

**To be completed by the Secretariat:**

Document No.: WG-EMM-13/29  
Date submitted: 16 June 2013  
Original Language: English

**To be completed by the author:**

Meeting: WG-EMM-13  
Agenda Item No(s): 2.1.4

Title **To what extent do type C killer whales (*Orcinus orca*) feed on Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica?**

Author(s) Leigh Torres<sup>1</sup>, Matt H. Pinkerton<sup>1</sup>, R. Pitman<sup>2</sup>, J. Durban<sup>2</sup>, Regina Eisert<sup>3</sup>

Address(s) <sup>1</sup>National Institute of Water and Atmospheric Research (NIWA)  
Private Bag 14901, Kilbirnie, Wellington, NEW ZEALAND

[l.torres@niwa.co.nz](mailto:l.torres@niwa.co.nz)

<sup>2</sup>Protected Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, 8604 La Jolla Shores Dr., La Jolla, California 92037, USA

<sup>3</sup>Gateway Antarctica, University of Canterbury, Christchurch, NZ

Name and email address of person submitting paper: ben.sharp@mpi.govt.nz

Published or accepted for publication elsewhere? Yes  No

If published or in press, give details:

To be considered for publication in *CCAMLR Science*?<sup>1</sup> Yes  No

<sup>1</sup> By indicating that the paper is to be considered for publication in *CCAMLR Science*, the authors have agreed that the paper can be considered by the Editorial Board of the journal and that, if the paper is accepted for peer review, it is the responsibility of the authors to ensure that permission to publish data and cite unpublished working group papers has been received.

**Abstract**

Information on type C killer whales in the Ross Sea region is reviewed, in particular on the trophic overlap between type C killer whales and Antarctic toothfish. Killer whale population ecology (high consumption rates, low abundances, low production rates, often specialised diets, unknown potential for foraging innovation) means that they are particularly vulnerable to changes in the ecosystem. It is also possible that changes in killer whale feeding can affect the structure and stability of whole ecosystems.

There is circumstantial evidence that suggests that toothfish are an important prey item for type C killer whales in the Ross Sea: (1) type C killer whales near McMurdo Sound have been commonly observed carrying toothfish in their mouths; (2) comparison of the relative nutrient density of toothfish with silverfish and other prey shows that toothfish represent a high-energy food resource of much higher quality than other potential prey in the Ross Sea region; (3) densities of other alternative potential prey (Antarctic silverfish, cryopelagic fish) seem too low to justify killer whales coming to the Ross Sea for feeding and the development of a fish-eating ecotype; (4) anecdotal observations of type C killer whales with toothfish in their mouths in McMurdo Sound have declined since 2000, consistent with reduced catch rates of toothfish by scientific fishing in McMurdo Sound, though the reasons for observed changes in this location are not known.

Other information reviewed here is inconclusive: (1) Habitat overlap information is inconclusive, because it is not known to what extent toothfish forage pelagically or how deep type C killer whales can dive. Recent and unpublished information shows that type C killer whales in the Ross Sea can routinely dive to 200-400 m, with a maximum of >700m. This is deep enough to reach demersal prey over much of the Ross Sea shelf. (2) Stable isotope values of killer whales and

toothfish do not support or refute the hypothesis that toothfish are a major prey item in the Ross Sea in summer. Information on the isotope values of skin of type C killer whales during the full time period in which they are in the Ross Sea, and in different locations inside and outside the Ross Sea, as well as turnover times for stable isotopes in killer whale skin, are required to interpret the isotope data. (3) Comparison between the consumption rates of killer whales and maximum biomass of toothfish potentially eaten by predators at two scales (McMurdo Sound, Ross Sea shelf) suggested that it was possible that type C killer whales could feed substantially on toothfish in summer, but much depends on the number and distribution of killer whales in the Ross Sea region.

At present, the balance of evidence suggests that toothfish are likely to form a significant part of the diet of type C killer whales in McMurdo Sound in summer, but it is not possible to say whether toothfish are an important prey item to type C killer whales in other locations on the Ross Sea shelf (e.g. Terra Nova Bay, Bay of Whales, Sulzberger Bay) or at the scale of the whole Ross Sea shelf and slope.

Basic information necessary to evaluate reliably the risk to type C killer whales in the Ross Sea from the toothfish fishery is urgently needed, including: prey type, foraging behaviour, abundance (and trends) and demographics. Suggested methods are biopsy sampling (analysis for isotopes, fatty acids, genetic tagging), focal-follows (e.g. from boat, ice-edge, helicopter), photographic sightings, tagging (satellite, suction-cup tags), aerial and acoustic surveys.

---

This paper is presented for consideration by CCAMLR and may contain unpublished data, analyses, and/or conclusions subject to change. Data in this paper shall not be cited or used for purposes other than the work of the CAMLR Commission, Scientific Committee or their subsidiary bodies without the permission of the originators and/or owners of the data.

## INTRODUCTION

Climate change and direct human activities such as commercial fishing are likely to affect Ross Sea<sup>1</sup> ecosystems, but our ability to predict, detect and manage these changes is presently limited by lack of basic data on key species (Pinkerton et al. 2010a). Here we focus on the “top top” Ross Sea predator (Pitman 2011), the killer whale (*Orcinus orca*). In particular, a potential risk to the ecotype C (“type C”) killer whale (Pitman & Ensor 2003) in the Ross Sea due to the fishery for Antarctic toothfish (*Dissostichus mawsoni*) (henceforth “toothfish”) has been suggested (Ainley et al. 2009, Pinkerton et al. 2007). Article II of the Convention for the Conservation of Antarctic Marine Living Resources explicitly requires management of fishing in the Southern Ocean region to protect the relationships between all species in the food web and to ensure that changes due to fishing are reversible within a few decades. In the absence of scientific certainty, the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR) is committed to applying the precautionary principle provided that the risk is considered significant. Here, we review available information on the abundance and ecology of type C killer whales in the Ross Sea region, focussing on what is and what is not known about this ecotype, and suggest priorities for killer whale research in the Ross Sea.

The toothfish fishery in the Ross Sea may affect type C killer whales by a number of means, including:

1. by causing death/injury to type C killer whales during fishing itself or afterwards (e.g. due to lost fishing gear);
2. by direct disturbance to type C killer whales (e.g. due to noise disturbance, human activity, pollution, etc.);
3. by allowing type C killer whales to depredate toothfish from longlines;
4. by affecting the ecosystem and/or habitat so that predation on type C killer whale is changed;
5. by affecting the ecosystem so that the abundance of prey items of type C killer whales are altered (direct trophic overlap), especially by reducing the availability of Antarctic toothfish as prey for type C killer whales.

(1) No direct mortality of killer whales by the toothfish fishery in the Ross Sea has been reported. The fishery is entirely based on long-lining so there are no nets available for entanglement, either during fishing operations or afterwards. The impact of lost long-line fishing gear on killer whales in the Ross Sea is unknown but is unlikely to be substantial because most fishing takes place in depths beyond the diving capability of killer whales...

(2) The disturbance impact of human activities (including fishing, research and tourism) on killer whales in the Ross Sea is not known and cannot be assessed at present. This is not considered further in the present paper.

(3) In the Ross Sea, depredation by killer whales on fish captured on long-lines has not been reported over 15 years during which ~40% of all hooks hauled have been directly observed. However, elsewhere in the Southern Ocean depredation by killer whales of toothfish from fishing longlines is a major and growing issue (Ashford et al. 1996, Clark & Agnew 2010, Hucke-Gaete et al. 2004, Pitman 2011, Roche et al. 2007, Tixier et al. 2010). A number of

---

<sup>1</sup> The “Ross Sea” in this paper includes the Ross Sea continental shelf and slope, i.e. shallower than 3000 m and between 160°W and 170°E.

ecotypes of killer whale have been reported as being involved in depredation in the Southern Ocean (type B near South Georgia, Clark and Agnew 2010; types A, C and D off Crozet). There is a risk to the viability of the fishery, to the killer whales, and to ecosystem stability if killer whales learn to depredate toothfish from longlines in areas of the Ross Sea shelf where commercial fishing overlaps with areas frequented by killer whales. At Crozet, populations of depredating killer whales have declined and this is thought to have been caused by fishermen shooting at the whales (Guinet & Tixier, 2011). In the north Pacific, changes in diet by killer whales have been implicated in major ecosystem alteration (Estes et al. 1998, Springer et al. 2003) though this hypothesis is disputed (e.g., see summary in Baird 2011).

(4) In terms of trophic impacts, type C killer whales experience low predation in the Ross Sea. The only possible predator of type C killer whales in the Ross Sea region may be type A killer whales (Pitman, 2011), though such predation has never been observed according to the authors' knowledge. The risk that fishing for toothfish in the Ross Sea could cause significant changes to predation on type C killer whales is hence very low.

(5) The most likely immediate potential impact of the toothfish fishery on type C killer whales in the Ross Sea region is by changes to their diet, and specifically, via the possible reduction in the availability of toothfish as a prey item. Mixed trophic impact (MTI) analysis (Libralato et al. 2006, Ulanowicz & Puccia 1990) was developed to investigate the potential for changes in the abundance of one species in an ecosystem to affect other species through trophic linkages. This MTI analysis approach was applied to the Ross Sea (Pinkerton & Bradford-Grieve, 2012) based on a balanced Ross Sea trophic model (Pinkerton et al. 2010a) and showed low impacts related to killer whales both as an impacting and impacted species. However, the MTI approach only evaluated impacts occurring through trophic interactions at the scale of the underlying Ross Sea trophic model, i.e. the whole Ross Sea shelf and slope area, averaged over a typical year, and in 35 trophic groups. Different ecotypes of killer whales and effects at smaller spatial and temporal scales were not resolved by the MTI analysis which limits its utility for investigating risk to type C killer whales (Pinkerton & Bradford-Grieve, 2012); a specific analysis of the risk to killer whales in the Ross Sea through indirect trophic effects from the toothfish fishery was recommended (Pinkerton & Bradford-Grieve, 2012).

The overall objective for this paper is to investigate to what extent fishing toothfish in the Ross Sea under the current management approach could affect type C killer whales by affecting their prey items, especially via changes to the availability of toothfish as prey. The paper has three specific objectives: (1) are toothfish an important prey item for type C killer whales in the Ross Sea? (2) to what extent has fishing reduced the availability of toothfish as a prey item to type C killer whales and how much is it likely to do so in the future? (3) if the availability of toothfish as a prey item for type C killer whales were reduced, what is the potential for the whales to consume alternative prey items?

## **1. KILLER WHALE BIOLOGY AND LIFE HISTORY**

### **2.1 Killer whale ecotypes**

Four ecotypes of killer whale have been described in Antarctic and adjacent waters that are distinguished through morphology, colour-patterns, diet, behaviour and genetics: these are referred to as types A, B (large and small forms), C and D (LeDuc et al. 2008, Morin et al. 2010, Pitman et al. 2011, Pitman 2011, Pitman & Ensor 2003). de Bruyn et al. (2013) suggest that the available information (especially genetic and social) is currently inadequate to

designate “ecotypes” of Southern Ocean killer whales, but state that “good discriminatory morphological evidence for Antarctic type C (Pitman & Ensor 2003) and Antarctic type D (Pitman et al. 2010) killer whales is sufficient for their classification as different morphotypes”. In contrast, genetic sequencing of killer whales by Morin et al. (2010) was used to recommend that these ecotypes be elevated to full species. Whether type C killer whales in the Ross Sea are denoted an ecotype, separate species or genetically-isolated morphotype does not matter in the context of this paper and hereafter we will use the “type C ecotype” label.

The four killer whale ecotypes are morphometrically distinct and have different markings (Pitman & Ensor 2003). Type A is perhaps the largest form, with black and white colouring that typically lacks a yellow tinge, lacks a visible dorsal cape, and the eyepatch is of medium size, generally oval, with the long axis roughly parallel to the body axis (Pitman & Ensor 2003). Types B and C killer whales are two-toned-grey and white and often have a strong, yellow cast due to a diatom film on the body, and sometimes a dark grey dorsal cape over a medium-grey lateral field (Pitman & Ensor 2003). Type B and type C whales are further distinguishable in the field based on the size and orientation of the eyepatch relative to the horizontal body axis between the gape and flipper: type B has a large eyepatch oriented parallel to the body axis and type C has a much smaller eyepatch that angles downward in the front at an angle of ca. 45° relative to the body axis (Pitman & Ensor 2003). In addition, Pitman et al. (2007) used aerial photogrammetry to measure body length in type C killer whales off Ross Island and showed that adult males grew to a maximum of 6 m, making it the smallest-sized killer whale currently known. By comparison, other killer whales in Antarctic waters (i.e., type A and probably large type B) can grow to more than 9 m in length (Pitman et al. 2007). de Bruyn et al (2013) present evidence of variation in these morphological features within proposed ecotypes, including varying size of type C killer whale eyepatches, and both with and without a prominent dorsal cape. Type D killer whales have an extremely small eyepatch and more bulbous head than the other types (Pitman et al. 2011).

Other than the sub-Antarctic type D killer whale, all these forms of killer whale are found in Antarctic waters during the austral summer. However, they show distinct foraging, distribution and habitat use patterns in Antarctic waters relative to the amount of ice present: type A whales only occur in open water and feed mainly on Antarctic minke whales (*Balaenoptera bonaerensis*); type B occasionally occur in open water but are seen more frequently travelling among loose sea ice and spyhopping next to ice floes, apparently looking for its main prey, seals; type C whales penetrate further into the ice than type B whales and regularly occur in dense pack-ice, along leads in fast ice and in polynyas. Fish is the only known prey of type C killer whales (Pitman & Ensor 2003). Additionally, type C whales are known only from East Antarctica, especially in the Ross Sea, and have never been recorded in the Antarctic Peninsula area (Pitman & Ensor 2003). To date, the only possible occurrence of mixed-type interactions was reported by Olson et al. (2012), apparently during a feeding situation. Very little is known about the ecology and biology of type D whales due to rare observations, but the sightings have been circumpolar and only in sub-Antarctic waters (Pitman et al. 2011, Pitman 2011).

These feeding-type characterisations are based on limited foraging observations and sparse knowledge of the spatial and temporal extent of killer whale distribution throughout the Southern Ocean. de Bruyn et al. (2013) question the dietary specialisation among killer whale types, saying that there is ‘considerable evidence’ from many locations in the Southern Ocean to suggest more generalist diets of all Antarctic ecotypes. For example, de Bruyn et al. (2013) report a sighting of type C killer whales apparently hunting emperor penguins *Aptenodytes forsteri* in the Ross Sea, but direct observation of consumption were lacking.

