

Opinion Paper

Physical–biological interactions influencing large toothfish over the Ross Sea shelf

JULIAN ASHFORD¹, MICHAEL DINNIMAN² and CASSANDRA BROOKS³

¹Center for Quantitative Fisheries Ecology, Old Dominion University, 800 West 46th St, Norfolk, VA 23508, USA

²Center for Coastal Physical Oceanography, Old Dominion University, 411 Monarch Way, Norfolk, VA 23508, USA

³Stanford University, Palo Alto, CA 94305, USA
jashford@odu.edu

Abstract: We add comments to a recent series of publications in peer-reviewed journals concerning the distribution of large Antarctic toothfish (*Dissostichus mawsoni*) found over the inner shelf of the Ross Sea. We note that earlier fish ecologists advanced innovative hypotheses invoking physical–biological interactions with life history, and that these, far from being disproved, have been relegated by more immediately pressing management concerns. We argue that, despite the considerable advances achieved by research groups working on *D. mawsoni*, an understanding of distribution and abundance is incomplete without reference to the physical structure that supports their life history. We briefly consider hypotheses highlighted by the recent literature in the context of major features of the shelf circulation in the Ross Sea, in particular intrusions of modified Circumpolar Deep Water along trough systems. We suggest physical–biological interactions that may be involved and call for improvements in the monitoring programme that can help test between the competing hypotheses.

Received 11 February 2017, accepted 22 June 2017, first published online 7 September 2017

Key words: Circumpolar Deep Water intrusions, life history connectivity, physical structuring, probability-based sampling, transport pathways, vertical distribution

A brief overview

An earlier generation of fish ecologists focused on physical–biological interactions and their relationship to the abundance and distribution of Antarctic fish. Prominent studies advanced a diverse array of innovative hypotheses. These included the various roles of fronts, for instance in structuring feeding and forming biological barriers (e.g. Loeb *et al.* 1993), currents as transport pathways facilitating immigration and emigration (e.g. Kellermann 1986), the wind field in structuring life history habitat over the continental shelf (e.g. Hubold 1984) and retention systems in mitigating advection mortality (e.g. White 1998). Nevertheless, the hypotheses were difficult to test with the empirical and analytic tools available at the time. With the advent of commercially valuable fisheries, research focus shifted to supporting the conservation and management of targeted species, in particular identifying population structure and parameterizing stock assessment models.

It is important to note that the shift was not the result of a systematic attempt to test and disprove the earlier hypotheses. Evidence has continued to accumulate for other species, most notably in the transport and life history habitat of krill (e.g. Hofmann *et al.* 1998, Fach & Klinck 2006, Piñones *et al.* 2011). Methodology has

advanced as well; the increasingly sophisticated toolbox that Antarctic scientists can call on today includes predictive models and vessels capable of sampling in heavy ice conditions. Moreover, theoretical advances in our understanding of the physical system around the Southern Ocean (e.g. GLOBEC, ANSLOPE, RAISED) have coincided with the development of simulation techniques that can predict the transport of particles over a range of spatial and temporal scales (e.g. Fach & Klinck 2006, Piñones *et al.* 2011, Renner *et al.* 2012). Separately, increased commercial fishing has led to growing research activity in support of the Commission for the Conservation of Marine Living Resources (CCAMLR) and interest in spatial and ecosystem perspectives for managing exploited marine populations.

These developments have not been overlooked by Antarctic fish population scientists. In *Pleuragrammatinae*, the neutrally buoyant clade of notothenioids, empirical studies suggested an important role for the Antarctic Circumpolar Current in structuring populations of Patagonian toothfish *Dissostichus eleginoides* Smitt (e.g. Shaw *et al.* 2004, Ashford *et al.* 2006, 2008). Hanchet *et al.* (2008) used particle simulations and evidence from conventional fisheries techniques to propose a life history hypothesis for Antarctic toothfish (*Dissostichus mawsoni* Norman) in the Ross Sea, in which advection during

early life was linked to the Ross Gyre. Their hypothesis successfully withstood testing using age distributions validated by lead–radium dating (Brooks *et al.* 2011), environmental exposures inferred from otolith chemistry and a shelf circulation model (Ashford *et al.* 2012). Near *et al.* (2003) demonstrated an ontogenetic shift to neutral buoyancy at maturity and Ashford *et al.* (2012) suggested that this facilitated life history movement of *D. mawsoni* along deep transport pathways. Principally, recently mature fish move from juvenile feeding grounds on the shelf via trough outflows into the South-east Pacific Basin, and adults move subsequently along the Ross Gyre between spawning areas on the Pacific–Antarctic Ridge and feeding grounds on the continental slope. In Antarctic silverfish (*Pleuragramma antarctica* Boulenger), another species in the *Pleuragrammatinae* on which *D. mawsoni* feeds, La Mesa

et al. (2010) found that environmental conditions influenced the distribution and abundance of larval stages in the Ross Sea. A series of multi-disciplinary studies indicated substantial genetic flow around the Antarctic continent (Zane *et al.* 2006, Agostini *et al.* 2015) and population structuring linked to currents along the coast and continental slope of the Antarctic Peninsula (Ferguson 2012, La Mesa *et al.* 2014, 2015, Parker *et al.* 2015). In a population review, Ashford *et al.* (2017) outlined how physical–biological interactions between glacial trough systems, circulation and life history processes could structure the extensive distributions of *P. antarctica* observed along and across the continental shelf (e.g. La Mesa & Eastman 2012).

