if it means occupying waters having lower food availability (Everson 1970). In contrast to conjecture by WG-FSA and Parker *et al*. (2016), we note that the extensive fast ice and pack ice in McMurdo Sound during the icebergs' presence (see MacAyeal *et al*. 2008) protected AnT from predation, by restricting access by air-breathing predators, rather than contributing to their disappearance (a possibility noted also by Buckley 2013). It might well be that the fish found by Parker *et al*. (2016), to reduce predation risk, had become confined to the deep bottom depressions, in one of which those researchers fished (Fig. 1). Indeed, Weddell seal numbers were lower in McMurdo Sound during the mega-iceberg years (2001–05), and only since 2010 has the abundance of Weddell seals that occupy southern McMurdo Sound during spring recovered from their slaughter for dog food in the 1950–80s (>2200 seals were taken from southern McMurdo Sound; Ainley *et al*. 2015a). It is possible that this recovery has contributed to the AnT trends evident during spring in McMurdo Sound, i.e. the disappearance of large AnT at shallower depths in the water column. Even when seal populations were low in the early 1980s, Testa *et al*. (1985) showed not only that AnT prevalence is greatly reduced where seals are concentrated, but also that once the seals began to disperse from pupping/breeding areas following pup weaning, the prevalence of AnT began to decrease farther away from the breeding haul-out location.

Much remains unknown about the life cycle of the AnT. If we were starting over with the 40-year time series, for the purpose of monitoring the fishery, we would implement a more sophisticated randomized sampling design over a wider geographical region and at a range in depth, as this would probably lead to more robust findings. In the meantime, we have tried to give an unbiased interpretation of the data that are currently available.

## Acknowledgements

Thanks to Paul Cziko for sharing his data and comments, and to Robert Pitman for sharing his and John Durban's killer whale foraging data. Comments by Mario La Mesa, two anonymous reviewers and the Editor, David Walton, improved our presentation immensely. DGA and GB time in preparing this paper was supported by National Science Foundation grants ANT-0944411 and -0944141.

## Author contribution

All authors participated fully in the writing and subsequent re-writing of this paper.

## References

Ainley, D.G. & Siniff, D.B. 2009. The importance of Antarctic toothfish as prey of Weddell Seals in the Ross Sea: a review. *Antarctic Science*, **21**, 317–327.

Ainley, D.G., LaRue, M.A., Stirling, I., Stammerjohn, S. & Siniff, D.B. 2015a. An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast. *Marine Mammal Science*, **31**, 1338–1361.

Ainley, D.G., Ballard, G., Barton, K.J., Karl, B.J., Rau, G.H., Ribic, C.A. & Wilson, P.R. 2003. Spatial and temporal variation of diet composition within a presumed metapopulation of Adélie penguins. *Condor*, **105**, 95–106.

Ainley, D.G., Ballard, G., Jones, R.M., Jongsomjit, D., Pierce, S.D., Smith Jr, W.O., & Veloz, S. 2015b. Trophic cascades in the western Ross Sea, Antarctica: revisited. *Marine Ecology Progress Series*, **534**, 1–16.

Ainley, D.G., Nur, N., Eastman, J.T., Ballard, G., Parkinson, C.L., Evans, C.W. & DeVries, A.L. 2012. *Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972–2011*. Document SC-CAMLR-WG-FSA-12/P04. Hobart, TAS: CCAMLR.

Ainley, D.G., Nur, N., Eastman, J.T., Ballard, G., Parkinson, C.L., Evans, C.W. & DeVries, A.L. 2013. Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972–2011. *Fish and Fisheries*, **14**, 343–363.

Barry, J.P. & Dayton, P.K. 1988. Current patterns in McMurdo Sound, Antarctica and their relationship to local biotic communities. *Polar Biology*, **8**, 367–376.

Blackwell, B.G., Brown, M.L. & Willis, D.W. 2000. Relative weight (Wr) status and current use in fisheries assessment and management. *Reviews in Fisheries Science*, **8**, 1–44.

Buckley, B.A. 2013. Rapid change in shallow water fish species composition in an historically stable Antarctic environment. *Antarctic Science*, **25**, 676–680.

