

Coping with the loss of large, energy-dense prey: a potential bottleneck for Weddell Seals in the Ross Sea

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Abstract. Extraction of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea began in 1997, following a management plan that targets the largest fish with a goal of reducing the spawning biomass by 50% over 35 yr. We investigate the potential long-term consequences of the reduced availability of this prey for Weddell seals (*Leptonychotes weddellii*). Energy demands in seals are acute, especially immediately following lactation, when females must recover substantial mass and cope with molting costs. We tested the hypothesis that toothfish are critically important for adult female seals during this period. Toothfish body mass is three orders of magnitude greater, and its energy density nearly double that of the most common seal prey, Antarctic silverfish (*Pleuragramma antarcticum*). Reduction or elimination of toothfish consumption could impair a female's ability to sufficiently recover and successfully produce a pup in the following pupping season. Our goals are to (1) illustrate mechanisms and conditions whereby toothfish depletion might plausibly affect seal population trends; (2) identify measurable parameters of the seals' ecology that may help better understand the potential negative impact of toothfish depletion on seal populations; and (3) promote a precautionary management approach for the fishery that includes monitoring of seal populations. We constructed a set of inter-linked models of seal diving behavior, physiological condition, and demography based on existing information. We evaluate the effect of the following factors on seal mass recovery and intrinsic population growth rates: fishery depletion rate, daily diving limits, probability of a successful dive, and body mass recovery target. We show that loss of toothfish has the greatest potential impact on seal populations' growth rate. Under some scenarios, populations may decrease at >10% per year. Critical parameters to better understand fishery impacts include prevalence and size of toothfish in the seals' diet; the relationship between diet and the rate of mass recovery; and female breeding propensity in relation to body condition at the end of the molting period. Our results lend support to concerns about the potential negative impact of toothfish extraction in the Ross Sea; and to advocate for a precautionary management approach by the fishery.

Key words: Antarctic silverfish; Antarctic toothfish; diving behavior; energy bottleneck; fisheries impacts; *Leptonychotes weddellii*; Leslie matrix; precautionary management; Ross Sea; Weddell seal.

INTRODUCTION

While it is widely appreciated that adequate prey availability is crucially important to marine predators, some prey are more energetically valuable than others, and adequate access to them at specific life history stages may play a critical role. Here we investigate the role that energy-rich Antarctic toothfish (*Dissostichus mawsoni*) may play in the demography of Weddell seals (*Leptonychotes weddellii*) in the Ross Sea, Antarctica, a role potentially in jeopardy in light of the fishery for this prey species. Both species are best known in the Ross Sea. Examples of the important role that energy-rich prey can play in predator life histories include (1) the great white shark (*Carcharodon carcharias*) which, prior to breeding season migration,

preys selectively upon seal species that provide double the energy density of other plentiful, potential fish prey (Klimley 1994, 2013, Klimley et al. 1996); (2) the seasonal importance of energy-dense eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), and various salmon species (*Oncorhynchus* spp.) to Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), and other predators (reviewed by Wilson and Womble 2006, see also Tollit et al. 1997, Sigler et al. 2009, Hofmeyr et al. 2010); (3) the effect of energy-rich Patagonian toothfish (*Dissostichus eleginoides*) on calving rate in killer whales (*Orcinus orca*; (Tixier et al. 2014); and (4) the importance of recently weaned ringed seals (*Pusa hispida*) to polar bear (*Ursus maritimus*) females, who depend on finding this highly energetic prey in late spring and early summer, and whose consumption affects female survival, reproductive output, and cub survival (Stirling and Øritsland 1995, Stirling et al. 1999, Regehr et al. 2007).

Manuscript received 9 September 2015; revised 24 June 2016; accepted 2 August 2016. Corresponding Editor: Paul K. Dayton.

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Here we model the importance of the Antarctic toothfish, an especially energy-rich prey, as an item in the diet of Weddell seals in the Ross Sea, Antarctica. Specifically, we evaluate the potential long-term population consequences of a loss of the toothfish to this seal population as a result of ongoing fishing and associated changes in the abundance and condition of this prey. The motivation for our work is that (1) energy-rich prey are known to be part of the Weddell seal diet, and may be a critical resource during the summer period when energetic demands on female seals are particularly high (summarized in Ainley and Siniff 2009, also Goetz 2015, Goetz et al. 2016); and (2) the Antarctic toothfish, the most energy-rich and largest prey species in the Weddell seal diet, has decreased in size and body condition in McMurdo Sound since about 2002 according to monitoring data collected by the fishery as well as independent researchers (SC-CAMLR 2012:318, 346; 2013:5–6; Ainley et al. 2013). Although Weddell seal diet in the Ross Sea, as well as elsewhere (Lake et al. 2003, Zhao et al. 2004), is dominated by the small, loosely shoaling, Antarctic silverfish (*Pleuragramma antarctica*; Castellini et al. 1992, Burns et al. 1998, Goetz 2015), the energy density of silverfish is just half that of toothfish (Lenky et al. 2012). Furthermore, the average size of these two fish captured by seals differs by nearly three orders of magnitude (50 g silverfish vs. 25000 g toothfish; Burns et al. 1998, Ainley and Siniff 2009). Catching one toothfish, in contrast to catching the energetic equivalent in silverfish, makes a large difference in terms of foraging effort and net energy gains, and thus, we hypothesize, may strongly impact the daily and seasonal energetic balance of breeding female Weddell seals (see also Goetz 2015).

The Weddell seal lives year-round in ice-covered Antarctic waters. In McMurdo Sound, intensive research on the physiology, ecology, behavior, and population dynamics of the local Weddell seal population has resulted in it being one of the best-studied marine mammals anywhere (e.g., Stirling 1969*a, b*, Kooyman 1981, Testa and Siniff 1987, Burns and Kooyman 2001, Cameron and Siniff 2004, Hadley et al. 2006, 2007*a, b*, 2008, Rotella et al. 2009, 2012, Garrott et al. 2012, Chambert et al. 2013, 2014, Goetz 2015). Reproduction is costly in Weddell seals, especially for females, and extends beyond the cost of gestation (Wheatley et al. 2006). In particular, it is known that subsequent annual survival rate of pupping females is lower for individuals that produced a pup in a given year compared to those that skipped reproduction or were still pre-breeders (Chambert et al. 2013); the difference is presumably mainly due to costs stemming from the enormous mass loss that occurs during lactation (Wheatley et al. 2006, Eisert and Oftedal 2009, Shero et al. 2015). Among females that reproduce, it is also known that maternal mass at pupping is positively related to lactation duration and pup mass gain, which may have important consequences for a pup's subsequent survival (Wheatley et al.

2006). Those females that can attain adequate body condition and breed more often than others have greater lifetime reproductive output and fitness (Chambert et al. 2013, 2014). Weddell seals are thus intermittent breeders, relying heavily on energy stored throughout the year (Wheatley et al. 2008), with some females breeding annually for many years while others skip breeding for one or several years, suggesting a trade-off strategy to balance current reproductive costs and gains against survival and future opportunities to breed (Hadley et al. 2007*a*).

Weddell seals in McMurdo Sound congregate for pupping and breeding beginning in early October. Pups born at 30 kg are nursed to 150 kg before weaning. Female seals appear to cope with this high energetic demand by having a prolonged nursing period (~2 mo) while gradually resuming foraging as the pup grows (Hindell et al. 2002, Wheatley et al. 2008, Eisert and Oftedal 2009, Shero et al. 2015). Most pups are weaned by the beginning of December. Female seals may lose >100 kg during lactation, as they remain on ice for long periods while nursing the newborn (Castellini et al. 1991, Eisert 2003). Adult males, too, may lose up to 40% of their mass, limiting foraging dives in order to defend underwater territories to restrict access by other males to females (Harcourt et al. 2006, Wheatley et al. 2006). This period of pronounced mass loss is followed by a foraging period in which some body condition is recovered, and then by an annual molt during which feeding is again restricted (Lake et al. 1997, Shero et al. 2015). After molt, most seals disperse and spend the winter in pack-ice-covered waters overlying the adjacent Ross Sea continental shelf (Castellini et al. 1992, Testa 1994, Ainley and Siniff 2009, Goetz 2015). There they continue regaining the mass and body condition needed for the following year's pupping and breeding effort (Shero et al. 2015). We and others (e.g., Stirling 1969*b*, Kooyman 1981, Ainley and Siniff 2009) hypothesize the existence of a mass recovery period, beginning near the end of lactation and extending through, and perhaps past, molting, during which the seals gain mass at a higher rate than at any other period of the year (henceforth the "post-lactation foraging period," Fig. 1). Here we explore the implications of differences in the availability of energy-rich toothfish, especially during this mass recovery period.

