Letter to the Editor

How overfishing a large piscine mesopredator explains growth in Ross Sea penguin populations: A framework to better understand impacts of a controversial fishery

ABSTRACT

We herein review the modeling approach of Pinkerton et al. (2016, Ecol. Modelling), who tested the hypothesis that fishery depletion of large, neutrally buoyant Antarctic toothfish (*Dissostichus mawsoni*) was implicated in the recent increase in the southern Ross Sea population of Adélie penguins (*Pygoscelis adeliae*). Toothfish are a trophic competitor of penguins for Antarctic silverfish (*Pleuragramma antarctica*) in the southern Ross Sea, hence Ainley et al. (2013) and Lyver et al. (2014) proposed that the effect of the removal of toothfish was through predation release of silverfish. Pinkerton et al. concluded that predation release could not provide sufficient energy to sustain the observed penguin population growth. Critically, however, they failed to consider certain spatial and size-by-depth aspects of diet overlap, and mechanisms associated with population dynamics that could cause the population growth through predation release. In order to effectively test the prey release hypothesis, we suggest a strong inference path that incorporates what we know about population dynamics in penguins and Ross Sea food webs into life history parameterizations of penguins, toothfish and silverfish population dynamics models.

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1. Introduction

The Adélie penguin (*Pygoscelis adeliae*) population size at four colonies in the southern Ross Sea (Ross and Beaufort islands), constituting ~10% of the species' global population (see Lynch and LaRue, 2014), showed no trend in the 1990s, but after 2001, with an annual growth rate of 6.7%, nearly doubled from ~230,000 pairs in 1999/2000 to >400,000 pairs by 2012 (cf Wilson et al., 2001; Ainley et al., 2007; Lyver et al., 2014). This recent trend is counterintuitive because, owing to increasing sea ice extent in the penguin's wintering area (Stammerjohn et al., 2012; Kwok et al., 2016), penguin population size, on the basis of results from previous demographic modeling (Wilson et al., 2001), should have been decreasing over the last decade. Moreover, as of the early 2000s, it was thought that at least the largest colony in this metapopulation (Cape Crozier), had reached an asymptotic energy balance limit and therefore could not grow any larger, as indicated by a colony-size-related increase in foraging effort and energy expenditure leading to reduced chick growth and fledging size –– a result in turn of increased intraspecific competition for food during the breeding season (Ballance et al., 2009). However, recently the colony has increased dramatically, perhaps reaching a higher asymptote (Fig. 1). Clearly, given the recent surge in the size of this metapopulation and especially the Crozier colony, something in the system recently has changed. The central question is, what could be the large-scale factor(s) behind the recent, unexpected penguin trend in this region?

Ainley et al. (2013) and Lyver et al. (2014) hypothesized that a possible explanation for dramatically increasing Adélie penguin numbers in the southern Ross Sea was that there were greater numbers of energy-dense silverfish (*Pleurgramma antarctica*) available owing to reduced trophic competition between penguins and toothfish (*Dissostichus mawsoni*), in turn related to fewer toothfish in the water column. While we address just Adélie penguins in this paper, it is worth pointing out that numbers of another silverfish predator, the emperor penguin (*Aptenodytes forsteri*) (Cherel and Kooyman, 1998), recently have attained levels at Cape Crozier never before seen in the past 65 years of counts (Ainley and Ballard, unpubl. data), indicating an unexpectedly rapid recovery from the early 2000s iceberg event (colony severely reduced: Barber-Meyer et al., 2008; Kooyman and Ponganis, 2016). The icebergs, present 2001–2005, had negative effects on numbers of Adélie penguins visiting Bird and Crozier during 2001 and 2003 (Dugger et al., 2014; Lyver et al., 2014).

