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OPINION PAPER

Comments on “The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross Sea region,” by S. Hanchet et al.

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Abstract We expand the paper by Hanchet et al. (Hydrobiologia 761:397–414, 2015), published in Hydrobiologia, by elaborating upon neutral buoyancy, a critical aspect of Antarctic toothfish life history that was only briefly treated by those authors. Neutral buoyancy, although not common among adult notothenioid fish, is an attribute that expands the water column niche space of this species beyond that available to the bottom-dwelling toothfish that were emphasized in the review. Conversely, also not well covered in the review are the implications involved in the suspected absence of neutral buoyancy in the so-called post-spawning, fat-depleted “axe-handle” fish.

Keywords Antarctic toothfish · Neutral buoyancy · Axe-handle body condition · Ross Sea · Southern Ocean

In their recent paper in Hydrobiologia, Hanchet et al. (2015) present a valuable summary of much of what is known about the natural history of Antarctic toothfish (*Dissostichus mawsoni* Norman 1937), the largest fish in the Southern Ocean and among the ~100 species of notothenioids, which together dominate the Southern Ocean fish fauna. It is one of only five notothenioid species that achieve neutral buoyancy as adults and large subadults thus allowing an expanded ecological role compared to other primarily benthic notothenioids (Near et al., 2003). Hanchet et al. (2015) summarize information from 60 reports, although >20% are not publicly available to scientists outside of members of the working groups that manage the species’ commercial fishery (CCAMLR: Convention for the Conservation of Antarctic Marine Living Resources, i.e., those papers listed as SC-CAMLR WG-EMM or WG-FSA). While the CCAMLR report guidelines are designed to protect the authors’ future publishing of results, often the reports are never published and therefore not peer reviewed or publicly available although some become central to CCAMLR’s management strategy. In any case, a significant portion of the Hanchet et al.’s (2015) review cannot be verified. Further, despite their

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attempt at a thorough review, these authors misinterpreted or overlooked some critical aspects of toothfish life history. Given the authors' well-warranted recommendations with respect to acquiring information about the "spawning behavior and [attributes of] early life history" of toothfish, we wish to build on their review by offering one correction and a few important additions, especially in regard to the species' capacity for neutral buoyancy. We further draw attention to some of the caveats and uncertainties inherent in the understanding of Antarctic toothfish biology, which largely relies on fishery-dependent data.

One major factor that Hanchet et al. (2015) confused was the geography of the Southern Ocean, stating that the Antarctic Convergence separates Antarctic toothfish from Patagonian toothfish (*D. eleginoides* Smitt 1898). This boundary between the two species actually occurs at the SBACC (Southern Boundary of the Antarctic Circumpolar Current; Orsi et al., 1995), as evident in Hanchet et al.'s (2015) Fig. 1 and affirmed by Roberts et al. (2011). This is important because temperatures are significantly colder south of the SBACC (requiring antifreeze in Antarctic toothfish and barring the permanent residence of Patagonian toothfish; Near et al., 2012). Further, dissolved oxygen is dramatically higher (Orsi et al., 1995) and biotic resources much richer than in waters north of the SBACC (Tynan, 1998; Nicol et al., 2000). On their respective sides of the SBACC, Roberts et al. (2011) found much fuller stomachs among Antarctic compared to Patagonian toothfish caught in the same Southern Ocean sector and same winter season (to date, there has been little winter sampling in the Ross Sea region).

Otherwise, in their valuable review, there are a few caveats about the available data that Hanchet et al. (2015) should have clarified for the benefit of readers who are not immersed in questions about Antarctic fish biology. First, on page 401, in a discussion of movements of tagged fish, Hanchet et al. (2015) point out that results are affected "spatially by the location of subsequent fishing effort and temporally by the relatively short austral summer season when fishing takes place." In fact, a large proportion of the studies in their review were based on data derived from the commercial catch and thus constrained in time and space by one of the highest sea-ice concentrations on the globe (growing in both extent and season; Stammerjohn et al., 2012). The concentrated ice cover limits commercial fishing to about 2–3 months of the year (December to January or February) and spatially confines the vessels to seasonally ice-free parts of the Ross Sea region, with vessels targeting the Ross Sea continental slope at 800–1200 m where large fish can be found.