It is in this context that we respond to recent debate over the life history and ecology of *D. mawsoni*. We commend engagement beyond management working

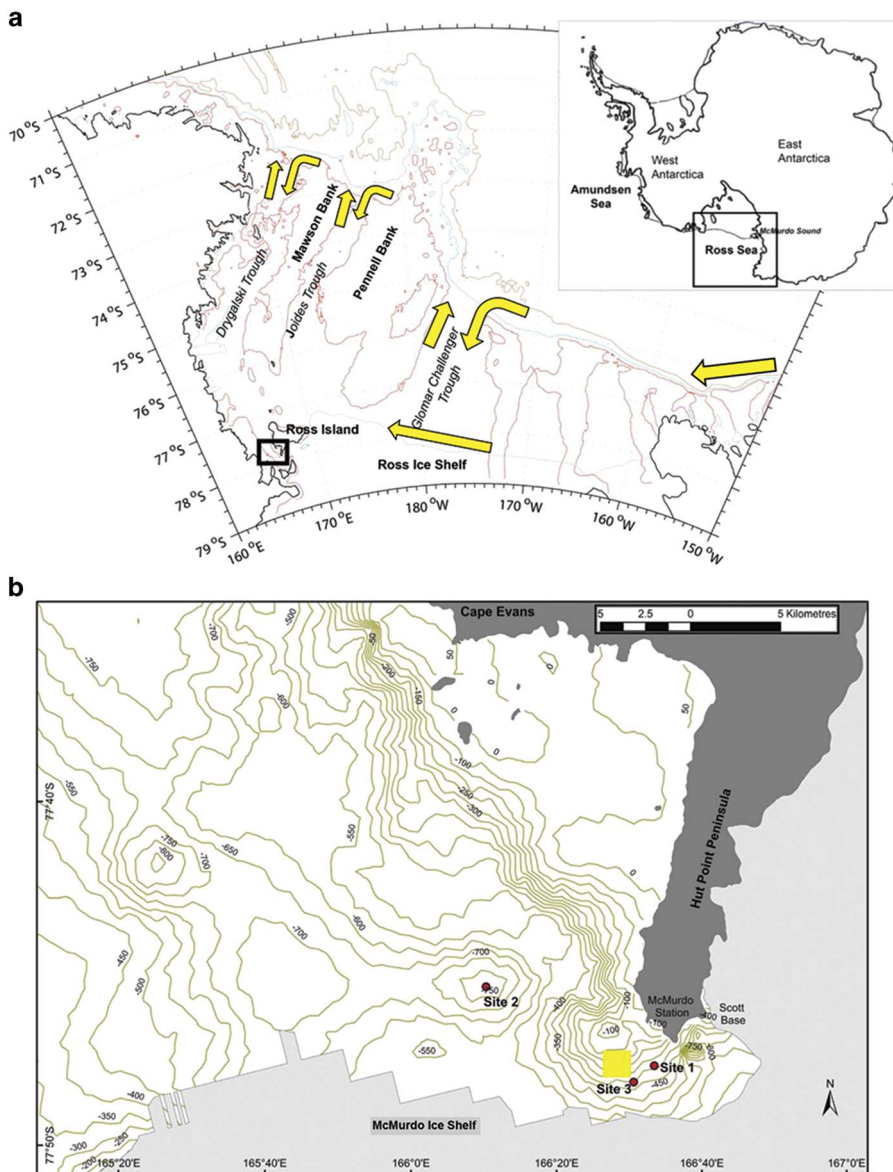


Fig. 1a. Map of the Ross Sea adapted from Ashford *et al.* (2012), with a schematic of the circulation (yellow arrows) showing main flows along the continental slope and Ross Ice Shelf and along troughs located north–south across the shelf. **b.** Detailed map of McMurdo Sound modified from Parker *et al.* (2016, fig. 2), showing their sampling sites (red circles) compared to the main area sampled in the time series (yellow square) taken from Ainley *et al.* (2017, fig. 1).

groups at CCAMLR and into the wider, peer-reviewed literature as a productive and welcome development. One strand of the wider discussion has focused on a decline observed in large, neutrally buoyant toothfish documented in McMurdo Sound (Fig. 1) after 2000 and attributed to commercial activity in the Ross Sea from 1997 onwards (Ainley *et al.* 2013, 2017, Parker *et al.* 2016). Another has centred around a recent comprehensive review of Antarctic toothfish biology (Hanchet *et al.* 2015, 2016; Ainley *et al.* 2016) that also referred to the decline in McMurdo Sound. We note that in both cases, the discussion reflected very different perspectives, between scientists working on fishery-related issues in the Ross Sea and others out of McMurdo Sound representing broader concerns, notably with predator–prey relationships. We also recognize the wealth of cross-disciplinary expertise brought to bear and the considerable advances achieved, as well as developing points of convergence. However, physical and spatial structuring is a critical component of the system, and further attention to these aspects may help resolve some of the issues raised. In this article, therefore, we consider the debate concerning abundance and distribution of large *D. mawsoni* near McMurdo Sound in light of their life history and the shelf circulation. We build on insights about vertical distributions afforded by neutral buoyancy that were highlighted in the earlier discussion, suggest circulatory mechanisms that may be involved and propose improvements in the monitoring programme that can help test between the competing hypotheses.