Antarctic toothfish is the largest fish in Antarctic waters (Eastman, 1993). Adult, sexually mature toothfish, about 1–2 m long and weighing ≥100 kg, are being fished in the Ross Sea at arguably unsustainable rates (Abrams, 2014; Abrams et al., 2016). Ainley et al. (2013) and Lyver et al. (2014) suggested a connection between the toothfish fishery take and the population growth of Adélie penguins. These authors speculated that the effect was mediated through a food web mechanism. Simply put, they suggested that silverfish, which is an important prey to both Adélie penguins and toothfish (Eastman, 1985a; Ainley et al., 2003; La Mesa et al., 2004; La Mesa and Eastman, 2012), may have become more abun-
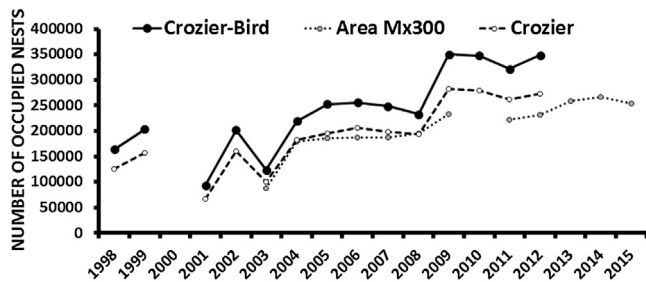
Fig. 1. The number of occupied Adélie penguin nests on about 1 December 1998–2015: Cape Bird and Crozier colonies combined to emphasize the regional aspect of penguin increase (from Lyver et al., 2014); and Cape Crozier only (from Lyver et al., 2014) to provide context to the several subcolonies common to all years located in Area M at Cape Crozier (DGA and collaborators, unpubl.), used as ground truthing of Antarctica NZ aerial photographs (source of the Lyver et al. data), thus extending the time series. Data are highly correlated (2004–2012): Crozier-Bird vs Area M, r = 0.965; Crozier vs Area M, r = 0.979. The 2001 and 2003 counts –- not included to show that correlations are robust –- were affected by the mega-icebergs, but by 2004 the penguins were able to negotiate around them (Dugger et al., 2014). The depression in 2007 and 2008, and those of 2001 and 2003, are the result of daunting sea ice conditions that inhibited birds, mostly youngers ones (who arrive late even normally) from arriving in time for egg laying and were absent at the time that aerial photos were taken (DGA and collaborators, unpubl.). Compare the pattern of growth 2003–2015 to that of the mid-1980s through the 1990s shown in earlier analyses (Wilson et al., 2001; Ainley et al., 2007), i.e., a similar plateauing of penguin numbers occurred in the 1990s, but at a lower level.

dant in Ross Sea surface waters after the removal of the toothfish, i.e. predation release, thereby facilitating the penguin population growth. The key information that is missing is the change in abundance of silverfish in shallow water over time and its impact on penguins at critical times in their life cycle.

The scientific fishery in McMurdo Sound (Ainley et al., 2013; Cziko et al., 2014) indicated that toothfish populations were relatively stable during the 25 years preceding the start of the Ross Sea fishery in 1997; after 2001, though, catch-per-unit-effort and fish size began to change. Changes became consistent with data gathered by the fishery itself suggesting a significant decline in toothfish population size (spawning stock biomass) combined with a decrease in mean size of individuals (CCAMLR, 2013, 2014). The population decline may be significantly greater than the 25% that CCAMLR estimated in 2013 (Abrams et al., 2016).

To test the predator release hypothesis, Pinkerton et al. (2016; henceforth, Pinkerton et al.) constructed a simple model, assuming that nothing else but toothfish, Adélie penguins, and silverfish were involved, thus, greatly simplifying the potential pathways of indirect effects of harvesting toothfish. They calculated the total mass of silverfish consumed by the toothfish removed, accounting for the proportion of silverfish in the toothfish diet and an average energy transfer efficiency. This mass of silverfish is the amount made available to other Ross Sea mesopredators by the extraction of toothfish. Pinkerton et al. showed that even if 100% of the predation release was consumed by Adélie penguins, correcting for energy transfer efficiency, it would not be sufficiently large enough to explain the doubling of the penguin population. They pointed to other possible causes of the expansion of penguin populations, such as temporary changes in the geophysical climate caused by the presence of large icebergs lodged in the southern Ross Sea that also occurred in 2001. Conditions, however, returned to normal by 2006, whereas penguin populations continued to grow for at least six more years and remain high (Fig. 1), a pattern for which they failed to provide a clear explanatory mechanism.