## 2.2 Large-scale movement patterns

The migratory patterns of type C killer whales are currently unknown. There is evidence of type C whales occurring in Antarctic waters during winter months. A group of at least 40 killer whales reported well inside the sea ice 100 km north of the Adélie Land coast in August 1995 (Gill & Thiele 1997) were identified as type C by Pitman and Ensor (2003) who also noted that some potential prey items of these fish-eating whales are non-migratory and could sustain these whales through the winter months in Antarctic waters. Van Dam & Kooyman (2004) reported a sighting of two killer whales over the Ross Sea shelf slope about 580 km from the ice edge in May 1998, but did not identify the whales to ecotype.

In contrast, there is also clear evidence that type C killer whales do at times move outside Antarctic waters, including a sighting off New Zealand in January 2001 (Pitman & Ensor 2003), and a sighting of a group of over 20 off New South Wales, Australia, in March 2008 (D. Donnelly, M. Morrice, pers. com. ). Additionally, Dwyer and Visser (2011) reported scars on type C killer whales that come from cookie cutter sharks (*Isistius* sp.), a species group whose distribution is limited to the tropics and sub-tropics. Finally, 7 type C killer whales satellite-tagged in the Ross Sea during the 2012-13 summer season were tracked to the east of northernmost New Zealand, reaching a northernmost latitude of ca. 35°S (J. Durban and R. Pitman unpublished data). This rapid north transit is similar to that reported for type B killer whales elsewhere in the Southern Ocean (Durban & Pitman 2012). Based on satellite tracks, five type B killer whales tagged near the Antarctic Peninsula travelled quickly (12 km h<sup>-1</sup>) and directly to subtropical waters off Uruguay and Brazil; two of these tags transmitted long enough to record return trips to Antarctic waters. The authors hypothesized that these rapid movements to warmer waters could represent a “physiological maintenance migration” to allow skin regeneration (Durban & Pitman 2012). The recently recorded satellite tracks of type C killer whales from the Ross Sea may represent long-distance, short-term movements to warmer waters for similar reasons.

Type C killer whales may be philopatric within the Ross Sea, as at least one individual photographed in McMurdo Station in 2002 was resighted at the same location 10 years later, in 2012 (R. Pitman, unpublished data).

## 2.3 Small-scale movement patterns

Limited fine-scale distribution data of type C killer whales in the Ross Sea are available, and there is a lack of data on diving patterns and spatio-temporal habitat use. Type B and type C killer whales are reported as arriving in the southwestern Ross Sea in early December by Ainley et al. (2009) from whence they patrol the receding edge of the fast ice in McMurdo Sound (Ainley et al. 2006), Terra Nova Bay (Lauriano et al. 2007a, Lauriano et al. 2007b), and perhaps similar habitat elsewhere in the Ross Sea, in notable numbers. Sightings of killer whales in the Ross Sea sector based on International Whaling Commission cruises have been made across the Ross Sea shelf, slope and to the north of the Ross Sea (as shown in Ainley et al. (2011, Figure 32). In Ainley et al. (2011), type B and type C killer whales were separated on the basis of group size: as reported in Pitman and Ensor (2003), type C killer whales generally form larger groups than type B (Figure 1b; Section 2.5). However, this method may be biased as partial observations of type C killer whale groups would tend to lead to misclassification as type B. In general, far more type C killer whales have been observed than type B in the Ross Sea region (Lauriano et al., 2007a; R. Pitman, unpublished data). Although most observations of type C killer whales have occurred in the vicinity of McMurdo Sound, it is clear that this ecotype occurs over the whole Ross Sea shelf and slope, and also to the north of the Ross Sea.

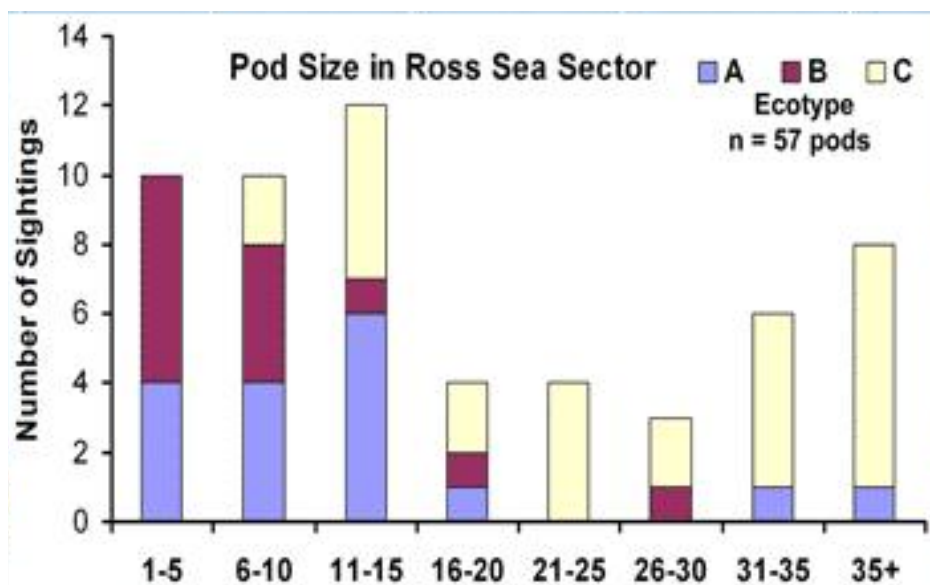
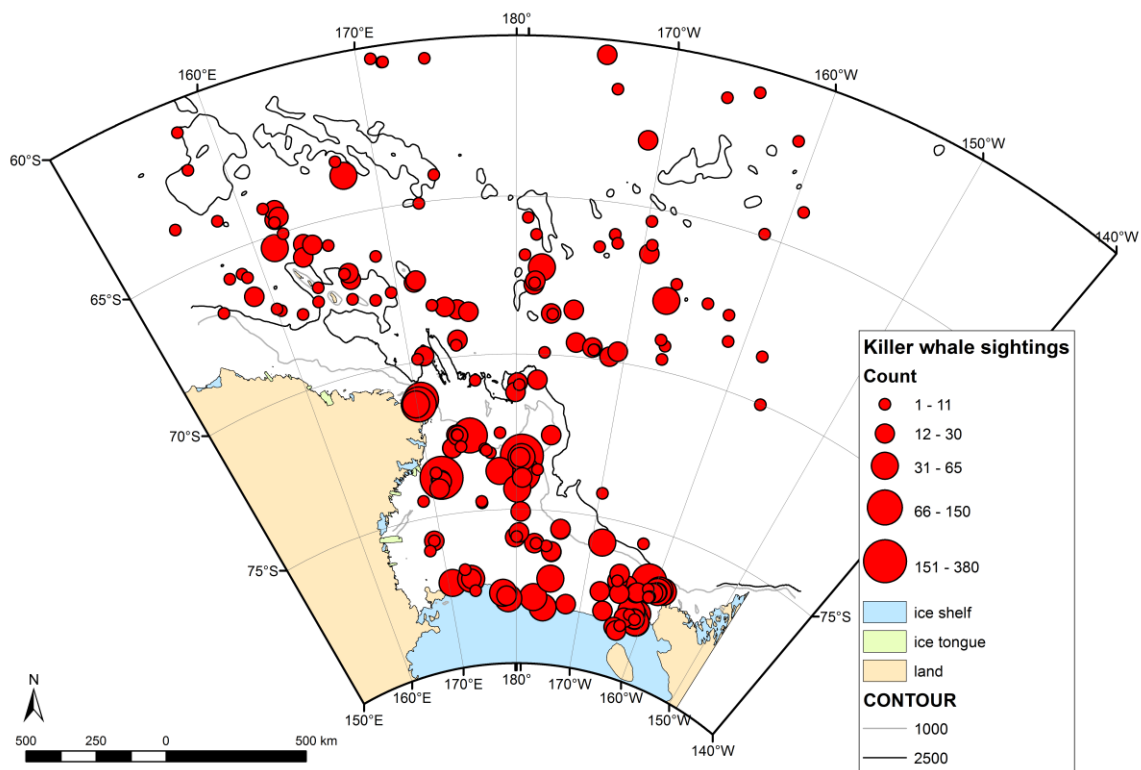


Figure 1. Upper: Sightings of killer whales in the Ross Sea sector based on International Whaling Commission cruises (Ainley et al., 2011, Figure 32). Sizes of circles relate to the number of whales seen in the group. Larger groups (more than about 20 animals) are likely to be type C killer whales, but small groups may be type B or type C killer whales. Lower: Group sizes of killer whales in the Ross Sea sector (Ainley et al. 2006a, 2009; n = 57 pods)

Andrews et al. (2008) satellite tracked four type C killer whales and one type B killer whale in January/February 2006 (Figure 2). These telemetry data do not include depth profiles or information on foraging events. Location-only satellite tracking data of the four type C killer whales in the Ross Sea indicated a mean daily travel distance of 20 km day<sup>-1</sup>, and 90% of satellite points were contained in an area of 5,223 km<sup>2</sup> (Andrews et al. 2008). During the last

week in January, all tagged type C whales spent nearly all their time in the icebreaker channel and adjacent leads and polynyas, but as the ice edge retreated into the southern end of McMurdo Sound they began to spend more time near the ice edge (Andrews et al. 2008). In comparison, the telemetry track of a type B killer whale over the same time period averaged  $57 \text{ km day}^{-1}$  and 90% of satellite points were within an area of  $49,351 \text{ km}^2$  (Andrews et al. 2008). It travelled much farther north in the Ross Sea compared to the localized daily movement patterns of the type C whales, which used a smaller area near McMurdo Station. The authors suggest that the contrast in movement patterns was due to differences in prey preferences between type B and fish-eating type C killer whales (see below).

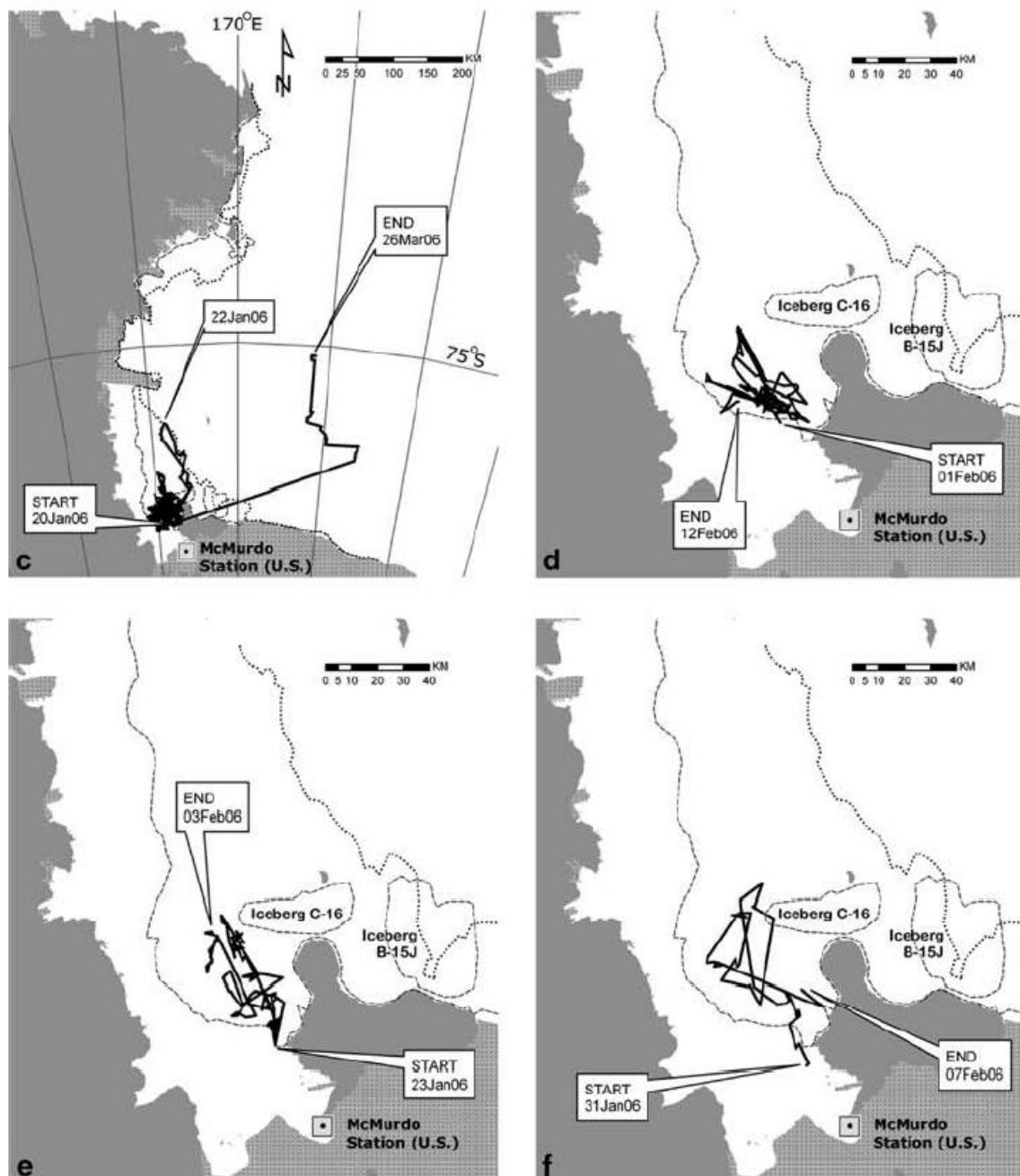


Figure 2. Satellite tracks of four type C killer whales in the southwestern Ross Sea (Andrews et al., 2008, Figure 1c-f; Figure 1a and b are not reproduced here.) Note that the spatial scale of panels d-f is smaller



than panel c. The margin of the land-fast ice edge on January 20 (dotted line) and February 15 (dashed line) are shown.

## **2.4 Depth of killer whale diving**

Published dive data are not available for any Antarctic killer whales. Diving data for northern hemisphere killer whales was provided in a study by Baird et al. (2005), who tagged 34 fish-eating killer whales using suction cup-attached time-depth recorders (TDRs) in the inshore waters of southern British Columbia, Canada, and Washington, USA. They reported a mean maximum dive depth of 140.8 m (SD = 61.8 m), with a maximum of 264 m. It is not known to what extent the depth of diving by these whales is limited by physiological capability. The authors also reported that dive rates did not change with age or differ among groups or between males and females, although analyses restricted to adults showed that during the day, adult males performed significantly more deep dives than adult females. For all whales, dive rates and swim speeds were greater during the day than at night, suggesting decreased activity levels at night.