The proportional consumption of toothfish in Weddell seals is not well established because the seals do not ingest toothfish hard parts that can then be identified in scats, and because there has been insufficient analysis of diet using biochemical methods (Ainley and Siniff 2009, Goetz 2015, Goetz et al. 2016, see *Discussion* in Appendix S1). The decrease in the prevalence of large toothfish in McMurdo Sound (Ainley et al. 2013) occurred a few years after initiation of a fishery that began in the Ross Sea region in 1997, the take increasing rapidly in subsequent years. Owing to the need to fill vessel holds quickly, the fishery targets large toothfish (Ainley and Pauly 2013,

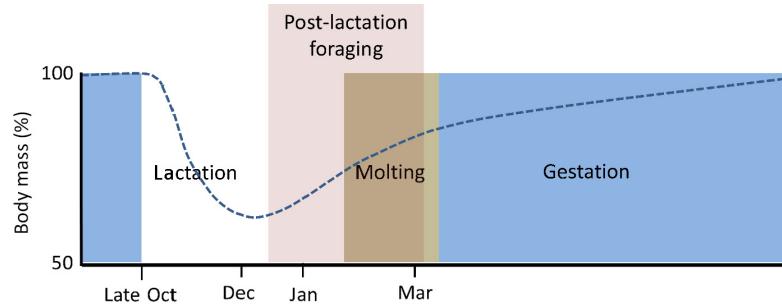


FIG. 1. Schematic representation (hypothetical) of mass changes, and the post-lactation foraging period in the annual cycle of adult female Weddell seals. (Color figure can be viewed at wileyonlinelibrary.com.)

Ainley et al. 2013, Hanchet et al. 2015), which are decreasing in prevalence within the overall stock; the fishery take now is dominated by smaller, pre-recruit fish (SC-CAMLR 2013:5–6, including their Fig. 1). While the fishery concentrates its effort in Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) Areas 88.1H, I, and K (Ross Sea continental shelf slope), it also fishes in deeper areas near Ross Island and McMurdo Sound, in Areas 88.1J, L, and previously M (SC-CAMLR 2013). The reduced prevalence of large fish is important to the seals. Owing to an ontogenetic accumulation of interstitial fat (they have no swim bladders), toothfish only reach neutral buoyancy at ~100 cm TL (Near et al. 2003, see also Ainley et al. 2016), at which point they ascend in the water column sometimes occurring close to the surface in pursuit of their silverfish prey (Fuiman et al. 2002). This buoyancy means that seals may capture bigger fish in shallower dives (Ponganis and Stockard 2007, Kim et al. 2011). Smaller toothfish will be still available to the seals at greater depths (Parker et al. 2015), but to acquire them requires metabolically costly, longer, deeper dives (Williams et al. 2004).

We hypothesize that the loss of the large, neutrally buoyant, fatty toothfish from the seals' diet might limit the ability of the seals to recover condition following breeding and molt, to successfully bear young and rear pups in the next breeding season. Understanding the potential long-term population-level impact of the reduced prevalence of large toothfish, especially at shallow–mid water depths, on the Ross Sea Weddell seal population requires a clear understanding of the degree to which toothfish may be sufficiently replaceable in the seal's diet—not only how much, where, and when are toothfish being consumed, but how important is this resource for maintaining stable Weddell seal numbers in the face of continued toothfish depletion in number, size, and condition.

The consequences of lowered availability of large toothfish on seals are likely complex. For example, large toothfish are also a competitor of the seal for silverfish (Eastman 1985a, b, Fuiman et al. 2002, La Mesa and Eastman 2012). Thus the loss of the large toothfish could,

by reducing predation on silverfish, increase the availability of silverfish to seals (Pinkerton et al. 2013) as it may perhaps do for penguins (Lyver et al. 2014).

There are no data or research on the direct impact of a decline in toothfish availability on Weddell seal population growth rates. Therefore, the fishery's management plan, contrary to CCAMLR articles of incorporation, was set without any such knowledge (Constable et al. 2000, Pinkerton et al. 2007). In this paper, we address the potential future impact of the toothfish fishery on Ross Sea Weddell seal populations by constructing relatively simple, linked models of seal behavior, condition, and demography based on existing parameter estimates and life cycle considerations, combined with information and inferences regarding the prevalence of prey species. We use the best data available in the literature (published and unpublished) to model the process of mass recovery by the seals through the joint consumption of toothfish and silverfish, and then link mass recovery to seal body condition, pup survival, and breeding propensity. Our goals specifically are to (1) illustrate mechanisms by which toothfish depletion may plausibly affect seal population dynamics and evaluate potential consequences of loss of toothfish as prey during the mass recovery period; (2) identify measurable parameters of the seals' diving behavior and foraging ecology that may help better understand these impacts; and (3) provide a scientific basis for a precautionary management approach that explicitly relates fishing quotas to seal population behavior by providing plausible mechanisms by which the fishery may be severely impacting seal populations, now or in the future. While the effects of the toothfish fishery are uncertain, our models help examine how the impact may occur (for example, under which conditions might there be little to no negative impact as well as identifying conditions under which impact may be severe), and to identify what parameters may be important to measure and monitor to better understand the relationships between the seals' diet, foraging behavior, and population dynamics. We discuss the consequences of our findings in terms of a precautionary approach to managing the fishery (*sensu* Abrams 2013, Abrams et al. 2016). Improved understanding of the seals' dependence

on particular food sources, and their ability or inability to compensate for a shortfall in availability of energy-dense prey during critical periods of their life cycle, should lead to adjustments in the management of Antarctic fisheries. This approach is consistent with the articles of CCAMLR and its Ecosystem Monitoring Program, which call for active, ecosystem-based, fishery management.

METHODS

We constructed a set of simple mass gain and demographic models and linked them in an overall modeling approach for the post-lactation foraging period. The overview of the overall modeling approach is presented in Fig. 2, and explained in more detail in the *Overview* section. Without empirical data on the length of the post-lactation foraging period, here we assume it to span 90 d.

Our modeling only considers two prey species, a simplification that is justified in Appendix S1. Parameters used are described in Appendix S1: Table S1; additional details on these parameters and functional relationships are provided in Appendix S1 and briefly described in the *Overview* section. We built our models based on minimal, but explicit, assumptions where the literature provided insufficient detail, consistent with what is known about the behavior, physiology, and demography of Weddell seals and their prey; we accommodate uncertainty by considering upper and lower bounds for important variables.

Overview: functional relationships between toothfish depletion and seal demography

To the best of our knowledge, there are no studies in the literature or being conducted now, to directly relate toothfish depletion to seal demographic parameters.

