A Critical Re-examination of the Evidence for a Possible Dependence of Weddell Seals (*Leptonychotes weddellii*) on Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica

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Abstract

There is presently debate over the degree to which the fishery for Antarctic toothfish (*Dissostichus mawsoni*; ‘toothfish’) in the Ross Sea may affect the ecological viability of top predators such as Weddell seals (*Leptonychotes weddellii*), but available evidence remains inconclusive as a result of both methodological limitations and knowledge gaps. We present new stable isotope data on Weddell seal prey, consider the assumptions underlying application of stable isotope methodology to Weddell seals, and estimate the potential contribution of toothfish to the diet of Weddell seals using an isotope mixing model. As a new approach, we also estimate Weddell seal food requirements by considering nutritional quality of potential prey species including toothfish in the context of updated estimates of Weddell seal energy requirements. The energy density of potential prey items (fish and invertebrates) covers a four-fold range. Nutritional analysis of Ross Sea prey suggests that toothfish may represent a unique high-energy food resource for Weddell seals that possibly cannot be adequately replaced by other prey, in particular during periods of high energy demand such as late-stage lactation and the post-breeding recovery of body weight and condition. The assumed dominance of Antarctic silverfish (*Pleuragramma antarcticum*) in Weddell seal diets should be re-examined given the known biases of methods used to derive diet estimates. While large (>30 g) silverfish occurring at high densities are a valuable nutritional resource, smaller size classes are unlikely to be adequate to meet the estimated energy requirements of adult Weddell seals. Our ability to conclusively determine possible dependence of Weddell seal populations on toothfish, and hence possible impacts of toothfish removal by fisheries, is primarily hindered by (a) insufficient information on Weddell seal diet, due to inadequate temporal coverage and biased methodology, and (b) uncertainty regarding Weddell seal abundance and spatial foraging patterns in the Ross Sea region.
I. INTRODUCTION

Marine mammals are potentially affected by fisheries both directly, e.g., through bycatch mortality, and indirectly, through a reduction of their prey biomass. Indirect impacts on marine mammals may be significant but are much more difficult to quantify than direct effects (Moore 2012).

There is presently debate over the degree to which the fishery for Antarctic toothfish (Dissostichus mawsoni; ‘toothfish’) in the Ross Sea may exert indirect trophic impacts on top predators such as Weddell seals (Leptonychotes weddellii; e.g., Ponganis & Stockard 2007; Ainley et al. 2009; Ainley & Siniff 2009). Weddell seals breed in summer in the vicinity of McMurdo Sound (Fig. 1) and elsewhere in the Ross Sea region (Stirling 1969a, 1971a). As reviewed by Pinkerton et al. (2008), the most likely potential impact of the fishery on Weddell seals in the Ross Sea is a reduction in prey availability arising from depletion of toothfish by the fishery, but the available body of knowledge is insufficient to (a) quantify toothfish intake by Weddell seals (of any subpopulation or at any time of year), and hence (b) to assess the risk of impacts of the fishery on Weddell seals, and possibly other species, in the Ross Sea. There are marked, unresolved discrepancies in existing diet information regarding toothfish consumption by Weddell seals: Direct methods (observation, stomach contents, photography) support significant predation on toothfish by Weddell seals, whereas indirect methods (stable isotope analysis, scat hard part analysis) appear to point to Antarctic silverfish (Pleuragramma antarcticum) and cryopelagic fish such as bald notothen (Pagathenich borchgrevinki) as the principal food resource of Weddell seals in McMurdo Sound.

In this paper, we critically re-examine available evidence regarding Weddell seal diet and the possible importance of toothfish for Weddell seals. Stable isotope analysis shows great promise for determining long-term diet. We present new stable isotope data on prey, discuss several key assumptions underlying application of stable isotope methodology to Weddell seals, and estimate the potential contribution of toothfish to the diet of Weddell seals using an isotope mixing model. As a new approach, we also estimate Weddell seal food requirements by considering nutritional quality of potential prey species in the context of updated estimates of Weddell seal energy requirements. The energy density of potential prey items (fish and invertebrates) covers a four-fold range, and the estimated energy requirements of Weddell seals vary greatly with season and among subpopulations (breeding vs. non-breeding adults, growing subadults). These factors have a direct effect on the mass (and possibly type) of prey consumed. Combining estimates of possible toothfish consumption derived from stable isotope analysis and energetic considerations, we estimate plausible rates of toothfish consumption by Weddell seals and compare them to estimates of Antarctic toothfish production and mortality in the vicinity of McMurdo Sound.

II. Weddell Seal Biology and Life History

Weddell seals (Leptonychotes weddellii) are one of five Antarctic pinniped species. Due to their unique ability to dive under closed sea ice, Weddell seals are the only marine mammal able to exploit continental shelf habitats around the Antarctic continent that are covered by contiguous sea ice for a large proportion of the year. Weddell seals occur in large numbers on the circumpolar fast ice, and offshore in the pack ice zone north to the Antarctic Convergence (Kooyman 1981). The northernmost breeding limit of Weddell seals is South Georgia (54° 30’ S; Vaughan 1968). Weddell seals are distributed throughout the Ross Sea, forming large breeding colonies of up to several hundred animals along the coasts of Victoria Land and Ross Island (Ainley 1985; Testa & Siniff 1987).
Weddell seals breeding in the southern Ross Sea have been extensively studied. In McMurdo Sound, Weddell seals were first studied by Wilson in 1902-04 (Wilson 1907), and later establishment of American and New Zealand research stations has resulted in almost continuous research activity directed towards local breeding colonies (e.g., Smith 1965; Stirling 1967, 1968, 1969b, a, 1971b, 1974; Testa 1987; Testa et al. 1989; Burns & Castellini 1996; Schreer et al. 1996; Burns et al. 1998; Testa & Scotton 1999; Stewart et al. 2003; Cameron & Siniff 2004; Proffitt et al. 2009; LaRue et al. 2011; Eisert et al. 2013a). An intensive study of the population ecology of a breeding population of Weddell seals in the Erebus Bay region of eastern McMurdo Sound, started during the 1960s by the New Zealand Antarctic Programme and continued by American researchers, continues to the present and is the longest-running study of any wild mammal (e.g. Stirling 1967; Rotella et al. 2009). Over the course of this study, over 17,000 animals have been tagged, with emphasis on maintaining and enhancing annual demographic data through the use of mark-recapture techniques (Rotella et al. 2009). In contrast to the wealth of information collected on demographics, few studies have targeted the nutritional ecology of the Weddell seal, and there is a paucity of information not just on diet, but on the energetic and nutritional requirements of all seal age classes.

