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Title: **ADDRESSING UNCERTAINTY OVER THE IMPORTANCE OF ANTARCTIC TOOTHFISH AS PREY OF SEALS AND WHALES IN THE SOUTHERN ROSS SEA: A REVIEW**

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ABSTRACT***.*** An uncertainty heretofore has existed over the importance of Antarctic toothfish (*Dissostichus mawsoni*) as prey of top predators in the Ross Sea. We reviewed the literature to assess the relative weight that should be given to direct, observational evidence of predator diet composition, as opposed to indirect evidence from scat and biochemical analysis. As a result of this assessment, it is evident that toothfish are an important prey of Weddell seals (*Leptonychotes weddellii*). Recent findings show the seals do not eat toothfish hard parts, thus providing the reason that toothfish have seldom been detected in scat or stomach samples; biochemical samples have been taken only from seal populations where toothfish do not occur. On the basis of data from an under ice observation platform, non-breeding seals in McMurdo Sound take 0.8-1.3 toothfish per day. Seals with video recording equipment were seen to closely encounter toothfish but for unknown reasons did not often pursue for capture. It is estimated that the non-breeding portion of the seal population in McMurdo Sound, during spring and summer, consume about 52 tonnes of toothfish. Too many unknowns exist to estimate what the larger, breeding portion consumes during that and other parts of the year, although it should not be trivial. Much less is known quantitatively about the importance of toothfish to type-C (fish-eating) killer whales (*Orcinus orca*), but observational evidence indicates toothfish consumption to be common. A decline in the abundance of toothfish in McMurdo Sound appears already to be leading to a decline in the number of foraging killer whales. Care must be taken in managing the Ross Sea toothfish fishery, as the potential is great that, given the high degree of trophic overlap and competition among top predators, likely cascades will lead to dramatic changes in the populations of charismatic megafauna, particularly the seals, should the toothfish, probably the most important predator of fish in the system, become overly depressed.

SUMMARY OF FINDINGS AS RELATED TO NOMINATED AGENDA ITEMS

Agenda Item	*Findings*
EMM 08-07	Justification is presented for establishing a CEMP for finfish fisheries in the high latitude Southern Ocean, and especially in the Ross Sea.

ADDRESSING UNCERTAINTY OVER THE IMPORTANCE OF ANTARCTIC TOOTHFISH AS PREY OF SEALS AND WHALES IN THE SOUTHERN ROSS SEA: A REVIEW

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ABSTRACT. An uncertainty heretofore has existed over the importance of Antarctic toothfish (*Dissostichus mawsoni*) as prey of top predators in the Ross Sea. We reviewed the literature to assess the relative weight that should be given to direct, observational evidence of predator diet composition, as opposed to indirect evidence from scat and biochemical analysis. As a result of this assessment, it is evident that toothfish are an important prey of Weddell seals (*Leptonychotes weddellii*). Recent findings show the seals do not eat toothfish hard parts, thus providing the reason that toothfish have seldom been detected in scat or stomach samples; biochemical samples have been taken only from seal populations where toothfish do not occur. On the basis of data from an under ice observation platform, non-breeding seals in McMurdo Sound took 0.8-1.3 toothfish per day. Seals with video recording equipment were seen to closely encounter toothfish but for unknown reasons did not often pursue for capture. It is estimated that the non-breeding portion of the seal population in McMurdo Sound, during spring and summer, consume about 52 tonnes of toothfish. Too many unknowns exist to estimate what the larger, breeding portion consumes during that and other parts of the year, although it should not be trivial. Much less is known quantitatively about the importance of toothfish to type-C (fish-eating) killer whales (*Orcinus orca*), but observational evidence indicates toothfish consumption to be common. A decline in the abundance of toothfish in McMurdo Sound appears already to be leading to a decline in the number of foraging killer whales. Care must be taken in managing the Ross Sea toothfish fishery, as the potential is great that, given the high degree of trophic overlap and competition among top predators, likely cascades will lead to dramatic changes in the populations of charismatic megafauna, particularly the seals, should the toothfish, probably the most important predator of fish in the system, become overly depressed.

1 INTRODUCTION

There is little doubt that the Antarctic toothfish (AT; *Dissostichus mawsoni*) is an important predator in waters overlying the Ross Sea continental shelf and the southern portion, in general, of the Southern Ocean (Eastman 1993, La Mesa et al. 2004). Among a suite of top-predators that otherwise include mammals and penguins, and assuming its role is equal to that of large, predatory fish in other marine ecosystems (e.g. Schindler et al. 2002, Scheffer et al. 2003, Frank et al. 2005), AT with little doubt exert an important pressure on structuring the Ross Sea foodweb.

There appears to be uncertainty, however, about the role of AT as prey, at least judging from comments expressed by the CCAMLR working group for Ecosystem Monitoring and Management (EMM) at its 2007 meeting (EMM 2007: para 5.77-5.79). Herein we address this uncertainty, thinking that much of it has to do with the unique characteristics of the Ross Sea neritic ecosystem, and particularly McMurdo Sound, where much of what we know about AT, as prey of Weddell seals (WESE, *Leptonychotes weddellii*) and type-C killer whales (KW, *Orcinus orca*), has been learned. Southern McMurdo Sound has been the site for intensive marine research for 50 years and, thus, much is known, but much remains to be learned, about its workings (Smith et al. 2006). Little pertinent research has been conducted elsewhere in the Ross Sea.

A large body of observational evidence indicates that many AT are taken annually by WESE and KW during the summer in McMurdo Sound (e.g., Murphy 1962; Dearborn 1965; Calhaem & Christoffel 1969; Thomas et al. 1981; Davis et al. 1999, 2003; Fuiman et al. 2002;; Wu & Mastro 2004; Kim et al. 2005; Ainley et al. 2006a; Ponganis & Stockard 2007). However, work using stable isotopes, fatty acids and scats (Testa et al. 1985, Castellini et al. 1992, Burns et al. 1998, Zhao et al. 2004, Krahn et al. 2008) is considered to have provided evidence that AT play much less of a role in top-predator diets than direct observations suggest. The issue appears to be one of weight given to indirect evidence from tissue analyses, where time lags play a major role in interpretations, and direct observations where time lags do not exist. It is thought by many that biochemical methods better integrate over time the contribution of prey in a species' diet. This is true, but only if the time lags and other contextual information is taken into account.