We find the evidence and explanations presented in Pinkerton et al. thus far incomplete and inadequate. First, Pinkerton et al. attempted to address the question: "Is the energy released by the removal of toothfish equal to the energy absorbed by the growth in penguin numbers?" This question is very different from

the predation release hypothesis. However, it implicitly assumes that Adélie populations are solely regulated bottom-up by lack of available food, which is not necessarily the reason to suspect predation release effects. The food web appears to have a 'wasp-waist' structure, involving close coupling among mesopredators and competition both exploitative and interference among them (Ainley, 2007; see also Testa et al., 1985; Ainley et al., 2006, 2007, 2015). Ainley et al. (2013) and Lyver et al. (2014), therefore, inferred causation: "Can a change in the food web due to the fishery cause the observed population growth?" To understand the distinction, imagine that the removal of toothfish released enough energy to match the energy that would sustain the observed penguin population growth. It still does not mean that the predation release caused or indeed is sustaining the growth. It is just an energy equivalence without an explanatory mechanism, unless Pinkerton et al. are implicitly proposing that Adélie populations are solely regulated by the total amount of energy in the system, without regard to when energy is available in the penguin life cycle or its consequences to life history parameters, and thus demographic processes.

Here we review the arguments presented by Pinkerton et al. and show that while their explanations are illuminating, the subject of predation release requires a more incisive explanation. Further, we briefly propose a path forward to better understand the penguin population growth and changes in the Ross Sea food web. To properly test the paradoxical position that the growth in penguin numbers is unrelated to toothfish extraction, as presented by Pinkerton et al., we must understand the causes of growth in terms of the processes that regulate Adélie penguin population numbers, as well as the changes in the Ross Sea food web that make existing, new, or enhanced food sources available to the penguins. Included would be geophysical changes that for now appear to be contrary to Adélie penguin population growth, i.e. increasing large scale sea ice extent in winter leading to population decrease (cf. Wilson et al., 2001; Stammerjohn et al., 2012; Kwok et al., 2016). In addition to the latter, geophysical changes had been proposed to explain Ross Sea penguin population growth during the 1980s, i.e. increasing winds and polynya persistence (Ainley et al., 2005). The latter continued to increase but beyond what could locally affect penguin productivity, and thus the populations ceased any increase during the 1990s (Ainley et al., 2007). First we review points raised by Pinkerton et al. about limited competition for silverfish between Adélie penguins and toothfish.

2. Depicting mesopredator and prey overlap in time and space

Important to the discussion is partitioning of the biomass of silverfish exploited by both species, silverfish being well known to sort age/size by depth with younger/smaller ones occurring shallower (La Mesa and Eastman, 2012). Also important is determining what portion of the silverfish biomass is subject to competition between toothfish and penguins. This was not considered by Pinkerton et al. (2016), who used in their model the total biomass of each of the main actors within this competition scenario.

Researchers have classified Antarctic silverfish maturation status differently, with respect to the sizes of "juveniles," "subadults," and "adults." In part this is due to the fact that only recently has it become known that maturity (adulthood) is reached at 12–18 cm SL, with "juveniles" being 3–5 cm SL, and subadults 6–12 cm SL (La Mesa and Eastman, 2012). In ice-covered waters of the southern Ross Sea, silverfish, along with crystal krill (*Euphausia crystallorophias*), are the principal prey species of most mesopredators, including the penguins (Eastman, 1985a,b; Burns et al., 1998; Ainley et al., 2003; Ballard et al., 2012). The high proportion of silverfish in the diet of adult toothfish, and presumably other meso-