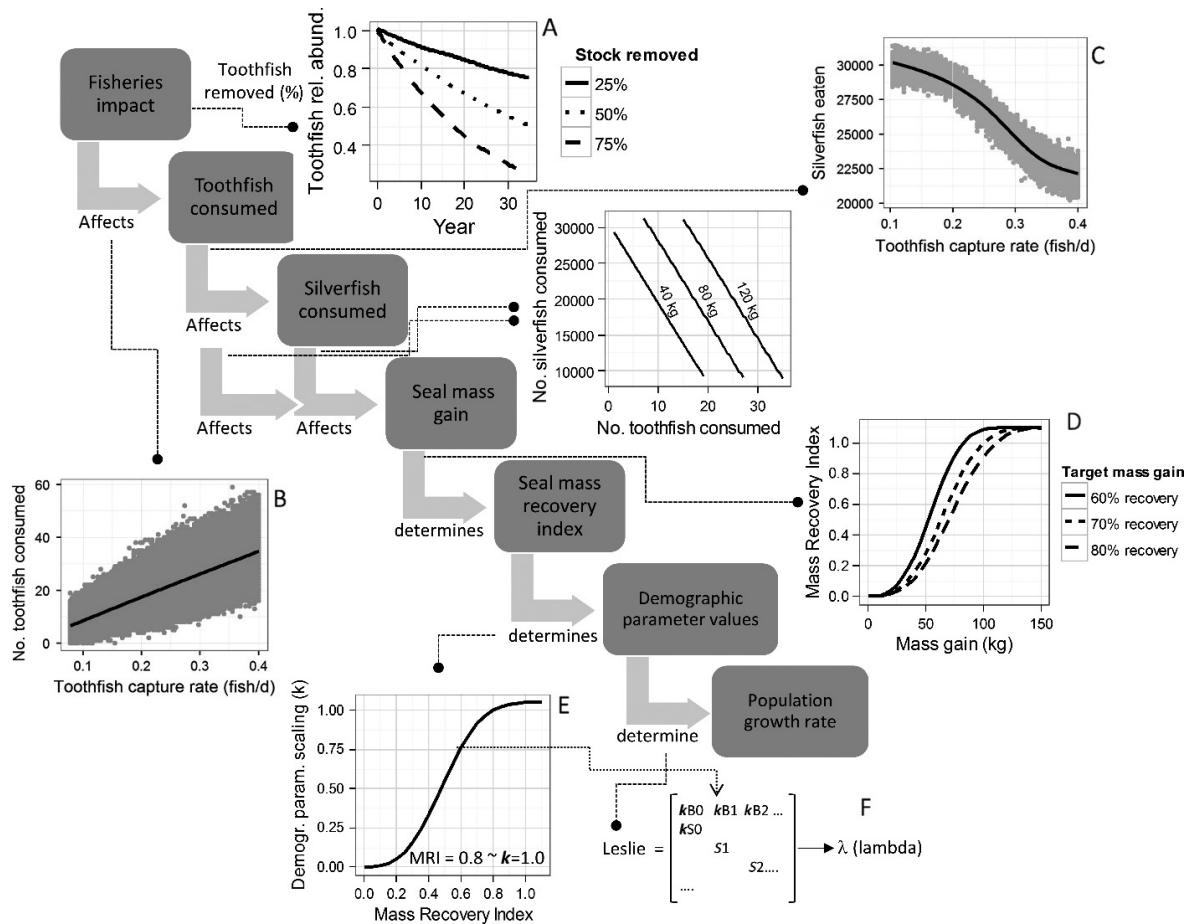


FIG. 2. Schematic representation of the modeling plan, with hypothetical relationships among parameters. (A) three hypothetical toothfish depletion rates (rel. abund., relative abundance); (B) number of toothfish consumed by Weddell seals during a 90-d post-lactation foraging period in relation to toothfish abundance (toothfish/d); (C) number of silverfish consumed by Weddell seals during a 90-d post-lactation foraging period in relation to toothfish capture rate (toothfish/d); (D) mass gain during post-lactation foraging is determined from the total mass of toothfish and silverfish consumed by the seals in the 90-d period, from which a mass recovery index (0–1.1) is estimated, based on three different mass recovery thresholds; (E) Mass Recovery Index becomes a scaling parameter (0–1.05); (F) scaling parameter (k) is used to adjust demographic parameters (demogr. param. - fecundity: B0, B1, etc.; and survival: S0, S1, etc.) in Leslie matrix, thus determining the growth rate (λ) for the seal population.

Therefore, we modeled this relationship by combining results of the mass gain model and the demographic model. The mass gain model consists of a daily diving sub-model that simulates energy gains and costs from consuming fish every day, for the 90-d period (Fig. 2A–D), and a simple function that translates the energy gains into seal mass. With the mass gain model we simulate the implications of a depletion of toothfish over the course of 35 yr, as planned by CCAMLR (Constable et al. 2000, Pinkerton et al. 2007). Year 1 corresponds to 2004, when extraction reached its current maximum level (we indicate year with reference to the respective austral summer, i.e., 2004 = 2004–2005; Fig. 2A). Over the course of the 35-yr simulation, we model how much toothfish and silverfish each seal consumed as a consequence of prey availability (Fig. 2B, C) and consider the consequences of that consumption for their physiological condition (Fig. 2E). We do this through a function that relates mass gain to a mass recovery index (MRI) of seals in a population. In the demographic model, we constructed a Leslie matrix based on values in Rotella et al. (2012), with demographic parameter values that vary annually as a function of the seals' physiological condition after the post-lactation foraging period (Fig. 2F, G). Thus, we estimated asymptotic λ in each year in each simulation as a function of physiological condition (Fig. 2).

Our mass gain model evaluates availability of toothfish to a seal following one of three hypothetical declining trends in toothfish availability (see *The mass gain model and modeled scenarios*; Fig. 2A). Because the rate of toothfish and silverfish consumption by seals in relation to their abundance is unknown, we instead model the diving behavior and success of seals over the 90-d period in the daily diving sub-model. It is based on extensive studies of diving behavior of the seals, with additional assumptions about daily diving and food consumption limits. Consumption of toothfish and silverfish varies in relation to the abundance of toothfish. As noted in a general sense by research, seals capture more silverfish where toothfish are lacking (cf Testa et al. 1985, Fuiman et al. 2002, Ainley and Siniff 2009). Toothfish mean daily capture rate by seals therefore declines with increased fishery extraction (Fig. 2B) and affects the number of silverfish consumed as well (Fig. 2C). From the daily diving sub-model simulations, we determine the total number of toothfish and silverfish consumed by a seal in the 90-d period. The daily diving sub-model thus simulates how much net energy seals obtain from the fish, the costs of prey capture and digestion, and other metabolic costs during the 90-d post-lactation foraging period each year, for the 35 yr of each depletion scenario (more details in Appendix S1). The mass gain model includes one additional function that translates energy gained into mass gained via a simple conversion function that accounts for the cost of mass storage.

On the basis of the mass gained in each year of the simulation, we determined the MRI value that reflects physiological condition (Fig. 2E). This index was scaled

using a sigmoidal functional form, so that if a female reached the target mass recovery percent, her index value was 1.0, implying no decrement in demographic parameter values (i.e., reduction in pupping success or post-weaning survival of pups). A 350-kg seal can lose 22–42% of its mass during lactation/breeding (i.e., 80–150 kg; Wheatley et al. 2006). Most, but not all, of this mass is recovered during the post-lactation foraging period (Fig. 1; Shero et al. 2015).

The amount of mass gained in the post-lactation foraging period, we hypothesize, is an important factor in the trade-off females must make between successfully gestating in the current year and pupping again next spring (i.e., maintaining high breeding potential), and surviving overwinter to take advantage of future breeding opportunities (Chambert et al. 2013, 2014). We model this relationship between mass gain and demographic parameters in our demographic model. Seals breed at the end of lactation and delay embryo implantation until later in the summer. Presumably, implantation is related to the seals' body condition and mass recovery up to that point. We hypothesized that the seal's target is to recover 100 kg during the post-lactation foraging period, or ~70% of the mass lost. However, because we lack any information about a critical mass recovery target and its relationship with embryo implantation, we also considered scenarios with the assumption that the target is 60% or 80% mass recovery during the 90-d period (Fig. 2E). Once the embryo implants, carrying the pregnancy to term will affect the seal's overwinter survival rate. To the degree that a seal controls the level of recovery from lactation during the post-lactation foraging period, mass gain early in the pregnancy determines whether it will pup again next spring. We reflect this trade-off in our demographic model.