Calhaem, I. & Cristofell, D.A. 1969. Some observations of the feeding habits of a Weddell seal, and measurements of its prey, *Dissostichus mawsoni*, at McMurdo Sound, Antarctica. *New Zealand Journal of Marine and Freshwater Research*, **3**, 181–190.

Castellini, M.A., Davis, R.W. & Kooyman, G.L. 1992. Annual cycles of diving behavior and ecology of the Weddell seal. *Bulletin of the Scripps Institution of Oceanography*, **28**, 1–54.

Causse, R., Ozouf-Costaz, C., Koubbi, P., Lamy, D., Eléaume, M., Dettaï, A., Duhamel, G., Busson, F., Pruvost, P., Post, A., Beaman, R. J. & Riddle, M.J. 2011. Demersal ichthyofaunal shelf communities from the Dumont d'Urville Sea (East Antarctica). *Polar Science*, **5**, 272–285.

Cziko, P.A., DeVries, A.L., Evans, C.W. & Cheng, C.H.C. 2014. Antifreeze protein-induced superheating of ice inside Antarctic notothenioid fishes inhibits melting during summer warming. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 14 583–14 588.

Dugger, K.M., Ballard, G., Ainley, D.G., Lyver, P.O. & Schine, C. 2014. Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. *Frontiers in Ecology and Evolution*, **2**, 10.3389/fevo.2014.00068.

Eastman, J.T. 1985a. The evolution of neutrally buoyant notothenioid fishes: their specializations and potential interactions in the Antarctic marine food web. *In* Seigfried, W.R., Condy, P.R. & Laws, R.M., *eds. Antarctic nutrient cycles and food webs*. Berlin: Springer, 430–436.

Eastman, J.T. 1985b. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biology*, **4**, 155–160.

Eastman, J.T. & Barry, J.P. 2002. Underwater video observation of the Antarctic toothfish (*Dissostichus mawsoni* (Perciformes: Nototheniidae) in the Ross Sea, Antarctica. *Polar Biology*, **25**, 391–395.

Eastman, J.T. & DeVries, A.L. 2000. Aspects of body size and gonadal histology in the Antarctic toothfish, *Dissostichus mawsoni*, from McMurdo Sound, Antarctica. *Polar Biology*, **23**, 189–195.

Eastman, J.T., Amsler, M.O., Aronson, R.B., Thatje, S., McClintock, J.B., Vos, S.C., Kaeli, J.W., Singh, H. & La Mesa, M. 2013. Photographic survey of benthos provides insights into the Antarctic fish fauna from the Marguerite Bay slope and the Amundsen Sea. *Antarctic Science*, **25**, 31–43.

Everson, I. 1970. The population dynamics and energy budget of *Notothenia neglecta* Nybelin at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 23, 25–50.

Fenaughty, J.M. 2006. Geographical differences in the condition, reproductive development, sex ratio and length distribution of Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (CCAMLR subarea 88.1). *CCAMLR Science*, **13**, 27–45.

Fenaughty, J.M., Eastman, J.T. & Sidell, B.D. 2008. Biological implications of low condition factor 'axe handle' specimens of the Antarctic toothfish, *Dissostichus mawsoni*, from the Ross Sea. *Antarctic Science*, **20**, 537–551.

Fuiman, L.A., Davis, R.W. & Williams, T.M. 2002. Behaviour of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology*, **140**, 815–822.

Hanchet, S.M., Rickard, G.J., Fenaughty, J.M., Dunn, A. & Williams, M.J.H. 2008. A hypothetical life cycle for Antarctic toothfish *Dissostichus mawsoni* in Antarctic waters of CCAMLR Statistical Area 88. *CCAMLR Science*, **15**, 35–53.

Hanchet, S.M., Stewart, A.L., McMillan, P.J., Clark, M.R., O'Driscoll, R.L. & Stevenson, M.L. 2013. Diversity, relative abundance, new locality records, and updated fish fauna of the Ross Sea region. *Antarctic Science*, **25**, 619–636.

Kim, S.Z., Ainley, D.G., Pennycook, J. & Eastman, J.T. 2011. Antarctic toothfish heads found along tide cracks of the McMurdo Ice Shelf. *Antarctic Science*, **23**, 469–470.

Kim, S.L., Conlan, K., Malone, D.P. & Lewis, C.V. 2005. Possible food caching and defence in the Weddell seal: observations from McMurdo Sound, Antarctica. *Antarctic Science*, **17**, 71–72.