1.1 BACKGROUND

Approximately 2000 breeding seals and appreciable numbers of non-breeders comprise what is considered the eastern McMurdo Sound WESE population (Smith 1965, Cameron & Siniff 2004). In total for all the Sound, the population may number about 4000 individuals (Siniff & Ainley 2008). This is one of the largest concentrations of this species in coastal Antarctica. The breeders congregate at traditional sites around tide cracks near to the shores of Ross Island, the Erebus Ice Tongue, and nearby Delbridge Islands, in the southeastern corner of the Sound (Fig 1); smaller breeding concentrations occur at tide cracks along the western side of the Sound. Non-breeding adults are mostly excluded from those colonies, owing to the territorial behavior of adult males and adult females with their pups. These non-breeders congregate at cracks along shore elsewhere as well as at cracks that cross McMurdo Sound, for example, the one that annually exists between Cape Royds, Ross Island, across to Marble Point, Victoria Land (distance ~50 km). The breeders are present from early spring (some even are present from the previous winter) through to mid-December (when pups are weaned, and breeding occurs). They then disperse from these pupping and breeding sites, although not far and some remain in the vicinity of the pupping areas; their numbers are swelled by an influx of immatures and weaners. A favorite haul out then is around the southernmost end of Hut Peninsula, between McMurdo Station and Scott Base (where the sea ice meets the Ross Ice Shelf; Smith 1965, Stirling 1969). A demographic study has been carried out on this population since about 1963, and currently most of the seals in this population are tagged and are of known age (Stirling 1969, Testa & Siniff 1987, Cameron & Siniff 2004, Hadley et al. 2007).

KWs arrive in the southern Ross Sea in early December, and patrol the receding edge of the McMurdo Sound fast ice (Ainley, pers. obs.; e.g. 40 and 47, respectively, counted by air on 14 Jan and 21 Jan 2008, when numbers of KW were actually decreased from earlier years; DeVries et al. 2008). The large majority of these are the ecotype-C (fish eater), with a few type-B (mammal eater) as well (see Pitman & Ensor 2003); the ratio of C's to B's on the dates above was 8:1 (Ainley, pers.obs.).

The edge of this fast ice, thick enough that an airstrip for military cargo aircraft exists to the south near McMurdo Station, usually lies just north of Cape Royds during the winter and spring, but by mid-January it breaks back several kilometers, piece meal, to be well south of the Delbridge Islands. Annually in January, an icebreaker breaks a channel from the edge to McMurdo Station, and the KWs use the channel to reach prey that otherwise would not be accessible (see also Jehl et al. 1980, Thomas et al. 1981), in the case of C's seeking fish and B's seeking WESEs. Given the latter, not long after the channel is made, WESEs disappear from the mid-Sound. The KWs begin to depart by late January or early February (Pitman 2004, Ainley et al. 2006b), with some probably remaining until darkness in late February-early March (van Dam & Kooyman 2004). No formal attempt has been made to precisely estimate the numbers of KWs in the southern Ross Sea, and there does appear to be a 'circuit' that the whales follow on the order of days to a week or so (Ainley, pers. obs.).

2 OBSERVATIONAL EVIDENCE

2.1 Weddell Seals. A key to understanding the importance of AT as prey to WESE is the experimental study by Testa et al. (1985), the report of which in itself is confusing. The main reason for the confusion is that, in spite of ample observational evidence of seals eating AT, no identifiable remains had been reported in the stomachs or scats of WESE in McMurdo Sound, or elsewhere: 367 stomachs in the Antarctic Peninsula region (Bertram 1940); 8 stomachs inspected in the South Shetland Islands (Clarke & Macleod 1982); 44 stomachs inspected from McMurdo Sound (Dearborn 1965); and numerous scats inspected up to 1985 (Testa et al. 1985) and subsequently in McMurdo Sound (Castellini et al. 1992, Burns et al. 1998) and elsewhere (Plötz 1986). Recently, however, research divers (Kim et al. 2005, Ainley et al. 2006a) published observations that the seals eat neither the head, skin nor vertebral column of AT, or at least ones >0.85 m in length (which comprise the majority of AT in McMurdo Sound; (DeVries et al. 2008; see also Appendix 1 for further observations on this aspect of WESE behavior). *Therefore, finding identifiable hard parts of AT, and particularly otololiths, in a WESE's stomach or scat would be unlikely.* The otoliths of smaller AT (<40 cm) have been recorded in 6 WESE stomachs in the southern Weddell Sea (Plötz 1986). The AT caught by research longline in McMurdo Sound range 85-200 cm in length, with the large majority ranging 101-160 cm (DeVries et al. 2008). Large numbers of scats have contained numerous otoliths of the much smaller Antarctic silverfish (AS; *Pleuragramma antarcticum*), and thus otoliths degradation owing to digestion is not the issue.

Testa et al. (1985) reported a curvilinear relationship between scientific catch rate of AT and distance from major seal colonies ($r^2 = 0.84$). This was based on fishing at 16 sites spread around McMurdo Sound (Fig 1) using a vertical longline deployed to the bottom, with 15-20 baited hooks. Soak time was 24 hrs. Such a longline operation has led to the catch of 200-500 large AT per year from fishing sites that were away from seals (DeVries et al. 2008). Testa et al. had no information as to the mechanism of the observed 'exclusion'. If foraging was the reason, it would have been contrary to what was commonly known at that time from stomach and scat analysis. Testa et al. speculated that the seals' activities chased the fish away. In other words, a form of intraspecific interference competition was operating.