Although parts of the banks in the Ross Sea (especially Ross, Pennell, Mawson and Crary Banks) are shallower than 400 m, most of the Ross Sea shelf is deeper than 500 m. If type C killer whales have similar diving capabilities, then prey which remain close to the seabed over the continental shelf of the Ross Sea will be inaccessible to killer whales (see Section 3.3 below). However, preliminary analysis of dive information collected by J. Durban and R. Pitman (unpublished data) during the 2012-13 season in McMurdo Sound suggest that type C killer whales in the Ross Sea routinely dive to depths of 200-400 m, with a maximum of >700m. The type C killer whales hence seem to dive much deeper than those studied by Baird et al. (2005) and are likely to be able to feed at or near the seabed (including on demersal fish) over much of the Ross Sea shelf, but not the continental slope (> 800 m).

## **2.5 Killer whale group size in the Ross Sea**

Type C killer whales are typically found in much larger groups (mean 46.1 animals in group; range 10-150; n = 14) than type A (mean = 13.6; range: 1-38; n = 28) or type B (mean = 11.8; range: 2-31; n = 37) (Pitman & Ensor 2003). See also Figure 1b. It has been suggested elsewhere (Barrett-Lennard et al. 1996) that the smaller group sizes of mammal-eating killer whale ecotypes relative to fish-eating ecotypes may be a strategy to minimize detection by mammal prey with increased sensory capability.

## **2.6 Population size of Ross Sea type C killer whales**

Although there have been preliminary estimates of killer whale abundance in the Ross Sea, there has been no formal attempt that used modern estimation techniques and distinguished among the different ecotypes (Ainley et al. 2009). Ainley (1985) estimated 3440 ( $\pm$  SD 2850) killer whales (all ecotypes combined) along ship tracks criss-crossing the Ross Sea over the entire continental shelf and slope during 1976 to 1981. Ainley (1985) suggested that this was probably an overestimate owing to an assumed propensity of killer whales to be attracted to ships. This is probably not correct, as killer whales in general in the Ross Sea are rarely attracted to ships (R. Pitman, unpublished data). In fact, the abundance estimate of 3,440 (Ainley, 1985) may be an underestimate because most of the killer whales in the Ross Sea tend to be found deep in the pack- and fast-ice (R. Pitman, unpublished data), where they are not sighted from ships.

## **2.7 Recent changes in the southwest Ross Sea**

Sightings of type C killer whales from the ice-edge between 2002–2010 are reported by Ainley et al. (2009) and Ainley & Ballard (2012). Although observations were not

standardised by duration of observational period or by the effect of differences in visibility, a change in the number of type C killer whales sighted over this period was described (Ainley & Ballard 2012, Ainley et al. 2009). The reasons for this change are not known, but could be due to, among other things, prey depletion by the whales, effects of the fishery, or oceanographic changes. Over this period, two massive tabular icebergs calved from the Ross Ice Shelf in 2000 (iceberg B-15) and 2002 (iceberg C-19), which perturbed regional ocean processes in the southwest Ross Sea for several years (Robinson & Williams 2012). Departures from typical McMurdo Sound seasonal oceanography noted after these calving events included the absence of Antarctic Surface Water in summer, a cooler and more homogeneous water column during winter and “super-fresh” High Salinity Shelf Water that gradually recovered its salinity (Robinson & Williams 2012). Iceberg B-15a, the largest piece of iceberg B-15, restricted surface circulation, cooled and freshened the upper water column and reduced melting near the ice shelf front for 4-5 years (2000-2004); iceberg C-19 affected the Ross Sea polynya, which impacted McMurdo Sound for three to four years (2002-2006), and was responsible for a geographic shift in the region of dense water formation for the south-western Ross Sea (Robinson & Williams 2012). These oceanographic effects from the icebergs were associated with reductions in primary production in the Ross Sea polynya (Arrigo & van Dijken 2003, Seibel & Dierssen 2003), and trophic disruption affecting top predators including Adélie penguins (Cockrem et al. 2006), emperor penguins (Kooyman et al. 2007) and Weddell seals (Ainley & Siniff 2009). If and how these changes directly or indirectly affected killer whales in the southwestern Ross Sea is unknown.

### **3. KILLER WHALE DIET IN THE ROSS SEA**

#### **3.1 Direct observations of feeding**

To date, type C killer whales have been reported preying only on fish, although which species of fish, other than toothfish, and proportional composition of the fish in their diet is unknown (Ainley et al. 2009, Andrews et al. 2008, Pitman & Ensor 2003).

**Toothfish:** In the McMurdo Sound region, type C killer whales have frequently been observed carrying large Antarctic toothfish in their mouths at the surface (Ainley & Ballard 2012; Ainley et al. 2009; Pitman & Ensor 2003). Type C killer whales with toothfish in their mouths have also been observed in the Terra Nova Bay region (G. L. Kooyman pers. comm. reported in Ainley et al. 2009). So, it is not in doubt that type C killer whales consume Antarctic toothfish to some extent.

**Other fish:** Lauriano et al. (2007b) describes observations of type C killer whales feeding off Cape Washington (just north of Terra Nova Bay). During an event lasting about 5 minutes, the 12 animals displayed a behaviour that was described by the authors as being “similar to the herding phase of the ‘carousel method’ (Simila & Ugarte 1993)”. Individuals swam with the white underside of their body towards the ice floe and emitted bubbles close to the surface, in a way comparable to the cooperative feeding reported by these authors for killer whales preying on herring (*Clupea harengus*) in northern Norway (Lauriano et al. 2007b). We note that delphinids often swim belly-up when pursuing fish, so this type of swimming is not necessarily indicative of herding.

Between 1996 and 2006 at Cape Crozier, groups of 10–30 type C killer whales have been frequently observed apparently foraging along the Ross Ice Shelf edge and nearby fast ice edges, near the surface with belly up (D. Ainley, G. Ballard pers. com. reported in Lauriano et al. 2007b). The whales were typically seen either travelling to and from the ice edges, or diving at or under the ice edge repeatedly over several hours, indicating that most foraging was associated with either glacial or fast ice edges. In both locations, the fish prey was not

observed, probably because small prey fish can be swallowed while underwater. Although Lauriano et al. (2007b) suggests feeding on Antarctic silverfish is most likely, it is possible that the killer whales were feeding on cryopelagic fish, as has been observed for Weddell seals by flushing these fish out using bubbles, or sucking them in while turned upside down (Davis et al. 1999, Kim et al. 2005). There are three species of cryopelagic fish occurring in the Ross Sea: *Pagothenia borchgrevinki*, *P. brachysoma*, and *Trematomus newnesi* (Andriashev 1970, Gutt 2002) with maximum body lengths ca. 15 to 20 cm, and these seem to be widely dispersed, largely in the platelet layer on the underside of ice floes (Kock, 1992; Eastman, 1993). The three main species are known mainly from inshore specimens collected from under sea ice and from around the shores of the Ross Sea in McMurdo Sound and Terra Nova Bay. During the 2012-13 season at McMurdo Sound, type C killer whales were observed and photographed spyhopping with *P. borchgrevinki*, in their mouths (R. Pitman, unpublished data). Weddell seals have also been observed feeding on *P. borchgrevinki* by blowing bubbles into the loose unconsolidated brash and frazil on the ice undersurface to startle the fish, and then catch them (Davis et al. 1999). The importance of *P. borchgrevinki* or other, smaller fish species in the diet of type C killer whales is unknown, but such a behaviour directed at ice-dwelling fish has been suggested as requiring much effort for little value (Ainley et al., 2009).

To the authors knowledge, there is no confirmed observation of killer whales in the Ross Sea feeding on Antarctic silverfish.

The relative lack of observations of type C killer whales foraging on smaller fish compared to direct observations of feeding on toothfish may be due to a 'handling bias'. Type C killer whales probably swallow smaller fish whole underwater, limiting any chance for above water observation. In contrast, killer whales may need to bring a much larger toothfish to the surface to divide, eat, or share it, increasing the likelihood of an observation.

**Other prey:** It is also unknown how specialised type C whales are on fish as there have been reports of them chasing, and potentially hunting, penguins and seals (de Bruyn et al. 2013, Pitman & Ensor 2003); to date, however, there are no confirmed reports of non-fish prey for type C killer whales. For example, de Bruyn et al.(2013) reported a sighting of type C killer whales purportedly hunting emperor penguins in the Ross Sea, but details were lacking.

### 3.2 Stomach contents analysis

Berzin & Vladimirov (1983) reported the stomach contents of 785 killer whales taken by the Soviet fleet in 1979/80 in or around Prydz bay. The sample included 156 'white' (suggested by Pitman & Ensor, 2003 to be probably type A) and 629 'yellow' (suggested by Pitman and Ensor, 2003 to be probably type C) individuals. The main prey items they found (in frequency of occurrence) were: "type A": 3.2% fish, 89.7% marine mammals, 7.1% squid; "type C": 98.5% fish, 0.4% marine mammals, 1.1% squid. The species of fish found in stomachs were either not identified or not reported by Berzin & Vladimirov (1983).

No stranded type C killer whales have been examined in Antarctica (Krahn et al. 2008) which could provide recent dietary data from stomach contents.

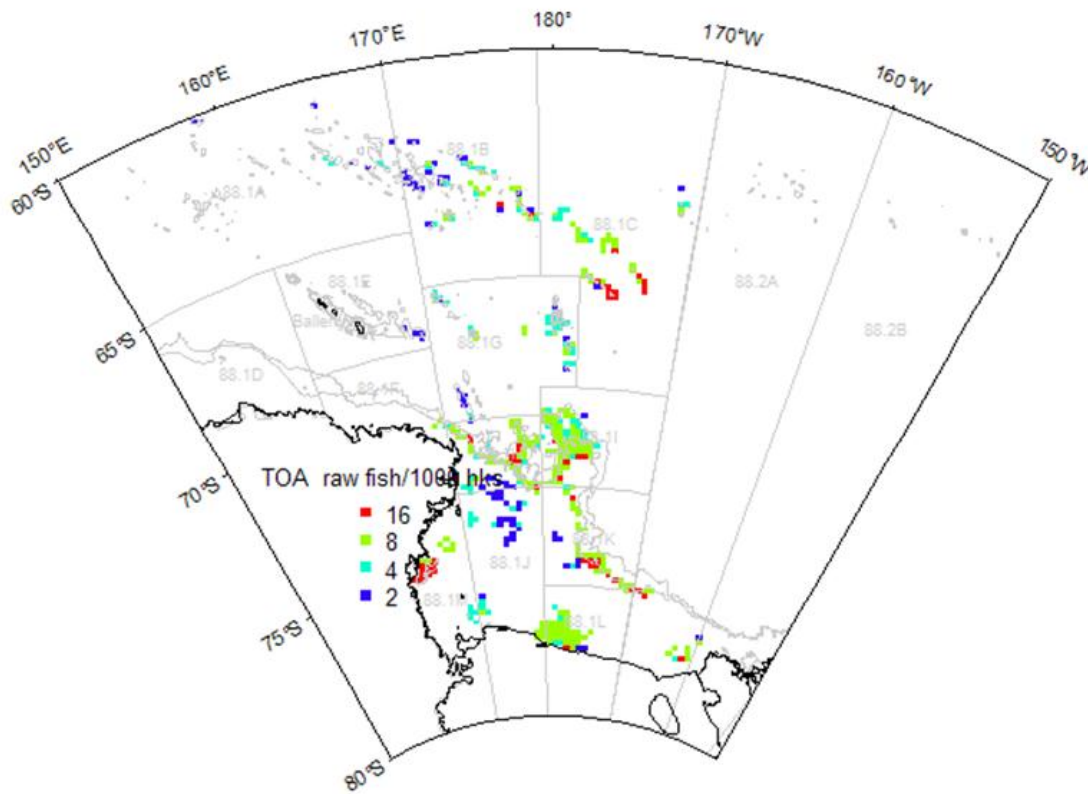
### 3.3 Distribution of potential prey species

**Antarctic toothfish:** In terms of Antarctic toothfish habitat preferences in the Ross Sea, there are two main sources of information: (1) the commercial fishery (Hanchet et al. 2008); and (2) scientific observations, mainly in the McMurdo Sound region (e.g. Ainley et al. 2012, Raymond 1975). Fishery catches show that adult toothfish are mainly found on the

continental slope and are most abundant in depths of 800–1500 m (Figure 3). Over the shelf, there was a relatively large number of subadult toothfish of <110 cm TL living at depths 500–800 m (). Although catch rates of toothfish shallower than 500 m were lower, large adult toothfish have been caught in depths shallower than 500 m in McMurdo Sound and Terra Nova Bay (Ainley et al. 2012, Raymond 1975).

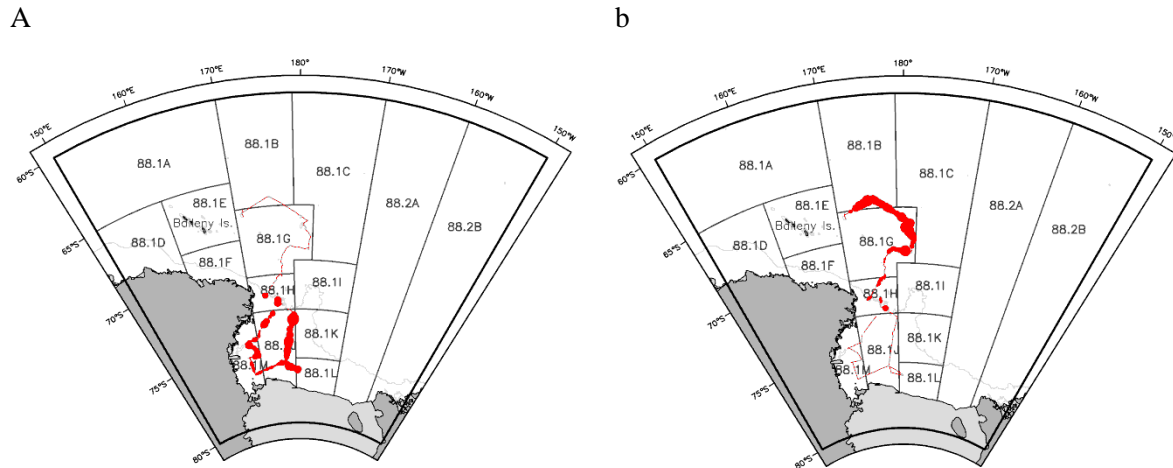
It is currently unclear to what extent adult toothfish forage in the water column rather than remaining close to the seabed. Antarctic toothfish are generally considered to be a demersal (“dwelling at or near the bottom”) or epibenthic species (“of or pertaining to close association with the sea floor”) (Gon & Heemstra 1990). Their physiology is such that they have very close to neutral buoyancy, but only at sizes greater than about 100 cm TL (Eastman and DeVries 1981; Near et al. 2003). Evidence that toothfish are pelagic to some degree includes: (1) observations from cameras on Weddell seals showing large toothfish in the top 200 m of the water column over a bottom depth of 570 m in McMurdo Sound (Fuiman et al. 2002); (2) presence of fresh toothfish in the stomachs of sperm whales, which had been taken over deep waters in the northern Ross Sea region, from an area extending from 150°E to 100°W and from 60°S to 78°S, where feeding on the seabed was deemed unlikely (Yukhov 1971); (3) suggestions that toothfish travel pelagically over deep water between seamounts to the north of the Ross Sea region (Hanchet et al. 2008); (4) presence of beaks of some species of pelagic cephalopods found in the stomachs of toothfish (Thompson et al. 2012; Yeon et al. 2012).