predators, is due to the relative lack of abundant alternative fish species in the water column (La Mesa et al., 2004; Pinkerton et al., 2016) and the high energy density of subadult and adult silverfish relative to krill (Ainley et al., 2003; Lenky et al., 2012). In contrast, larval, post-larval, and juvenile silverfish have no exceptional energy value (Chapman et al., 2011). The silverfish taken by Ross Sea mesopredators are subadults and adults: those silverfish taken by Adélie penguins range 6–13 cm SL (two age classes, 2 and >2 years; Ainley et al., 2003; who erroneously termed the 2-year-olds as juvenile fish), by Weddell seals (*Leptonychotes weddellii*) 10–18 cm SL (Burns et al., 1998; Fuiman et al., 2002), and by toothfish in the water column of McMurdo Sound, 6–16 cm SL (Eastman, 1985a). Clearly, diet composition overlaps in species composition and over a narrow spectrum of size/maturity classes among these mesopredators.

Specifically in regard to toothfish (more on penguin diet below), the spring-summer diet of those in the water column contains 89% silverfish by mass (71% frequency of occurrence in toothfish stomachs sampled; Eastman, 1985a,b; see also La Mesa et al., 2004; La Mesa and Eastman, 2012). Davis et al. (2013; also Fuiman et al., 2002) showed that Weddell seals track the diel movement of silverfish in the water column within 250–350 m of the surface (as do toothfish; Fuiman et al., 2002), but also consume fish at shallower depths. Only the large, buoyant toothfish forage at these or shallower depths, and these large toothfish are the ones targeted by the fishery. Toothfish begin to attain neutral buoyancy at ∼100 cm TL owing to accumulation of lipid; smaller subadults remain on the bottom (Near et al., 2003). So, it is distinctly possible that the silverfish high in the water column that would otherwise have been consumed by toothfish had become available as penguin prey as a result of toothfish depletion.

These results are in stark contrast to bottom-dwelling toothfish considered by Pinkerton et al. (mostly from depths >400 m), whose diet contains ∼4% silverfish by mass (7% frequency of occurrence), the value used in Pinkerton et al. These authors emphasized the fact that their results showed that bottom-dwelling toothfish do not eat silverfish, assumed that all toothfish are bottom dwelling, and therefore concluded that toothfish could not be competing with penguins for food. Indeed, the non-buoyant bottom-dwelling toothfish may have a diet with a composition relatively devoid of silverfish, but the older and larger toothfish predate heavily on silverfish (references above). The vast majority of the 5588 toothfish in the data set reported by Ainley et al. (2013) were caught above the bottom, some to within ∼100 m of the surface. Moreover, prior to full development of the fishery (when there was limited removal of neutrally buoyant fish), using crittercams attached to 15 Weddell seals in fast-ice covered areas of McMurdo Sound over three spring periods, Fuiman et al. (2002) noted prey encounters on 58 dives. Among 13 toothfish encountered, >75% were within 150 m of the surface with some as shallow as 12 m. Subadult/adult silverfish can also be found close to the surface: 3% of the 336 adult/subadult silverfish encountered by the seals with crittercams, who were at the same time depleting silverfish (Testa et al., 1985), were also within 150 m of the surface. This is noteworthy because Adélie penguins in the Ross Sea, especially in pack-ice covered areas, forage to 150 m deep (recorded as deep as 175 m elsewhere), though many dives are shallower (Lyver et al., 2011; Ainley et al., 2015), and because silverfish sort depth by size, measureable depletion of shallow silverfish, predated by penguins, could well occur. [Note that in spring, the penguins and seals are not competing owing to ice-defined habitat differences] In summary, it is clear that appreciable overlap occurs between the water column depths, and silverfish age classes/sizes consumed by neutrally buoyant toothfish and Adélie penguins.