We explored the effect of variability in this mass recovery target on MRI and thus, ultimately, λ (the discrete population growth rate), relative to the effect of other adjustments (e.g., increased time diving) that seals may make to cope with the loss of toothfish. Under a 70% recovery target, MRI = 1 is defined to be equivalent to a 100-kg mass recovery (350 kg \times 0.4 lost \times 0.7 regained); seals that gain >100 kg attain MRI values > 1 (capped at MRI = 1.1). Every year, the MRI values obtained from mass gain simulations under each scenario are sampled. Resultant MRI values are rescaled with a demographic "scaling" parameter (Fig. 2F), which is then incorporated into the Leslie matrix. Each demographic scaling parameter, with values between 0 and 1.05, is a multiplier of specific elements of the Leslie matrix, and in this way the Leslie matrix determines a unique population trajectory for each simulation within each scenario (Fig. 2G). The demographic model uses the resulting matrix to calculate asymptotic λ in each year of each simulation for each scenario. Our overall modeling approach therefore links Weddell seal population growth rate to toothfish availability through the inter-linked functions displayed in Fig. 2 (see also Appendix S1).

The mass gain model and modeled scenarios

The daily diving sub-model simulates how much toothfish and silverfish seals consume in 90 d every year for 35 yr, by modeling their behavior on a daily basis. Diving energetics equations and caloric content estimates for the two fish species are used to estimate how much energy the seals gain on average every year, as well as the variance in gains, as toothfish becomes scarcer over the 35-yr time span. We do not model a direct relationship between toothfish abundance and its consumption rate. Instead, it is determined from the sub-model by specifying the well-studied diving behavior of the seals, and the following assumptions: (1) a toothfish capture rate per day that decreases following an exponential decay based on the toothfish depletion rate (we evaluate two starting mean values for this rate); (2) an increasing capture rate (following a sigmoidal form) for silverfish in accordance to a predation release effect, as toothfish (an important silverfish predator; Eastman 1985a, b) become scarcer; (3) a limit to the number of dives and the total amount of time the seals spend diving each day; and (4) a limit to how much mass the seals consume in a day. Our mass gain modeling scenarios and assumptions are described in more detail in Appendix S1.

Toothfish fishery depletion rates.—We considered three plausible toothfish trends due to fishery extraction: 25%, 50%, and 75% numeric decline of large toothfish available for capture by seals over 35 yr. We hypothesize these trends specifically in relation to the CCAMLR management goal to deplete Antarctic toothfish spawning biomass (toothfish >140 cm; Parker and Grimes 2010) in Subarea 88.1 (Ross Sea region) to 50% of its pre-fished level within over the course of 35 yr. The fishery targets the large fish by concentrating effort where these are found (Ross Sea slope and northern sea mounts; Ashford et al. 2012, SC-CAMLR 2013: Fig. 1). A 50% spawning biomass reduction from harvesting the largest fish will entail a reduction <50% of the total number of adult fish in the stock because heavier, spawning-sized fish comprised <25% of the initial fishable stock (see SC-CAMLR 2013, Fig. 1). The removal of 50% spawning biomass, however, will possibly result in a 50% numeric reduction of the toothfish most easily accessible to seals, those having the body fat allowing them to frequent the water column over the shelf at shallow depths (e.g., from 300 to within 12 m of the surface; Fuiman et al. 2002). A 25% numeric reduction (regardless of spawning status) of all fish would occur if the fishery is extremely selective about the sizes targeted, removing only the most massive fish, which is possible, but unrealistic (see SC-CAMLR 2013: Fig. 1; fishery still confined mostly to the Ross Sea slope, yet catching smaller fish over time). A 75% reduction would represent an extreme case of overfishing. Therefore, reality from the perspective of the seals appears to be spanned by our three scenarios.

Toothfish starting abundance in Weddell seal diet.—The number of toothfish caught per day by Weddell seals is not well established and is apparently highly variable among individual seals (median values, 0.8–14.5% of diet; see Appendix S1: Table S1 in Goetz 2015). Because toothfish capture rates decrease as a function of distance to concentrated seals, e.g., the breeding colony (Testa et al. 1985), and available estimates come from locations away from seal colonies, we considered two starting mean daily capture rates for a Poisson-distributed random variable: 0.3 and 0.4 toothfish/d. These rates decrease following an exponential decay based on the toothfish depletion rate. Fig. 2B shows the resulting pattern of toothfish consumed in 90 d in relation to mean daily toothfish capture rate, as the capture rate of large toothfish (those in water column) decreases with fishery extraction. The pattern is a nearly linear relationship between toothfish abundance and its capture rate by seals, which is a common simplifying assumption in predator–prey models where predation rate depends solely on prey abundance (Abrams and Ginzburg 2000). Variance around the number eaten per seal decreases with mean daily capture rates because the samples are taken from a Poisson distribution (where mean = variance). Consequently, when the mean capture rate is <0.1 toothfish/d, some seals may not eat a single toothfish in 90 d, whereas if daily capture rate is close to 0.4, some seals may consume >50 in 90 d.

Average number of silverfish per successful dive.—Davis et al. (2013) studied 12 seals in October to December near pup-rearing colonies and estimated the capture by seals of 5.6–15.7 silverfish per dive depending on habitat (see also Fuiman et al. 2002, Ainley and Siniff 2009). Importantly, these were not pupping seals nor individuals dwelling where seals concentrate for breeding, and therefore were not under the same energetic constraint as the seals simulated in our model. The daily diving sub-model assumes seals consume silverfish with an initial mean in Year 0 of 6.8 fish per successful dive, so that catches >10 fish/dive would occur ~5% of the time, assuming a Poisson distribution for captures. This mean value of number of silverfish per successful dive is consistent with what is known about seals' consumption of silverfish: some dives can be bountiful with 10 or more fish caught, leading to the possibility of seals catching hundreds of silverfish in a day.

Although silverfish represent >90% of the mid-water fish biomass on the shelf waters of the western Ross Sea (La Mesa et al. 2004), more than a dozen different species of fish prey on silverfish, including Antarctic toothfish, as well as penguins, seals, killer whales (*Orcinus orca*), and minke whales (*Balaenoptera bonaerensis*; Eastman 1985a, b, Smith et al. 2007, Pinkerton et al. 2010). Therefore, owing to competition, potential predation release effects from fisheries removal of toothfish may not translate directly into large numbers of silverfish available to the seals. We assume that mean rate of silverfish caught increases 30%, from 6.8 to 8.4 fish per successful dive (following a sigmoidal functional form) as large, mid-water

toothfish vary from the starting abundance to the abundance after 35 yr of fishery extraction. We explored alternative predation release effects, but this effect proved unimportant, and thus these alternatives are only referenced in Appendix S1.

Percentage of successful dives.—It is unknown how often seal dives result in successful capture of silverfish. Grey seals (*Halichoerus grypus*) reportedly capture prey, on average, in 46% of their dives (Austin et al. 2006), while Davis et al. (2013) report 55 dives in October to December in which Weddell seals encountered silverfish, out of a total 758 dives (or 7.2%). Fuiman et al. (2007) identified a subset of 109 among these 758 dives, in which there were 51 encounters with fish, not all with silverfish (for example, in very shallow dives, the seals often foraged on *Pagothenia borchgrevinki*, which reside on the underside of fast ice; see also Goetz 2015, Goetz et al. 2016); thus more than 50% of dives did not result in fish encounters at all. Davis et al. (2013) found that seals were successful in catching fish (not necessarily just silverfish) on ~25% of dives (sometimes more) depending on circumstances. We simulated two scenarios of silverfish foraging success: 25% and 35% of dives successful.

Percentage benthic dives.—Seals require energetically expensive, often anaerobic, dives (Williams et al. 2004) to search for, and capture, fish on the bottom, most of which is deep in McMurdo Sound, as opposed to fish encountered in the water column during shallower dives. Fish on the benthos typically hide among sponges and corals (Eastman and Barry 2002). Given these costs, there must be occasional positive incentives incurred from searching for food at greater depths. Based on data from Fuiman et al. (2007), we set 10% of all daily dives as benthic, with only a small pre-set average net energy gain after diving costs (see Appendix S1).

Maximum daily diving limits.—There is no published information on the average daily diving limits of seals during the post-lactation foraging period. Diving may amount to 80% of the 24-h day (J. Burns, *unpublished data*). However, since the post-lactation foraging period as here defined includes part of the molting period, during which the seals may limit diving time, it is likely that, on average, the time spent diving is <80% of the day during this period. We considered two limit scenarios in the daily diving sub-model: 80% of the day diving (equivalent to 120 dives/d or diving 1,150 min/d), or 62.5% of the day diving (which translates to 90 dives/d or diving 900 min/d). The limit in our simulations was imposed by whichever was reached first (number of dives or total minutes) during each day.