There is also strong evidence of a predominantly benthic lifestyle for adult toothfish: (1) stomach contents of toothfish on the Ross Sea shelf and slope include an overwhelming predominance of benthic prey (Fenaughty et al. 2003, Stevens et al. 2012). In particular, recent analysis of stomach contents from subadult toothfish (<110 cm TL) from surveys in the Southern Ross Sea in 2011-12 and 2012-13 seasons reported mainly benthic prey, including small demersal fishes, Antarctic benthic shrimps and other benthic invertebrates, with very few Antarctic silverfish or euphausiids (Hanchet et al., 2012; J. Forman, D. Stevens, NIWA, pers. com.); (2) scientific fishing in McMurdo Sound found almost all catches of toothfish occurred in the bottom 100 m of the 500 m depth (Ainley et al. 2012, Raymond 1975); (3) demersal prey species (especially *Trematomus loennbergii*) linked to toothfish by fatty acid analysis (Yeon et al. 2012).



**Figure 3. Distribution of Antarctic toothfish in the Ross Sea region based on catch rate in the longline fishery (fish per 1000 hooks) based on data from seasons 1997/98–2009/10.**

**Distribution of silverfish and myctophids:** Acoustic data from the International Polar Year Census of Antarctic Marine Life (IPY-CAML) voyage in February-March 2008 were used to estimate biomass of silverfish, krill and myctophids in the Ross Sea region (O'Driscoll et al. 2011). Multi-frequency acoustic data (12, 38, 70, and 120 kHz) allowed discrimination of silverfish marks from those of krill and other associated species. Mark identification was achieved using targeted midwater trawls. Acoustic target strength for silverfish at 12, 18, 38, 70, and 120 kHz were estimated from anatomically detailed scattering models based on computed tomography (CT) scans of frozen specimens, and used to estimate absolute biomass of silverfish from acoustic backscatter (O'Driscoll et al. 2011). Depth integrated relative biomass distributions (backscatter strength per m<sup>2</sup> for a particular class of organisms) are given in Figure 4. Silverfish are known to be widespread in the midwater over the Ross Sea shelf at depths of 100-400 m (O'Driscoll et al., 2011, Figure 7)



**Figure 4. Relative biomass (backscatter strength per m<sup>2</sup> for a particular class of organisms) of (a) Antarctic silverfish, and (b) myctophids from New Zealand’s International Polar Year Census of Antarctic Marine Life (IPY-CAML) voyage in February-March 2008 (O’Driscoll et al., 2011). Note that values are not comparable between panels.**

**Habitat overlap between type C killer whales and potential prey:** The above described studies indicate that there could be significant spatial overlap between the occurrence of type C killer whales (Figure 1) and potential prey: toothfish (Figure 3) and silverfish (Figure 4a). There seems to be less overlap between type C killer whales and myctophids (Figure 4b). Also, type C killer whales, toothfish and silverfish are known to occur, often with relatively high abundance, in McMurdo Sound when ice conditions permit whales to penetrate into this area. The key unknowns in terms of assessing habitat overlap between type C killer whales and toothfish, and hence the likelihood of a significant trophic link, are (1) to what extent toothfish forage in the midwater rather than on the sea bed over the Ross Sea shelf and slope, and (2) the depth of type C killer whale foraging dives and to what extent they feed in the water column compared to near the seabed.

### 3.4 Information from stable isotopes

Krahn et al. (2008) collected 28 biopsy samples from type C killer whales from the ice edge in McMurdo Sound, off the west side of Ross Island. Stable isotope analysis was conducted on epidermis (skin) from these samples. The stable isotope values for type C killer whales have low variability: mean for males (n=13):  $\delta^{15}\text{N} = 13.4 \pm 0.4$ ; mean for females (n=15):  $\delta^{15}\text{N} = 13.3 \pm 0.4$  (mean  $\pm$  s.d.).

Bury et al. (2008) analysed the isotopic signature of 100 Antarctic toothfish tissue samples from the Ross Sea region and found  $\delta^{15}\text{N} = 13.6 \pm 1.1$  (mean  $\pm$  s.d.). This study provides a more robust sample for comparison to the type C killer whales stable isotope values reported in Krahn et al. (2008). Carbon and nitrogen stable isotope values for other potential prey items were measured, based on samples from New Zealand’s International Polar Year Census of Antarctic Marine Life (IPY-CAML) voyage to the Ross Sea in February-March 2008 (Pinkerton et al. 2010b). Stable isotope values for 140 Antarctic silverfish were determined:  $\delta^{15}\text{N} = 10.3 \pm 0.8$  (mean  $\pm$  s.d.; Pinkerton et al. 2013). Five species of lanternfish were measured (*Electrona carlsbergi*, n=23; *E. antarctica*, n=84; *Gymnoscopelus nicholsi*, n=30; *G. opisthopterus*, n=27; *G. braueri*, n=40) giving  $\delta^{15}\text{N} = 9.1 \pm 1.1$  (mean  $\pm$  s.d., all species combined, n=203, unpublished data). Isotope values for other potential fish prey items for toothfish were given by Krahn et al. (2008), but the samples sizes were very small: dusky notothen (*Trematomus newnesi*, n = 2 adults):  $\delta^{15}\text{N} = 10.9$  (mean); bald notothen (*Pagothenia borchgrevinki*, n = 2 adults):  $\delta^{15}\text{N} = 10.7$  (mean). Isotope data are shown in Figure 5.

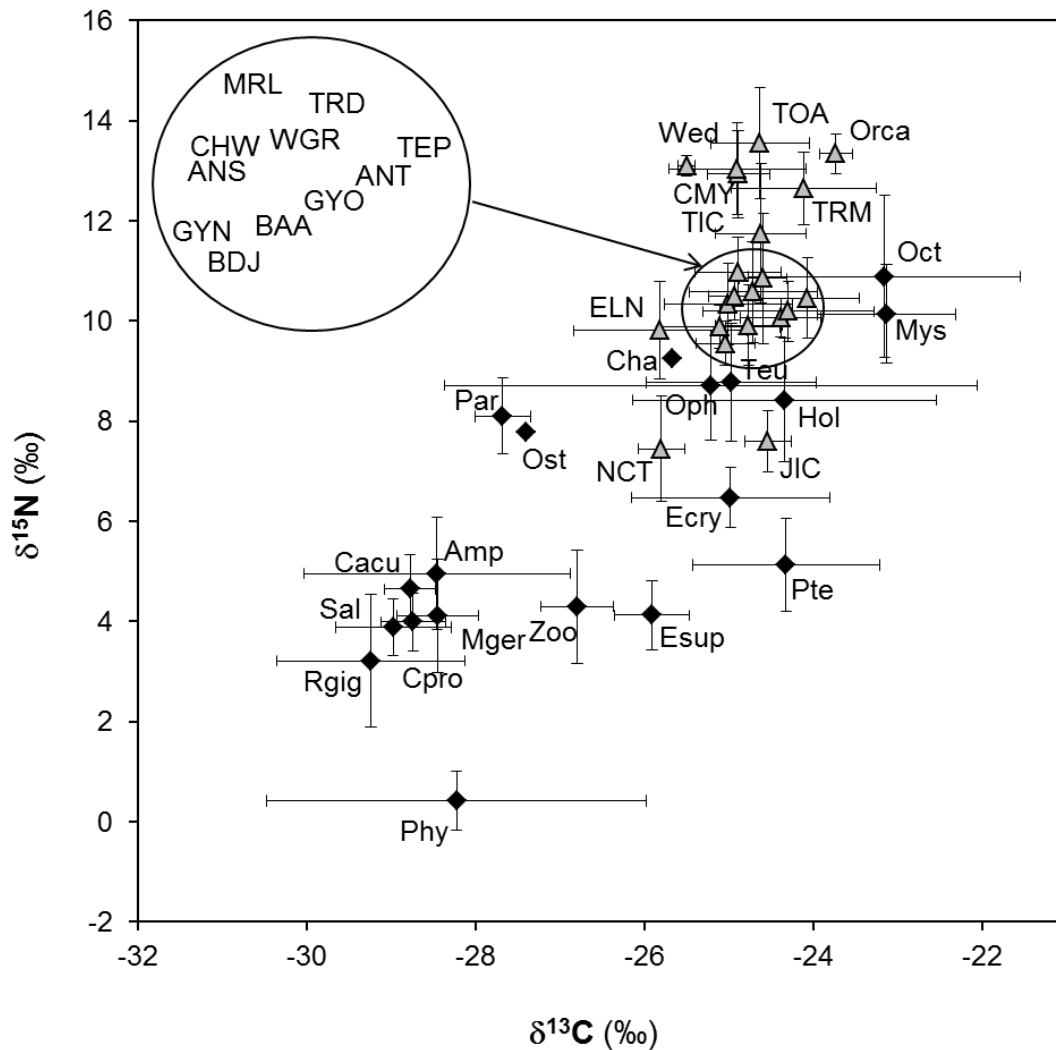


Figure 5. Carbon-nitrogen stable isotope values for biota in the Ross Sea (mean and standard deviations). Means for invertebrates are shown as black diamonds and vertebrates as grey triangles. Codes are:

Amp=Amphipod; ANS=*Pleuragramma antarcticum*; ANT=*Antimora rostrata*; Ast=Asteroid; BAA=*Bathylagus antarcticus*; BDJ=*Bathydraco marri*; Cacu=*Calanoides acutus*; Cha=Chaetognath; CHW=*Chionobathyscus dewitti*; CMY=*Cryodraco myersi*; Cpro=*Calanus propinquus*; Ecry=*Euphausia crystallophorias*; ELN=*Electrona antarctica*; Esup=*Euphausia superba*; GYN=*Gymnoscopelus nicholsi*; GYO=*Gymnoscopelus opisthopterus*; Hol=Holothurian; JIC=*Neopagetopsis ionah*; Mger=*Metridia gerlachei*; MRL=*Muraenolepididae*; Mys=Mysid; NCT=*Notolepis coatsi*; Oct=Octopoda; Oph=Ophiuroid; Orca=*Orcinus orca* (Krahn et al. 2008); Ost=Ostracod; Par=*Paraeuchaeta antarctica*; Phy=Surface phytoplankton; Pte=Pteropod; Rgig=*Rhincalanus gigas*; Sal=Salp; TEP=*Trematomus eulepidotus*; Teu=Teuthida; TIC=*Cryodraco hamatus*; TOA=*Dissostichus mawsoni*; TRD=*Trematomus lepidorhinus*; TRM=*Trematomus scotti*; Wed=*Physeter macrocephalus* (Weddell seal, Burns et al. 1998, Zhao et al. 2004); WGR=*Macrourus whitsoni*; Zoo=Size fractionated zooplankton <1000um.

According to isotope mixing theory, the  $\delta^{15}\text{N}$  in the tissues of a predator equal the sum of the  $\delta^{15}\text{N}$  values of the prey items, weighted by their contribution to the diet over the preceding

period of integration, plus a fractionation (enrichment) factor (Fry, 2006). It is not known over what period the isotope signal in skin of killer whales integrates the diet, but it is likely to be months-year. Measurements on captive killer whales fed a controlled diet indicates that carbon and nitrogen stable isotope ratios in blood are substantially affected by the type of prey consumed in about the last 1–4 months (half lives of 14–60 days, Caut et al., 2011). Trophic enrichment factors for killer whale skin is reported as 3.05‰ (Caut et al., 2011; n=1), close to 3.2–3.4‰ often used (Post 2002; Sweeting et al. 2007), but we note that this was for a single sick animal.

If we assume this trophic enrichment factor and that the isotope signal in killer whale epidermis integrates their consumption from feeding within the Ross Sea and outside the Ross Sea in proportions  $t_{RS}:t_N$  (respectively), the relationship between the isotope values in prey and diet proportions are given in Equation 1, and shown graphically in Figure 6.

$$N_{kw} = 3.05 + t_N N_N + t_{RS} \left[ p_{TOA} N_{TOA} + (1 - p_{TOA}) N_{RS} \right] \quad [1]$$

Where:

$N_{kw} = \delta^{15}N$  value for killer whales (13.35 based on Krahn et al. (2008))

$N_N = \delta^{15}N$  value of prey consumed by killer whales when not in Ross Sea

$N_{TOA} = \delta^{15}N$  value of toothfish consumed by killer whales in Ross Sea (13.6, Bury et al. (2008))

$N_{RS} = \delta^{15}N$  value of prey other than toothfish consumed by killer whales in Ross Sea

$t_N$  = proportion of isotope signal from diet consumed while out of the Ross Sea (assumed to be 0.75, e.g. 9 months per year with annual turnover)

$t_{RS}$  = proportion of isotope signal from diet while within the Ross Sea (assumed to be 0.25, e.g. 3 months per year with annual turnover)

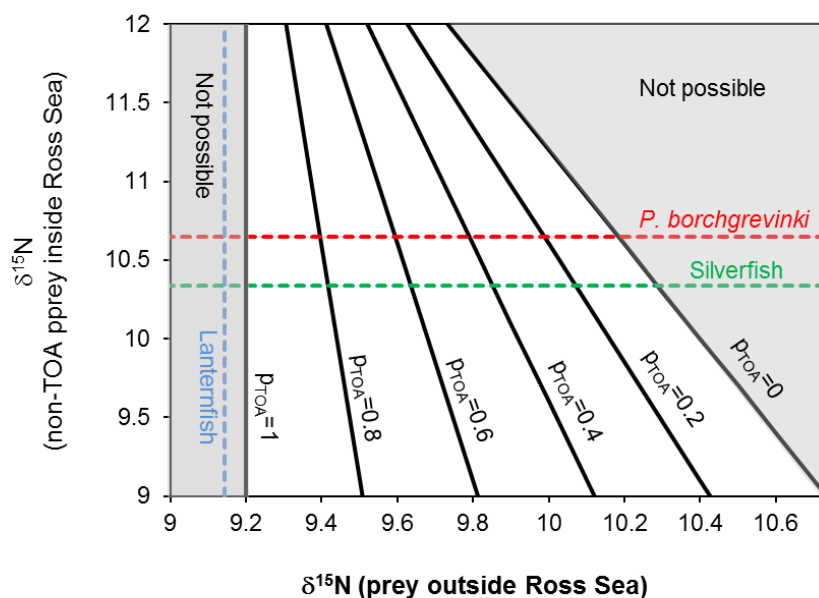
$p_{TOA}$  = proportion of toothfish in diet of killer whales while in the Ross Sea (assumed to be zero when the killer whales are not in the Ross Sea)

The diet of killer whales when not in the Ross Sea is not known. By incorporating the isotope data on killer whales in Krahn et al. (2008) and plausible prey items in the Ross Sea, Figure 6 shows that the  $\delta^{15}N$  value of killer whale prey when not in the Ross Sea are likely to be between 9.2 and 10.7. If killer whale prey outside the Ross Sea has  $\delta^{15}N$  towards the upper part of this range, this simple model suggests that toothfish are likely to be a small component of their diet in the Ross Sea. If killer whale prey outside the Ross Sea has  $\delta^{15}N$  towards the lower part of this range, this simple model suggests that toothfish could be a significant component of type C killer whale diet in the Ross Sea. Killer whale prey outside the Ross Sea could not have a  $\delta^{15}N$  equal to that of lanternfish (mean  $\delta^{15}N = 9.1$ , Pinkerton et al., 2010b) according to this model.