Review of evidence: physical structuring and sampling

Summary of prior discussion

The decline in large, neutrally buoyant toothfish observed in McMurdo Sound after 2000 (Ainley *et al.* 2013) was based on a 40 year time series that sampled through a hole cut in sea ice using baited hooks on a longline. As part of a monitoring programme to address the issues raised by Ainley *et al.* (2013), a similar configuration was used by Parker *et al.* (2016) during 2014 at three sampling sites in the same vicinity (Fig. 1). No fish were caught at a single site (site 1 in Fig. 1) that was shallower than used during the time series. At the other two sites, deeper than used during the time series, the catch-rate was similar to before the decline. Rather than commercial activity, Parker *et al.* (2016) suggested the observations by Ainley *et al.* (2013) were the result of detection issues related to depth or temporary absence influenced by the grounding of two large icebergs off Ross Island.

In response, Ainley *et al.* (2017) emphasized the importance of neutral buoyancy and interactions with diving predators and *P. antarctica* in structuring the vertical distribution of large *D. mawsoni* in the water column. They suggested this resulted in a ‘cloud’ that extended up from the bottom and, even over depths

of >500 m, reached near the surface at times. However, the cloud no longer extends above depths of 500 m in McMurdo Sound, and selective removal of large fish by the fishery would explain reduced numbers of neutrally buoyant individuals capable of moving throughout the water column. Rather than mega-icebergs, the authors hypothesized that predator effects, including fishing, have depressed the cloud below the diving range of many species and contributed to spatial mismatches with vertical distributions of *P. antarctica*.

As a result, the discussion highlighted the importance of variation in spatial distributions over time and the relationship to depth. There was also agreement over continued monitoring using a spatially stratified, standardized approach. While the exchange raised a number of useful points, we note that the hypotheses suggested to explain the decline observed by Ainley *et al.* (2013) included very little consideration of major circulation features over the shelf. We agree that fishery removals, fishing and predator avoidance by movement to depth and the unusual presence of mega-icebergs are potential explanations worth testing in future monitoring. However, transport pathways may also contribute to the variation observed.

Physical structuring

Large toothfish are typically caught by benthic longline between 1000–1600 m along the continental slope of the Ross Sea (Hanchet *et al.* 2016), where the Antarctic Slope Current and Front system (ASF) flows westward (Fig. 1) carrying warm Circumpolar Deep Water (CDW) in its intermediate depths (e.g. Dinniman *et al.* 2003, Orsi & Wiederwohl 2009). Variable but persistent intrusions of warm CDW are initially driven from the slope onto the Ross Sea shelf by momentum advection resulting from changes in the curvature of the shelf break (Dinniman *et al.* 2003), by eddies along the ASF (Stewart & Thompson 2015) and by tides (Wang *et al.* 2013). The shelf is characterized by trough systems that are oriented north–south and connect the shelf break to the inner shelf. The cross-shelf circulation is generally bathymetrically controlled and the CDW, mixing with adjacent waters to form modified CDW (MCDW), is carried along the eastern side of the troughs (Dinniman *et al.* 2003, Orsi & Wiederwohl 2009, Kohut *et al.* 2013). The intrusions are generally fast-flowing, with velocities of 0.3 m s^{-1} found along the western side of the Mawson and Pennell banks (Kohut *et al.* 2013). However, their core is shallow relative to the depths at which most large fish are taken commercially. Deeper shelf water forms outflows that sink down the slope in gravity currents that make counter-current swimming ineffective in the benthic layer (Ashford *et al.* 2012).

The vertical cloud suggested by Ainley *et al.* (2017) helps resolve this paradox. Simulation techniques can

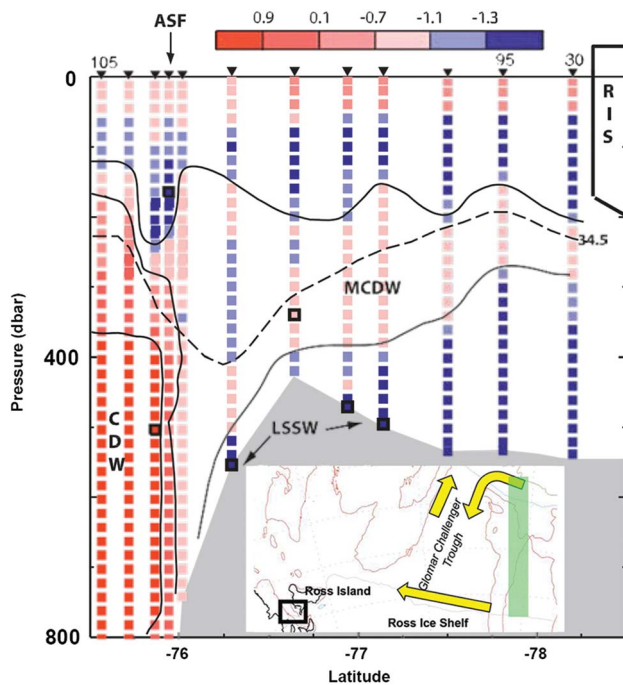


Fig. 2. North–south temperature section from the continental slope to Ross Ice Shelf (RIS; study area shown in inset as green rectangle), modified from Jacobs & Giulivi (2010, fig. 10; used with permission from the American Meteorological Society), showing intruding modified Circumpolar Deep Water (MCDW) in relation to depth. ASF = Antarctic Slope Current and Front system, LSSW = Low Salinity Shelf Water.