Demographic parameter scaling, and demographic model

The mass gain model produces estimates of mass recovered each year under each scenario, based on 200

simulations per scenario. The results are used to estimate a probability distribution of MRI values for each scenario and year through the functional relationship explained above (Fig. 2E). The mass gain model is linked to the demographic model, for each scenario in each year, through samples taken from the respective distributions of MRI values. Our demographic model simulates 200 seal population trajectories. For each population under each modeling scenario, an MRI sample for the appropriate year is taken and used to calculate the scaling parameter, modify the values of demographic parameters in the matrix model, and calculate λ , the annual, finite population growth rate. The demographic parameters being scaled are the probabilities of reproducing, and pup survival. λ is then calculated as the dominant eigenvalue of the Leslie matrix for each simulation in each year. Each population trajectory is thus unique, as it results from modifying the demographic parameters with respect to different samples of the MRI.

Altogether, we simulated 24 possible scenarios of how fishery extraction may affect seal mass gain during the post-lactation foraging period, under different sets of assumptions: 3 toothfish depletion rates \times 2 starting toothfish daily capture rates \times 2 probabilities of diving success \times 2 daily diving limits. Results were then evaluated with regard to their impact on seal mass recovery, body condition, and ultimately demographics, assuming one of three mass recovery targets: seals need to regain 60%, 70%, or 80% of the mass previously lost during the post-lactation foraging period in order to attain a MRI index value of 1. That is, under a 70% recovery target, a seal that regained <70% of the mass lost would attain MRI < 1, which translates into reduced breeding propensity, which would reduce reproductive rates and, to the degree that female body mass relates to weanling size in the next pupping season and its consequences on future survival and recruitment (Wheatley et al. 2006), first-year survival. Combined, we present the result of 72 scenarios (24 mass gain scenarios \times 3 recovery target scenarios).

Parameter importance

We fit a simple multivariable linear model to determine the relative importance of single-parameter effects on λ . Because many other factors not considered in our model may dictate the state of the McMurdo Sound seal population over time, including density-dependence effects not considered here, we do not simulate population trends and rather estimate λ . Each λ value is estimated for each year and scenario. Consequently, we considered all possible values of λ from all 200 trajectories under all scenarios combined to look at the relative effect of the most relevant parameters in our simulations through the regression analysis.

We standardized each parameter in order to understand the magnitude of its effect by using one level (the most impactful, e.g., lowest probability of diving success) as reference and expressing the other(s) as a proportional

difference. We include the toothfish mean daily capture rate under each scenario and year as a covariate in our regression model, and used the median value of the capture rate across all scenarios as the reference value. We relate our results to the fishery depletion rate through its impact on the seals' mean daily capture rate (increased depletion leading to reduced capture rates). Although we simulated all possible combinations of levels of parameters, we fit a simple additive model to understand the relative importance of single parameter effects

$$\lambda \sim \text{toothfishCaptureRate} + \text{probDivingSuccess} \\ + \text{dailyDivingLimit} + \text{targetPercentMassRecovery}$$

We calculated the change in R^2 values from the regression when each parameter is removed with all other parameters present, i.e., a partial R^2 value, using this as a metric of relative sensitivity of λ to the simulated parameter values in our scenarios. We report both the standardized coefficients and partial R^2 values.

As an additional, absolute metric of parameter importance, we used model results to estimate the amount of parameter value change (proportional change from the reference value) required to alter λ by +0.01 when all parameters are set at their reference value. To do so, we predicted the value of λ from the model fit while changing each parameter separately and holding all others constant at mean values, thus obtaining the amount of change for each parameter that caused the defined change in λ , akin to an elasticity analysis (henceforth “elasticities”). Our elasticity results depend on the reference value used for toothfish mean daily capture rate, used as reference. We also report results using the minimum value as reference. Because of how we standardized the covariates, elasticity values directly read as percent change needed to increase λ by +0.01.

All R code files to run the simulations and summarize results are found in the following github repository (*available online*).⁶

RESULTS

Contribution of toothfish to mass recovery

Fig. 3 shows (A) the impact of decreasing mean daily capture rate on mass gain of post-lactating seals and consequently (B), on λ . Fig. 3A illustrates that seals fail to gain 100 kg on average even when the mean daily capture rate has only been reduced by 38%, if the probability of diving success is 25% (red lines). If the probability of diving success is 35% (blue lines), seals fail to gain 100 kg only if the mean daily toothfish capture rate has been reduced by >50%. Regression analyses show that the most significant effect on lambda is related to the mean daily toothfish capture rate, and thus, to the depletion rates (Table 1). Daily diving limit and probability of foraging success had

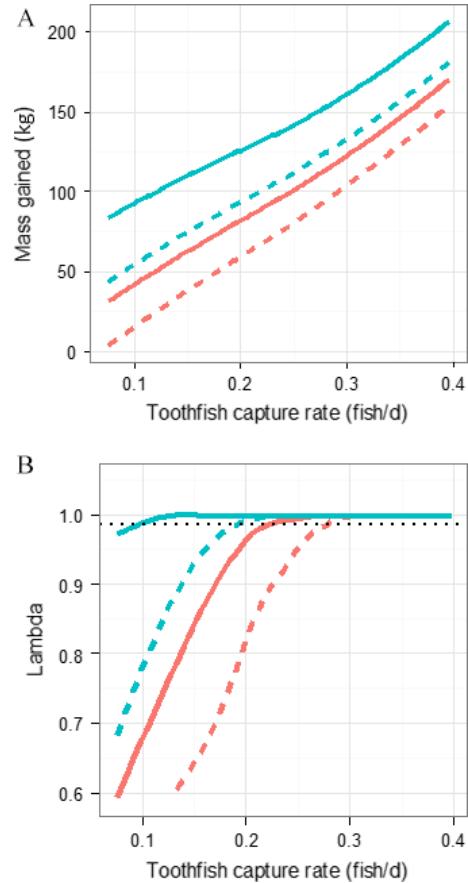


FIG. 3. Impact of toothfish depletion on (A) mass gain and (B) λ in Weddell seals. Blue lines show the effects when probability of diving success is 0.35 and red lines when it is 0.25. Solid lines show the effect when the daily diving limit is 80%, and the dashed lines when it is 90 dives/d. The black dotted line represents $\lambda = 0.985$, the rate that would result in a drop of 40% in population numbers in 35 yr. (Color figure can be viewed at wileyonlinelibrary.com.)

TABLE 1. Regression coefficients, change in R^2 value (i.e., “partial R^2 ”), and elasticity value of multivariable regression of λ vs. change in each simulated parameter.

Parameter	Regression coefficient	Change in R^2	Elasticity
Toothfish capture rate	0.1751	0.282	0.057†
Probability of successful dive	0.1549	0.086	0.064
Daily diving limit	0.1436	0.036	0.070
Target mass recovery	-0.1080	0.011	0.092

Notes: Parameter values were scaled (see *Parameter importance* in Methods). Partial R^2 values represent a standard metric of parameter importance relative to its effect on λ . Elasticity reflects the proportional change of parameter value required to increase λ by 0.01. All coefficients are highly significant ($P < 0.0005$). For λ model, $F_{3,102} = 48.85$, adjusted $R^2 = 0.691$.

†Value calculated using median of toothfish abundance as reference. If reference is set at minimum toothfish abundance, the elasticity value is 0.078.

⁶ <https://github.com/pointblue/weddell-seal-toothfish-model>

similar effects on λ , as both directly limit how much mass the seals may recover from eating silverfish, but neither parameter is as influential as the daily toothfish capture rate on λ , as evidenced in the partial R^2 values reported in Table 1. Early on in all scenarios, seals were able to gain >100 kg of mass. In a few scenarios, particularly under low depletion rates (25% decline) and high starting toothfish capture rate (0.4 fish/d), seals were able to gain >100 kg of mass throughout the 35-yr toothfish depletion period if allowed ≥ 90 dives/d.