Additional observational data comes from the experiments of Ponganis & Stockard (2007). In this case, a large hole (1.3 m across) drilled through the McMurdo Sound fast ice was used to investigate the diving physiology of Emperor Penguins (*Aptenodytes forsteri*). The penguins were 'captive' as they could not hold their breath long enough to find another air breathing hole farther away, thus to escape. A fence prevented the penguins from walking away. Importantly, the researchers did not feed these birds, as the penguins were allowed to forage at will. Another hole was drilled 15 m away where a sub-ice observation chamber was inserted. From this, penguins and seals using the other hole could be observed beneath the ice. At this location, which became known as "Penguin Ranch" (Fig 1), these holes were discovered by subadult WESEs. These seals can hold their breath up to 82 minutes depending on type of dive (Castellini et al. 1992) and, thus, from various sites they can swim the required distance under the fast ice to reach this location. The seals subsequently used the hole, for breathing, for weeks. These researchers were not expressly observing the seals, but in the course of 37 observation days during October –November 2003, on 28 occasions they recorded a seal with an AT; in January 2001 they noted 10 seals with an AT in 11 days. These are rates equivalent to those reported by Calhaem & Christoffel (1969). Seals were not tagged for known age identification, but were classified as subadults, or at least non-breeders since the site was located several kilometers from the nearest breeding colony. Some were recognizable on a day-to-day basis by spots and scars; one seal took 4 AT in three days. On the basis of Ponganis & Stochard's observations, these seals were taking on the order of 0.8 -1.3 AT per day. On some occasions, the seals did not eat the AT right away, but rather cached it on the lip of the ice hole (see below).

Kim et al. (2005), while studying benthic communities, reported the caching of an AT by a WESE on the ocean bottom in one of their study plots. The case can be made that this is not a rare event. In most research divers' work in McMurdo Sound, areas are avoided where it is likely that WESE would use the holes drilled for diver access. It's a serious matter, when seals arrive at the same time as divers at the surface of an access hole, since seals are sometimes aggressive and pose some danger for divers. Therefore, benthic researchers are not often in a position to make observations such as these. In this case, the WESE 'defended' the AT carcass upon the researchers' approach to inspect it, the seal blowing a cloud of bubbles in the divers' faces. In an unpublished observation made since their publication (S. Kim, pers. comm.), these researchers encountered a WESE caching a large octopus; and in another such unpublished observation, and only recently coming to light, researchers in January 1962 found three large AT cached in an artificially drilled hole (through the ice) near Scott Base (G.L. Kooyman, pers. comm.; see also Ponganis & Stockard 2007).

Davis et al. (1999, 2003) placed a small video, with infra-red lighting, on the heads of 31 WESEs during the course of six spring seasons, 1997-2002. Until 2001, the seals were captured in the breeding colonies and transported to an isolated hole too far away from any other holes/cracks to allow escape (Fig 1) or interference from other seals. Beginning in 2001, these researchers moved their study to the seal breeding colonies in Erebus Bay (see Fig. 1). In 500 hours of video recording, seals 'ecountered' 12 adult AT and about 1200 AS; Davis et al. 2004; R.W. Davis pers. comm.). The AT were encountered at depths of 12 – 363 m; bottom depth was ~575 m; most AS were taken >160 m deep. Capture rate for either fish species was not disclosed by these researchers, as they were not always absolutely sure of this. Both AT and AS escaped pursuit; WESE apparently pursued, and eventually captured all AS they saw but few AT (R. Davis & L. Fuiman, pers. comm.). Why they did not pursue some AT is not known but large, powerful fish would likely be able to elude capture thus to waste WESE energy (Fuiman et al. 2002; L. Fuiman, pers. comm.). In fact, of the 12 AT encountered, only one was pursued, though these researchers for an unspecified number of occasions saw these seals, before being instrumented, bring AT to the surface (L. Fuiman & R. Davis, pers. comm.). On some dives, instrumented-seals flushed bald notothen (*Pagothenia borchgrevinki*) from cavities full of platelet ice on the underside of the fast ice, by exhaling air into these cavities (n = 6 observations); not all were captured.