In the austral spring, adult Weddell seals congregate in breeding colonies to give birth, raise their young, and mate. Colonies tend to form near tidal cracks in fast ice in traditional locations, often at considerable distance from open water. Once female Weddell seals are of breeding age, they show a high degree of philopatry for colonies (Hastings et al. 1999). Mean parturition and weaning dates...
depend on colony location and occur earlier in the northern part of the range (Mansfield 1958; Vaughan 1968). In McMurdo Sound (Fig. 1), one of the most southerly breeding locations, pupping starts around October 12, with peak pupping occurring during the last week of October. Pregnant females arrive at colony sites a few days before giving birth. Non-breeding adults are excluded from the colonies by aggressive behaviour of adult males and females with pups (Stirling 1969b). Weddell seal pups are born at an advanced stage of maturity (Eisert et al. 2013b), start diving in their second week of life, and are weaned after nursing for only 5 to 8 weeks (Eisert et al. 2013a). Lactating females fast initially before the majority starts to feed near the breeding colonies at two to four weeks postpartum (Hindell et al. 2002; Eisert et al. 2005). Adult males defend underwater territories (= maritories) associated with fast-ice colonies and compete for access to females, which come into oestrus towards the end of lactation (late November to mid-December; Hill 1987). Weddell seals have an extreme ‘capital breeding strategy’, i.e., they catabolise a large proportion of their body mass (BM) to support the energetic demands of reproduction during the austral spring and summer (Eisert & Oftedal 2009). Female Weddell seals may lose ≥40% of their postpartum BM during lactation (Eisert & Oftedal 2009), and sexually active males also sustain high rates of mass loss (Bartsh et al. 1992; Table 4). Because lactating Weddell seals have one of the largest mass losses of any pinniped, it was previously thought that food intake during lactation was opportunistic and did not contribute significantly to energy requirements (Oftedal 2000; Eisert & Oftedal 2009). However, preliminary data on the energetics of lactation and food consumption in lactating Weddell seals indicate that food intake is significant and possibly essential for successful completion of lactation (Eisert, Oftedal et al., unpublished data; Oftedal & Eisert 2010). There is evidence that weaning mass has a direct effect on pup survival in Weddell seals, indicating that any factors that decrease lactation performance (such as inadequate prey availability or quality) may have a detrimental effect on offspring survival (Hadley et al. 2008; Proffitt et al. 2008).

After the six-week lactation period (late Oct-early Dec), adult Weddell seals move short distances (~2-10 km) away from breeding colonies and aggregate in other areas of sea ice; for example, many Weddell seals in the Erebus Bay region move to haul-out areas near Turtle Rock and the pressure ridges near Scott Base, where they remain for the annual moult (Jan-Feb; Smith 1965). The annual moult takes place shortly after the breeding season (late December-January) and is likely to represent an additional, energetically demanding period for Weddell seals (Boily 1996; Table 4). Weddell seals have delayed implantation (Smith 1966), i.e., there is a variable delay between fertilisation and implantation of the blastocyst. This mechanism serves to synchronise parturition dates among individuals of a population to take advantage of the narrow window of optimal ice and climatic conditions during the short Antarctic spring and summer. Body condition is known to have a decisive influence on whether blastocyst implantation takes place at all in other carnivorans (Lindenfors et al. 2003), and successful implantation and subsequent foetal development in Weddell seals may be contingent on the ability to recover the massive weight loss incurred during the preceding lactation period. If this is the case, it would imply not only a strong dependency of seals on local, high-quality prey during the immediate post-breeding season, but it also means that a decrease in prey availability or quality at this time may have a disproportionate detrimental impact on this species. There is very little information on feeding activity in Weddell seals during the period from December to February, partly because access on unstable sea ice may be difficult, and because no instruments can be attached to seals to monitor their behaviour during the moult. Late lactation and post-breeding are periods when seals would be expected to benefit greatly from feeding on abundant and/or high-quality prey to replace lost body stores.
The spatial distribution of Weddell seals between March – October is not certain. Some individuals remain year round in the fast ice at latitudes as high as 78°S in McMurdo Sound, whereas others, particularly newly weaned and subadult animals, appear to spend the winter in the pack ice to the north of the Ross Sea (Stewart et al. 2003). Ice conditions, the availability of prey, and the abundance of predators such as leopard seals and killer whales likely determine where adults and young go when they disperse from the breeding colonies (Testa 1994). Tagging experiments show that some pups born in McMurdo Sound return there within a year, while others stay more than 400 km distant for a number of years (Burns et al. 1999). Fewer than 15% of pups born in the Erebus Bay area of McMurdo Sound have been observed recruiting into the breeding population near their birth locality by six years of age (Testa 1987; Hastings et al. 1999). The low return rate may be because pups suffer high mortalities in their first few years of life, because pups recruit into other colonies, and/or because studies are not long enough to observe pups returning to their natal areas (Burns et al. 1999). Satellite tracking of adult females from breeding colonies in McMurdo Sound showed that most remained in the northern part of the Sound during winter, although some travelled as far as 500 km north beyond the Sound (Testa 1994).

In summary, the extreme capital breeding strategy of Weddell seals indicates two periods of potentially critical dependence on local, high-quality food resources: (1) during late lactation, if food intake is required to allow lactating females to successfully raise their pups to a weaning weight consistent with subsequent pup survival; and (2) during the post-breeding period, assuming that implantation of the blastocyst and early foetal development depend on the ability of females to regain mass lost during lactation.

III. Weddell Seal Diet

Because prey consumption may exhibit both short- and long-term variability, meaningful determination of prey consumption by predators requires methods that can integrate diet information across multiple time scales from days to months and beyond. A limitation of existing methods of determining diet is that there is an inverse relationship between specificity and time scale. Methods that allow determination of prey to species level and/or quantification of biomass intake represent dietary snapshots (underwater video cameras and scat and stomach sampling), whereas methods that integrate dietary intakes over weeks to months provide information on the average trophic level of the diet (stable isotope analysis of predator tissues). Fatty acid analysis appears to offer both a useful time scale as well as moderate specificity (Budge et al. 2006). However, in the only study that has applied fatty acid analysis to Weddell seals to date, findings were inconclusive due to difficulties of interpretation and lack of a reference data base for prey fatty acids (Wheatley et al. 2007). The status of available knowledge on Weddell seal diet and foraging was reviewed in a previous paper (Pinkerton et al. 2008), and there has been a recent detailed review of diet determination in pinnipeds that examines inherent biases of existing methods (Bowen & Iverson 2012).

III.1 Evidence from Stable Isotope Analysis

Stable isotope ratios of carbon and nitrogen (δ^{15}N, δ^{13}C) are widely used in marine ecology and ecophysiology to study trophic relationships and ecosystem dynamics (Newsome et al. 2010). Ingestion and assimilation of prey results in fractionation of naturally occurring isotopes in prey due
to metabolic processes in the predator (e.g., amino acid turnover and urea formation), and this results in diagnostic changes in isotope abundance across trophic levels (Newsome et al. 2010).