predict the transport of particles, based on circulation models like the high-resolution version of the Regional Ocean Modelling System used by Ashford *et al.* (2012). If large fish move high in the water column, particles released from shallower depths can provide insight into the change in transport pathways they would encounter. Simulations of particles released across the slope indicated that a proportion consistently reached the inner shelf of the south-western Ross Sea and Glomar Challenger Basin: 8–12% released from depths of 300 m and 9–19% from 100 m (Ashford *et al.* 2012, table 5). Thus, the extent and frequency of the intrusions containing MCDW that penetrate into the Glomar Challenger trough may contribute to a mechanistic explanation for the historic abundance and distribution of larger toothfish near McMurdo Sound. Poleward inflow forms a tongue of MCDW that occupies the intermediate layer along the eastern side of the trough (Fig. 2). In front of the Ross Ice Shelf (RIS) at 173°W, it forms a layer 150 m thick below a depth of 200 m (Orsi & Wiederwohl 2009). Flow along the ice shelf is generally westward (e.g. Jacobs *et al.* 1970). Along its western half, Antarctic Surface Water (AASW) is found to a depth of 225 m (Orsi & Wiederwohl 2009). Below this, a layer of

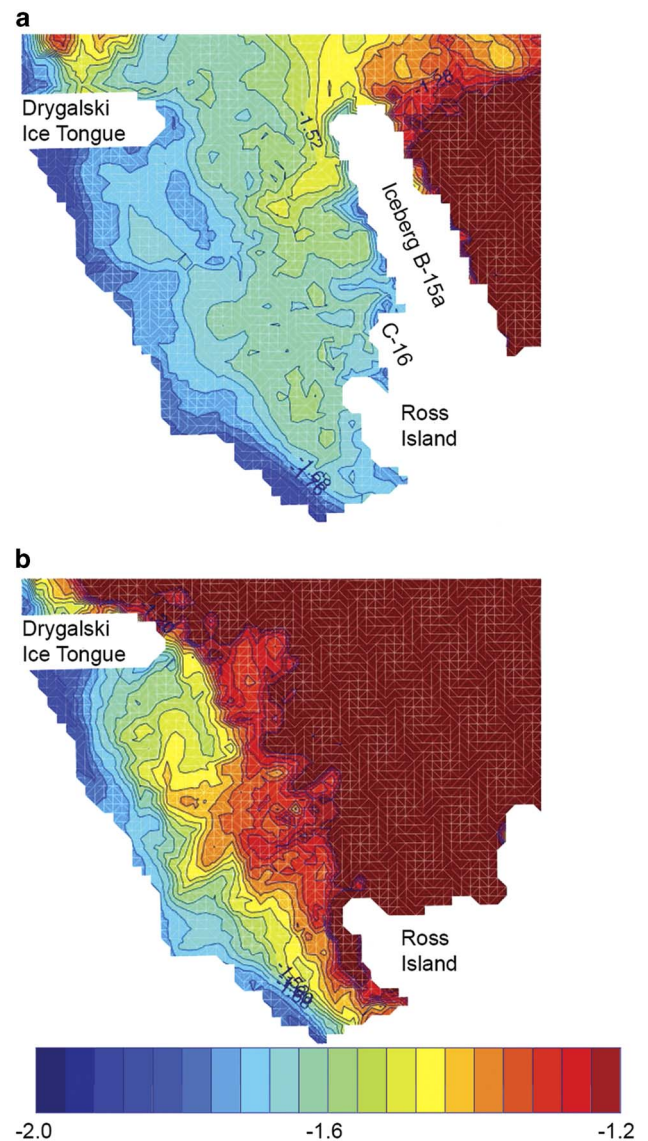


Fig. 3. Modelled temperature (°C) distributions around Ross Island at 30 m depth in January 2003, modified from Dinniman *et al.* (2007, fig. 14), comparing **a.** iceberg and **b.** baseline scenarios.

MCDW occurs to Ross Island, thinning considerably to a thickness of *c.* 50–75 m (Orsi & Wiederwohl 2009). Nutrient transport in CDW in the intrusions is probably important for biological production (McGillicuddy *et al.* 2015), particularly where it mixes with iron-rich sources from suspension and meltwater. If transport and production are correlated, active feeding is likely to reinforce movement of toothfish entrained in the intrusions across the shelf.

By corollary, depression of the cloud can help explain the decline observed by Ainley *et al.* (2013), as fish along the slope become less exposed to water upwelling on to the shelf. The proportion of simulated particles reaching

shelf areas dropped considerably with increasing depth of release over the slope (Ashford *et al.* 2012). The percentage reaching the Glomar Challenger trough halved to 9–10% between a release depth of 100 m in the surface layer and those at 500 m and 1000 m. The reduction was even more marked, from 9% to 3%, for particles reaching further west into the basin north of Ross Island. Increasing depth of the cloud may also facilitate off-shelf movement through greater exposure to outflowing shelf water. Thus, 48% of simulated particles released in the benthic layer near Ross Island reached the northern Ross Sea continental slope and the western boundary of the model domain, compared to 36% released at 100 m.