Better information on these relationships is required to understand and interpret these isotope data, including further information of the trophic fractionation factor and turnover times of  $\delta^{15}N$  in killer whale skin. According to Ainley et al. (2009), killer whales arrive in the southwestern Ross Sea in early December, as ice conditions allow the whales to follow leads. The skin biopsy samples in Krahn et al. (2008) were taken in late January, so the whales may only have had 4 to 6 weeks to feed in the Ross Sea prior to tissue sample collection. If similarly short turnover time of isotopes in killer whale blood (1–4 months) found by Caut et al. (2011) also apply to killer whale skin, the isotope signature in the killer whale skin analysed in Krahn et al. (2008) would show a stronger effect of their diet in the Ross Sea than is assumed here. However, type C killer whales may replace their skin cells at different rates



in sub-zero waters than in warmer waters, and may feed at lower levels when replacing their skin in temperate waters (R. Pitman, unpublished data). In this case, the isotope signature in killer whale skin analysed in Krahn et al. (2008) may show a weaker effect of their diet in the Ross Sea than is assumed here. Finally, Ainley et al. (2012) report that toothfish may have become less abundant since about 2001 in McMurdo Sound near where the Krahn et al. (2008) samples were taken. The Krahn et al. (2008) study gives no insight into killer whale diet other than in the 2007-2008 period.



**Figure 6. Relationship between nitrogen isotope values in prey items outside the Ross Sea and those inside the Ross Sea consistent with measured  $\delta^{15}\text{N}$  value for killer whales (Krahn et al. 2008) and toothfish (Bury et al., 2008) for different proportions of toothfish in the diet of killer whales while in the Ross Sea. Solid black lines indicate various toothfish diet fractions ( $p_{\text{TOA}}$ ). The areas shaded grey are not possible because proportions of toothfish in the diet of killer whales cannot be less than zero or greater than 1. The mean isotope values of silverfish (Pinkerton et al., 2013), bald notothen (*Pagothenia borchgrevinki*) are shown as possible prey items inside the Ross Sea (red and green dashed lines). The prey of type C killer whales outside the Ross Sea is not known. The mean  $\delta^{15}\text{N}$  value from five species of lanternfish is shown (blue dashed line, Pinkerton et al., 2010b) but, under the assumptions here, cannot be the sole prey of type C killer whales outside the Ross Sea.**

### 3.5 Other biomarkers

Krahn et al. (2008) also analysed fatty acids and persistent organic pollutants (POP) levels in the 28 tissue samples collected from type C killer whales in the Ross Sea. Krahn et al. (2008) found fatty acid profiles of type C killer whales to be marginally more similar to the mammal-eating transients than they were to the fish-eating populations in Alaska. The authors suggested three possible explanations for this result: (1) type C killer whales supplement a fish diet with marine mammal prey; (2) there are highly dissimilar fatty acid compositions in the fish species that inhabit these two largely dissimilar ecosystems; or (3) there is different stratification of individual fatty acids within the blubber column in the two regions owing to factors such as highly dissimilar oceanographic conditions (e.g., temperature, salinity). Krahn et al. (2008) reported that, with the exception of the highly volatile pesticide hexachlorobenzene (HCB), mean lipid-normalized POP concentrations in adult male type C

killer whales were the lowest of any killer whale population studied to date, including the fish-eating Alaska resident or offshore killer whales. Although not physiologically harmful at present, it may be useful to track concentrations of organic pollutants (and mercury) in the tissue of type C killer whales in the Ross Sea in order to discount contaminant loading as a factor in any ecological changes observed in these populations in the future.

### 3.6 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)<sup>2</sup> 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 CO<sub>2</sub>, NO<sub>x</sub>, 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). This calculation is simplified in fish-eating mammals, as fish is generally highly digestible and the principal macronutrients are fat and protein (Donnelly et al. 1990; Lenky et al. 2012). Carbohydrates are present in only trace amounts. Relatively large losses are incurred in the assimilation of protein, which reduce the energy content of dietary protein from 23.6 kJ.g<sup>-1</sup> (GE) to 16.7 kJ.g<sup>-1</sup> (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) by type C killer whales, as both are poorly digested by terrestrial mammals (Place 1992; Mårtensson et al. 1994). Wax esters account for a large proportion of the total lipid (>80%) in some, but not all, species of myctophids, with the remainder of the fat in myctophids being triglycerides (Connan et al. 2010). If wax esters are indigestible to killer whales, myctophids with wax esters will contain far less ME than suggested by their very high GE content. Prey ME content for six potential prey species (five fish and an octopod) are given in Table 1, assuming chitin and wax esters are not digested by type C killer whales. Metabolisable energy for these prey species was calculated based on measured GE content and proximate composition (Lenky et al. 2012; Eisert, unpublished data). Note that the myctophid prey (*Gymnoscopelus nicholsi*) contains triglycerides rather than wax esters (Connan et al. 2010) and so represents an upper estimate of ME for myctophids.

### 3.7 Prey consumption rates for killer whales

Mean maintenance consumption rates of type C killer whales are estimated to understand the quantities of prey required. “Mean maintenance” is used on the assumption that the animal is not incurring additional metabolic costs due to pregnancy, lactation, fasting, growth or recovery of lost mass, or disease states. For example, Kriete (1995) reported that in captive killer whales, food intake increased by 25% during late stage pregnancy and by 100% during lactation. The mass-specific metabolic rate for young, growing animals will also be higher than for adults. For animals to meet their energy requirements, the average net energy from food needs to equal energy expenditure (=field metabolic rate). Data from three different studies on energy expenditures in killer whales (Kriete, 1995; Williams et al., 2004; Noren

---

<sup>2</sup> Predators obviously also require micronutrients such as vitamins and minerals, but no information is available for Antarctic megafauna.

2011) were used to estimate an average net energy intake of 722 MJ day<sup>-1</sup> (range 594-873 MJ day<sup>-1</sup>) for type C killer whales based on an estimated body mass of 3,000 kg corresponding to a mean length of 5.6 m.

Estimated consumption rates for seven potential prey species in the Ross Sea (six fish and an octopod) are given in Table 1. The mass consumption rates for fish are in the range 76-181 kg d<sup>-1</sup>, with a median of 138 kg d<sup>-1</sup>. For comparison, the estimate of consumption rate (Q/B) for type C killer whales in the Ross Sea trophic model (Pinkerton et al., 2010a, 2010c) was 10.7 y<sup>-1</sup>, estimated using an average of two methods: (1) allometric method (based on Innes et al. 1986, 1987); and (2) based on metabolic rate (Sigurjonsson & Vikingsson 1997). In other studies, based on metabolic rates and assimilation efficiency for killer whales in the Aleutian Islands, Williams et al. (2004) estimates Q/B=11 y<sup>-1</sup>, and Trites (2003) gives 11–18 y<sup>-1</sup>. A Q/B of 10.7 y<sup>-1</sup> implies a mean mass consumption rate of 88 kg d<sup>-1</sup> per individual whale (mass 3000 kg), within the range estimated for high-energy fish prey items in Table 1.

Consumption estimates given in Table 1 are likely to represent a lower limit to consumption in the Ross Sea. As predators with high energetic demands it is possible that killer whales will maximise their energetic intake by capitalising on seasonally abundant food resources (de Bruyn et al. 2013). Killer whales in Norway take advantage of seasonally abundant herring (*Clupea harengus*; Simila & Ugarte 1993); Baird (2011) found that some killer whales can more than double consumption rates when prey are abundant. Such seasonal variation in food intake is difficult to predict (Baird, 2011). We have not changed consumption rates on this basis; values in Table 1 are based on estimated maintenance requirements of adult, non-breeding animals.

The mass consumption rates for fish are in the range 76-181 kg d<sup>-1</sup>, with a median of 116 kg d<sup>-1</sup>. For comparison, the ME content of marine mammal and bird prey consumed by Antarctic killer whales such as adult king penguins, whole seals, and minke whale blubber plus muscle is ca.9.5, 13-16, and 10.1 MJ.kg<sup>-1</sup>, respectively (calculated from data in Lockyer 1991, Chérel et al. 1993, Kvadsheim et al. 1996, and R. Eisert, O. Oftedal, unpublished data), which would indicate prey mass consumption rates of 45 to 76 kg d<sup>-1</sup>.

**Table 1: Potential prey items for type C killer whales in the Ross Sea showing average individual prey mass, metabolisable energy (ME) and estimated daily consumption rates in terms of mass and number of individual prey items. The consumption rates are based on an average net energy intake of 722 MJ/day (range 594-873 MJ/day) as described in the text.**

| Prey species                         | Prey mass<br>(g WW) | Prey ME<br>(MJ kg <sup>-1</sup> ) | Mass consumption<br>rate (kg day <sup>-1</sup> ) |         | Number consumption<br>rate (N day <sup>-1</sup> ) |             |
|--------------------------------------|---------------------|-----------------------------------|--|---------|---|-------------|
|                                      |                     |                                   | Mean   | Range   | Mean  | Range       |
| <i>Dissostichus mawsoni</i>          | 18,000              | 8.5                               | 85   | 70-103  | 5   | 4-6         |
| <i>Pleuragramma antarcticum</i>      | 25                  | 4.3                               | 168  | 138-203 | 6725  | 5,523-8,123 |
| <i>Trematomus bernacchii</i>         | 80                  | 4.0                               | 181  | 149-219 | 2263  | 1,859-2,733 |
| <i>Trematomus lepidorhinus</i>       | 217                 | 6.2                               | 116  | 96-140  | 536   | 440-647     |
| <i>Pagothenia borchgrevinki</i>      | 133                 | 4.5                               | 161  | 132-194 | 1210  | 994-1,461   |
| <i>Gymnoscopelus nicholsi</i>        | 37                  | 9.5                               | 76   | 63-92   | 2062  | 1,693-2,490 |
| <i>Pareledone turqueti</i> (octopod) | 100                 | 2.3                               | 311  | 255-375 | 3106  | 2,551-3,752 |

### 3.8 Toothfish mortality versus killer whale consumption

Here we compare consumption rates of killer whales with natural mortality of toothfish at two indicative scales: (1) in the McMurdo Sound region; (2) over the Ross Sea shelf (including

McMurdo Sound). The intention is to generate a maximum plausible estimate for the amount of toothfish consumed by killer whales. We employ two scales to assess (1) the localized importance of toothfish in McMurdo Sound where type C killer whales are known to forage on toothfish (at least historically) and occur with regularity and high densities during summer months, and (2) the significance of toothfish in the larger Ross Sea shelf area where the occurrence and foraging patterns of type C killer whales is less well known. We consider McMurdo Sound separately because more information is available for this region than elsewhere in the Ross Sea. However, there are other areas that may be similar to McMurdo Sound in the Ross Sea region, for example the Bay of Whales and Sulzberger Bay in the southeast of the Ross Sea. We make several assumptions which lead to highest proportional amount of toothfish in killer whales diets, namely: (1) killer whales are present in the region for three months during the summer; (2) all annual natural mortality of toothfish occurs only in these three months; (3) there are no other sources of natural mortality (i.e. no predation by Weddell seals, sperm whales or other potential predators of toothfish, and no natural mortality due to non-predation causes such as starvation); (4) killer whales are eating at maintenance level during this period.