As noted, Pinkerton et al. considered only the total biomass of toothfish, silverfish and penguins. They used a figure of 500,000 t of silverfish estimated to occur over the Ross Sea shelf based on the acoustic assessment of O'Driscoll et al. (2011). The latter assessment included all age/size classes of silverfish, but O'Driscoll et al. (2011) defined "juveniles" as fish 4–6 cm SL and "adults" as all fish >6 cm, which differs from the conventions reviewed above. In the mid-water trawls used by O'Driscoll et al. (2011) in support of acoustics, the "adult" silverfish caught ranged 5–19 cm SL, with − by extrapolation from their Fig. 5 − ∼90% occurring within the penguins' and toothfish' diet size range noted above. Their targeted trawling, however, failed to obtain the largest adult silverfish (to 25 cm; La Mesa and Eastman, 2012) but presumably this size class (likely too deep for penguins) was included in their acoustic results. Using relative acoustic backscatter to partition silverfish by depth, O'Driscoll et al. (2011, their Fig. 7) indicated (another extrapolation) that ∼15% of the ∼200,000 t of appropriately-sized silverfish, i.e. "adults", occur within the penguins' diving range, or 30,000 t. This biomass approximation by depth is consistent with Hubold (1984) who estimated that ∼11% of "adult" silverfish occur in the upper 250 m of the Weddell Sea water column; Hubold (1984) classified "adults" as silverfish >9 cm SL.

While our various extrapolations are necessarily approximate, and would be improved by access to the actual data, it appears that the portion of the Ross Sea biomass of silverfish contested by toothfish and penguins thus, in actuality, could be as much as an order of magnitude lower than what Pinkerton et al. used in their modeling. Therefore, again noting that silverfish distribution by age/size is sorted by depth, the potential intensity of trophic competition between toothfish and penguins is likely to be much higher than what Pinkerton et al. assumed. And, as we show later, silverfish are likely to be key dietary components for penguin reproduction and could influence subsequent survival.

3. Can the extraction of toothfish explain the penguin population growth?

Pinkerton et al. used a set of simple energy transfer equations that can be reduced to:

$$\Delta\_ADPE_m = mrr x etSF x erATF$$

where Δ_ADPE_m is the change in total mass of Adélie penguins (ADPE) in the Ross Sea, $erATF$ is the energy released from the mass of toothfish (ATF) removed, mrr is the metabolic rate ratio between toothfish and penguins, and $etSF$ is a correction parameter for the energy transfer efficiency between toothfish and penguins through the consumption of silverfish (SF; i.e., the efficiency of energy transfer from silverfish to toothfish, times the efficiency of energy transfer from silverfish to Adélie penguins, adjusting for the proportion of silverfish in the diets of toothfish and penguins). The parameters mrr and $etSF$ are not found in Pinkerton et al.; they are the result of simplifying their equations into more basic parameters. This is a simple linear relationship depicted by Pinkerton et al. that excludes all other species and processes in the Ross Sea food web to maximize the energy transfer to penguins. The critical parameter justifying Pinkerton et al.'s conclusion is mrr in our basic equation above, as it accounts for the differential metabolic rate between penguins and toothfish. It is indeed the reason why the direct transfer of energy as modeled by Pinkerton et al. cannot explain the penguin population growth. To understand what it means, assume that it takes 1 J to maintain 1 g of toothfish tissue for 1 year. Further assume that it takes 2 J to maintain 1 g of Adélie tissue for 1 year. In this example, mrr = 0.5, since it takes twice the energy per unit mass per unit time to maintain Adélie tissue vs toothfish tissue. In reality, it takes ∼55 times more energy per gram of mass to maintain an Adélie penguin than to maintain a toothfish. This can be discerned from the ratio of the $(E/B)^t\_ADP$ and $(E/B)^t\_TOA$ parameters in Pinkerton et al. (267 kJ/gWW/y vs
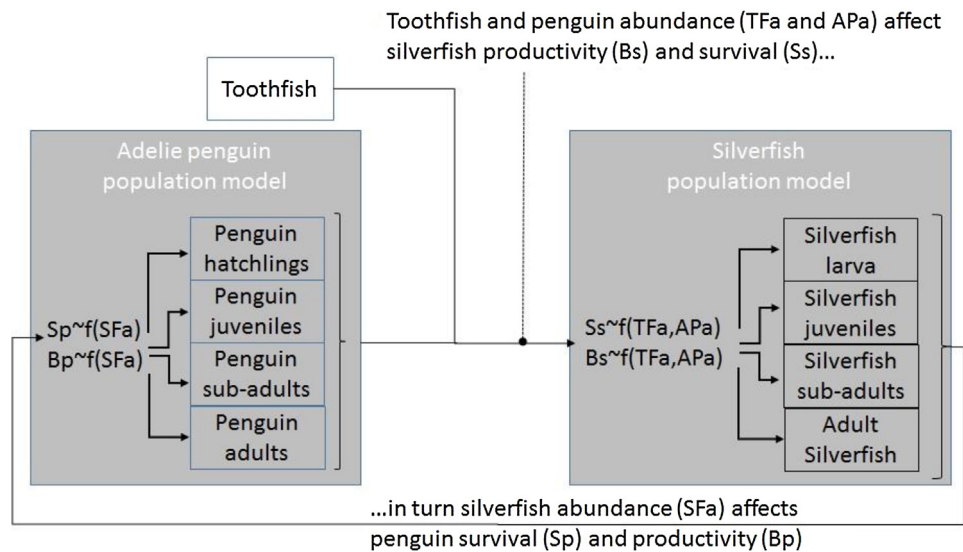
Fig. 2. Hypothetical integrated population demographic model for a system that includes (but not exclusively restricted to) toothfish, silverfish and Adélie penguins. The consumption of silverfish of various age classes by toothfish and penguins has an effect on silverfish populations, mediated through demographic parameter equations of silverfish productivity (Bs) and survival (Ss). Thus toothfish and Adélie penguin abundance (TFa and APa, respectively) affect silverfish survival and productivity – the equations in the silverfish population model. Conversely, silverfish abundance (SFa) affects the growth of penguin populations through its effects on penguin survival (Sp) and productivity (Bp) – the equations in the Adélie penguin population model.