Moreover, physical structuring can help explain the association with iceberg activity noted by Parker *et al.* (2016). Six massive tabular icebergs calved off the RIS between 2000 and 2002. A portion of B-15 (B-15a) and B-16 drifted north of Ross Island in 2001, where they remained until 2005 and 2006 oriented north–south from the edge of the RIS (MacAyeal *et al.* 2008, fig. 1). Tabular icebergs calving off the RIS generally have a thickness of 250 m (MacAyeal *et al.* 2008), and observations (Robinson & Williams 2012) and simulations (Dinniman *et al.* 2007) indicated that the presence of B-15a and B-16 would mitigate flow of relatively warm surface water into McMurdo Sound (Fig. 3). Ainley *et al.* (2017) cautioned whether the icebergs would act as a barrier to toothfish moving at depth over the shelf near Ross Island. However, stratification is weak and the tabular icebergs significantly reduced the height of the water column, which may have diverted westward flow equatorwards throughout the water column as a result of potential vorticity constraints (Dinniman *et al.* 2007). Moreover, iceberg activity led to temporary freshening of the water column and changes in the formation of High Salinity Shelf Water that contributes to outflows off the shelf (Dinniman *et al.* 2007, Robinson & Williams 2012). Changes in vertical density may reinforce movement to depth, depressing the cloud, altering distributions relative to sampling by Ainley *et al.* (2013) as well as exposure to shelf outflows.

Sampling

How much the decline observed by Ainley *et al.* (2013) reflects fishery removals, fishing and predator avoidance by movement to depth or iceberg activity can be addressed in future sampling around McMurdo Sound. However, while we strongly support a monitoring programme that is independent of the fisheries, we note that the sampling designs used by Ainley *et al.* (2013) and Parker *et al.* (2016) were essentially opportunistic. Opportunity or convenience sampling is when samples are taken from a part of the population that is easy to access. The disadvantages are a lack of representativeness

and the risk of serious biases. In this case, understandably limited by the logistical constraints of sampling through sea ice, the programme was originally established to obtain specimens for laboratory experiments and remained spatially restricted and logistically driven even after resumption by Parker *et al.* (2016). Activity was limited mostly to one site that sometimes changed between years. The spatial limits of inference were consequently unclear and the representativeness of the samples open to question. Sampling error and bias, as well as changes in spatial and temporal availability of toothfish, may have influenced estimates. However, opportunistic sampling designs generally do not allow these effects to be examined or quantified, and limited numbers of sampling sites constrain the ability to tease apart changes in abundance from shifts in distribution.

These issues contribute to uncertainty in the conclusions drawn. While useful for detecting local temporal trends in catch-rate, the design was unable to separate potential confounding between a decline in abundance and movement to depth. Catch rates are notoriously susceptible to distribution effects. For example, given that the catch rate estimated by Parker *et al.* (2016) at the two deeper sites was similar to those found prior to the decline, it remained unclear whether a contraction in the depths, and therefore area, occupied by larger toothfish could be indicative of an overall reduction in abundance. Discrepancies in measures of toothfish condition highlighted by Ainley *et al.* (2017) may have been an artefact of sample size: differences in the means of body condition index *K* were small, while differences in the range may simply have reflected the low numbers of fish captured by Parker *et al.* (2016), that were inadequate to stabilize the tails of the distribution. There may have been confounding between depth and spatial features that are not necessarily related. For instance, most fish caught in the study by Parker *et al.* (2016) were caught in a bathymetric depression. Were higher catch rates really due to depth, or constraints of topography? The areas of contention between Ainley *et al.* (2017) and Parker *et al.* (2016) reflect such confounding effects and it is difficult to resolve these satisfactorily using a limited number of sampling sites that are chosen opportunistically.

In response, while we fully understand that the logistics of sampling on fast ice can be challenging, a well-conceived probability-based survey would nevertheless help resolve the issues over depth, providing a clearly defined spatial frame and sampling units, samples drawn according to a depth-stratified randomized sampling design and an optimum sample size. A properly randomized design would also help test between the various competing hypotheses concerning toothfish distribution. The design does not need to be complicated. CCAMLR surveys usually stratify by three depth strata and multiple sites randomly chosen within each stratum would simply demand opening a hole in the sea ice for each sampling

event. The frame can be drawn up based on the logistical limits of day travel around McMurdo Sound, allowing the spatial limits of inference to be defined clearly. Even three sites randomly chosen each year within each stratum would add a great deal of statistical rigor at the logistical cost of cutting holes for nine sampling sites (compared to the three cut by Parker *et al.* 2016). However, repeated sampling at each site would be correlated over time and independent sampling events would be better. Drawing from sampling theory and experience elsewhere, estimates will be most precise when a population is partitioned so that sampling units are as similar as possible (e.g. Thompson 1992). Measuring the important sources of variation would facilitate more efficient designs and allocation of sampling effort. The precision and accuracy of estimates could then be improved, while reducing the cost of sampling (e.g. Ashford *et al.* 2013).