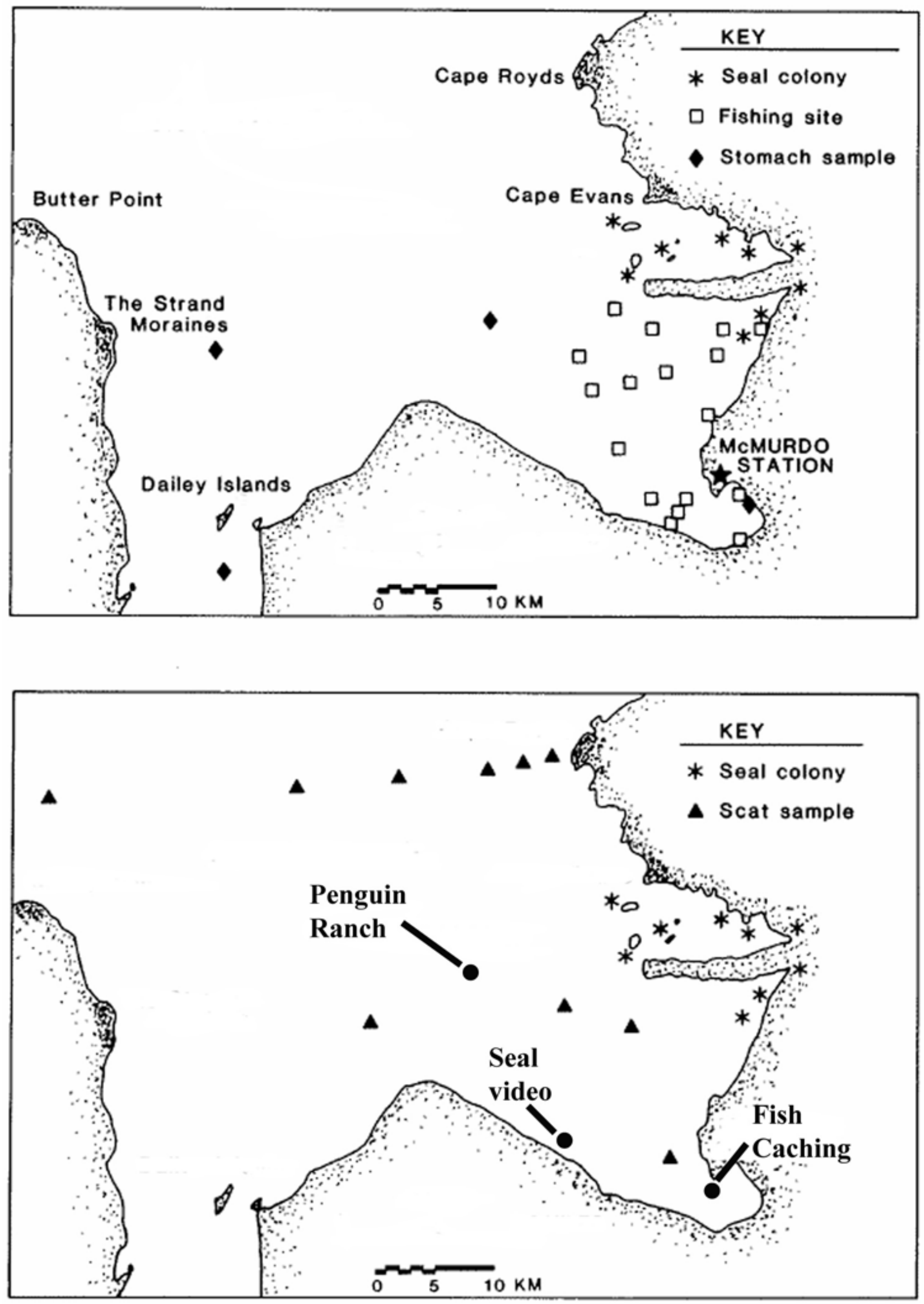


Figure 1. Sites where Testa et al. (1985) collected seal scats and fished for toothfish. Also shown are the location of seal colonies, as well as that of the “Penguin Ranch” (Ponganis & Stockard 2007), the site where video of seals hunting fish was taken during 1997-2000 (Davis et al. 1999), and site where toothfish caching behavior was seen (Kim et al. 2005).

When these researchers' efforts are parced by study area, encounter rates with AT become consistent with the observations of Testa et al. (1985). At the site isolated from seal breeding concentrations, the ratio of AT:AS encountered by WESEs was either 1:24 (72 fish-encountering dives, total of 350 fish) or 1:31 (65 fish-encountering dives, 321 fish) depending on dive criteria used in the analysis. After the research moved to work within the seal breeding colonies, where no more AT were seen in the videos, overall AT:AS encounter rate plummeted, the ratio becoming 1:100 (cf. Davis et al. 2003, 2004; Fuiman et al. 2002) for the six years of study.

2.2 Killer Whales. Each year since 1957, beginning on about 1 January, ice breakers have chopped a channel from the edge of the fast ice, usually at a location out from Cape Royds, to McMurdo Station (Fig 1). Sailors on board these vessels have often reported KWs surfacing in the open water astern with AT in their mouths (as noted in Ainley et al. 2006b). Not many other persons have spent much time in the vicinity of the channel, but those who have done so have seen this as well, including two cetacean research groups who have published photographs (Thomas et al. 1981, Wu & Mastro 2004). Therefore, this is by no means an observation of a rare event, although at present we have no knowledge of the rate by which this would occur (i.e., KW with fish per hour of observation). Most of the observations of AT in the grasp of KWs come during the first week of the channel chop-in.

The taking of AT by KWs is not confined to McMurdo Sound. In 1978, while investigating Emperor Penguins along the fast ice edge of Terra Nova Bay, G.L. Kooyman and co-authors (pers. comm.) observed KW taking large AT and bringing them to the surface as they've been observed repeatedly to do in McMurdo Sound. In this case, the outer portion of the Terra Nova Bay fast ice was fracturing rapidly to leave leads farther and farther into the Bay. The AT, thus, suddenly were losing cover and the KWs were exploiting the rapidly developing leads.

3 BIOCHEMICAL AND OTHER EVIDENCE

3.1 Weddell Seals. As noted above, extensive collections of scats of WESEs in Erebus Bay (Fig 1) were made by Testa et al. (1985), Castellini et al. (1992) and Burns et al. (1998). The scats were collected during October and November. Not one sample contained an AT otolith or bone, though as noted above many AS otoliths.

Burns et al. (1998) also analyzed the stable isotopes of C and N in the blood of 12 adults and 16 yearlings *collected at seal colonies*. Using blood would reveal trophic information about what these seals ate within the previous 48 hours (Tieszen et al. 1983, Hobson & Clark 1992). These researchers also determined isotopes in the muscle of various fish, a procedure that would integrate fish diet over weeks. The blood samples for WESE had a δN of 13.1 for adults, and 12.6-13.3 for yearlings, compared to 10.9 for AS and 13.5 for AT (n = 2; see also

Ainley et al. 2003 for AS values). The values for AT are equivalent to those from a much larger sample taken from the Ross Sea continental slope (Pinkerton et al. 2007; where actually the diet is dominated by fish deeper-living than AS (Fenaughty et al. 2003)).

The values in McMurdo Sound are consistent with a diet of AS for both predators; had the WESEs' values been higher, by theory, this would have reflected the significant consumption of AT. Given that these WESE, living in colonies, *would not be eating many AT at the time that biochemical samples have been taken* (owing to results of interference competition; see above), but like the AT would be feeding mainly on AS (as seen in the WESE scats), these biochemical results are to be expected. Values of δN for WESE were equivalent to those determined by Zhao et al. (2004) from the blood of 31 WESE taken in pelagic waters of the western Amundsen Sea. The chances that WESE would be eating AT in that habitat, ocean depth >2000 m, are not high. There, AS would be the likely prey of the seals.