Fig. 2 shows δ^{15}N values for a range of megafaunal predators and fish and invertebrate prey based on published data from (Burns et al. 1998; Bury et al. 2008; Krahn et al. 2008) and additional data on prey from McMurdo Sound and on blood plasma collected from lactating Weddell seals (Eisert, Newsome, Oftedal, unpubl. data). The average of reported δ^{15}N of Weddell seals is 13.0 ‰ (Burns et al. 1998; Zhao et al. 2004; Eisert, Newsome, Oftedal, unpubl. data). If one assumes a trophic shift of +3.4 ‰ (Newsome et al. 2010) and a diet primarily composed of a single prey species, stable isotope values are consistent with silverfish as the principal prey for Weddell seals; significant consumption of toothfish by Weddell seals and Type C killer whales (Orcinus orca) appears to be ruled out on the basis that δ^{15}N signatures of these marine mammals are the same or slightly lower than those of toothfish (Krahn et al. 2008; Fig. 2). Given that the two megafaunal predators with the highest δ^{15}N, Weddell seals and type C killer whales (Fig. 2), have δ^{15}N on par with toothfish, this implies that toothfish do not have any predators in the Ross Sea. This seems implausible, and ignores the effect of isotopic mixing in predators consuming prey from a range of trophic levels, as well as direct observations of predation on toothfish by both predators. For example, tissue of a McMurdo octopod (Pareledone turqueti) had δ^{15}N values higher than either toothfish or Weddell seals (Fig. 2), even though octopods are a known prey item for Weddell seals in McMurdo Sound; remains of Pareledone and/or related octopods were found in 14% of 36 seal stomachs (Dearborn 1965) and 10% of 290 seal stomachs collected in McMurdo Sound (Smith 1966). These discrepancies likely derive from differences in isotopic enrichment among different tissue types, plus the effects of diet mixing in which prey of low isotopic enrichment counterbalance prey of high enrichment.

Table 1. Maximum proportions of prey species in the diet of Weddell seals based on δ^{15}N values as explained in the text. The values in grey indicate that the secondary constraint has been reached (diet items not to be greater than 50% of diet).

<table>
<thead>
<tr>
<th>Prey species</th>
<th>DM</th>
<th>PA</th>
<th>PG</th>
<th>TL</th>
<th>TB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leptonychotes weddellii</td>
<td>0.15</td>
<td>0.7</td>
<td>0.5</td>
<td>0.45</td>
<td>0.4</td>
</tr>
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</table>

DM, Dissostichus mawsoni; PA, Pleuragramma antarcticum; PG, Psychroteuthis glacialis; TB, Trematomus bernacchii; TL, Trematomus loennbergii

We therefore employed a mixing model (IsoSource: Phillips & Gregg 2003) to determine the range of diets of Weddell seals that is consistent with existing stable isotope data. We set the diet resolution to 5% and the tolerance to 0.1 ‰ (Phillips & Gregg 2003). We further constrain IsoSource by requiring that Pleuragramma antarcticum should not be less than 30% of the diet, and that Psychroteuthis glacialis, Trematomus loennbergii and Trematomus bernacchii should each not be more than 50% of the diet. These are termed “secondary constraints”. The primary constraints come from the nitrogen isotope information itself. There is considerable uncertainty on the use of δ^{13}C to infer diet given differences in lipid extraction protocols; since we are primarily interested in determining trophic level, we only use the nitrogen isotope and assume changes in δ^{15}N of +3.4 ‰ per trophic level (Newsome et al. 2010). Assuming that these secondary constraints are reasonable,
the $\delta^{15}N$ stable isotope data are consistent with a $\leq 15\%$ contribution of toothfish to the diet of adult Weddell seals.

**Figure 2:** Stable isotope ($\delta^{15}N$) enrichment in Antarctic prey and predators. Sources of data include Burns *et al.* (1998), Bury *et al.* (2008), Krahn *et al.* (2008), and Eisert, Newsome, Oftedal, unpublished data. The dashed line indicates the expected trophic shift between Weddell seals and prey.

The question remains whether existing stable isotope information for Weddell seals adequately reflects diet in McMurdo Sound. An important consideration for inferring predator diets from tissue stable isotope patterns is the time scale of incorporation. Dietary isotopes are assimilated via tissue turnover, which depends on the metabolic rate of the tissue and animal (MacAvoy *et al.* 2006, 2012). In Weddell seals, stable isotope values have been determined in blood plasma (Burns *et al.* 1998). As ca. 97% of the nitrogen in blood plasma resides in plasma proteins (Krebs 1950), changes in the nitrogen signature of plasma are primarily determined by the turnover of plasma proteins, which scales to the quarter power of adult BM ($BM^{0.25}$) among mammals (Allison 1960; Jarnum 1975). For a 400-kg adult Weddell seal, estimated half-lives of the two dominant plasma proteins, albumin and $\gamma$-globulin, are ca. 24 days for albumin and ca. 28 days for $\gamma$-globulin (Allison 1960). Incorporation of a new dietary signal into plasma proteins takes 2 to 3 half-lives, corresponding to replacement of 75% to 87.5% of the resident proteins. This process would require approximately 52 to 78 days in an adult Weddell seal, not a few days, as it sometimes assumed (e.g., Ainley & Siniff 2009). Reported
half-life values for δ\textsuperscript{15}N in plasma proteins in captive cetaceans are ca. 20 days for bottlenose dolphins (\textit{Tursiops truncatus}, 200 kg BM) and 42 days for killer whales (\textit{Orcinus orca}, ~2,000 kg BM; Caut \textit{et al.} 2011), and are in perfect agreement with predicted plasma protein half lives of 20-24 days and 40 to 46 days for mammals weighing 200 and 2,000 kg, respectively. Burns \textit{et al.} (1998) measured δ\textsuperscript{13}C and δ\textsuperscript{15}N blood from pup \textit{(n = 16)}, yearling \textit{(n = 14)}, and adult \textit{(n = 12)} Weddell seals at breeding colonies in McMurdo Sound, and blood samples were taken over a number of seasons (1992–1994). While the dates of collection are not given by Burns \textit{et al.} (1998), sampling most probably occurred sometime between mid-October (arrival of seals) and early January, as travel on sea ice tends to be difficult after this time. Plasma samples collected during November to December reflect the diet during September and October; to infer diet in the late lactation/post-breeding season (late November to late December), when seals sustain very high rates of energy expenditure and/or are recovering from massive weight loss, plasma samples would need to be collected after the end of January. Near-annual fishing for toothfish in McMurdo Sound (1972–2011) indicates that catch rates of toothfish from research longlines increases markedly after September (Ainley \textit{et al.} 2012). Stable isotope values reported for Weddell seals captured in the pack ice of the eastern Ross Sea between late December and early February (13.04±0.92 ‰, \textit{n = 22}; Zhao \textit{et al.} 2004) likely reflect the diet of non-breeding seals foraging over deeper water (Ackley \textit{et al.} 2003). It follows that existing stable isotope information is insufficient to provide conclusive evidence either for or against toothfish consumption by Weddell seals in McMurdo Sound, because it is likely that plasma samples collected from Weddell seals represent dietary information during a time of year when seals have little or no access to toothfish.