### **Antarctic toothfish mortality**

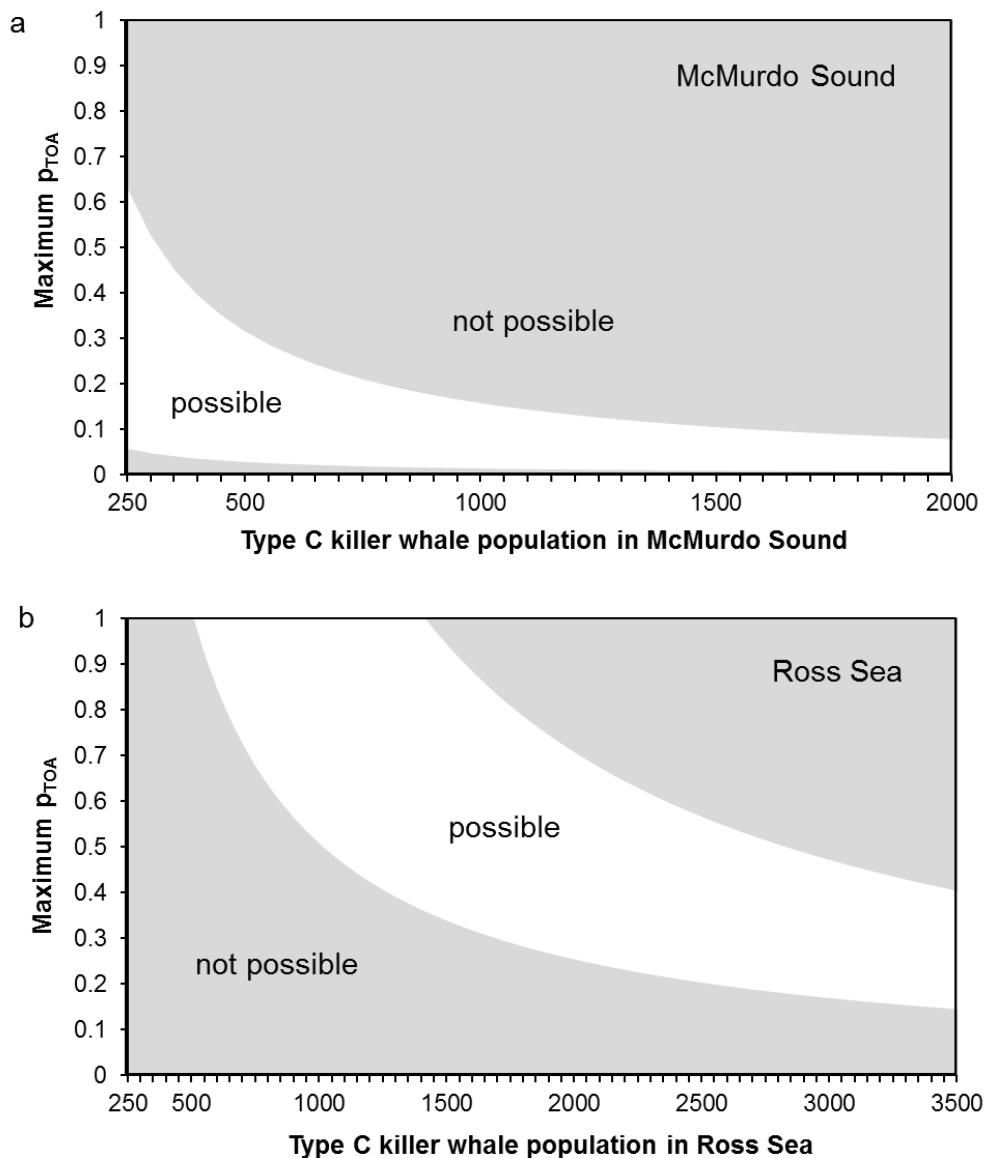
**(1) McMurdo Sound scale:** The biomass of toothfish in the McMurdo Sound region in the summer (ice free) period January-February, before fishing for toothfish started (i.e. pre-1997), is not known. The development of a spatially-explicit model of toothfish in subarea 88.1 (Dunn and Rasmussen 2008; Mormede et al. 2013) is on-going. The present version suggests a toothfish biomass in the McMurdo Sound region as 1040 t. Pinkerton et al. (2008) estimated 4400-7770 t for mass of toothfish in the McMurdo Sound region bounded to the north by 76°S and to the east by 175°E (a greater area than extracted from the model of Mormede et al. 2013). Scientific tagging/recapture rates were used to give an early estimate of the biomass of toothfish in the McMurdo Sound region of 2700 t (Raymond, 1975). Hence, we use a plausible toothfish biomass range in the McMurdo Sound region of 1040–7770 t.

**(2) Ross Sea scale:** The proportion of the Ross Sea toothfish stock over the shelf and slope was estimated to be about 85% of the total stock (Pinkerton et al., 2010a), equivalent to a toothfish biomass before fishing of about 69 500 t. The draft spatial stock model would suggest a toothfish biomass over the Ross Sea shelf and inner slope of about 36 700 t (Mormede et al. 2013). We use these as bounds of the possible biomass of toothfish over the shelf and inner slope.

Mortality of toothfish is likely to be age-dependent, with higher mortality for young and old fish than for mid-age fish. In the absence of information on variation in natural mortality of toothfish with age in the Ross Sea, we set toothfish mortality equal to the age-invariant value used in stock modelling (Mormede et al., 2011). Natural mortality for toothfish in the shelf region was estimated to be 0.11–0.15  $y^{-1}$ , with a typical value of  $M=0.13 y^{-1}$  (Dunn et al. 2006).

**Mortality-consumption comparison:** Combining the estimated mass of toothfish with the natural mortality rate of 0.13  $y^{-1}$  gives an estimate of the maximum amount of toothfish which may be consumed annually by predators. The estimate is (1) McMurdo Sound: 135–1010 t; (2) Ross Sea: 4800–9040 t. The plausible number of type C killer whales in the Ross Sea in summer is likely to be in the range 380–3000 (Section 2.6). The plausible number of type C killer whales in the McMurdo Sound region in summer is likely to be in the range 250–3000. Maintenance level consumption rates of toothfish by killer whales are 85 (70-103)  $kg d^{-1}$  (Table 1). Estimates of the maximum amount of toothfish in the diet of type C killer whales are hence shown in Figure 7.

At the McMurdo Sound scale, this analysis suggests that if there are 250 type C killer whales in McMurdo Sound in summer, there may be enough toothfish available to provide between 6 and 63% of their diet. This high variability occurs because the biomass of toothfish in the McMurdo Sound region is not well known. If there are 1000 killer whales present in McMurdo Sound, there is likely to only be enough toothfish available to satisfy 1-16% of their diet. In the larger scale analysis, if there are 2000 killer whales present over the Ross Sea shelf, the analysis suggests that there are sufficient toothfish available to provide 25-71% of their diet, but this falls to 15-40% if there are 3500 killer whales present.



**Figure 7.** Maximum proportion (by weight) of toothfish in the diet of type C killer whales during the 3 months of summer that may be supported by estimated natural mortality of toothfish.  $p_{TOA}$  = proportion of toothfish in diet of killer whales while in the Ross Sea (assumed to be zero when the killer whales are not in the Ross Sea). The analysis is presented at two scales a: the McMurdo Sound region, b: Ross Sea (shelf and slope). The upper limit of the grey region corresponds to the highest estimated toothfish biomass in region and the lowest estimated consumption rate for whales. The lower limit of the grey region corresponds to the lowest estimate of toothfish biomass in the region and the highest estimated consumption rate of whales. The method assumes no consumption of toothfish by other predators, all toothfish natural mortality occurs in the summer 3 months, and toothfish natural mortality of  $0.13 \text{ y}^{-1}$ . See text for more details of method.

Note that similar calculations performed for Weddell seal predation (Eisert et al. 2013) estimated that natural mortality in the McMurdo region was sufficient to support a maximum of the order of 20% of the diet of Weddell seals in the same time period (i.e. with no remaining toothfish available for killer whale predation). The feasible maximum fractions of toothfish in the diet of killer whales will be reduced if Weddell seals also consume toothfish (Pinkerton et al., 2008; Ainley & Siniff 2009). We note that these estimates for killer whale consumption and toothfish mortality rely on a number of assumptions and, although they represent the only estimates currently available, they include considerable uncertainty.

### 3.9 Prey density of silverfish

Camera systems lowered through the water column from research vessels (J.T. Eastman, personal observations), and ‘critter cams’ deployed on Weddell seals (Fuiman et al. 2002) indicate Antarctic silverfish exist as loose midwater shoals (unstructured aggregations), with individuals estimated to be spaced 2–4 m apart and densities of one fish per 7–43 m<sup>3</sup> (Fuiman et al. 2002, La Mesa & Eastman 2012). This estimate of the density of silverfish corresponds well with that observed acoustically on New Zealand’s IPY-CAML voyage in February–March 2008. On this research voyage, multifrequency acoustic data (12, 38, 70, and 120 kHz) was partitioned into backscatter due to silverfish, krill, myctophids, and other marks using the frequency response of the target (O’Driscoll et al., 2011). The peak silverfish densities within a silverfish aggregation were obtained from direct inspection of echograms (ping by ping data) and these give maximum densities of about 0.2 adult silverfish per m<sup>3</sup> (back-scattering strength recordings SV of -70 dB, O’Driscoll pers. com.). Taking adult silverfish to have mean 115 mm standard length and weigh 14.1 g<sub>WW</sub> (O’Driscoll et al., 2011, Table 4), the silverfish density estimates together suggest silverfish biomass densities in the range 0.3–2.8 g m<sup>-3</sup>.

Killer whales feed on seasonally abundant herring (*Clupea harengus*) in Norway cooperatively by herding their prey into a tight ball using a ‘carousel’ method (Simila & Ugarte 1993). Acoustic estimates of herring density off Norway during predation by killer whales showed that herding had increased herring densities by a factor of about 2.5, giving densities of 0.6–2.2 fish m<sup>-3</sup> while being attacked by killer whales (Nottestad & Simila, 2001). Average fish weight was 208 g, giving biomass densities of 125–458 g m<sup>-3</sup> during the killer whale attack. In a separate study off Norway using video cameras rather than acoustics, herring density was measured while herring were under attack from killer whales. In this case the increase in density during corralling by killer whales was estimated to have been about a factor of 12 (Domenici et al., 2000, based on Misund 1993). Measured density of corralled herring was 24.6 fish m<sup>-3</sup>, equivalent to biomass density of 8000 g m<sup>-3</sup> (herring 35 cm TL; Domenici et al., 2000).

If type C killer in the Ross Sea can concentrate silverfish by the same factor as killer whales do with herring off Norway (up to a factor of about 12), it may be possible for killer whales to herd silverfish into densities of up to 35 g m<sup>-3</sup>. This density is still only 0.4–28% of prey densities found while killer whales are feeding on corralled herring. Hence, it seems unlikely that killer whales could make silverfish densities as high as herring densities observed off Norway (Simila & Ugarte 1993; Nottestad & Simila, 2001; Domenici et al., 2000) because of two key differences: (1) silverfish are about 1/10<sup>th</sup> of the size of herring (ca. 20 g compared to 200 g per individual); and (2) silverfish naturally do not seem to form structured aggregations (compare 0.02–0.2 silverfish m<sup>-3</sup> in La Mesa & Eastman (2012) with 1–3 herring m<sup>-3</sup>, Misund 1993). To achieve similar corralled densities of silverfish to those observed while killer whales are feeding on herring off Norway, silverfish would need to be concentrated 4–200 times as effectively as herring.

## 4. DISCUSSION

By virtue of their high trophic position, top predators integrate ecosystem processes and thus are not only at the forefront of change, but also represent sentinels for ecosystem state (Ramos and González-Solís, 2012). Top predators are widely used in monitoring the ecosystem effects of fishing in the Southern Ocean (Reid et al. 2005; Constable 2006; CEMP 2004; Agnew 1997). However, given that predators respond in complex ways to many factors simultaneously, ascertaining causes of observed change in predator ecology or abundance, and hence the appropriate management response is difficult without a robust understanding of the ecology of the species and ecosystem in which it lives (Boyd et al. 2006).

Various features of killer whale life history and ecology increase their vulnerability (see Barrett-Lennard & Heise 2011 and references therein): (1) being at the top of food chains, killer whales are not abundant because food availability decreases with increasing trophic level. Low abundance puts them at greater risk of extinction (or extirpation) than common species; (2) killer whales have a very low reproductive rate, with one calf at a time and siblings being usually separated by four years or more; (3) killer whales have high consumption rates; (4) killer whales are long-lived (perhaps 60 and 80 years for males and females, respectively) and this, coupled with their high trophic position, means they tend to accumulate contaminants such as heavy metals and PCBs; (5) the highly social nature of killer whales makes populations vulnerable to one-off catastrophic events or loss of key 'cultural elements' or individuals, such as older adult females.

We have discussed a number of pieces of evidence to quantify the importance of toothfish as a prey item for type C killer whales in the Ross Sea, but the picture is far from clear. An important prey item is one that is crucial to the survival and/or reproductive success of the population (or metapopulation) of predators and one that cannot be replaced by an alternative prey without substantial detrimental effect on the predator. Such a critical trophic dependency could occur by the coupling between life history stages (e.g. growth, reproduction) and a seasonal peak in food supply or availability of a particularly high-quality prey. Any reduction in the availability of food resources that are coupled to critical life cycle stages has a high probability of triggering a disproportionate population decline or ecological change. It appears that type C killer whales occur in Ross Sea region (including McMurdo Sound and Terra Nova Bay) for the purpose of feeding; there is no evidence of any other special activity (such as reproduction) in these regions. If killer whales are indeed in the Ross Sea to feed, the availability and type of prey in these regions must be such that feeding by type C killer whales is better here than elsewhere.

In the CCAMLR context, management is required to preserve ecosystem linkages and ensure reversibility of fishing-related ecosystem changes within a few decades (principles IIa and IIb). Prey-switching by killer whales in other regions has been implicated in ecosystem changes such as trophic-cascades and system destabilisation (Estes et al. 1998, Springer et al. 2003; Baird 2011). The requirements of CCAMLR principles Article II(3) paragraphs b and c suggests management of fisheries by CCAMLR should avoid changes which lead to type C killer whales switching diet and the potential ecosystem consequences of such changes.

There is circumstantial evidence that suggests that toothfish are an important prey item for type C killer whales in the Ross Sea, as follows:

- (1) It was reportedly common before 2000 to see type C killer whales in the icebreaker channel near McMurdo Sound with toothfish in their mouths (Ainley et al., 2009).
- (2) Type C killer whales near McMurdo Sound have not been observed carrying toothfish since 2000 which is consistent with a suggested reduced abundance of toothfish in McMurdo

Sound since about 2000 (Ainley et al., 2012). If genuine, the reasons for reduced abundance of toothfish in McMurdo Sound since about 2000 are not known. We note that the Ross Sea stock model indicates that in 2000 the spawning stock biomass of toothfish was at more than 98% the unfished level (Dunn et al. 2011).

(3) Assuming the correlation between morphotypes/ecotypes and diet proposed by Pitman & Ensor (2003) is correct, there can only be C type killer whales in the Ross Sea if there is a sufficiently abundant prey base to motivate dietary specialisation. Evolution of the type C ecotype indicates that dietary specialisation on fish is significant and has persisted for long enough to allow development of morphological and genetic differences from the ancestral stock of killer whales. The existence of a killer whale ecotype specialising on fish for at least part of the annual cycle hence implies the availability of energy-rich, sufficiently clustered (large or occurring in dense shoals) fish prey. There is no ecological or evolutionary reason for part of the killer whale population to concentrate on prey other than marine mammals and birds, unless this alternative food source is profitable; the energy density (ME) of minke whale muscle plus blubber, and of whole seals and king penguins is in the range of ca. 10-16 MJ.kg<sup>-1</sup> WW, and therefore higher than in any fish prey with the possible exception of some species of myctophids. Bird and mammal prey species are also large enough (10–500+ kg mass) to meet the absolute food requirements of killer whales. Comparison of the relative nutrient density of toothfish with silverfish and other fish or invertebrate prey (Lenky et al. 2012) shows that toothfish represent a high-energy food resource of much higher quality than other potential fish or invertebrate prey in the Ross Sea region.

(4) Densities of other potential pelagic prey seem too low to justify killer whales coming to the Ross Sea for feeding. In the northern hemisphere, fish-eating killer whales are known to herd herring into high concentrations for feeding (Simila & Ugarte 1993; Nottestad & Simila, 2001; Domenici et al., 2000). However, silverfish are about 1/10<sup>th</sup> of the size of herring and naturally do not seem to form structured aggregations. We acknowledge that there is no evidence on the degree to which silverfish densities may be increased by killer whale herding.