La Mesa, M., Eastman, J.T. & Vacchi, J.M. 2004. The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biology*, **27**, 321–338.

Lenky, C., Eisert, R., Oftedal, O.T. & Metcalf, V. 2012. Proximate composition and energy density of nototheniid and myctophid fish in McMurdo Sound and the Ross Sea, Antarctica. *Polar Biology*, **35**, 717–724.

Lyver, P.O., Barron, M., Barton, K.J., Ainley, D.G., Pollard, A., Gordon, S., McNeill, S., Ballard, G. & Wilson, P.R. 2014. Trends in the breeding population of Adélie penguins in the Ross Sea, 1981–2012: a coincidence of climate and resource extraction effects. *PLoS ONE*, **9**, 10.1371/journal.pone.0091188.

MacAyeal, D.R., Okal, M.H., Thom, J.E., Brunt, K.M., Kim, Y.J. & Bliss, A.K. 2008. Tabular iceberg collisions within the coastal regime. *Journal of Glaciology*, **54**, 371–386.

Nash, R.D.M., Valencia, A.H. & Geffen, A.J. 2006. The origin of Fulton's Condition Factor – setting the record straight. *Fisheries*, **31**, 236–238.

Near, T.J., Russo, S.E., Jones, C.D. & DeVries, A.L. 2003. Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (Perciformes: Nototheniidae). *Polar Biology*, **26**, 124–128.

O'Driscoll, R.L., Macaulay, G.J., Gauthier, S., Pinkerton, M. & Hanchet, S. 2011. Distribution, abundance and acoustic properties of Antarctic silverfish (*Pleuragramma antarcticum*) in the Ross Sea. *Deep-Sea Research II - Topical Studies in Oceanography*, **58**, 181–195.

Parker, S.J., Mormede, S., DeVries, A.L., Hanchet, S.M. & Eisert, R. 2016. Have Antarctic toothfish returned to McMurdo Sound? *Antarctic Science*, **28**, 29–34.

Ponganis, P.J. & Stockard, T.K. 2007. The Antarctic toothfish: how common a prey for Weddell seals? *Antarctic Science*, **19**, 441–442.

Reisinger, R.R., Keith, M., Andrews, R.D. & de Bruyn, P.J.N. 2015. Movement and diving of killer whales (*Orcinus orca*) at a Southern Ocean archipelago. *Journal of Experimental Marine Biology and Ecology*, **473**, 90–102.

Robinson, N.J. & Williams, M.J.M. 2012. Iceberg-induced changes to polynya operation and regional oceanography in the southern Ross Sea, Antarctica, from *in situ* observations. *Antarctic Science*, **24**, 514–526.

Robison, B.H. 2003. What drives the diel vertical migrations of Antarctic midwater fish? *Journal of the Marine Biological Association of the United Kingdom*, **83**, 639–642.

Saenz, B.T. & Arrigo, K.R. 2014. Annual primary production in Antarctic sea ice during 2005–2006 from a sea ice state estimate. *Journal of Geophysical Research - Oceans*, **119**, 3645–3678.

SC-CAMLR. 2012. *Report of the 31st Meeting of the Scientific Committee* (*SC-CAMLR XXXI*)*, Annex 7*. Hobart, TAS: CCAMLR.

SC-CAMLR. 2013. *Report of the 32nd Meeting of the Scientific Committee* (*SC-CAMLR-XXXII*)*, Annex 6*. Hobart, TAS: CCAMLR.

SC-CAMLR. 2014. *Fishery report 2014: exploratory fishery for* Dissostichus *spp. in Subareas 88.1 and 88.2*. Hobart, TAS: CCAMLR.

Smith, W.O., Ainley, D.G., Arrigo, K.R. & Dinniman, M.S. 2014. The oceanography and ecology of the Ross Sea. *Annual Review of Marine Science*, **6**, 469–487.

Testa, J.W., Sinniff, D.B., Ross, M.J. & Winter, J.D. 1985. Weddell seal–Antarctic cod interactions in McMurdo Sound, Antarctica. *In* Seigfried, W.R., Condy, P.R. & Laws, R.M., *eds. Antarctic nutrient cycles and food webs*. Heidelberg: Springer, 561–565.