4.8 kJ/gWW/y, respectively; in this case ADP is Adélie penguin, TOA is Antarctic toothfish). This marked difference in energy consumption between penguins and toothfish makes sense, because penguins are endothermic while toothfish are ectothermic animals. Furthermore, as an ectotherm, the toothfish's metabolic rate is greatly influenced by water temperature, which is low (e.g., Clarke and Johnston, 1999). In addition to these stark differences in thermal physiology, the Adélie penguin is, on average, at least 20 times smaller than toothfish, and since metabolic rates scale in an allometric fashion with body size, the metabolic demands (per gram of body mass) of the penguin must far exceed those of the toothfish. To put the numbers in perspective, assume $etSF = 1$; if so, removing 1000 g of toothfish results in only a 18 g gain in Adélie mass. According to Pinkerton et al. $etSF$ is <1 because silverfish is more prevalent in the diet of Adélie penguins than in the diet of toothfish (but see contrary arguments above); if so, the gain is <18 g. Pinkerton et al.'s calculations show that the amount of energy released from the removal of toothfish can only explain a very small gain in Adélie mass compared to the mass gain observed in the recent population growth and thus, concluded that the hypothesis of a predation release effect causing the penguin population growth must be rejected.

4. Why is penguin demography important in the modelling?

There are many assumptions by Pinkerton et al. that merit a closer review, because if incorrect they may render their main conclusion invalid. Here we focus on the two most obvious and most likely to be incorrect: the proper understanding and modeling of population growth and regulation, and whether the effects of toothfish removal are limited to simply a predation-release growth in availability of silverfish, and not to other aspects of the Ross Sea food web.