3.2 Killer Whales. Krahn et al. (2008) analyzed the fatty acids and stable isotopes of N and C found in KW skin biopsies obtained in McMurdo Sound at the end of January 2005 and 2006. Analysis of skin tissue would integrate diet over the previous few weeks (Tieszen et al. 1983). However, the fact that samples were obtained from the outer, non-metabolically active epidermis makes it problematic for closely assessing current diet, and can only reveal qualitative information and not proportions of prey species consumed (Krahn et al. 2008). The δN of 13 males averaged 13.2 (range 12.8-14.1) and that of 15 females also averaged 13.2 (range 12.5-13.7). These numbers average slightly above those reported for WESE by Burns et al. (1998) and equivalent to those of AT, see above; four samples exceeded slightly the δN determined for AT as reported by Burns et al. (1998) and Pinkerton et al. (2007). One AT sampled by Krahn et al. had a δN of 14.0.

The fatty acids revealed little information as results were compared with two fishes that likely are not part of the KW diet, *P. borchgrevinki* and dusky notothen (*Trematomus newnesi*; body length ca. 15-20 cm), both of which occur widely dispersed largely in the platelet layer on the underside of ice floes (Koch 1992, Eastman 1993). It is possible, however, that the KWs could flush these fish, using bubbles like WESE, or suck them in while turned upside down, a technique apparently used on the loose-schooling but deeper AS (Lauriano et al. 2007). Such a behavior would require a lot of effort for little value, and otherwise the KW's long dorsal and huge pectoral fins would not be conducive to foraging in the ragged 'substrate' of floe undersides. Indeed, all the cetaceans of the Arctic, which feed to a great degree on Arctic cod (*Boreogadus saida*; Ainley & DeMaster 1990), a fish that inhabits ice floe undersides, lack dorsal fins all together and whose pectoral fins are reduced in size compared to most other cetaceans.

4 DISCUSSION

While biochemical analysis can reveal the trophic level of foraging and even the identity of individual prey in the case of fatty acids, these techniques can not quantify diet composition unless the number of prey are few and represent widely disparate trophic levels. In that case an isotopic mixing model can be constructed with a high degree of credence (Phillips & Koch 2002). In the case of the predators considered in this paper, all eating fish within one trophic level of one another (AT vs AS), use of this procedure is problematic (see diet review in Ainley et al. 2006b).

4.1 How many toothfish are taken by seals during the summer in McMurdo Sound? It is clear that AT are an important prey of WESE during spring and summer in McMurdo Sound, but how much AT might WESEs actually consume? We will consider just non-breeders for the sake of simplicity. About 1,000 non-breeders may be present in southern McMurdo Sound during summer (Smith 1965). Plötz (1986) estimated an average wet weight of 12.8 kg of fish in the stomachs of WESE collected in the southern Weddell Sea, and estimated a daily fish intake of 18 kg for a 250 kg seal (a non-breeder judging by mass) during summer. Over a four-month period in McMurdo Sound, non-breeders' fish harvest would be 72 tonnes. What would be the composition of that catch?

The non-breeding seals in McMurdo Sound in the Spring, in the past, appeared to take about one fairly large AT per day of foraging (a fish weighing 10-20 kg, as pictured in Ponganis & Stockard 2007; see also Fuiman et al. 2002). WESEs on numerous occasions have been seen with much larger AT, including the one being cached as illustrated in Kim et al. (2005). Therefore, many AT are caught over the four-month period when seals are concentrated in the area, including late October to March, when about 4000 animals would be foraging here (see summary of seal populations in Siniff & Ainley 2008). We will consider just four months, as fishing success indicates that AT become hard to catch (at least by humans) by mid-December. Whether that has to do with depletion of the fish by predators, or migration out of the area, remains to be determined (see DeVries et al. 2008). There are McMurdo Sound sightings of WESE with AT during January and February at the extreme southern edge of the Sound near Scott Base (see above).

WESE also take many AS (as noted above). Judging from otoliths, and also the video images (Davis et al. 1999, 2004; Fuiman et al. 2002), AS taken by WESE are similar in size to those taken by Adélie Penguins (*Pygoscelis adeliae*; Ainley et al. 2003: 20-25 cm, or ~ 50 g each: J. Eastman, pers. comm.). To consume 18 kg of these fish in a day would require catching about 360 individuals (see below), or about equal to one of the subadult AT illustrated in Ponganis & Stockard (2007).

What is the ratio of AT to AS in a WESE's diet? Davis et al. (2004, pers. comm.) in 500 hrs of video saw WESEs encountering 12 AT (~ 1 m TL, or ~13.6 kg each; A. DeVries, pers. comm.) and ~1200 AS. Assuming that seals unfettered by technology caught the majority of AT they encountered and all of the AS, on a weight basis, the importance to WESE of AT relative to AS is therefore ~2.7:1. Since the WESE reject the head, vertebral column and skin, i.e. a dress-out rate of 60% (L. Fuiman, pers. comm.), the weight ratio of consumed fish becomes ~1.6:1, the benthic invertebrates benefiting and perhaps somewhat dependent upon the AT offal (Ainley 2004).