Discussion

In this paper, we suggest physical–biological interactions between life history and circulation that may influence large *D. mawsoni* over the inner shelf of the Ross Sea. Specifically, we suggest that large neutrally buoyant toothfish found in McMurdo Sound may have moved from the slope using transport pathways that are well-established in the literature. Particle simulations strongly suggest that depression of the cloud, as well as reduced numbers of large fish over the slope, would lead to fewer reaching areas near Ross Island. Abundance of these toothfish may be partly a function of this movement along shelf inflows and export along shelf outflows, as well as local recruitment from resident juveniles as they grow and experience buoyancy changes associated with maturity. While we agree with our colleagues that fishery removals, fishing and predator avoidance by movement to depth, and the unusual presence of mega-icebergs are all important hypotheses to test, we observe that variation in the circulation is also likely to affect numbers of large toothfish over the inner shelf and the properties of the cloud defined by Ainley *et al.* (2017). As well as depression of the cloud, regional causes such as the relative curvature of the shelf, the strength and depth of upwelling onto the shelf and along troughs, the extent and distribution of CDW and shelf water, and effects on flow by topography or icebergs may all influence distribution of large *D. mawsoni* around McMurdo Sound.

These physical–biological interactions raise questions over variation on longer time scales. Multi-decadal freshening of shelf water in the south-western Ross Sea is consistent with increased melting of continental ice in the Amundsen Sea and transport westward in the ASF and along the coast (Jacobs *et al.* 2002, Jacobs & Giulivi 2010). Intrusions reaching the RIS have freshened and cooled as well (Jacobs & Giulivi 2010). The trend may

result in reduced production of AABW (Swift & Orsi 2012, Purkey & Johnson 2013) and less CDW coming onto the Ross Sea shelf (Stewart & Thompson 2015). Although unlikely to cause decline on the rapid timescale observed by Ainley *et al.* (2013), long-term changes in shelf inflows and export along shelf outflows may nevertheless have implications for toothfish movement, and hence abundance and distribution over the inner shelf. Moreover, the freshening has resulted in lower density throughout the water column in the south-western Ross Sea and more vertical stratification (Jacobs *et al.* 2002, Jacobs & Giulivi 2010). Like those potentially associated with recent iceberg activity, such changes in the vertical density structure on decadal time scales may depress the toothfish cloud over the long term, altering exposure to shelf inflows and outflows and contributing to spatial mismatches with *P. antarctica* (Ainley *et al.* 2017).

Testing between the competing hypotheses is vital and we use this opportunity to explicitly call for a monitoring programme that is probability-based, with a fixed spatial frame and sampling units, and samples drawn according to a depth-stratified randomized sampling design. We welcome recent sampling of seven more sites in a study currently being prepared for publication (Steven J. Parker, personal communication 2017). We note that a probability-based sampling design is necessary, but not in itself sufficient to measure properties of the cloud. Its height in the water column and important variables such as condition, length, age and sex of fish are all likely to vary over time, depth and space. Testing will demand vertical sampling that has not so far been undertaken using longlines. With ice-strengthened vessels, approaches that are independent of fisheries may be effective for pelagic sampling, but problems due to gear effects and the size and density of the fish targeted would need to be addressed. Predator cameras also present an opportunity but careful attention is needed to avoid biases exerted by selective foraging. Finally, we predict strong physical–biological relationships, so measurement of physical variables at the local and regional scale would be a valuable corollary. The measurements can be used to quantify associations with biological variables over the inner shelf and assess their contribution to the variation observed. A more rigorous probability-based approach combining biological monitoring with measures of physical processes would be a valuable step forward in resolving the important questions raised by Parker *et al.* (2016) and Ainley *et al.* (2017) concerning the abundance and distribution of large toothfish in McMurdo Sound.

Acknowledgements

We wish to acknowledge two anonymous reviewers for comments that substantially improved the manuscript. We thank Steven J. Parker for permission to reproduce

the map of McMurdo Sound in Fig. 1 and generous communication of unpublished material on recent sampling.

Author contribution

JA wrote the initial draft of the manuscript. All authors contributed text revisions and editing, and approved the final version. MD and CB were co-authors on the original publication by Ashford *et al.* (2012), funded by the US National Science Foundation. MD undertook the particle simulations on which this manuscript draws and CB undertook the age analyses, including their validation, that underpin application to connectivity over the life history. Additional intellectual contributions by MD in this paper include disruption of transport due to iceberg activity and freshening of the water column. CB made important contributions in the presentation of the arguments and their articulation in relation to the debate at CCAMLR.