III.2 Evidence from other Methods of Diet Determination

In addition to stable isotope analysis, the bulk of evidence for Weddell seal diets has been derived from scat hard part analysis, \textit{i.e.}, the recovery and identification of diagnostic prey remains (such as sagittal otoliths, vertebrae, cephalopod beaks) from Weddell seal faeces. Scat hard part analysis is biased in favour of prey with resistant hard parts (Bowen & Iverson 2012). Weddell seals selectively feed on the soft tissues of toothfish so that scat hard part analysis will almost certainly fail to detect toothfish consumption (Calhaem & Christoffel 1969; Ainley & Siniff 2009; Kim \textit{et al.} 2011). This method also provides frequency rather than mass estimates, a point particularly relevant for assessing the dietary importance of silverfish vs. toothfish and other prey species. Silverfish otoliths are readily detected in large numbers in Weddell seal scats (Castellini \textit{et al.} 1992), and, through confounding of frequency and mass data, this has led to the assumption that silverfish is the predominant prey for Weddell seals. For example, Burns & Kooyman (2001) state that

"Green and Burton (1987) demonstrated that Weddell seals were even more specialized fish consumers (99.3% diet by mass). In addition \textit{Pleuragramma antarcticum}, the Antarctic silverfish, is the primary fish prey for both predators (88.6% by numbers for penguins, 95.3% for seals; Castellini \textit{et al.}, 1992; Cherel and Kooyman, 1998)."
However, it is invalid to equate numerical dominance with biomass dominance (and incidentally equally invalid to assume that all fish prey are silverfish). A small abundant prey item can have a high frequency of occurrence – possibly even through secondary ingestion –, yet contribute relatively little to the total amount of food and energy consumed. The magnitude of error introduced by confusing data on prey number with data on prey mass has been pointed out by (Ainley & Siniff 2009). To illustrate, if a Weddell seal consumed one toothfish (18 kg BM, ingested portion 10.8 kg) and 100 silverfish of 31 g each, the resulting ratios would be 3.5:1 (toothfish: silverfish) for ingested biomass. The error is exacerbated further by the fact that seals can obtain considerably more energy (metabolisable energy, ME; see section below) from toothfish than from silverfish (Table 3). When relative prey intakes are considered in terms of energy (ME), the ratio becomes 5.4:1 in favour of toothfish, while scat analysis would show only silverfish consumption.

Further direct evidence of toothfish availability to Weddell seals comes from underwater video recorded using cameras attached to free-ranging Weddell seals in McMurdo Sound. In one study, seals encountered 336 silverfish in 58 dives and toothfish 26 times in 14 dives (Fuiman et al. 2002). The silverfish had a reported total length (TL) of 20 to 25 cm, corresponding to a standard length (SL) of 17.6 to 22 cm (Azzali et al. 2010) and a mean BM of ca. 65 g (O’Driscoll et al. 2011), which is larger than the reported modal SL and mass of adult silverfish in the Ross Sea (SL 17 cm, BM 40 g; O’Driscoll et al. 2011). If we consider only the 13 encounters between seals and toothfish reported by Fuiman et al. (2002) that are known to be different fish, and further assume that seals ate the toothfish following only one in ten encounters, then the energy intake from the two prey types would be 9.4 MJ ME per dive for toothfish vs. 3.9 MJ ME per dive for silverfish. Davis et al. (1999) reported that in addition to encounters with silverfish and toothfish, seals equipped with underwater video cameras flushed bald notothens (*Pagothenia borchgrevinki*) out of crevices in the under-ice surface.

While direct observations of stomach contents (Dearborn 1965; Green & Burton 1987) from McMurdo Sound indicate that fish remains occur in close to 100% of sampled seals, it is not true that silverfish is the only or even the dominant fish species taken by Weddell seals. In Dearborn (1965), fish remains were present in 35 of 36 seal stomachs, but silverfish were positively identified in only 4 samples (11%); by comparison, fishes of the genus *Trematomus* occurred in 14 stomachs (39%). Smith (1966) examined 290 stomachs of Weddell seals collected in McMurdo Sound and reported that the results “were similar to those of Dearborn”, and “in the Cape Armitage region [near Scott Base in McMurdo Sound], channichthyids were the predominant fish taken by Weddell seals”. There is also evidence that cryopelagic fish (species living in or near the under-ice surface) may be important prey items for Weddell seals. Cryopelagic fish in the Ross Sea include *P. borchgrevinki*, *P. brachyosoma*, and *Trematomus newnesi* (Andriashev 1970; Gon & Heemstra 1990). In addition to camera observations reported by Davis et al. (1999) (above), *P. borchgrevinki* have been found cached in ice holes (Kim et al. 2005) and as otoliths in seal scat (Castellini et al. 1992). *Trematomus newnesi* has been reported as prey of Weddell seals near Mawson Station, 67°36’ S 62°52’ E (Lake et al. 2003); *T. newnesi* occurs in the Ross Sea and fishes of the genus *Trematomus* are frequently eaten by Weddell seals in McMurdo Sound, although they are rarely identified to species level (Dearborn 1965; Burns et al. 1998; Table 2). Consumption of *T. newnesi* by Weddell seals is therefore plausible.
Table 2: Reported prey species of Weddell seals in the Ross Sea region. Identification refers to the lowest taxonomic level reported in the original source. For prey items reported in multiple sources, only the most direct method is given in order of priority. Taxonomy follows ITIS (www.itis.gov). MCM, McMurdo Sound.

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* identified simply as “Gymnodraco” in the source but there is only one species in this genus; †found in the stomach of a weaned pup; ‡this may in fact be Pareledone turqueti (Oftedal, Vecchione, Eisert et al., unpubl. data)
Table 3: Energy content of fish and invertebrate prey species calculated from data in Lenky et al. (2012) and additional sources as indicated. Metabolisable energy (ME) content was calculated from proximate composition using values of 38.1 kJ.g\(^{-1}\) for lipid and 16.74 kJ.g\(^{-1}\) for crude protein (CP); gross energy (GE) was measured directly or calculated using equivalents of 39.3 kJ.g\(^{-1}\) for lipid and 23.6 kJ.g\(^{-1}\) for CP. GE values that were calculated rather than measured are indicated by an asterisk (*). ME: GE ratios of less than 75% are shown in **bold** type. BM, body mass; DM, dry matter; SL, standard length

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\(\) Oftedal, Vecchione, Eisert et al., unpublished data; † ca. 85% of lipids are wax esters (Phleger et al. 1999) with an assumed digestibility of 50% (Place 1991); ‡ ca. 10% of GE is chitin; *) composition data from Clarke (1980) and Pond et al. (1995); †) based on data Friederich & Hagen (1994), CP and ash were estimated by difference and using the CP: ash ratio for *P. antarcticum* in Lenky et al. (2012)
Even if silverfish are consumed in abundance at some times and locations, this is by no means universal. Note that Fuiman et al. (2002) found in McMurdo Sound that “The relative abundance of *Pleuragramma* varied greatly from year to year, as indicated by “catch per unit effort”. [...] No *Pleuragramma* were observed in 1997, 34 were observed in 1998 (all by one seal between 27 and 29 November), and 302 in 1999 (by all five seals)”. Similar observations were made in the Weddell Sea by Plötz et al., who found that while Weddell seals preyed heavily on silverfish in two of three study seasons at the same site, silverfish were completely absent from stomach contents and replaced by other prey (primarily channichthyids) in one year (Plötz 1986; Plötz et al. 1991, 2001).