Mean daily toothfish capture rate has the strongest overall effect on λ , too (Fig. 3B), but that the effect only becomes evident after the realized capture rate has dropped some amount. The effects of toothfish capture rate on λ increase exponentially under conditions when the combined effects of capture rate, the probability of diving success, mass recovery target, and the daily diving limits, result in the seals' being unable to recover sufficient mass. Though in some scenarios (high diving success, high daily diving limits, lowest mass recovery target), λ decreased relatively little, there may be long-term negative consequences to seal populations if λ remains <1 . In fact, in all scenarios there is the potential for λ to drop below 0.985 (dotted line in Fig. 3B), a growth rate that would cause $>40\%$ drop in population numbers in 35 yr.

Can seals compensate the loss of toothfish with silverfish to recover lost mass?

In many scenarios, the seals were unable to maintain body mass during the post-lactation foraging period. Fig. 4 shows the relationship between amount of toothfish and silverfish consumed in 90 d and resultant mass gain, combining results from all simulations using all three diving limits. We found that at high levels of toothfish consumption, seals are able to gain ≥ 100 kg even with moderate silverfish consumption. Conversely, there are

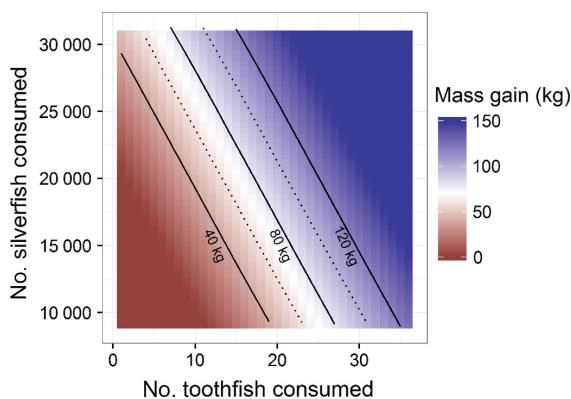


FIG. 4. Mass gain in Weddell seals in relation to number of toothfish and silverfish consumed in 90 d of post-lactation foraging. Mass gain is shown as contours of color shading, and with "iso-gain" contours depicted for 40, 60, 80, 100, and 120 kg. (Color figure can be viewed at wileyonlinelibrary.com.)

also conditions under which low numbers of toothfish are consumed such that no "realistic" (as defined in our simulation) amount of silverfish consumption will suffice to recover at least 100 kg of mass. For example, if a seal is able to eat 28 toothfish during the post-lactation foraging period (or about one toothfish every 3 d), it can gain ≥ 100 kg if it also consumes 80–90 silverfish/d. If only 25% of the dives are successful and on average a seal catches 6.8 silverfish per successful dive, it would take ~ 56 dives to catch 90 silverfish. On the other hand, if a seal is only able to consume ≤ 20 toothfish in the 90-d period, the seal would need to dive more than 80% of the time or >120 times/d to catch enough silverfish (at minimum, 26,000 over 90 d) to recover 100 kg, once dive energetics are considered. Based on the available (albeit sparse) data on silverfish captures, we deem this and similar scenarios unrealistic.

Consequences of toothfish depletion on sustaining population numbers and λ

Table 1 shows the regression coefficients of simulation parameters on λ , including the effect of target mass gain. Toothfish mean daily capture rate has the largest coefficient and, most notably, the largest change in R^2 value, indicating its higher effect. Probability of diving success has a slightly higher effect than daily diving limits, and the target mass recovery has the lowest effect. Elasticity values, as we define them, corroborate these results: it takes a 5.4% change in toothfish daily capture rate to change λ by 0.01, compared to 6.4% in probability of successful dive, 7.0% in percent time diving, and 9.2% in target mass recovery. However, if evaluated using the lowest toothfish mean capture rate in the data as reference, the elasticity value of toothfish capture rate is 7.8%, i.e., a proportionally larger change in depletion rate is required to alter λ by 0.01, than a change in probability of diving success and daily diving limit. This is because at the low toothfish capture rates (i.e., in the proximity of the minimum value, which is used as the reference), how much silverfish is being consumed becomes more important, because in the model it is the only alternative for seals to compensate for the low toothfish intake. The number of silverfish consumed is influenced by the diving success rate and the diving limit.

Fig. 5A, B shows the resulting average of λ for all simulations in each scenario simulated. The blue coloring of dots indicates scenarios with mean $\lambda < 0.985$ (i.e., scenarios where seal population numbers would drop by $>40\%$ in 35 yr). The scenarios under high diving limits (80% of the day) and coupled with low depletion rate resulted in little relative effect on λ . In contrast, $\sim 75\%$ of the simulations under the high fishery depletion rate, and 1/3 of those under the 50% depletion rate resulted in λ values < 0.985 . Effects are more marked under the lower starting capture rate (Fig. 5A).

The fishery depletion rate, through its effects on the seals' mean daily toothfish capture rate, has the highest

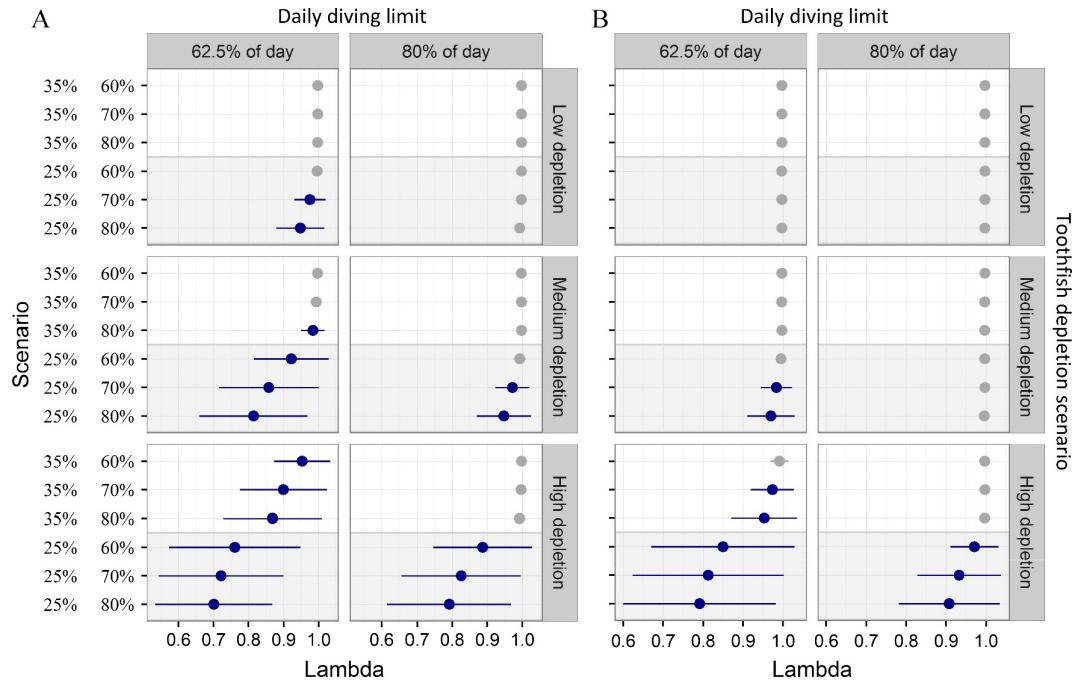


FIG. 5. Effect of toothfish depletion rate (rows in the lattice), daily diving limits (columns in the lattice), probability of diving success (leftmost scenario column), and target percent mass recovery (rightmost scenario column), on the population growth rate (λ) mean of simulations for each scenario (bars show standard deviation). In blue are those scenarios where $\lambda < 0.985$ (equal to a drop of 40% or more in seal numbers in 35 yr). (A) Effects on lambda for starting toothfish capture rate 0.3 fish/d; and (B) for capture rate 0.4 fish/d. (Color figure can be viewed at wileyonlinelibrary.com.)

impact on the population growth rate of Weddell seals in our simulations, followed by probability of diving success and daily diving limits (Fig. 5). The partial R^2 analysis in Table 1 provides a quantification of the importance of each variable, with mean daily toothfish capture rate more than four times as impactful as the other parameters, and target mass recovery the least influential. Some parameters are unimportant under some scenarios, but become relevant under others (also Fig. 5). For example, target mass recovery is of little importance in determining λ under high depletion rates, but become very relevant under other conditions (e.g., medium depletion rates and high daily diving limits).