References

- AGOSTINI, C., PATARNELLO, T., ASHFORD, J.R., TORRES, J.J., ZANE, L. & PAPETTI, C. 2015. Genetic differentiation in the ice-dependent fish *Pleuragramma antarctica* along the Antarctic Peninsula. *Journal of Biogeography*, 10.1111/jbi.12497.
- AINLEY, D.G., EASTMAN, J.T. & BROOKS, C.M. 2016. Comments on “The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross Sea region,” by S. Hanchet *et al.* *Hydrobiologia*, 10.1007/s10750-015-2607-4.
- AINLEY, D.G., BALLARD, G., EASTMAN, J.T., EVANS, C.W., NUR, N. & PARKINSON, C.L. 2017. Changed prevalence, not absence, explains toothfish status in McMurdo Sound. *Antarctic Science*, 10.1017/S0954102016000584.
- 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.
- ASHFORD, J.R., ARKHIPKIN, A.I. & JONES, C.M. 2006. Can the chemistry of otolith nuclei determine population structure of Patagonian toothfish *Dissostichus eleginoides*? *Journal of Fish Biology*, 69, 708–721.
- ASHFORD, J.R., JONES, C.M. & FEGLEY, L. 2013. Within-day variability in catch taken by public access fishers during a recreational fishing survey. *Transactions of the American Fisheries Society*, 142, 974–978.
- ASHFORD, J.R., ZANE, L., TORRES, J.R., LA MESA, M. & SIMMS, A.R. 2017. Population structure and life history connectivity of Antarctic silverfish (*Pleuragramma antarctica*) in the Southern Ocean ecosystem. In VACCHI, M., PISANO, E. & GHIGLIOTTI, L., eds. *The Antarctic silverfish: a keystone species in a changing ecosystem*. Basel: Springer, 193–234.
- ASHFORD, J.R., JONES, C.M., HOFMANN, E.E., EVERSON, I., MORENO, C.A., DUHAMEL, G. & WILLIAMS, R. 2008. Otolith chemistry indicates population structuring by the Antarctic Circumpolar Current. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 135–146.
- ASHFORD, J.R., DINNIMAN, M., BROOKS, C., ANDREWS, A.H., HOFMANN, E., CAILLIET, G., JONES, C. & RAMANNA, N. 2012. Does large-scale ocean circulation structure life history connectivity in Antarctic toothfish (*Dissostichus mawsoni*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 1903–1919.
- BROOKS, C.M., ANDREWS, A.H., ASHFORD, J.R., RAMANNA, N., JONES, C.D., LUNDSTROM, C. & CAILLIET, G.M. 2011. Age estimation and lead-radium dating of Antarctic toothfish (*Dissostichus mawsoni*). *Polar Biology*, 34, 329–338.
- DINNIMAN, M.S., KLINCK, J.M. & SMITH, W.O. 2003. Cross-shelf exchange in a model of the Ross Sea circulation and biogeochemistry. *Deep-Sea Research II - Topical Studies in Oceanography*, 50, 3103–3120.
- DINNIMAN, M.S., KLINCK, J.M. & SMITH, W.O. 2007. Influence of sea ice cover and icebergs on circulation and water mass formation in a numerical circulation model of the Ross Sea, Antarctica. *Journal of Geophysical Research - Oceans*, 10.1029/2006JC004036.
- FACH, B.A. & KLINCK, J.M. 2006. Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part I: Circulation and particle tracking simulations. *Deep-Sea Research I - Oceanographic Research Papers*, 53, 987–1010.
- FERGUSON, J.W. 2012. *Population structure and connectivity of an important pelagic forage fish in the Antarctic ecosystem, Pleuragramma antarcticum, in relation to large scale circulation*. MSc thesis, Old Dominion University, 132 pp. [Unpublished].
- 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 the Ross Sea region. *CCAMLR Science*, 15, 35–54.
- HANCHET, S., DUNN, A., PARKER, S., HORN, P., STEVENS, D. & MORMEDE, S. 2015. The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross Sea region. *Hydrobiologia*, 10.1007/s10750-015-2435-6.
- HANCHET, S., DUNN, A., PARKER, S., HORN, P., STEVENS, D. & MORMEDE, S. 2016. Response to the opinion paper by Ainley *et al.* *Hydrobiologia*, 10.1007/s10750-015-2607-4.
- HOFMANN, E.E., KLINCK, J.M., LOCARNINI, R.A., FACH, B. & MURPHY, E. 1998. Krill transport in the Scotia Sea and environs. *Antarctic Science*, 10, 406–415.
- HUBOLD, G. 1984. Spatial distribution of *Pleuragramma antarctica* (Pisces: Nototheniidae) near the Filchner and Larsen ice shelves (Weddell Sea, Antarctica). *Polar Biology*, 3, 231–236.
- JACOBS, S.S. & GIULIVI, C.F. 2010. Large multidecadal salinity trends near the Pacific–Antarctic continental margin. *Journal of Climate*, 23, 4508–4524.
- JACOBS, S.S., AMOS, A.F. & BRUCHHAUSEN, P.M. 1970. Ross Sea oceanography and Antarctic Bottom Water formation. *Deep Sea Research and Oceanographic Abstracts*, 17, 935–962.
- JACOBS, S.S., GIULIVI, C.F. & MELE, P.A. 2002. Freshening of the Ross Sea during the late 20th century. *Science*, 297, 386–389.
- KELLERMANN, A. 1986. Geographical distribution and abundance of postlarval and juvenile *Pleuragramma antarctica* (Pisces, Notothenioidei) off the Antarctic Peninsula. *Polar Biology*, 6, 111–119.
- KOHUT, J., HUNTER, E. & HUBER, B. 2013. Small-scale variability of the cross-shelf flow over the outer shelf of the Ross Sea. *Journal of Geophysical Research - Oceans*, 118, 1863–1876.
- LA MESA, M. & EASTMAN, J.T. 2012. Antarctic silverfish: life strategies of a key species in the high-Antarctic ecosystem. *Fish and Fisheries*, 13, 241–266.
- LA MESA, M., PIÑONES, A., CATALANO, B. & ASHFORD, J. 2015. Predicting early life connectivity of Antarctic silverfish, an important forage species along the Antarctic Peninsula. *Fisheries Oceanography*, 10.1111/fog.12096.
- LA MESA, M., RIGINELLA, E., MAZZOLDI, C. & ASHFORD, J. 2014. Reproductive resilience of ice-dependant Antarctic silverfish in a rapidly changing system along the western Antarctic Peninsula. *Marine Ecology*, 10.1111/maec.12140.
- LA MESA, M., CATALANO, B., RUSSO, A., GRECO, S., VACCHI, M. & AZZALI, M. 2010. Influence of environmental conditions on spatial distribution and abundance of early life stages of Antarctic silverfish, *Pleuragramma antarcticum* (Nototheniidae), in the Ross Sea. *Antarctic Science*, 22, 243–254.