### III.3 Evidence for Toothfish Consumption by Weddell Seals

There is a marked discrepancy between direct evidence for toothfish consumption by Weddell seals – *i.e.*, observation by underwater cameras, in stomach contents, or by eye witnesses (Murphy 1962; Dearborn 1965; Calhaem & Christoffel 1969; Ross *et al.* 1982; Plötz 1986; Davis *et al.* 1999; Fuiman *et al.* 2002; Kim *et al.* 2005; Ponganis & Stockard 2007; Ainley & Siniff 2009) – and conclusions drawn from less immediate methods for estimating diet (analysis of stable isotopes and scat hard part analysis). Possible explanations for this discrepancy include:

- Weddell seals only feed on toothfish under specific, relatively rare circumstances (such as when ice holes are prepared by scientists);
- preying on toothfish represents a dietary specialisation that is only practiced by a subpopulation of seals, which is not adequately represented by existing methods (dietary specialisation was suggested by Ponganis & Stockard 2007);
- methods other than direct observation are biased, *i.e.*, likely to underreport or miss toothfish consumption entirely.

Reports of observed toothfish consumption by Weddell seals describe predation on subadult and adult toothfish, with an approximate range of 7 to 30 kg body mass and total length of up to 1.3 m (Murphy 1962; Dearborn 1965; Calhaem & Christoffel 1969; Ponganis & Stockard 2007; Hanchet *et al.* 2008; Ainley & Siniff 2009). Most observations of toothfish predation by Weddell seals were incidental to an unrelated research activity (*e.g.*, fish biology, penguin dive physiology) that required drilling and maintaining large holes in the sea ice, which were subsequently utilised by Weddell seals to catch and process toothfish. Due to the anecdotal nature of reports, there may be a bias towards reporting the largest fish caught. For example, Calhaem and Christoffel (1969) give a detailed description of one of the largest fish taken from a Weddell seal (29.3 kg and 1.25 m total length), but provide fewer details on smaller specimens. However, it is clear that despite their somewhat specialised dentition (Stirling 1969c), Weddell seals are capable of preying on adult toothfish, although they may not be able to catch the largest size classes (>1.4 m TL). It is possible, as suggested by Ponganis & Stockard (2007), that toothfish hunting represents a specialised skill limited to older or more experienced seals (but note that a large toothfish carcass was defended by a subadult Weddell seal; Kim *et al.* 2005).
IV. Energy Requirements of Weddell seals in Relation to Prey Nutritional Value

IV.1 Prey Nutritional Value

The nutritional quality of prey is not only essential for estimating biomass intake, it also determines how predators respond to changes in the availability of particular prey (Moore 2012), and is therefore a key variable in ecological modelling (Raubenheimer et al. 2009). Nutritional quality of prey is defined by its proximate composition (lipid, protein, water, carbohydrate, minerals) and metabolisable energy concentration, i.e., the amount of energy that the predator can extract from the food. The total or gross energy content of food (GE) is equal to the energy released by combustion, i.e., the complete oxidation of all constituents to CO₂, NOₓ, and water. The utilisation of energy from food is always less than the GE content and is primarily limited by (1) incomplete digestion (e.g., due to presence of refractory compounds), (2) the metabolic costs of digestion and assimilation, and (3) loss of energy in urine and faeces. Subtracting these costs from dietary GE allows the calculation of the energy available to animals from food, called metabolisable energy (ME).

Figure 3: A comparison of gross (GE) and metabolisable (ME) energy concentration of fish and invertebrate prey. See Table 3 for further details.

This calculation is simplified in fish-eating mammals, as fish is generally highly digestible and the principal macronutrients are fat and protein, with only traces of carbohydrate (Donnelly et al. 1990; Lenky et al. 1991). Predators obviously also require micronutrients such as vitamins and minerals, but no information is available for Antarctic megafauna.
Relatively large losses are incurred in the assimilation of protein, which reduce the energy content of dietary protein from 23.6 kJ.g\(^{-1}\) (GE) to 16.7 kJ.g\(^{-1}\) (ME; Blaxter 1989). There is uncertainty regarding the digestibility of some compounds found in Antarctic prey, such as chitin (e.g., krill; Clarke 1980) or wax esters (e.g., some myctophids; Phleger et al. 1999), as both are poorly digested by terrestrial mammals (Place 1992; Mårtensson et al. 1994).

As shown in Figure 3 and Table 3, the ME concentration of fish and invertebrate prey in the Ross Sea studied to date varies by more than a factor of 4, and ME accounts for less than 75% of GE in low-fat prey and prey containing a significant proportion of indigestible components (Table 3). It follows that estimates of predator biomass intake need to take into account prey energy content, as predators have to eat proportionately more of a lower-quality prey to meet their requirements. In some Antarctic fish, proximate composition is correlated with age/size, with larger size classes generally lower in water and higher in lipid and energy (Donnelly et al. 1990), and this applies also to silverfish (Table 3; Wöhrmann et al. 1997). As a result, the nutritional value of silverfish depends on the age/size class selected by, or available to, the predator. Together with biomass density, ME content is likely to be the primary factor determining whether predators can substitute one prey for another (e.g., silverfish vs. toothfish).

**IV.2 Estimating Weddell Seal Energy Requirements**

While information on Weddell seal energetics is scarce, mammalian metabolism is based on fundamental concepts that can be applied to estimate Weddell seal energy requirements with a reasonable degree of confidence. The guiding principle of mammalian energetics is that energy metabolism scales allometrically with species size. This means that the rate of energy production, or metabolic rate, of mammals does not increase linearly with BM, but scales to mass raised to the three-quarter power, BM\(^{0.75}\) (Brody 1945; Kleiber 1975). Hence it is useful to express metabolic rates on a ‘metabolic mass’ basis (Joules per kg BM\(^{0.75}\) per day).

We present estimates for the annual energy budget of different subpopulations of Weddell seals (breeding females, breeding males, non-breeding adults, and subadults) in Table 4, and a conceptual model for the annual changes in BM, energy expenditure, and food energy intake of breeding female Weddell seals (as the subpopulation expected to have the highest overall energy expenditure) in Figure 4. Younger age classes (BM < 150 kg) are unlikely to prey on toothfish and were not considered in this analysis. To estimate the annual energy budget of Weddell seals, we used reported data on resting metabolic rates of Weddell seals in McMurdo Sound, and added in the costs of reproduction, recovery of mass lost during the breeding season, and the annual moult using published parameters for pinnipeds, terrestrial mammals, and unpublished data from our own studies on the energetics of lactation in Weddell seals (Oftedal & Eisert 2010). We assumed a priori that (a) over the course of a year, energy expenditure would equal food intake, with no net change in body energy, and (b) Weddell seals practice hyperphagia during the post-breeding period (December-February) and rapidly recover two-thirds of the body mass lost during the breeding period in the three months after weaning.