Thus, the general knowledge about Ross Sea Antarctic toothfish is confined to the early summer months and skewed toward those fish that are caught in the limited areas the fishery occupies, which essentially are ice-free waters. Because vessels target large fish that live close to the bottom on the slope, scientists know very little about fish that occur at greater or shallower depths on the slope and elsewhere or about life history stages that the benthic longline gear does not target (e.g., fish <60 cm, and larger fish in the water column). Moreover, benthic longlining, because it uses baits on hooks, introduces biases because fish effectively select themselves; hungry fish are more likely to take bait (and faster), and larger ones may have advantages over smaller ones in terms of orienting to and competing for the bait. Although large sample sizes for testing some life history parameters are achieved through sampling the commercial catch (e.g., age and growth via otoliths, with its own biases: Horn, 2002; Brooks et al., 2011), other aspects remain less well known, especially spawning or very early life history.

In regard to the spatiotemporal constraint on the sampling emphasized by Hanchet et al. (2015), we would like to highlight a unique fishery independent tag-and-release study of Ross Sea toothfish completed over 39 years in the ice-covered waters of McMurdo Sound (Ainley et al., 2013). The McMurdo Sound ice conditions, which prevail from March into January, represent those for most of the Ross Sea commercial fishing area *during the period when sampling from commercial fishing is not possible*. The August–December scientific fishing expands the temporal constraints of the commercial fishery, as well as the vertical dimension in the water column (a vertical set line was used). This time series showed decadal variation in size, body condition, and abundance, and revealed that decreases in fish size and catch per unit effort were correlated with the initiation of the commercial fishery which, for most of its years, has operated in deep areas close to McMurdo Sound (Hanchet et al., 2015). A group of scientists (Parker et al., 2015), including many among Hanchet et al. (2015), despite what has been said to characterize the 39-year effort as a localized endeavor of limited application to the species at large, in fact, has initiated its own monitoring project, using much the same fishing gear and doing so near to the older time series' fishing site.

An additional caveat that should have been emphasized more by Hanchet et al. (2015) at the outset of their review is the existence of considerable uncertainty about many aspects of this species' natural history. Hanchet et al. (2015) highlight some of these uncertainties, like the lack of knowledge about early life history and reproductive ecology. Other uncertainties having to do with demographic factors were highlighted in Abrams (2014), but not acknowledged by Hanchet et al. (2015). One subject that Hanchet et al. (2015) expressly classified as holding great uncertainty (p. 409) is that concerning predation of subadults and adults, despite increasing evidence of their importance to a variety of predators, especially Weddell Seals (*Leptonychotes weddellii* Gill 1872; Ainley & Siniff, 2009). While Hanchet et al. (2015) did briefly review the multiple papers that investigate toothfish predation, a few of which are not publically available, they placed little to no emphasis on the importance of toothfish as a prey item for these species. The assumed lack of predation, an assumption based on a less-than-ideal amount of evidence rather than on evidence of absence, is used by CCAMLR to justify a fishery management strategy to reduce spawning biomass at a rate that would achieve 50% in 35 years (Constable et al., 2000). This contrasts the 25% level reserved for Antarctic krill (*Euphausia superba* Dana 1850), acknowledged by CCAMLR as an important forage species (Constable et al., 2000; but see Constable, 2004, who acknowledged ample predation on toothfish). On the other hand, there are some subjects that have become less uncertain, and many lend themselves to laboratory work and are more thoroughly investigated by different methods, e.g., size and growth by age as noted above.

Finally, pertinent to the issues of uncertainty is that Hanchet et al.'s (2015) discussions of various aspects of toothfish natural history are often separated among broad maturity classes, i.e., sub-adult vs adult. However, there is potentially much confusion in the review when relating patterns and trends to maturity stages or breeding status. This is because much of the literature that they summarized predates the 2012 finding by National Institute of Water and Atmosphere scientists, unpublished but cited in Mormede et al. (2014), that adulthood is achieved at 135 cm TL rather than the previously determined 110 cm TL. For example, when Hanchet et al. (2015) describe life history patterns of subadults, does this refer to fish <110 cm or <135 cm TL?