It has been concluded in a number of studies that survival of juveniles plays an important role in population size change among Adélie penguins, as investigated by Wilson et al. (2001), Jenouvrier et al. (2005), Ballerini et al. (2009), Chapman et al. (2011), Hinke et al. (2014), and Cimino et al. (2014). Moreover, the effort to fledge

robust chicks, which have a better chance for survival (see below), can well affect parental survival, and at some point, colony growth can reach a size of diminishing returns related to the energy necessary for successful chick provisioning (Ballance et al., 2009; see Fig. 1). The situation, then, appears to be similar to that analyzed by Weller et al. (2014) who modeled African penguin (*Spheniscus demersus*) prey availability in the breeding season, within and without the foraging "halo" (i.e., the area in the vicinity of the colony wherein fish populations are locally reduced by penguins). Prey availability within the halo had little effect on breeding success; more important to population growth was prey availability outside of the "halo" and its effect on yearling survival.

In regard to juvenile survival among Adélie penguins, a diet of energy-dense silverfish appears to play a critical role, as detailed below, but it is important to note that the percentage of subadult and adult silverfish that contribute importantly to Adélie penguin diet in the southern Ross Sea is not constant, as also detailed below. Indeed, the silverfish contribution to the penguin diet increases as the breeding season progresses. Diet during incubation appears to be mostly krill, but by the time chicks are fledging the proportion of fish is 50–100% (Ainley et al., 2003, 2006, 2015). It appears that the change, in part, is related to the seasonal arrival of trophically competing whales who, along with the penguins, consume the shallow krill, forcing the penguins to dive deeper where they then encounter silverfish; the whales also force the penguin foraging "halo" to expand proportional to colony size (Ainley et al., 2006, 2015). Given that subadult and adult silverfish are energy dense, especially compared to krill (Ainley et al., 2003; Chapman et al., 2011; Lenky et al., 2012), foraging on them compensates for the greater effort needed in diving deeper and foraging farther away.

Importantly, the more the chicks' diet is weighted toward silverfish, the heavier the chicks become and the more robust they are at fledging (Whitehead et al., 2015; Jennings et al., 2016). Accordingly, Chapman et al. (2011) found that a mere 17% increase in the proportion of diet contributed by silverfish translated to a 5% increase in Adélie penguin fledging mass. More robust chicks have a larger cushion during their initial months at sea when they are learning to forage, and thus experience enhanced survival (Chapman et al., 2011; Cimino et al., 2014 and references therein). The significance

of maintaining or surpassing a body mass threshold by foraging on silverfish could also explain why variability in silverfish abundance is playing an important role in Adélie penguin population change in other parts of the Southern Ocean (Sailley et al., 2013).

Lacking any consideration of penguin population dynamics, it is not surprising that Pinkerton et al. concluded that the availability of more silverfish, owing to fewer toothfish, played no role in the recent Adélie penguin population increase. Instead they invoked the mega-icebergs that were present 2001–2005 in waters off the northern shore of Ross Island as somehow playing the major role. They state that the icebergs affected: 1) Ross Sea oceanography (relationship to toothfish, silverfish or penguins unspecified), yet Robinson and Williams (2012) confirmed altered currents only in eastern McMurdo Sound (see also Dinniman et al., 2007); 2) primary production, a negative effect that was very short term during the iceberg event, but when variability in primary productivity was studied over the recent two decades was found to have no effects on Adélie penguin breeding biology (Dugger et al., 2014), as well as little connection with middle trophic level prey (Ainley et al., 2015); 3) abundance of "zooplankton," citing Seibel and Dierssen (2003), who studied only pteropods in eastern McMurdo Sound (1 of 3 years had anomalously low prevalence); and 4) predators, however Weddell seals and emperor penguins only temporarily emigrated from the local region, returning when their breeding habitat was restored soon after iceberg departure (Barber-Meyer et al., 2008; Siniff et al., 2008). In regard to pteropods, the latter are the upper level predators in that part of the Ross Sea ecosystem based on the colonial alga *Phaeocystis antarcticam*, which dominates the Ross Sea primary production. The food web, based on the much less prevalent diatoms, however, sustains the krill, fish, birds and mammals and is associated with Ross Sea sea ice (Smith et al., 2014). Overall, pteropods contribute very little to silverfish diet (Eastman, 1985a,b; La Mesa and Eastman, 2012; Pinkerton et al., 2013); thus, it is unclear how they would play a role in explaining the growth of penguin populations. Considering that the Adélie penguin population continued to increase even after the icebergs had disappeared, and remain high still, it follows that none of the explanations can account for icebergs representing the underlying factor responsible for penguin population growth.