Williams et al. (2004) report resting metabolic rates (RMR) of 117.8 kJ.kg\(^{-1}\) BM for adult Weddell seals with a mean BM of 387.4 kg, equivalent to 0.523 MJ.kg\(^{-0.75}\).day\(^{-1}\). We multiplied the RMR by a factor of 1.5 to arrive at an estimate for the field metabolic rate (FMR) for adult Weddell seals at maintenance of 0.784 MJ.kg\(^{-0.75}\).day\(^{-1}\) (Sparling et al. 2008). This FMR estimate was used to estimate maintenance metabolism from body mass (i.e., metabolic expenditure without any added costs such as gestation, moult, or mass recovery) for seals that were not lactating. For energy expenditure during the lactation
period, we determined mean values of 0.576, 0.522 and 1.56 MJ.kg\(^{-0.75}\).day\(^{-1}\) in Weddell seals during early, mid-, and late lactation using the double-labelled water method (Eisert, Oftedal, Michener, unpublished data; Sparling et al. 2008).

The cost of gestation was estimated by assuming that the GE content of the neonate (30 kg, 6.84 MJ.kg\(^{-1}\); Eisert, Oftedal, Hood, Mitchell, unpubl. data) accounted for 82% of the energy content of the conceptus (term foetus plus placenta, uterus, and associated structures), as is the case in terrestrial ungulates with single offspring of similar maturity at birth as Weddell seals (Oftedal 1985; Eisert et al. 2013b). The efficiency of energy retention of the conceptus was assumed to be 13.3% (Oftedal 1985). Foetal growth in Weddell seals was modelled using unpublished data from Weddell seals in Smith (1966), assuming that foetal growth followed the same general pattern as in the harp seal Pagophilus groenlandicus (Yunker et al. 2005).

The energy cost of lactation was estimated by multiplying an average milk yield of 3.54 kg.d\(^{-1}\) in Weddell seals (Tedman & Green 1987) with measured GE content of Weddell seal milk (Eisert et al. 2013a) and a lactation period of 42 days. No allowance was made for the costs of milk synthesis, as we measured oxidative metabolism during the lactation period and this already includes the energy expended for milk synthesis (as opposed to the energy content of the milk produced).

Mass loss of breeding females (Eisert & Oftedal 2009) and males (Bartsh et al. 1992) was estimated from published values. The cost of recovery for lost mass was calculated by assuming a ratio of fat to lean mass gain of 1:1 and a growth efficiency of 70% (Blaxter 1989; Eisert 2003; Oftedal & Eisert 2010). For the construction of the annual model of energy expenditure in breeding females (Fig. 4), it was assumed that seals would regain mass at a rate sufficient to achieve 85% of their postpartum BM within three months of weaning, and recover the remaining body weight slowly between March and October.

To simplify model calculations, we assumed that BM of adult seals would stay constant from year to year, which is not strictly true as adult Weddell seals continue to grow at a slow rate (Bryden et al. 1984). For subadult seals, we assumed a mean BM of 150 kg, an FMR of 0.586 MJ.kg\(^{-0.75}\).day\(^{-1}\), and a growth rate of 50 kg per year (Bryden et al. 1984; Boily & Lavigne 1995), using the same parameters for estimating cost of growth as for recovery of lost mass in adult seals (above).

To estimate the cost of the moult, an increment of on average 15% was added to the estimated RMR for a period of 30 days based on findings in captive grey seals, Halichoerus grypus (Boily 1996). Like grey seals and unlike many other pinnipeds, Weddell seals do not fast during the moult (Smith 1966).

An interesting outcome of the analysis presented here is that the energy costs of reproduction significantly elevate the mean annual energy expenditure relative to non-breeding seals (based on FMR), by a factor 1.44 and 1.13 in breeding females and males, respectively (Table 4). Secondly, peak energy expenditures of Weddell seals during certain periods are predicted to be very high, for example during the late lactation period (100 – 200 MJ.day\(^{-1}\)), and presumably also during the post-breeding recovery (note that this is driven by the assumption of rapid mass recovery post-breeding). Weddell seals not only lose a lot of mass during the breeding season, they lose lean mass and body fat in approximately equal proportions (Eisert 2003; Oftedal & Eisert 2010). The efficiency of regaining lost lean mass is poor (≤0.7), and hence mass recovery requires significant overfeeding (hyperphagia). We have no information over what time scale lost mass is recovered after the end of the breeding season; it was assumed as a first approximation that seals regain ca. two-thirds of the lost mass during the first three months after the end of lactation, and regain the remaining mass slowly until parturition the following year. This was based on the assumption that food will be more abundant during the summer months. Obviously, the daily rate of energy expenditure and the shape of the food intake curve shown in Fig. 4 will depend on

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rate of mass gain and the timing of when hyperphagia takes place, but assumed timing does not affect the estimate of the overall annual expenditure. The assumption that Weddell seals practice post-breeding hyperphagia is supported by the observations of Calhaem & Christoffel (1969), who reported that one Weddell seal caught four toothfish with a combined weight of 54 kg within 24 hours on December 10, 1966, and kept up high rates of toothfish consumption during the entire 14-day observation period (the authors estimated that the average daily toothfish catch was ca. 68 kg). Assuming a dress-out rate of 60% (Ainley & Siniff 2009), 54 kg of whole toothfish equates to an intake of ca. 32.4 kg and 275 MJ of energy (ME), vastly in excess of the estimated daily FMR for adult seals of 66 MJ.d$^{-1}$ (Table 4) but similar to peak rates of ME intake predicted by the model shown in Fig. 4. While it has been reported that Weddell seals cache toothfish in crevices in the sea ice (Kim et al. 2005; Ponganis & Stockard 2007), Calhaem & Christoffel (1969) specifically stated that the seal ate the toothfish it caught, starting with the viscera. Both immediate consumption of toothfish and caching behaviour by Weddell seals are described by Ponganis & Stockard (2007). A fish biologist reported that he once recovered a toothfish from which a seal had removed only the viscera but left most of the dorsal musculature intact (Prof. William Davison, pers. comm.).