To provide a more comprehensive picture of what we know about Antarctic toothfish natural history, Hanchet et al. (2015) should have emphasized the importance of neutral buoyancy in the life history. The coupled morphological and phylogenetic diversification that allowed transition from the ancestral benthic habitat to neutral buoyancy was not an aberration, but instead a key evolutionary innovation that appeared early in the history of the Southern Ocean lineage and allowed toothfish and a few other species to expand into water column niches that were unfilled by the sparse non-notothenioid fauna (Near et al., 2012). Buoyancy is therefore a central aspect of Antarctic toothfish biology although it is variable over the course of the life cycle. Eggs, larvae, and early juveniles are likely pelagic (Hanchet et al., 2008), but at about 10 cm SL their buoyancy begins to decrease (Near et al., 2003). Juvenile fish of 10–60 cm TL are negatively buoyant and benthic based on (1) measurements of buoyancy in the 2.5–4.0% range, with 0% indicating neutral buoyancy (Eastman & Sidell, 2002; Near et al., 2003), and (2) photographs of similarly sized fish resting on the substrate at 1277–2002 m on the slope of the western Antarctic Peninsula (Eastman et al., 2013; Amsler et al., 2015), as well as at 454 m in the southern Ross Sea (Eastman & Barry, 2002). After reaching ~100 cm TL and acquiring a lipid store, Antarctic toothfish attain neutral buoyancy (Near et al., 2003). Thereafter, they range throughout the water column preferring depths of 300–500 m while on the shelf but moving up or down throughout their depth range (12–2210 m; Fuiman et al., 2002; Hanchet et al., 2015) as necessary to feed, when on the shelf, on Antarctic silverfish (*Pleuragramma antarctica* Boulenger 1902), which exhibit diel vertical migration (Fuiman et al., 2002; Robison, 2003; see below). Preferred depths, as pointed out by Near et al. (2003), may represent the lower end of upper level predators' foraging depth capabilities, and thus occupying these depths, or deeper, reduces predation pressure (see Ballard et al., 2012 and also

Everson, 1970 for spatial avoidance of predators by adult nototheniids).

Owing to their minimal treatment of neutral buoyancy, it is mistaken for Hanchet et al. (2015) to infer a strictly benthic habitat based on large sample sizes of toothfish caught by benthic longlines. If they are in good condition, mature adults at slope depths are more likely to be demersal or benthopelagic (DeWitt et al., 1990; Stevens et al., 2014) rather than strictly benthic. Based on the morphology of the brain, cranial nerves, and olfactory apparatus (Eastman & Lannoo, 2011), chemosensation is well developed in Antarctic toothfish. They are known scavengers (Petrov & Tatarnikov, 2011; Roberts et al., 2011; Stevens et al., 2014) and, like the closely related Patagonian toothfish, are capable of tracking the current-dispersed odor plume emanating from decaying carcasses, traps, or longline bait (Collins et al., 1999; Yau et al., 2001). These odors can potentially draw fish from positions in the water column to the substrate depending on the axes of water flow.

Moreover, in the "sheltered waters" of McMurdo Sound—a result of extensive, almost year-round ice cover (see above)—large, neutrally buoyant toothfish rise from the depths to within 12 m of the surface (Fuiman et al., 2002) to feed primarily on silverfish. Not emphasized in Hanchet et al.'s (2015) review of benthic-caught toothfish diet, neutrally buoyant toothfish in ice-covered waters of the shelf gorge on energy-dense silverfish (Eastman, 1985a, b: 90% with identifiable food of which silverfish contribute 71% frequency of occurrence, 90% diet composition by mass). This is in contrast to the benthic-dwelling fish summarized by Hanchet et al. (2015; 40% with no food, ~30% with mere "trace"), which, not surprisingly, often take lower energy-dense benthic prey and no silverfish.

Pleuragramma antarctica aggregate in loose schools, thus increasing their availability to mesopredators, and have the highest lipid content and energy density (Friedrich & Hagen, 1994; Lenky et al., 2012) of any fish likely to be consumed by toothfish at any location or depth on the shelf. *P. antarctica* are a primary prey of almost all Ross Sea mesopredators (Eastman, 1985a, b; Ballard et al., 2012; La Mesa et al., 2004; La Mesa & Eastman, 2012), thus opening the question about the extent of interspecific trophic competition between toothfish and these other predators. In support, in a study employing stable isotopes, δ15N values for toothfish indicated that on the shelf they occupied a similarly high trophic position to the channichthyid *Dacodraco hunteri* Waite 1916 (Jo et al., 2013), which is also a near-neutrally buoyant pelagic predator on *P. antarctica* (Eastman, 1999). In general, we wish to point out that many phylogenetically diverse deep-sea fishes, including the Patagonian toothfish, have phases especially during their early ontogeny when they exploit food-rich, shallower or surface waters where they are able to grow and mature more rapidly (Gon & Heemstra, 1990; Drazen & Haedrich, 2012).