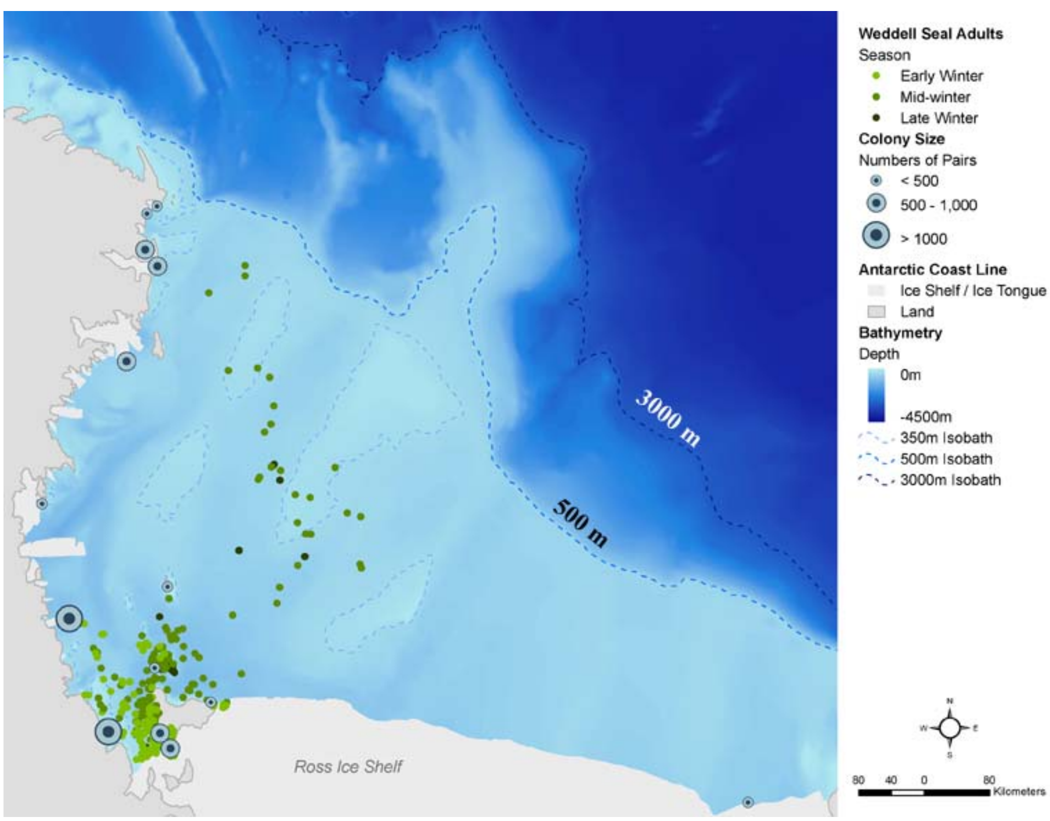
An actual preference for AT by WESE based on energetics would be consistent with these ratios, especially as Davis et al. (1999) saw that WESE could closely approach AT or AS with little effort. Further, Davis et al. (2003) logged the seals taking 311 AS on 58 dives, or about 6 fish per dive. In support of that, Castellini et al. (1992), on the basis of energetics, proposed that WESEs needed to catch 2 AS per dive in order to compensate for diving effort (but not any body weight increase); in general a seals' daily foraging comprised a bout of 20-30 dives of about 6 min each. Obviously, the best strategy for a WESE is to find an AT, of a suitable size for capture, early in their foraging session. The fact also that WESE cache prey items, especially AT (see above), a behavior never before reported in a pinniped but which is common among wolves, large cats, etc (Vanderwall 1990), indicates that AT are somewhat a special resource during spring and summer. This would indicate, it seems, that it is cost-effective to guard an AT, consuming it as needed, rather than leaving the fish upon satiation and searching for other prey later.

Considering the above ratios and calculations, the 72 tonnes of fish that would be taken by 1000 *non-breeding* seals in McMurdo Sound over a four-month period would equal up to about 52 tonnes of AT, with the remainder, 20 tonnes, being AS; these numbers would be adjusted slightly to account for minor prey items (see Dearborn 1965) as well as adjustments depending on AT availability (see below). How many AT would be taken during summer by the *breeders*, which reach (and then lose) a body mass about 1.5 times a non-breeder, awaits a full season investigation of their foraging but must also be a notable amount. Apparently, the breeders quickly deplete or chase away AT in range of colonies (see above), and then turn to AS for the remainder of the summer (as indicated by scat and stable isotope data).

Certainly the catch of AT by all seals in McMurdo Sound is on par with more than one commercial longliner in a typical Ross Sea fishing season (250 tonnes, caught in 6 weeks by setting 30,000 hooks per day; "Antarctic Encounters", NZ TV3, April 2007). In addition, the same foraging scenario is more than likely played out among the large numbers of WESE that occur along the Victoria Land coast (see population summary in Siniff & Ainley 2008).

One should note in considering the ratios and numbers of fish taken by WESEs, as presented here, that AT began to decline in McMurdo Sound after 2001 (DeVries et al. 2008). Therefore, WESE encounter rate of AT was likely decreasing during the period when a number of the observations reported herein were made.

4.2 Foraging by Weddell seals during the non-breeding season. Once the breeding and molting season (Oct-Feb) is completed, some of the WESE from McMurdo Sound disperse north as far as the Ross Sea shelf break, i.e. throughout CCAMLR SSRU 88.1J and 88.1H (see Hanchet et al. 2006; Figure 2). In addition, there are numerous pupping and breeding colonies along the coast of the western Ross Sea, i.e. at least 10,000-12,000 adults concentrated in numerous discrete locations (Smith 1965, Stirling 1969, Siniff & Ainley 2008). These seals, too, as well as their offspring, would occur over the shelf during the non-breeding season. There, they all feed, gaining or regaining the weight and condition lost during lactation, breeding and molt. Readily available food would be critical for gaining the condition needed to successfully reproduce the following spring (see Hadley et al 2007), and the bio-energetic advantage of taking AT over AS would be equally as important at this time of year as during the pupping season. While few studies have been conducted on WESE diet during fall and winter, we can only assume that AT and AS remain important. Castellini et al. (1992) sampled scats at the tiny White Island colony at the extreme southern end of McMurdo Sound over the course of one year, and while AS was the main prey item, they did find AT flesh in one regurgitation.