Observations of both prey caching and possibly selective consumption indicate that at least some Weddell seals some of the time are faced with an overabundance of toothfish, based on analogous behaviour in terrestrial carnivores such as felids (Leyhausen 1979). As pointed out by Ainley & Siniff (2009), prey caching and defence indicate that toothfish are ‘valuable’ to Weddell seals. Large predators such as tigers and leopards will also return to and defend prey carcasses that are too large to be consumed at once (Dr. John Seidensticker, pers. comm.).
Table 4: Annual energy budget for different subpopulations of Weddell seals, including the ratio of field metabolic rate (FMR) and overall expenditure. A conceptual model of the annual variation in energy expenditure for breeding female Weddell seals is shown in Fig. 4. Please see text for details of the calculation.

<table>
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<tbody>
<tr>
<td>adult female, breeding</td>
<td>394</td>
<td>70.3</td>
<td>188</td>
<td>188</td>
<td>6,055</td>
<td>1,809</td>
<td>244</td>
<td>36.8</td>
<td>1.44</td>
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<tr>
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<td>63.6</td>
<td>88</td>
<td>88</td>
<td>2,796</td>
<td>--</td>
<td>191</td>
<td>26.2</td>
<td>1.13</td>
</tr>
<tr>
<td>non-breeding adult</td>
<td>371</td>
<td>65.6</td>
<td>0</td>
<td>0</td>
<td>--</td>
<td>--</td>
<td>197</td>
<td>24.1</td>
<td>1.01</td>
</tr>
<tr>
<td>subadult</td>
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<td>37.7</td>
<td>0</td>
<td>50</td>
<td>1,597</td>
<td>--</td>
<td>113</td>
<td>15.5</td>
<td>1.12</td>
</tr>
</tbody>
</table>
Figure 4: A conceptual model of the seasonal variation in body mass, food intake (as metabolisable energy, ME), and daily energy expenditure of an adult female Weddell seal. All three variables were measured only during the lactation period (Eisert, Ofstedal, Michener, et al. unpubl. data). The model includes the energy costs of maintenance, gestation, lactation, moult, and recovery of mass lost during lactation. It was assumed a priori that (a) over the course of a year, energy expenditure would equal food intake, with no net change in body energy, and (b) Weddell seals practice hyperphagia during the post-breeding period (December-February) and rapidly recover two-thirds of the body mass lost during the breeding period in the three months after weaning. Total annual energy expenditure is ca. 36.8 GJ.y\(^{-1}\), equivalent to a daily average expenditure of 101 MJ.d\(^{-1}\) (see also Table 4). Further sources and assumptions are explained in the text. EB, embryonic diapause; F, fertilisation; I, implantation; P, parturition; W, weaning.
IV.3 Comparison of Weddell Seal Energy Requirements with Prey Energy Content

We combined information on the energy content of prey (section IV.1) with estimated energy expenditure of adult Weddell seals (section IV.2) to determine the amounts of prey required per day by Weddell seals in two different states, at maintenance (FMR) and relative to the mean annual daily expenditure of a breeding female, as the subgroup expected to have the highest energy expenditure (Table 3). We calculated requirements for three types of prey that are purportedly consumed by Weddell seals, juvenile silverfish, adult silverfish, and toothfish, and plotted the results both in terms of prey biomass (kg per day, Fig. 5A) and number of individual prey items (number per day, Fig. 5B).

The ME concentration of the three prey types differs by a factor of four, from 2.2 kJ.g$^{-1}$ wet mass in juvenile silverfish to 8.6 kJ.g$^{-1}$ wet mass in toothfish muscle (Table 3), and biomass requirements of Weddell seals are predicted to vary linearly with prey ME content (Fig. 5A). It should be noted that the maximum recorded stomach fill for Weddell seals is 17 kg (Plötz 1986), which does not mean that daily consumption cannot exceed this amount, but it provides an approximate reference point. Weddell seals may be physically unable to consume sufficient prey with a low ME content to meet their energy requirements. Weddell seal foraging behaviour in McMurdo Sound and elsewhere follows a diurnal or quasi-diurnal pattern (Smith 1965; Siniff et al. 1971; Bornemann et al. 1998), with one broad peak of foraging activity per 24-hour period. This suggests that Weddell seals fill their stomach and then haul out to digest their prey. Transit time from ingestion to defaecation or defaecation frequency are not known for Weddell seals. Reported transit times for fish prey in harp and leopard seals are approximately 8 to 17 hours and 18 to 25 hours, respectively (Mårtensson et al. 1998; Hall-Aspland et al. 2011).

An important factor affecting the feasibility of meeting feeding requirements is the size of individual prey items and the degree of clustering of the prey – toothfish are both very large and energy-rich and thus represent a highly clustered resource (Mangel & Adler 1994). Silverfish are small-bodied but occur in shoals, so that their energy density depends on abundance and shoal density in addition to size class. Camera systems lowered through the water column from research vessels (J.T. Eastman, pers. obs.), and ‘critter cams’ deployed on Weddell seals (Fuiman et al. 2002) indicate Antarctic silverfish exist as loose shoals (unstructured aggregations), with individuals estimated to be spaced 2–4 m apart at densities of one fish per 7–43 m$^3$ (Fuiman et al. 2002; La Mesa & Eastman 2012). Multi-frequency acoustic estimates of silverfish density in the Ross Sea (O’Driscoll et al. 2011) indicate maximum silverfish densities of one fish per 5 m$^3$ (back-scattering strength recordings SV of -70 dB; R. O’Driscoll, pers. comm.). Due to the small size and low ME content of juvenile silverfish, an implausible large number (~4,000 fish per day) would be required to meet Weddell seal daily energy expenditures. Burns & Kooyman (2001) have suggested that Weddell seals and emperor penguins both feed primarily on juvenile silverfish of ≤10 cm SL (i.e., with an individual BM of ca. 5-10 g), but energetic considerations indicate that this is unlikely for Weddell seals. By contrast, large, more lipid-rich adult silverfish (≥30 g, SL 15-16 cm) can be taken by Weddell seals in numbers adequate for meeting daily requirements (Fig. 5B; Plötz 1986: “The number of P. antarcticum taken by the individual seals ranged between 139 and 508.”).

Given the strong positive correlation between silverfish age/size and energy content, it is interesting to note that direct evidence from stomach sampling (Plötz 1986; Green & Burton 1987; Plötz et al. 2001) and underwater cameras (Fuiman et al. 2002) indicates that Weddell seals consume a larger size range of silverfish (mean reported SL 15 to 20 cm, equivalent to BM of 25 to 65 g) than the size range calculated indirectly from otoliths recovered in seal faeces (mean reported SL 10 to 14 cm, equivalent to BM of 7 to 21 g; Castellini et al. 1992; Burns et al. 1998; Burns & Kooyman 2001; O’Driscoll et al. 2011).
Figure 5: Amount (A) and numbers (B) of toothfish and two different size classes of silverfish (8 and 31 g body mass; see Table 2) required to meet mean daily average energy expenditures for an adult Weddell seal at maintenance and for a breeding female Weddell seal (annual average; refer Table 4).
This suggests that the silverfish size preferred by Weddell seals may have been underestimated due to a failure to adequately compensate for otolith erosion during digestion (Grellier & Hammond 2006). While seals are likely to consume all silverfish available and hence ingest a range of fish sizes (Plötz et al. 2001), larger fish will make a greater contribution in terms of biomass and ME.