Hanchet et al. (2015) do note that neutral buoyancy is not life-long but is affected by ontogeny and breeding status, with body condition lost during spawning but then hypothetically regained once fish have returned to the productive Ross Sea shelf and slope (note that to date no one actually knows what proportion successfully return, nor how long it takes to recover to spawn again; see below). Yet, Hanchet et al. (2015) downplay the importance and prevalence of this condition and in so doing limit their breadth of treatment of the toothfish diet (as noted above). Consistent with overlooking the importance of neutral buoyancy among larger Antarctic toothfish, Hanchet et al. (2015) also do not fully explore the significance and potential negative demographic consequences of the large number of "axe-handle" fish (starving individuals depleted of fat and white axial muscle, and thus negatively buoyant). Found predominantly in the northern portion of their range around the sea mounts where mature individuals of the Ross Sea population purportedly spawn, axe handles compose ~50% of fish of both sexes captured on longlines set near the seamounts (though that proportion could be biased upwards owing to baited hooks attracting hungry fish), but only ~5% on the slope and shelf in the south (Fenaughty et al., 2008; Hanchet et al., 2008). In McMurdo Sound, axe handles contributed an average of <3% of the fish caught over the 39 years sampled, though the proportion increased sharply after 2001 (Ainley et al., 2013).

Axe handles are presumably post-spawning individuals that have depleted their lipid stores, and possibly some white muscle protein, during migration, gametogenesis, and spawning, and have been unable to regain condition in oligotrophic northern waters (Fenaughty et al., 2008). Do they drift in the currents using their pectoral fins in an extended fixed position as lifting surfaces, never to spawn again, with potentially severe consequences for the breeding population? While such a seemingly unproductive life cycle is not expected in nature, the Ross Sea region is an extreme environment and there may be unforeseen consequences of the axe handle stage of the toothfish life cycle. For example, the hypothesized metabolic loss of white muscle protein in axe-handle fish (Fenaughty et al., 2008) may be difficult to replace given that, in Antarctic ectotherms, protein synthesis is effected at temperatures ≤0°C to a greater extent than are other metabolic processes (Peck, 2015). In addition, in the closely related Patagonian toothfish there may be loss of a component of the Falklands Islands breeding population ("non-breeding vagrants") due to unfavorable transport by currents during their life cycle (Ashford et al., 2012a). A similar scenario could exist in Ross Sea Antarctic toothfish (Ashford et al., 2012b).

The fate of axe-handle fish as well as other life stages and buoyancy, or lack thereof, also would figure importantly into the supposed passive or assisted movement around the Ross Gyre, north of the Ross Sea but south of the SBACC, as investigated by Hanchet et al. (2008) and Ashford et al. (2012b). These two groups of authors included simulations of the movements of presumed neutrally buoyant toothfish as a function of the flow and circulation of waters in the upper water column, down to 1000 m, with results showing little difference in flow rate as a function of depth in the models. Hanchet et al. (2008) argued that young stages were advected around the Ross Gyre and older fish moved directly between the Ross Sea slope and sea mounts by active swimming. However, Ashford et al. (2012b) pointed to physiological and hydrographic constraints on active swimming given the distances involved, and suggested that neutrally buoyant adult and immature fish moved along transport pathways. However, with regard to post-spawning axe-handle fish, it is not clear how, in their depleted state, their return to the slope would be facilitated, because some of the bathymetry reaches 5000 m (obviously beyond the known depth range of toothfish). Circulation would likely be slower in the deeper depths of the Ross Gyre (M. Dinniman, pers. comm.; S. Jacobs, pers. comm.). Very few fish tagged at sea mounts (proportion of axe-handle fish unknown) have been recovered; those that were recovered were caught on the slope after many years at liberty (Hanchet et al., 2015), apparently taking a considerable time getting there. Skip spawning was noted as potentially being involved. Clearly, much more work is needed in relating the role of ocean circulation to the movements of buoyant and non-buoyant Antarctic toothfish, as well as the role of neutrally buoyant toothfish in the Ross Sea ecosystem. Research should be directed to tagging northern axe handles to determine the following: survival rate, whether body condition is regained, whether more than 5% return to the slope or shelf, and whether they spawn again.

We would again like to emphasize that Hanchet et al. (2015) offered a useful and appreciated summary of Ross Sea Antarctic toothfish life history. We hope that we have been able to build on that summary by consideration of additional aspects of toothfish life history and by addressing many of the uncertainties and biases inherent in fishery-dependent data. Given that sustainable management relies on accurate life-history information, we encourage continued study of Ross Sea Antarctic toothfish. Filling the gaps in our knowledge about toothfish will require efforts and data beyond those achieved through the fishery. Questions of early life history, reproduction, and the fate of axe-handle fish, as well as about the role of toothfish as predator and prey can only be resolved through in-depth, fishery independent studies.

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