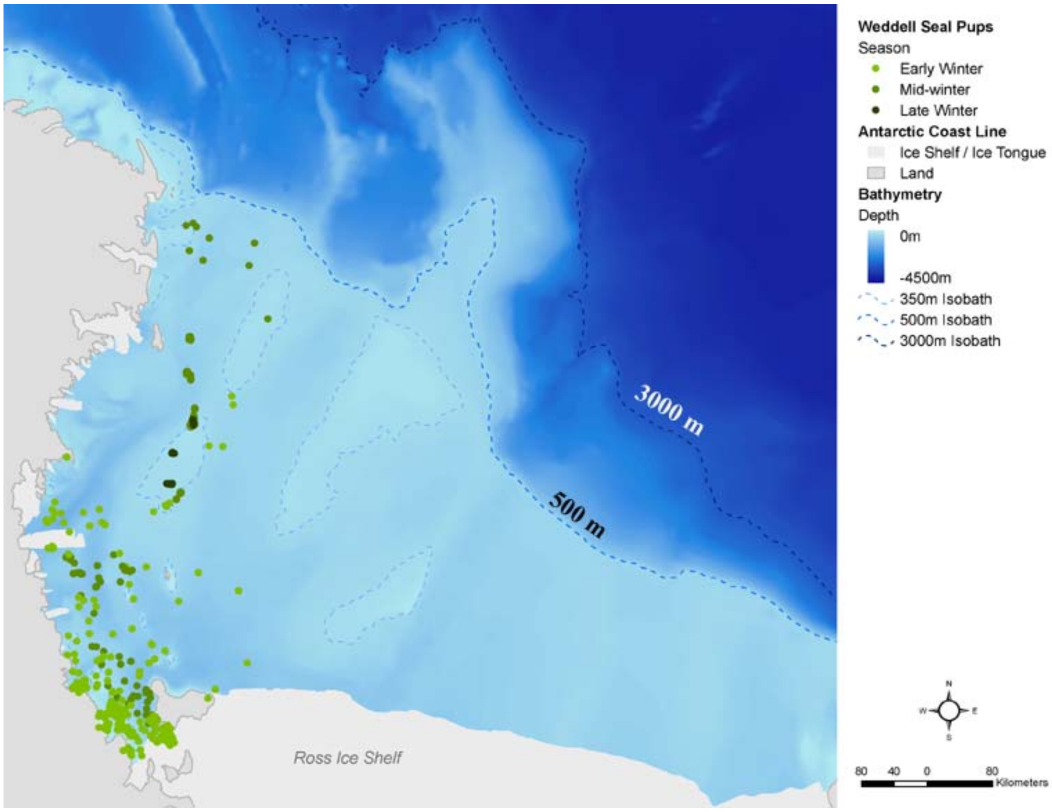


Figure 2. Movements of Weddell seals from breeding sites in McMurdo Sound, as tracked by ARGOS satellites, including both adult females (top panel) and weaned pups (3 to 12 months old; bottom panel) during early- (April-May), middle- (June-July) and late-winter (August-September) following the spring breeding season, 1990-2000 (data sources in Ainley et al. 2006b).

4.3 Is consumption of toothfish important to Killer Whales? Compared to WESEs, much less can be said about the degree to which KWs prey on AT versus AS. The fact that biochemical analysis was conducted on tissues obtained at the end of January, a few weeks after the seasonal invasion of the whales into southern McMurdo Sound and a period when at least humans find it hard to catch AT in those waters, renders those analyses inconclusive.

Given the frequency of observations of AT in the grasp of KW, and the fact that this has been observed both in McMurdo Sound and Terra Nova Bay, it can not be considered a minor phenomenon, although it may be seasonally short-lived. The same size-weight relationship relative to the energetics of foraging as discussed for WESE would apply to KWs and likely to an even greater degree given the size of a KW. According to Fuiman et al. (2002), AS under the ice of McMurdo Sound, typically exist in small mid-water shoals in which the fish are spaced 2-4 m apart. It appears that KWs in the Ross Sea, presumably when feeding on AS, exhibit fish-concentrating behavior reminiscent of that used to catch herring (*Clupea* spp.) in northern seas (see Lauriano et al. 2007). Otherwise, it would not be worth a KW expending much effort to capture single, 20-25 g AS or any fish other than AT that do not form schools or shoals. On the basis of long residency times of large numbers of KWs in the Ross Island area (i.e. several weeks, based on satellite telemetry), R. Pitman (pers. comm.) hypothesizes that only AS could generate the biomass to keep KWs interested for that long.

4.4 Effects on Weddell seals should toothfish become depleted. On the basis of energetics it is better for a WESE to capture AT compared to making lots of dives to capture a lot of AS. We know a great deal about the life history, population dynamics and overall behaviors of WESEs within the wide ecological context of McMurdo Sound and the Ross Sea, because of the long- term studies on the McMurdo Sound population. Of course there is a lot we do not know. However, if we can consider the big picture, we can try to draw some conclusions in regard to how environmental and human interactions might impact the seals' life history patterns.

In a general sense, WESE have evolved in a relatively stable environment. They return to historical pupping and breeding areas in what is physically and ecologically stable fast ice habitat. Cameron et al. (2007) have shown that there is benefit to reproductive fitness to individuals who return regularly to these locations. Hadley et al. (2007) showed that there is reproductive cost to females giving birth and raising a pup, in that those who reproduce, on the average, have a lower annual survivorship than females who do not. Proffitt et al. (2007) demonstrated linkages between variations in large-scale climate and oceanographic factors and weaning mass for pups, which in turn is thought to influence pup survival through the first year of life. Cameron & Siniff (2004) found that periodic immigration (from colonies elsewhere in the Ross Sea) plays an important role in population stability. Therefore, the McMurdo Sound population is neither ecologically nor demographically isolated.

The above is a very brief overview of some of the facts we know about the demography of McMurdo WESEs. These factors taken together suggest that no one factor is likely to be the deciding one influencing the dynamics of the McMurdo population on a year-to-year basis. We would suggest that because the life history of the WESE has evolved to expect a very stable environment, including the food web, small perturbations could have major influence on their livelihood. An example was the temporary but dramatic response that WESEs exhibited when a large ice berg briefly changed the sea-ice regime in McMurdo Sound (see Siniff et al. 2008). Another example might be annual variation in the prevalence of AT vs AS in seal foraging areas, as noted by Fuiman et al. (2002). Therefore, prey switching based on fish prevalence could be an important strategy for the seals and one fostering problems should such an option become less available.