In summary, it appears that large, high-fat silverfish occurring at relatively high densities that allow a daily ingestion of 200-500 fish (i.e., a high rate of catch per unit effort in terms of ingested energy) represent a feasible nutritional resource for Weddell seals, and may be preferred by seals. On the other hand, it is unlikely that Weddell seals can meet their energy needs feeding on smaller silverfish or silverfish occurring at low densities, in particular during periods of high energy demand. This proposition is in good agreement with the observation (see section III.2) that the contribution of silverfish to Weddell seal diets is highly variable and that seals readily switch to other prey when silverfish abundance is low (Plötz et al. 1991; Fuiman et al. 2002).

V. Weddell Seal Abundance Estimates

In contrast to extensive demographic information available for the Erebus Bay/eastern McMurdo Sound region, abundance estimates for the Ross Sea are based on aerial surveys from the late 1960s (Stirling 1969a) and urgently require revision. This represents a significant knowledge gap, because accurate estimates of Weddell seal abundance for the Ross Sea are required to estimate total prey biomass consumption and the plausible proportion of toothfish in Weddell seal diets (based on the comparison of toothfish mortality with seal biomass consumption; see below). In the absence of more spatially comprehensive population monitoring, it is also currently not possible to detect whether populations are changing in response to external factors.

Estimating seal abundance from satellite observation has recently been developed as an option (LaRue et al. 2011) but to be accurate, this method requires extensive ground-truthing and better information on seal diurnal activity patterns, as seals diving below the ice will not be seen. Accuracy of satellite surveys was particularly poor (recovery <50 %) for aggregations of fewer than 200 seals relative to ground surveys (LaRue et al. 2011), suggesting that a significant proportion of the population may be missed. While Weddell seals are the only pinniped breeding in the Ross Sea, hence all seal colonies can be assumed to consist of Weddell seals, satellites may fail to detect parts of the population not present in breeding colonies. In McMurdo Sound, seals in breeding colonies represent approximately 70% of the total population (Stirling 1969b). Breeding males defend underwater territories (maritories) and their visibility may therefore be reduced until after the mating season (Harcourt et al. 2007). Satellite surveys probably cannot distinguish between different seal species in the pack ice. Since it is likely that subadult Weddell seals disperse into the pack ice, surveys of breeding colonies are a necessary, though perhaps not sufficient, requirement for obtaining accurate information on Weddell seal abundance in the Ross Sea region.

VI. Comparison of Estimates of Toothfish Mortality and Weddell Seal Consumption in the McMurdo Sound region

A spatially explicit estimate of toothfish biomass and mortality was derived in Pinkerton et al. (2008) and used to estimate a plausible upper bound on toothfish biomass of 4,400-7,770 t in the region bounded to the North by 76°S and to the east by 175°E. Scientific tagging/recapture rates were used to give an early estimate of the biomass of Antarctic toothfish in the McMurdo Sound region of 2,700 t (Raymond 1975),
which is of a similar order of magnitude. Toothfish natural mortality has been taken as $M = 0.13 \text{ y}^{-1}$ (Dunn et al. 2006). Assuming that annual mortality scales with biomass, estimated toothfish mortality in the defined region is equivalent to ca. 950 t. The majority of this mass of fish are assumed to be consumed by predators. The most likely predators in the McMurdo Sound region are Weddell seals and Type C killer whales. It is possible that most of the annual predation on toothfish in this region occurs between November and February, when the largest number of Weddell seals are present (Smith 1965), toothfish appear higher in the water column (Ainley et al. 2012), and seals have access to a greater portion of the sound due to break-up of the sea ice (Stirling 1969b).

Currently available data on stable isotope enrichments in Weddell seals and their prey are consistent with a dietary contribution of toothfish of 15% (Table 1), although this estimate should be considered provisional as discussed in section III.1. Assuming that toothfish represents 15% of the total annual energy intake of all subpopulations listed in Table 4, the estimated total consumption of toothfish by Weddell seals, calculated from the ME content shown in Table 3, is 2,128 t.yr$^{-1}$. If consumption of toothfish is assumed to be restricted to the months of November, December, and January (i.e., Weddell seal energy expenditure includes 3 months of FMR, plus the costs of reproduction and of 50% of the mass recovery), the total consumption estimate is 626 t of toothfish. This estimate is lower than estimated toothfish mortality. If 100% of toothfish natural mortality in this region is assumed to arise from Weddell seal predation in summer (i.e., no mortality during the other 9 months of the year and no predation by Type C killer whales), then a diet composition of up to 22% toothfish (= 918 t) for the period November to January would be consistent with estimated toothfish biomass and mortality. It has been suggested that successful toothfish hunting may represent a dietary specialisation in Weddell seals and may be restricted to older, larger, or more experienced seals (Ponganis & Stockard 2007). If this the case, then individual seals or subpopulations may have a significantly higher intake of toothfish than estimated here, but this is speculative in the absence of further research.

SUMMARY

Nutritional analysis of Ross Sea prey suggests that toothfish may represent a unique high-energy food resource for Weddell seals that possibly cannot be adequately replaced by other prey, in particular during periods of high energy demand such late-stage lactation and the post-breeding recovery of body weight and condition. The assumed dominance of silverfish in Weddell seal diets should be re-examined given the known biases of methods used to derive diet estimates. While large (>30 g) silverfish occurring at high densities are a valuable nutritional resource, smaller size classes are unlikely to be adequate to meet the estimated energy expenditures of adult Weddell seals, in particular during periods of high energy demand. Preliminary calculations based on energetic considerations and estimated population sizes of both toothfish and Weddell seals in the McMurdo Sound region suggest that toothfish may be a minor (up to 20%) but potentially critical component of Weddell seal diet in this area. Our ability to conclusively determine possible dependence of Weddell seal populations on toothfish, and hence possible impacts of toothfish removal by fisheries, is primarily hindered by (a) insufficient information on diet, due to inadequate temporal coverage and biased methodology, and (b) uncertainty regarding Weddell seal abundance in the Ross Sea.
RECOMMENDATIONS

• we urgently need better information on diet of Weddell seals, specifically (a) during periods not currently covered and (b) utilising methodology that can conclusively detect toothfish consumption
• we need updated Weddell seal abundance estimates for the Ross Sea; satellite surveillance may be an option, but needs to be complemented by extensive ground-truthing to ensure accuracy
• we require refined estimates of energy requirements of Weddell seals, in particular during the post-breeding season
• we need improved understanding of spatial habitat utilisation and foraging behaviour, especially in the post-moult period and during winter
• accurate estimation of predator requirements would benefit greatly from a comprehensive prey database for the Ross Sea that includes information on GE content, ME content, proximate composition, and information on non-standard constituents (wax esters, chitin)
• we need to take into account other potential predators of toothfish (killer whales, leopard seals)

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