(5) Feeding predominantly on cryopelagic fish seems unlikely. Type C killer whales have been observed feeding on *Pagothenia borchgrevinki* in the Ross Sea, which is of a similar size to herring and occurs under sea ice in the Ross Sea. The abundance of cryopelagic fish under Ross Sea pack ice is not known, but consumption of 1200 of these fish per whale per day seems unlikely.

The pieces of circumstantial evidence (3)–(5) suggest together that the combination of high individual mass, and high fat content mean that toothfish are likely to be by far the most concentrated and hence attractive prey available to fish-eating killer whales in the Ross Sea.

There are several important pieces of evidence that are inconclusive at present:

(1) Habitat overlap information is inconclusive because it is not known to what extent toothfish occur pelagically or how deep type C killer whales can dive. Hence, at present we cannot assess to what extent toothfish are available to killer whales.

(2) Stable isotope values of killer whales and toothfish did not support or refute that toothfish are a major prey item in the Ross Sea in summer. More biopsy samples, information on the diet of killer whales at other times of the year, and measurements of isotope turnover times in killer whale skin and blubber are required.

(3) Comparison between the consumption rates of killer whales and the natural mortality of toothfish was carried out at two scales: McMurdo Sound and the Ross Sea shelf. The analysis neither supported nor refuted that type C killer whales could feed substantially on toothfish during 3 months of summer. The results depend crucially on the number of type C killer whales present in these regions during summer, the spatial distribution of toothfish in the region, natural mortality rates of toothfish, and to what extent other predators are consuming toothfish at the same time, none of which is robustly known at present.



(4) There is a suggestion that the seasonal overlap of toothfish and type C killer whales in the southwestern Ross Sea is short: Ainley et al. (2009) notes that killer whales arrive in McMurdo Sound in early December; scientific fishing in the 1970s suggested that toothfish were present in McMurdo Sound only from early September to mid-December (Raymond, 1975). However, this is only applicable to McMurdo Sound and when/where type C killer whales arrive in the Ross Sea in general is not known, and likely dependent on sea ice conditions. It is unlikely that toothfish abundance over the Ross Sea shelf is highly variable seasonally (Hanchet et al., 2008).

We have not found any robust evidence that toothfish cannot be an important prey item for type C killer whales in the Ross Sea.

### **Substitution of other prey**

The degree to which killer whales are ecologically, behaviourally and/or culturally able to alter their foraging strategies and diet is not clear. Some researchers believe that killer whales generally have low innovation and capacity for diet change:

- (1) When three mammal-eating transient killer whales were captured in 1970, after 75 days of refusing to eat the fish they were offered, one of the whales died. When returned to the wild after several months, the surviving whales resumed their diet of marine mammals (Barrett-Lennard & Heise, 2011; Barrett-Lennard, 2011). This led Barrett-Lennard (2011) to conclude that killer whale populations tend to be remarkably narrow and fixed in their prey preferences;
- (2) Resident killer whale foraging in the Pacific Northwest is highly focused on Chinook salmon, and the smaller but far more abundant species such as pink and sockeye salmon are not significant in their diet (Ford, 2011). A comparison of resident killer whale survival rates to coast-wide Chinook salmon abundance over a 25-year period revealed a highly significant correlation, suggesting that resident populations may be limited by this one key prey species (Ford, 2011);
- (3) The fact that Crozet killer whales already ate fish is suggested as a reason why they learnt to take toothfish from longlines so quickly (Guinet & Tixier, 2011);
- (4) In the Gulf of Alaska, resident killer whales seek out primarily the fatty Chinook and Coho salmon, and some chum salmon; little or no sockeye or pink salmon are consumed (Matkin & Durban, 2011).

In contrast, other studies suggest that killer whales can adapt their diet in changing conditions:

- (1) The killer whales at South Georgia which have learned to take Patagonian toothfish from longlines of fishing vessels have been identified as type B, the killer whale ecotype that preys on pinnipeds (Moir Clark & Agnew 2010).
- (2) In western Alaska where salmon are much less abundant, killer whales appear to feed on other fish species, such as Atka mackerel (Matkin & Durban, 2011). Around the Aleutians and Bering Sea, resident killer whales remove black cod, halibut, and turbot from hooks on their lines and also eat bycatch and discards that are dumped off the decks of the trawlers (Matkin & Durban, 2011).
- (3) A number of types of killer whales seem to be responsible for depredation of Patagonian toothfish from longlines at Kerguelen and Crozet, including whales tentatively identified as type A (though this ecotyping may not be valid outside the high Antarctic), with possibly one type C sighted, and type D may also be involved (Pitman et al., 2011; P. Tixier, pers. comm.; Moir Clark & Agnew, 2010). The killer whales that occur near Crozet appear to have a generalist diet; it has been observed taking minke whales, southern elephant seals, and penguins and fish near the islands (Guinet 1992; Guinet et al. 2000).
- (4) Antarctic type B killer whales (large form) preferentially take Weddell seals (*Leptonychotes weddellii*) when prey is abundant but can take other seal species when necessary (Pitman & Durban 2012).

According to ecological theory, killer whales in tropical and oceanic areas (i.e., low-productivity areas) should be less likely to exhibit prey specializations (Baird 2002); diet breadth should increase as the availability of the most highly profitable prey decreases (Baird 2002; see also Pitman & Dutton 2004). It is also possible that the degree of dietary flexibility is highly variable between different groups of killer whales, largely irrespective of ecotype. For example, only a few family groups of killer whales at Crozet have learned to depredate toothfish from longlines; Guinet & Tixier (2011) report that only 4 pods totalling 35 individuals were involved in 80% of the fish depredation events; most pods at Crozet have little interaction with fishing vessels.

### Summary of knowns and unknowns

A summary of knowns and unknowns regarding type C killer whales is given in Table 2.

**Table 2. Summary of knowns and unknowns regarding type C killer whales in the Ross Sea, of direct relevance to understanding the risk of ecosystem effects of the Ross Sea toothfish fishery.**

| Knowns   | Unknowns  |
|--|---|
| Type C killer whales occur in the Ross Sea shelf and slope region in the summer  | <ul style="list-style-type: none"> <li>• Type C Ross Sea abundance</li> <li>• Distribution across Ross Sea in summer</li> <li>• Seasonal and interannual variability in summer abundance in Ross Sea</li> <li>• Location during rest of year</li> </ul>   |
| <ul style="list-style-type: none"> <li>• Type C killer whales are likely to be predominantly fish eaters</li> <li>• Some type C killer whales in Ross Sea consume a proportion of Antarctic toothfish</li> <li>• Some type C killer whales in Ross Sea consume a proportion of smaller fish under ice</li> </ul> | <ul style="list-style-type: none"> <li>• Mean diet of type C killer whales while in the Ross Sea</li> <li>• Variation in diets across the type C killer whale population in the Ross Sea</li> <li>• What is eaten during rest of year</li> <li>• Ability to alter diet</li> </ul>   |
| <ul style="list-style-type: none"> <li>• Killer whale consumption rates are high</li> <li>• Killer whale populations have low production and recovery rates</li> </ul>   | <ul style="list-style-type: none"> <li>• Why type C killer whales come into the Ross Sea in summer (probably for feeding, but not definite)</li> <li>• Ecological consequence of diet changes on killer whales and rest of ecosystem</li> <li>• If feeding in the Ross Sea is crucial for life cycle of type C killer whales</li> </ul> |
| Stock model for toothfish estimates spawning stock biomass of Ross Sea stock over time   | Impact of fishery on availability of toothfish to type C killer whales  |
| Satellite and oceanographic observation in Ross Sea  | Reason for recent changes in type C killer whales in southwest Ross Sea   |

### Potential for the fishery to affect availability of toothfish

The latest Ross Sea toothfish stock model suggests that toothfish spawning biomass in 2011 is about 83% of the unfished level (Mormede et al. 2011, Table 9). Fishing at the present level is predicted to lead to the spawning stock biomass of the Ross Sea stock of toothfish to be reduced to 50% of the unfished level over 35 years (Mormede et al. 2011) consistent with CCAMLR Decision Rules. There are 4 ways in which the fishery could alter the availability of toothfish for type C killer whales in the Ross Sea:

(1) Local depletion by fishing within a season. It is known that fishing locally depletes toothfish abundance (catch rates fall when an area is fished) but those catch rates tend to increase back to the previous values by the start of next season (Hanchet, pers. com.). If fishing occurs in an area where killer whales forage, the availability of toothfish to killer whales is likely to be reduced within that season. At present, fishing is not allowed in water

shallower than 500 m or in some SSRUs, including 88.1M where McMurdo Sound is located in the southwestern Ross Sea. Spatial fishing closures have been proposed as one potential mechanism to eliminate the risk of localised depletion potentially affecting killer whales in preferred foraging habitats (Sharp & Watters, 2011).

(2) By reducing the number of toothfish recruits by the effect on toothfish spawning. There is no evidence in the stock assessments that toothfish recruitment has reduced from before the fishery started (though such an effect would only become apparent through the stock assessment about 10 years after it happened). The subadult survey in the southern Ross Sea was started in the 2011/12 season to monitor recruitment (Hanchet et al., 2012). An annual subadult survey is likely to be able to detect changes to recruitment about 5 years after the change occurred.

(3) By stock contraction (density-dependent effects). If some parts of the Ross Sea are more attractive to toothfish than others, reducing the abundance of toothfish in one area may affect the abundance in another. For example, fishing effort is currently concentrated on the Ross Sea slope and it is not known if reduced toothfish abundance on the slope will lead to reduced toothfish abundance over parts of the Ross Sea shelf, such as McMurdo Sound. Ongoing fishery characterisation (Stevenson et al., 2012) shows no change in size frequency of toothfish since the fishery began. Over time, the subadult survey will be able to monitor for changes in the spatial distribution of toothfish as the fishery progresses (Hanchet et al., 2012).

(4) By changing the movement patterns of large toothfish in the Ross Sea. The spatial distribution and movement patterns of toothfish in the Ross Sea region are not understood, and we do not know whether fishing will alter these. Large toothfish (>100 cm TL) are known to occur in the southern Ross Sea but why these fish occur there is not known. If these fish are the ones targeted by killer whales, it is not known to what extent their abundance (and availability to killer whales) will be affected by the fishery, especially considering that the abundance of large toothfish is likely to be reduced more than the abundance of smaller toothfish by the fishery.

## **5. RESEARCH PRIORITIES**

A summary of the methods used to study killer whales is given by Durban & Deecke (2011). These include photography, acoustics, aerial surveying, various methods to determine diet (including stable isotopes, fatty acids biomarkers, faecal examination), tagging and telemetering methods, and examination of bones and teeth from historic specimens. In this section we suggest the priorities for research to predict and monitor for changes to type C killer whales in the Ross Sea. These are presented in suggested order of priority.

### **5.1 Population size of type C killer whales in the Ross Sea**

The abundance of type C killer whales in the Ross Sea is not known, which limits any ability to assess population trends or variability. The establishment of a data series on the type C killer whales population trend is crucial. Two methods are likely to be useful for establishing population size of type C killer whales in the Ross Sea: photo-identification and aerial surveys (either from fixed-wing aircraft or helicopters).

**Photo-identification:** This is a robust method for individual-based monitoring over long time periods to understand life histories and population dynamics, long-term changes in social structure, and movement and residency patterns (Pitman 2011). Photo-identification data can also be used to estimate population abundance through mark-recapture models. R. Pitman and J. Durban (Protected Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, CA, USA) are currently conducting a mark-recapture study of type C killer whales in McMurdo Sound in order to estimate abundance and describe population structure. Field work in the 2012-13 summer resulted in photo-identification of the

majority of individuals in McMurdo Sound, and next season's field work will replicate this effort to provide the 'recapture' data and allow for a robust population estimate.

Photo-identification work by observers aboard toothfish fishing vessels in the Ross Sea can expand the area of data collection to assess movement patterns of individuals between areas and, if depredation occurs, determine the ecotype of killer whales responsible. Photo-identification work aboard toothfish fishing vessels near the Crozet islands lead to important new findings including the documentation that four pods of 35 individuals were involved in 80% of the fish depredation events, while other pods never interacted with the fishery (Pitman 2011, Tixier et al. 2010).

**Aerial surveys:** Standardise aerial surveys, such as line-transects with distance sampling methodology (Buckland et al. 2001), can produce robust population estimates of cetaceans. Aerial surveys over the known range of type C killer whales in the Ross Sea can be used to obtain a population estimate to compliment the mark-recapture efforts underway (See Photo-identification above), and to gain improved data on the distribution patterns and habitat preferences of type C whales. Aerial methods have already been used in the Ross Sea to confirm body lengths of type C killer whales (Pitman et al. 2007).

**Trend monitoring:** Methods used to collect data toward an abundance estimate, whether aerial surveys or photographic mark-recapture data, should be replicated periodically (i.e., yearly or every other year) to obtain population trend data.

## 5.2 Killer whale diet

Very little is known about the diet of type C killer whales in the Ross Sea. Their degree of dietary specialization and ability to vary between years or groups of whales is also unknown. Accessing Russian stomach sampling data is a high priority as this may give information on the species of fish found in the stomachs of type C killer whales (Berzin & Vladimirov 1983). To our knowledge, no historical tissue samples of type B or type C killer whales exist. If such samples were available however, these may be able to provide data on to what extent type C killer whale stable isotope signatures have changed over decadal scales.

**Biopsy samples:** Direct observations of killer whale feeding events are often rare or difficult, and qualitative inferences of diet through chemical analyses of tissue samples is likely to be most practical. An integrated picture of diet over the last year or so can be obtained through analysis of small biopsy samples collected by biopsy darts (Pitman 2011). A common practice is to infer the dietary preferences of animals through stable isotope ratios in a skin sample. Compound specific mass spectrometry (CSMS) of these tissues is likely to provide more nuanced information on feeding. The average or bulk nitrogen isotope signature of a tissue represents the mean of enriching ('trophic') and non-enriching ('source') amino acids and depends on amino acid composition. While  $\delta^{15}\text{N}$  enrichment of trophic amino acids (e.g., glutamate) indicates isotope enrichment from prey to predator, source amino acids (e.g., phenylalanine) preserve the nitrogen isotope enrichment at the base of the food web (McClelland & Montoya, 2002; Chikaraishi et al. 2009), and can be used to detect movement of predators between different regional food webs (Lorrain et al. 2009; Olson et al., 2010; Graham et al. 2010).

## 5.3 Killer whale movement and foraging

More empirical data at a range of spatial scales on the distribution patterns of type C killer whales in the Ross Sea are needed to obtain an improved understanding of their habitat use and foraging ecology.