Another ecological unknown in regard to AT is the locations and ecological requirements of young fish. This is a species that, from existing information, is not sexually mature until age 8-10 years (Eastman & DeVries 2000). Thus, there must be large numbers of young AT that we essentially know very little about. It could be that both WESEs and KWs make extensive use of these younger age classes in locations that are unknown to us. Plötz (1986), in fact, found small AT in some of his samples from the Weddell Sea. It would seem essential that more knowledge be obtained about the total life history of AT before commercial extraction begins to influence the distribution and recruitment of young AT to the adult population

Thus, while we are uncertain about what effects the absence of AT in McMurdo Sound (see DeVries et al. 2008) might have on WESEs, the correlations exist and point to a need for attention and careful monitoring. Certainly, the potential exists for major effects, particularly on the younger non-breeding WESEs, which of course are the future for the population. Further, the weight loss by adults, both males and females, during the period of pupping, breeding and molt must be recovered before the next reproductive season. We have limited data on how or where this weight gain is achieved. However, based on the data shown above in Figure 2, it seems rather likely that the foraging by some WESEs is in competition with the Ross Sea AT fishery. Again, this possibility emphasizes the need for monitoring and further research to document the extent of this competition for calories.

4.5 Effects on the Ross Sea foodweb should toothfish become depleted. The food web of the Ross Sea is tightly structured, with the members of the upper level showing competition and population compensation with variation in foraging pressure and lower to mid levels showing tight pelagic-benthic coupling (Smith et al. 2006: Ainley 2004, 2007). Given the likely numbers of AT and its voracity (see Eastman 1993), and assuming that patterns are similar to marine ecosystems elsewhere (see Scheffer et al. 2003 and references in Introduction), this fish is probably the most important upper-trophic level predator in the Ross Sea neritic food web.

Ainley et al. (2006b) summarized the diet information for top predators that are components of the neritic food web of the Ross Sea. An appreciable amount of research indicates that AS make up the large part of the diet during spring and summer of Adélie Penguins, Emperor Penguins, Snow Petrels (*Pagodroma nivea*), South Polar Skuas (*Catharacta maccormicki*), WESEs, KWs, Minke Whales (*Balaenoptera bonaerensis*), and AT. As shown also by Ainley et al., a disparate stratification in foraging depth occurs among these predators, as it does in AS (Eastman 1993). In the case of AS, the small ones are avoiding being eaten by larger individuals; in the case of the top predators, stratification would mitigate interference and exploitative competition. All of these species vacate the Ross Sea during winter, except for WESE, Emperor Penguin, and AT (as far as anyone knows). Each of the latter is capable of foraging throughout the entire water column over the Ross Sea shelf, but owing to the extensive ice during winter, the amount of foraging habitat is severely restricted at least for the air-breathing predators. Therefore, the potential for trophic competition is enhanced. Indeed, several authors have noted that WESEs are extremely sensitive to variation in ice cover during winter, with weaner survival and incidence of pupping among females being significantly affected (Testa et al. 1991, Proffitt et al. 2007, Hadley et al. 2007).

At this point, given the lack of our understanding of the integrative nature of the Ross Sea foodweb, one can only speculate what the ramifications to the foodweb might be should industrial fishing severely depress AT numbers. A probable result is that the abundance of AS would increase dramatically, but we have learned from the depletion of predatory fish elsewhere that the food web response is not simple (e.g., Österblom et al. 2006, Meyers et al. 2007, Heithaus et al. 2008) and the evidence exists that this would be true in the Ross Sea as well. AS, although preyed upon extensively by all the above predators, even in the present structure of the food web, are abundant enough in the southern Ross Sea to depress the availability of their prey, euphausiids, to the extent that the fish becomes cannibalistic in late summer; abundant minke whales would also help in the depletion of krill (Ainley et al. 2006a). One result of decreased krill and larval fish is that a portion of the phytoplankton is ungrazed (see review and references in Ainley et al. 2006a, b; Ainley 2007). Therefore, it is not a simple matter that losing AT means more AS, and therefore, as the argument probably would go, there would be more penguins, seals and KWs and thus why would anyone complain? Due to interference competition, the largest penguin colonies may not be capable of further growth regardless of an absolute increase in prey abundance (Ballance et al. 2008), and that argument could apply, too, to the WESE in which the breeders are excluding some portion of the population (non-breeders) from using a limited number of tide cracks for breathing (and ultimately breeding). On the other hand, on the basis of the greater energetic cost for WESE to be foraging on AS instead of also including AT in the diet, a likely scenario might well be fewer WESE (and perhaps KWs). A decline in the prevalence of KWs in the southern Ross Sea has already been observed, as the fishery passed through its 12th season (see DeVries et al. 2008). The long life-span, and k-selected life history of WESE would preclude any detectable reduction, at this time, in the McMurdo Sound population, particularly the breeding portion.

In conclusion, the evidence is strong that AT are of considerable importance to the diet of top predators, such as WESEs, and to the role they play in the neritic Ross Sea trophodyamics. Obviously, more research, and some monitoring (i.e., initiation of CEMP in regard to toothfish fisheries), would be fruitful and would provide needed information on foodweb dynamics, and thus to effectively practice ecosystem management of the AT fishery.

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APPENDIX 1. Presented here is a summary of the observations of seal physiologist, Randy Davis who has been working in McMurdo Sound since the 1980s (R. Davis, pers. comm., 19 June 2008):

“We've observed this [WESE removing the heads of AT before consumption] many times over the years when we had a hut over an ice hole. When a seal brings a large toothfish to the surface, it kills it by flinging it vigorously in the air or shaking it underwater until the neck is broken, then continues until the head breaks off or is shreaded. This is the only way the seal can expose the lateral musculature - it can not or does not attempt to penetrate the skin from the sides. Once the head is off, [the seal] breaks off large chunks of muscle by shaking the carcasss vigorously underwater. The skin rolls back as the seal eats its way towards the tail. This process may take several hours, and the seal does not always consume the entire fish. We have seen [this process] by looking down into the water through the ice hole and from the subice chamber. I think Rob Robbins shot some underwater video of the behavior [see Kim et al. 2005]. After the head is gone, the carcass floats and may be left under the ice near the hole. I can not tell you how many times I've seen this behavior, but it must be at least a dozen.”