Another notable effect evident in Fig. 5 is that the variance around λ increases as its mean value drops. Provided that toothfish remain moderately abundant in the water column, where they are more accessible, seals can capture enough of them to ensure full mass recovery in the 90-d period, and hence, λ exhibits little variance across population simulations. As large toothfish become scarcer and the main daily capture rate decreases, by chance alone some seals are able to consume enough to fully recover body condition while others do not. This variability permeates from individuals through to the λ values for the population. So, some simulated population trajectories result in high λ values while others end up with lower values, causing the high variability shown in the figure.

DISCUSSION

Relevance of toothfish as prey of Weddell seals

Our results demonstrate that foraging on energy-dense toothfish may play an important role in body mass recovery in Weddell seals during a critical period of their life cycle, especially the post-lactation foraging period of females. Our analyses indicate that toothfish capture rate is the most important determinant of the ability of seals to recover body mass in the post-lactation foraging period, and thus, as demonstrated in Table 1, toothfish capture rate is the most influential variable determining λ . The potential importance of toothfish is high when considering the energy content of the seals' other main prey, the Antarctic silverfish, as well as other less common prey with equal or lower energy value (cf. Burns et al. 1998, Lenky et al. 2012, Goetz 2015, Goetz et al. 2016).

On the basis of size and energy density and not considering diving costs, it would require the capture of ~470 50-g silverfish to replace a 15-kg toothfish (Lenky et al. 2012), but when considering diving costs, replacement requires ~1000 silverfish (Fig. 4). Our results also show that seals might adjust to some decrease in large toothfish and still be able to recover breeding-season mass loss. Indeed, toothfish is not a common seal prey. Isotope analyses suggest it being on average <10% of the seal's diet on an annual basis, though other studies found

toothfish to comprise up to 15% of the diet of individual seals (Burns et al. 1998, Zhao et al. 2004, Goetz 2015, Goetz et al. 2016). Our modeling is concerned with a short time period for one, albeit very important, segment of the population, post-lactating females, specifically when energetic demands are high. During such an energetic bottleneck, the contribution made by toothfish might well be substantial.

Using data acquired by limited sampling to represent toothfish consumption for the entire year and entire Ross Sea continental shelf habitat of the seal, as was done for Pinkerton et al.'s (2007) food web model, is problematic if, in reality, consumption during specific, short periods, such as the post-lactation foraging period, is particularly critical. Pinkerton and Bradford-Grieve (2014) acknowledged this problem in assessing toothfish importance to meso-predators, including Weddell seals.

Goetz (2015) showed individual variability in consumption of toothfish among seals, 0.8–14.8% of seals' diet. That study was conducted on seals already experiencing toothfish depletion (earliest sample from 2010), for males and females, regardless of reproductive status. Seals may recover body mass sufficiently to produce a pup without consuming toothfish, but our model shows that this does not necessarily translate into comparable survival and recruitment probabilities to those from mothers that are more successful at capturing and consuming the highly energetic and large toothfish. Thus, variability in a seal populations' ability to sustain decreased densities of toothfish may be related to the specific characteristics of the adult seal population. A population with more seals adept at capturing toothfish would, all else being equal, fare better than one in which toothfish-adept seals are rare. Our model also clearly shows that seals with a diet low in, or absent of, toothfish may not be able to maintain a high enough breeding propensity rate that, in conjunction with lower pup and sub-adult survival rates, still results in a stable seal population. In order to maintain breeding propensity that leads to stable seal populations, our modeling results indicate that at least some females (e.g., experienced females, or the "super-breeders" hypothesized by Chambert et al. 2013) must consume toothfish in sufficient amounts. The individual variability reported by Goetz (2015) supports this conclusion. This individual variance, important to maintain the overall seal population growth rate, will likely be eroded as the ability to find buoyant toothfish decreases.

We assume that seals must recover 60–80% of their lost mass during the post-lactation foraging period, and that those seals who fail cannot simply catch up overwinter (i.e., there are long-term consequences to inadequate mass recovery). Owing to this assumption's simplicity, it is unclear what the minimum number of toothfish must be consumed, in combination with other prey, to recover, in a timely manner, a sufficient amount of mass. Nevertheless, our simulations help illustrate that there may be a lower limit to the number of toothfish the seals need to maintain high breeding propensity and first-year survival rates.

Relevance of fishery effects and present status

Our results indicate that as toothfish are depleted, under some conditions, more seals are unable to fully recover body mass. We contend that at some point the reduction of toothfish in the Weddell seals' diet may lead to insufficient breeding season recovery, a drop in breeding propensity, and negative population growth. Our results also show two possible ways in which this impact will become evident. First, the impact becomes exponentially worse as toothfish presence (and its capture rate by seals) decreases below a certain level (Fig. 3B). Second, the impact may manifest itself through high variance in λ values (i.e., interannual variation), because in some years enough seals may find enough toothfish to regain mass despite low overall toothfish abundance (see Fig. 5), while in other years, lack of toothfish capture results in especially low λ . Although in some scenarios the average result is a λ close to 1, our results show numerous simulations in those scenarios that include some years with very low lambda values (<0.8), which would reflect severe negative impacts on seal populations. Therefore, scenarios with high variance should be considered potentially harmful to seal populations.

The mean daily toothfish capture rate was more than four times more influential than parameters dictating how much silverfish the seals may catch. Thus, our simulations support the conclusion that the fisheries at current extraction levels have a realistic potential to be detrimental to the Weddell seal populations in the southern Ross Sea in the long-term. We do not claim that such will be the case, but rather that the probability of this occurring must be considered in a precautionary approach to managing the fishery.

Currently, after 12 yr of fishery extractions, McMurdo Sound Weddell seal breeding population may or may not show negative impacts, despite the fact that seals seem to be taking increasingly smaller toothfish (see Appendix S1: Table S2). Our model offers three plausible explanations for the possible current lack of measurable fishery impacts to the breeding seal population. First, among potential impact scenarios, our simulations indicate that seals may cope with high depletion rates of large toothfish if the starting capture rate is high. Though not reported here, we explored simulations with starting toothfish capture rates >0.4 fish/d. Under these higher toothfish capture rates, seals are more often able to recover mass and maintain high MRI values, with less dependence on silverfish. Current observations in McMurdo Sound may in fact reflect a great skill in seals for finding toothfish, even as large toothfish become less abundant. For example, Goetz (2015) shows that seals have a strong preference for particular foraging habitats during the summer, presumably areas of high prey density (see also Barry et al. 2003, also Hindell et al. 2002). Second, our results show that a significant drop in the daily toothfish capture rate should occur before any impacts on λ occur (Fig. 3B), and thus, it may be that the McMurdo

population has not yet experienced a sufficient drop in toothfish abundance (i.e., there may be a time lag for effects to become notable). Third, the removal of the larger toothfish by the fisheries may have triggered predation release effects on toothfish prey, especially silverfish, but other species as well that are consumed by the seals (Goetz 2015, Goetz et al. 2016). It is possible that these prey species became abundant enough to become more prominent in the diet of the seals and help seals cope, for now, with the loss of toothfish. If seals are finding other species more abundant and using them to cope for the loss of toothfish, it remains unclear to what degree these replacement prey will help seal populations maintain breeding propensity into the future, when large toothfish are rarer.