While Pinkerton et al. inferred that geophysical factors may have been involved in the reduced prevalence of large toothfish reported by Ainley et al. (2013) and/or the change in penguin abundance reported by Lyver et al. (2014), whether or not geophysical factors played a role would not be a straight forward proposition to uncover. Included would have to be geophysical changes that for now appear to be contrary to Adélie penguin population growth or no longer a factor (see above, and Ainley et al., 2016).

5. Dynamic modelling framework for future investigation of the Ross Sea food web

Resolving the question of why an unusual spurt of population growth occurred among southern Ross Sea penguins requires a dynamic modeling approach that considers not just penguin demography, but also that better partitions the components of the food web are likely to be involved. The ecological relationship between breeding penguin population size and large toothfish, and their common prey, is not necessarily a direct relationship, and requires attention to the complex pattern of penguin demographics, which as noted include a critical period of foraging and prey thresholds, to explain penguin population change. It is also true that other mesopredators of the southern Ross Sea are likely involved (e.g., emperor penguins, as noted).

Herein we propose an approach that couples population dynamics with the hypothesized causes of penguin population growth. It is possible to re-construct the simple food web assumption that Pinkerton et al. presented, but this time the life history parameters would be modeled as functions of the silverfish-mediated predation release. This so-called Integral Projection Model (IPM) approach (Easterling et al., 2000) provides a flexible framework to test the predator release hypothesis by permitting the simultaneous evaluation of effects and causes expected by all factors involved.

The life history functions would link population numbers of one species to the life history parameters of the other species. Importantly, the relationship between species numbers does not need to satisfy any constraints in energy transfer, at least not initially, as presumed by Pinkerton et al. The system can still be open to unaccounted energy sources, as long as the model is a reasonably accurate representation of the regulatory mechanisms of population numbers of species in the Ross Sea food web. Energy transfer constraints can be added to the population numbers later (e.g., by forcing the total energy of the system to remain within some bounds, or through the use of regression weights that reflect the magnitude of specific trophic interactions, or both).

Fig. 2 offers a simple representation of an integrated demographic population model. In this model, abundances of Adélie penguins and toothfish affect abundance of silverfish through population demographic parameters. Conversely, the abundance of silverfish affects Adélie penguin numbers through demographic parameters. Through a moderately complex model such as this, it is possible to establish hypothetical values of the critical silverfish and penguin demographic parameter functions, such that the removal of toothfish could indeed be causal to the observed penguin population growth. The development of alternative hypothetical values of demographic parameter relationships to silverfish consumption could then guide research to test the mechanisms of impact of the fishery through a strong inference approach.

Though challenging, the approach we propose can be constructed with currently available computing techniques (e.g., https://www.novamodeler.com/). To be clear, our intent is not to develop a predictive model that would aim to fully explain the observed changes. The poor knowledge and paucity of data for the system precludes all but the simplest approximations at understanding the system. Our interest is to model scenarios that could provide alternative hypothetical mechanisms of effects on silverfish and penguins by the removal of toothfish, including one that explains the observed changes in penguin populations. Thus we are proposing to develop competing hypotheses of mechanisms that can be tested and through which, via an inductive process, we may better understand the possible role of the toothfish in regulating Adélie penguin populations. Another promising approach to incorporating energy budgets into demographics is presented in Smallegange et al. (2016). The authors show how the IPM can incorporate the energetics of individual growth, resulting in a population dynamics model with energy budgets. This approach could be used to explain the growth in Adélie numbers and its relationship to toothfish removal and associated changes in the food web, while at the same time accounting for the energy needed to sustain the growth.

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