- LOEB, V.J., KELLERMANN, A.K., KOUUBI, P., NORTH, A.W. & WHITE, M.G. 1993. Antarctic larval fish assemblages: a review. *Bulletin of Marine Science*, **53**, 416–449.
- 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.
- MCGILICUDDY, D.J., SEDWICK, P.N., DINNIMAN, M.S., ARRIGO, K.R., BIBBY, T.S., GREENAN, B.J.W., HOFMANN, E.E., KLINCK, J.M., SMITH, W.O., MACK, S.L., MARSAY, C.M., SOHST, B.M. & VAN DIJKEN, G.L. 2015. Iron supply and demand in an Antarctic shelf ecosystem. *Geophysical Research Letters*, **42**, 8088–8097.
- 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.
- ORSI, A.H. & WIEDERWOHL, C.L. 2009. A recount of Ross Sea waters. *Deep-Sea Research II - Topical Studies in Oceanography*, **56**, 778–795.
- PARKER, M.L., FRASER, W.F., ASHFORD, J., PATARNELLO, T., ZANE, L. & TORRES, J.J. 2015. Assemblages of micronektonic fishes and invertebrates in a gradient of regional warming along the western Antarctic Peninsula. *Journal of Marine Systems*, 10.1016/j.jmarsys.2015.07.005.
- PARKER, S.J., MORMEDE, S., DEVRIES, A.L., HANCHET, S.M. & EISERT, E. 2016. Have Antarctic fish returned to McMurdo Sound? *Antarctic Science*, **28**, 29–34.
- PIÑONES, A., HOFMANN, E.E., DINNIMAN, M.S. & KLINCK, J.M. 2011. Lagrangian simulation of transport pathways and residence times along the western Antarctic Peninsula. *Deep-Sea Research II - Topical Studies in Oceanography*, **58**, 1524–1539.
- PURKEY, S.G. & JOHNSON, G.C. 2013. Antarctic Bottom Water warming and freshening: contributions to sea level rise, ocean freshwater budgets, and global heat gain. *Journal of Climate*, **26**, 6105–6122.
- RENNER, A.H.H., THORPE, S.E., HEYWOOD, K.J., MURPHY, E.J., WATKINS, J.L. & MEREDITH, M.P. 2012. Advective pathways near the tip of the Antarctic Peninsula: trends, variability and ecosystem implications. *Deep-Sea Research I - Oceanographic Research Papers*, **63**, 91–101.
- ROBINSON, N.J. & WILLIAMS, M.J.M. 2012. Iceberg-induced changes to polynya operation and regional oceanography in the southern Ross Sea, Antarctic, from *in situ* observations. *Antarctic Science*, **24**, 514–526.
- SHAW, P.W., ARKHIPKIN, A.I. & AL-KHAIRULLA, H. 2004. Genetic structuring of Patagonian toothfish populations in the southwest Atlantic Ocean: the effect of the Antarctic Polar Front and deep-water troughs as barriers to genetic exchange. *Molecular Ecology*, **13**, 3293–3303.
- STEWART, A.L. & THOMPSON, A.F. 2015. Eddy-mediated transport of warm Circumpolar Deep Water across the Antarctic shelf break. *Geophysical Research Letters*, 10.1002/2014GL062281.
- SWIFT, J.H. & ORSI, A.H. 2012. Sixty-four days of hydrography and storms: RVIB *Nathaniel B. Palmer's* 2011 SO4P Cruise. *Oceanography*, **25**, 54–55.
- THOMPSON, S.K. 1992. *Sampling*. New York, NY: John Wiley and Sons, 343 pp.
- WANG, Q., DANILOV, S., HELLMER, H., SIDORENKO, D., SCHRÖTER, J. & JUNG, T. 2013. Enhanced cross-shelf exchange by tides in the western Ross Sea. *Geophysical Research Letters*, **40**, 5735–5739.
- WHITE, M.G. 1998. Development, dispersal and recruitment: a paradox for survival among Antarctic fish. In DI PRISCO, G., PISANO, E. & CLARKE, A., eds. *Fishes of Antarctica. A biological overview*. Milan: Springer, 53–62.
- ZANE, L., MARCATO, S., BARGELLONI, L., BORTOLOTTI, E., PAPETTI, C., SIMONATO, M., VAROTTO, V. & PATARNELLO, T. 2006. Demographic history and population structure of the Antarctic silverfish *Pleuragramma antarcticum*. *Molecular Ecology*, **15**, 4499–4511.