The status of the McMurdo Weddell seal population may not be indicative of impacts in the entire Ross Sea. While the main breeding population in McMurdo Sound (Erebus Bay vicinity) has only recently recovered from sealing that ceased in the mid-1980s, the larger molting population in the Ross Sea has yet to recover (Ainley et al. 2015). Owing to availability of habitat, assemblages of molting seals likely are much more concentrated than breeding concentrations, with fast ice being preferred by both. As well, a formerly large breeding/molting population in at least one site in the northern Ross Sea has decreased severely since the 1960–1970s (Ainley et al. 2015). Ainley et al. (2015) sought to explain the change as a consequence of alteration of fast ice persistence but found no supporting evidence. Because of these uncertainties, we recommend the precautionary approach espoused by CCAMLR. Such an approach will help discern what the fishery effects may be on the Ross Sea seal populations before these become severe, through measurements of informative metrics and behaviors, and help to adjust the fishery target accordingly.

Model assumptions

We made several simplifying assumptions in our approach that likely render our model results as conservative. These include, but are not limited to, a realized linear relationship between toothfish abundance and its capture rate; no change in the age structure of the toothfish population due to the fishery; no impacts on pups due to the loss of toothfish beyond first year survival; no differential scaling factors for breeding propensity, pupping rates, and pup survival (i.e., all were equally affected by loss of toothfish); no differential impacts among individual seals (e.g., young vs. experienced females), no costs of molting, and that toothfish and silverfish are more influential on seal mass gain during the post-lactation foraging period than any other components of the Antarctic food web. We discuss two among these here; a review of the others can be found in Appendix S1.

We did not specifically model a change in toothfish age structure. The fishery has been targeting the largest and

oldest of the fish so that, over time, seals are being left with a population of the younger and smaller toothfish that are exclusively benthic-dwelling, which is proving to be the case (see SC-CAMLR 2013, Fig. 1 therein). Our models considered only a change in toothfish numbers over time, not in sizes. The energy gain from a single toothfish may diminish over time, as seals are left to catch smaller toothfish; the smaller toothfish are negatively buoyant, due to lower lipid loads (Near et al. 2003). As a result, small toothfish are confined to the bottom, access to which may require deeper and more energetically costly dives by the seals, including more searching among the benthic invertebrates (Eastman and Barry 2002). The change in size caused by the fishery, and consequent implication of deeper dives to locate smaller toothfish, points to our results being conservative about the impact of the fishery on seal populations.

Our model assumed that impacts of the loss of toothfish did not affect sub-adult seal survival and recruitment rates. Seals take 5–10 yr to recruit (Rotella et al. 2012), perhaps also modulated to some degree by the consumption of toothfish to affect body condition. If this is the case, our model underestimated the impacts of toothfish loss. This is also a mechanism whereby time lags may operate. The reduction in recruitment rates may result in a reduction in seal numbers only after a decade or more of the seal population's experiencing the loss of toothfish. A time lag in effects may explain why the McMurdo population took such a long time to recover from exploitation (30 yr), and whether it can maintain the current recruitment levels remains to be seen.

Toward a better understanding of impacts

The removal of large biomass and energy from the Ross Sea food web by the fishery will undoubtedly have some effect on the seals; one of our conclusions is that gauging such effect will be difficult without an intensive, directed research effort. We contend that a consideration of the basic assumptions underpinning our model, and its results, will help determine what parameters to measure to better understand the potential for these effects. Here we list four.

First, following Goetz (2015), more accurate measurements of proportion of toothfish vs. other prey in the seal diet, in relation to age, breeding stage, and breeding propensity, will help understand which seals will be most impacted by the loss of toothfish. The proportion of toothfish-consuming seals in the population may also help estimate the overall population impact. These measurements may also help validate or improve our model's assumptions.

Second, we assumed that seals had only the 90-d post-lactation foraging period to recuperate from the 60 to 80% mass loss during breeding. One way seals may cope with fewer large, shallow-dwelling toothfish is by investing more time foraging at other times of the year. However, there may be adverse consequences to

increasing foraging at other times of the year to make this adjustment. Thus, also following Goetz (2015), it is important to relate change in foraging behavior across seasons to changes in breeding propensity, pupping rate, and subsequent pup survival to see which seals are being impacted and how.

Third, our results indicate that as abundance of large toothfish in the water column drops, the likelihood of mass recovery will become increasingly more subject to stochastic variation. This effect is understandable considering that water-column-capable toothfish are two to three orders of magnitude larger than, and twice as energy dense as, other seal prey. Capturing one or a few toothfish in a post-lactation foraging period may thus make a significant difference in a seal's ability to fully recuperate and bear a pup in the next spring. Thus, if this necessary recovery becomes less and less certain, it may be reflected in higher variance in breeding propensity. Tracking individual seal breeding propensity over time (which is being done, e.g., Rotella et al. 2009, 2012), and correlating it with age and size, may help show if variance in propensity is increasing over time and why.

Last, the seal population in McMurdo and elsewhere in the Ross Sea may or may not be showing numeric impacts from the fishery (Ainley et al. 2015), demonstration of which is made more difficult to detect because of immigration; for instance the molting population of seals in southern McMurdo Sound once was much larger than the breeding population (Stirling 1969a, b) but now is not (Ainley et al. 2015). Recent novel approaches to crowdsourcing the counts of seals using high-resolution satellite images (LaRue et al. 2011) is now being tested, and may be used to monitor seal numbers in the entire Ross Sea, thus to understand large-scale vs. localized dynamics, and determine the magnitude and extent of fishery impacts.

Incorporating uncertainties in management

The trial-and-error management of wildlife is undesirable (Nichols et al. 2015), especially in long-lived slow-growing vertebrate populations. Lacking a clear understanding of how the fishery may be affecting the Ross Sea ecosystem, as is presently the case, calls for caution, close evaluation, and monitoring for possible adverse impacts with long repercussions in the food web. Hanchet et al. (2015) review the presumed precautionary approach to managing toothfish stocks in the Ross Sea, and revealed that no considerations nor adjustments have been made to mitigate potential effects on mesopredators such as the Weddell seal or fish-eating killer whale. Abrams et al. (2016) discuss the principles behind a precautionary approach to managing the fishery, including considerations toward impacts to other wildlife in accord to CCAMLR principles. Our results suggest impacts on seal populations can vary from very limited to very severe, which under the precautionary principle justify management adjustment: the establishment of a seal monitoring program, as part of the CCAMLR

Ecosystems Monitoring Program that spans the entire Ross Sea and not just the McMurdo population. Further, killer whales are known to selectively prey on toothfish and can track fishing vessels (Söffker et al. 2015). Other authors have shown that consumption of key prey species may affect female killer whale fecundity rates (e.g., Patagonian toothfish *D. eleginoides* caught by killer whales around the Crozet Islands; Tixier et al. 2014), such that the fishery may also affect killer whale population dynamics in the Ross Sea (Ainley and Ballard 2012).

OVERALL CONCLUSIONS

Despite our simple approach and multiple assumptions, we provide evidence that the depletion of large, neutrally buoyant (high energy density) toothfish, can under some circumstances, be the most influential factor affecting the seals' capacity to recover mass lost during the lactation period, with potentially serious implications for demographic stability. This result is to be expected given the great differences in mass and energetic content between large toothfish and all other seal prey in the Ross Sea. Regarding the most important question of whether the seals may cope with reproductive costs in the absence, or under significant loss, of this potentially valuable prey, we show that there are several measurable parameters that may help us understand if and how the seals may be adapting to the loss of toothfish. We also show that under some conditions, given the CCAMLR target of 50% depletion of toothfish spawning biomass, there can be substantial seal population declines. Thus, there is reason for concern regarding possible deleterious consequences of toothfish depletion on Weddell seals, and we suggest areas for further study in order to support the ecosystem-based management of the Ross Sea ecosystem as called for in the CAMLR Convention. Our results justify a more precautionary approach to managing the fishery, including the immediate establishment of a monitoring program to better understand the impacts of the fishery on Weddell seal and other wildlife populations.

ACKNOWLEDGMENTS

Funding for this project was provided by Mission Blue and Biotherm. The National Science Foundation, Division of Polar Programs, provided additional support through grants no. ANT-1141326 (J. Rotella, R.A. Garrott, and Donald B. Siniff); ANT-0944411 (D. Ainley); ANT-0944141 (G. Ballard); and ANT-1246463 (J. Burns). This is Point Blue Conservation Science contribution No. 2105.

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