**Focussed following:** “Focal follows” are an appropriate method to examine the fine-scale movement patterns of cetaceans that allows for the collection of simultaneous behaviour data (Altmann 1974, Mann 2000). With this method, scientists in a research vessel follow a group of whales, tracking their movements, while conducting scan-sampling at regular intervals (e.g., 5 mins) to record behaviour, group size, and habitat variation. Standardized observations of type C killer whale groups over long-periods (i.e., > 30 min) could provide information on foraging behaviour, prey type, and habitat variation. The vessel used during focal follows of type C killer whales in the Ross Sea could be equipped with an Acoustic Doppler Current Profiler (ADCP) to synoptically record data on available prey fields (e.g., Hazen et al. 2009). Fine-scale relationships between killer whale distribution, habitat variability, and prey availability could be derived from data. However, we note that the association of type C killer whales with dense pack ice in the Ross Sea may affect the feasibility of focal follows. Ice edge or helicopter observations may be more appropriate.

**Small-scale movements from tags:** To improve our understanding of type C killer whales foraging ecology in the Ross Sea, data on fine-scale distribution and habitat use patterns would be highly informative. These data would ideally provide information on small scales (including depth) to look at foraging behaviour and locations. Tags with acoustic arrays, and data loggers (with depth, compass accelerometer sensors) on the tags may provide insights into the type of prey being targeted. For instance, the D-tag, (M. Johnson, P. Tyack, Woods Hole Oceanographic Institution) is a suction cup tag deployed externally on the dorsal fin using crossbows or pneumatic rifles, which can stay on individuals for > 24 hrs. In addition to time, depth and location, the D-tag also includes a compass, accelerometer and two hydrophones to record the three-dimensional movements of tagged whales at very high resolutions with simultaneous recordings of the ambient noise of the tagged individual. The D-tag could be deployed on type C killer whales to record the vocal behaviour and fine-scale movements of individuals, above and below water, which can be used to describe foraging behaviour, habitat use patterns, and social organizations. Evidence of “herding” of fish schools or multiple passes through the same area would be indicative of feeding on small fishes like silverfish. Short, sporadic lunges or separate pursuits may be indicative of feeding on larger fishes like toothfish. However, D-tags must be recovered to access data and therefore tag loss may be significant in the McMurdo Sound region due to the tendency of type C killer whales to forage near and under the ice.

**Large scale movements:** Recent advances in satellite tag electronics have allowed tags to be developed that are small enough to be deployed externally on the dorsal fin using crossbows or pneumatic rifles, without the need for physical capture and restraint (Pitman 2011). These LIMPET tags can be used to monitor the movements of individual killer whales on the scale of months (e.g., Andrews et al. 2008, Durban & Pitman 2012), and data can also be processed in near real-time to enable field teams to find whales and gather more frequent and detailed observations (Pitman 2011). R. Pitman and J. Durban recently deployed satellite tags on type C killer whales in McMurdo Sound to record longer term and larger scale movement patterns, and will continue tagging type C killer whales in McMurdo Sound in the 2013–14 season, pending support for tags.

#### **5.4 Depth of Antarctic toothfish over the Ross Sea shelf**

To quantify habitat overlap of killer whales and toothfish, better information on the degree to which toothfish occur in the midwater rather than on or near the seabed is needed. New Zealand has initiated a tagging programme for toothfish that will record depth information for fish. No data are available at present. Vertical longlines from research vessels may also be useful in this regard.

## 5.5 Toothfish movement and spatial distribution

An improved understanding of the spatial distribution and movement patterns of toothfish in the Ross Sea region is needed to predict to what extent the fishery may affect the availability of toothfish as prey for killer whales.

## 5.6 Social and genetic structure of killer whales

**Genetic structure:** de Bruyn et al. (2013) argue that social and genetic structure are key to understanding ecotypes and interconnectivity between groups of killer whales. Genetic analysis of biopsy material can be used to (1) study reproductive connectivity within the Ross Sea killer whale populations, and (2) perform a genetic mark-recapture analysis.

**Acoustic data:** Acoustic data has been frequently used to identify killer whale populations (ecotypes) and groups within populations based on pod- or family-specific dialects. Killer whales often produce stereotyped repertoires of sounds that can be monitored and used to differentiate groups and document occupancy patterns. Richlen & Thomas (2008) provided the only detailed description of purported type C killer whale vocalisations and acoustics in the Ross Sea. Although no other acoustic studies have been published on other Antarctic ecotypes (de Bruyn et al. 2013), this initial study indicates that ecotypes in the Ross Sea may also employ specific dialects that can be used to identify ecotypes and occurrence patterns. Acoustic data can also reveal foraging events due to changes in vocal patterns (Pitman 2011). An acoustic logger array could be deployed in the Ross Sea to determine the occupancy patterns of different killer whale ecotypes across the region and potentially identify foraging events.

## 6. CONCLUSIONS

1. Killer whale population ecology (high consumption rates, low abundances, low production rates, often specialised diets, unknown potential for innovation) means that they are particularly vulnerable to changes in the ecosystem. It is also possible that changes to killer whale feeding can affect the structure and stability of whole ecosystems. Both these are relevant to assessing risks with respect to CCAMLR Article II(3)b and c.
2. Basic information necessary to evaluate reliably the risk to type C killer whales in the Ross Sea from the toothfish fishery is lacking. If toothfish are (or were recently) a major prey item for type C killer whales, either at a local or Ross Sea scale, it is precautionary to assume that reducing the availability of toothfish carries a significant risk of adversely affecting their ecological viability.
3. At present, it is not known to what extent toothfish are consumed by type C killer whales in particular areas (e.g. McMurdo Sound) or in the Ross Sea in general. At present, the balance of evidence suggests that toothfish are likely to form a significant part of the diet type C killer whales in McMurdo Sound in summer. It is not possible to say whether toothfish are an important prey item to type C killer whales in other locations of the Ross Sea shelf (e.g. Terra Nova Bay, Bay of Whales, Sulzberger Bay) or at the scale of the Ross Sea (i.e. including the whole Ross Sea continental shelf and slope).
4. Basic information necessary to evaluate reliably the risk to type C killer whales in the Ross Sea from the toothfish fishery is needed, including: prey type, foraging behaviour, abundance (and trends) and demographics. Suggested methods are biopsy sampling (analysis for isotopes, fatty acids, genetic tagging), focal-follows (e.g. from boat, ice-

edge, helicopter), photographic sightings, tagging (satellite, suction-cup tags), and aerial and acoustic surveys.

## 7. ACKNOWLEDGEMENTS

This work was part-funded by the New Zealand Ministry of Science and Innovation project C01X1001 (“Protecting Ross Sea Ecosystems”) (Pinkerton, Torres) and by Gateway Antarctica (Eisert). Pitman and Durban are supported by NSF (US), the Southern Ocean Research Partnership (SORP), NOAA/NMFS, and the National Geographic Society. Richard O’Driscoll (NIWA) provided information on silverfish and myctophid distributions and silverfish density. Sophie Mormede (NIWA) provided preliminary SPM results. The New Zealand Antarctic Fisheries Working Group is thanked for input to an earlier draft.

## 8. REFERENCES

- Agnew, D.J. (1997). The CCAMLR Ecosystem Monitoring Programme. *Antarctic Science* 9(3): 235-242.
- Ainley, D. (1985). The biomass of birds and mammals in the Ross Sea, Antarctica. *In*: Siegfried, W.R.; Condy, P.R.; Laws, R.M. (eds). Antarctic nutrient cycles and food webs, pp. 498-515. Springer-Verlag, Berlin.
- Ainley, D.; Ballard, G.; Dugger, K.M. (2006). Competition among penguins and cetaceans reveals trophic cascades in the Ross Sea, Antarctica. *Ecology* 87: 2080-2093.
- Ainley, D.; Ballard, G.; Weller, J. (2011). Ross Sea biodiversity, Part I: Validation of the 2007 CCAMLR bioregionalization workshop results towards including the Ross Sea in a representative network of marine protected areas in the Southern Ocean. *CCAMLR document*. WG-EMM-10/11.
- Ainley, D.G.; Ballard, G. (2012). Trophic Interactions and Population Trends of Killer Whales (*Orcinus orca*) in the Southern Ross Sea. *Aquatic Mammals* 38(2): 153-160.
- Ainley, D.G.; Ballard, G.; Olmastroni, S. (2009). An apparent decrease in the prevalence of 'Ross Sea killer whales' in the southern Ross Sea. *Aquatic Mammals* 35(3): 334-346.
- Ainley, D.G.; Nur, N.; Eastman, J.T.; Ballard, G.; Parkinson, C.L.; Evans, C.W.; DeVries, A.L. (2012). Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972–2011. *Fish and Fisheries*.
- Ainley, D.G.; Siniff, D.B. (2009). The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. *Antarctic Science* 21(4): 317-327.
- Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* 49: 227-276.
- Andrews, R.; Pitman, R.; Ballance, L. (2008). Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biology* 31(12): 1461-1468.

- Andriashev, A.P. (1970). Cryopelagic fishes of the Arctic and Antarctic and their significance in polar ecosystems. *In*: Holdgate, M.W. (ed.). Antarctic Ecology, pp. 297-304. Academic, London.
- Arrigo, K.R.; van Dijken, G.L. (2003). Impact of iceberg C-19 on Ross Sea primary production. *Geophysical Research Letters* 30(16).
- Ashford, J.R.; Rubilar, P.S.; Martin, A.R. (1996). Interactions between cetaceans and longline fishery operations around South Georgia. *Marine Mammal Science* 12(3): 452-457.
- Baird, R.W. (2011). Predators, prey and play. *Journal of the American Cetacean Society* 40(1): 54-57.
- Baird, R.W.; Hanson, M.B.; Dill, L.M. (2005). Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 83(2): 257-267.
- Baker, A.N. (1983). Whales and dolphins of New Zealand and Australia: An identification guide. Victoria University Press, Wellington, NZ. p.
- Baird, R.W. (2002). Killer whales of the world – natural history and conservation. Voyageur Press, Stillwater, Minnesota.
- Barrett-Lennard, L. (2011). Killer Whale Evolution. *Journal of the American Cetacean Society* 40(1): 48-53.
- Barrett-Lennard, L.; K. Heise (2011). Killer whale conservation: the perils of life at the top of the food chain. *Journal of the American Cetacean Society* 40(1): 58-62.
- Barrett-Lennard, L.G.; Ford, J.K.B.; Heise, K.A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour* 51: 553-565.
- Berzin, A.A.; Vladimirov, V.L. (1983). Novyi vid kosatki (Cetacea, Delphinidae) iz vod Antarktiki. *Zool. Zh.* 62(2): 287-295. [Translated in 1984 as "A new species of killer whale (Cetacea, Delphinidae) from Antarctic waters" by S. Pearson, National Marine Mammal Laboratory, Seattle, WA 98115, USA].
- Blaxter, K.L. (1989). Energy metabolism in animals and man. Cambridge University Press, Cambridge, United Kingdom. p.
- Buckland, S.T.; Anderson, D.R.; Burnham, K.P.; Laake, J.L.; Borchers, D.L.; Thomas, L. (2001). Introduction to Distance Sampling: Estimating abundance of biological populations. Oxford University Press Inc., New York. 432 p.
- Burns, J.M.; Trumble, S.J.; Castellini, M.A.; Testa, J.W. (1998). The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biology* 19(4): 272-282.
- Bury, S.; Pinkerton, M.H.; Thompson, D.R.; Hanchet, S.; Brown, J.; Vorster, I. (2008). Final Report ANT200603-OBJ1: Trophic study of Ross Sea Antarctic toothfish (*Dissostichus mawsoni*) using carbon and nitrogen stable isotopes.



Caut, S.; Laran, S.; Garcia-Hartmann, E.; Das, K. (2011). Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). *Journal of Experimental Biology* 214: 538-545.

CEMP (2004). CCAMLR Ecosystem Monitoring Programme, CCAMLR Document, Hobart, Australia. Pp 268.

Cherel, Y.; Charrassin J.-B.; Handrich, Y. (1993). Comparison of body reserve buildup in prefasting chicks and adults of king penguins (*Aptenodytes patagonicus*). *Physiological Zoology* 66(5): 750-770.

Chikaraishi, Y.; Ogawa, N.O.; Kashiwama, Y.; Takano, Y.; Suga, H.; Tomitani, A.; Miyashita, H.; Kitazato, H.; Ohkouchi, N. (2009). Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnology and Oceanography-Methods* 7: 740-750.

Clark, J.M.; Agnew, D.J. (2010). Estimating the impact of depredation by killer whales and sperm whales on longline fishing for toothfish (*Dissostichus eleginoides*) around south georgia. *CCAMLR Science* 17: 163-178.

Cockrem, J.F.; Potter, M.A.; Candy, E.J. (2006). Corticosterone in relation to body mass in Adelie penguins (*Pygoscelis adeliae*) affected by unusual sea ice conditions at Ross Island, Antarctica. *General and Comparative Endocrinology* 149(3): 244-252.

Connan, M.; Mayzaud, P.; Duhamel, G.; Bonnevie, B.T.; Cherel, Y. (2010). Fatty acid signature analysis documents the diet of five myctophid fish from the Southern Ocean. *Marine Biology* 157: 2303-2316.

Constable, A.J. (2006). Setting management goals using information from predators. In: Top predators in marine ecosystems: their role in monitoring and management. Boyd, I.L. S. Wanless, C. J. Camphuysen (eds) Conservation Biology 12. Cambridge University Press. 324-346.

Davis, R.W.; Fuiman, L.A.; Williams, T.M.; Collier, S.O.; Hagey, W.P.; Kanatous, S.B.; Kohin, S.; Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283(5404): 993-996.

de Bruyn, P.J.N.; Tosh, C.A.; Terauds, A. (2013). Killer whale ecotypes: is there a global model? *Biological Reviews* 88(1): 62-80.

Domenici, P.; Batty, R.S.; Similä, T. (2000). Spacing of wild schooling herring while encircled by killer whales. *Journal of Fish Biology* 57: 831-836.

Donnelly, J.; Torres, J.J.; Hopkins, T.L.; Lancraft, T.M. (1990). Proximate composition of Antarctic mesopelagic fishes. *Marine Biology* 106(1): 13-23.

Dunn, A.; Rasmussen, S. (2008). Development of a spatially explicit age-structured statistical catch-at-age population dynamics model for modelling movement of Antarctic toothfish in the Ross Sea. CCAMLR document WG-SAM-08/14, Hobart, Australia.

Dunn, A.; Mormede, S.; Hanchet, S.M. (2011). Toothfish, mid-year plenary. Ministry of Fisheries, New Zealand. Pp 24.

- Durban, J.; Deecke, V. (2011). How Do We Study Killer Whales? *Journal of the American Cetacean Society* 40(1): 6-14.
- Durban, J.W.; Pitman, R.L. (2012). Antarctic killer whales make rapid, round-trip movements to subtropical waters: evidence for physiological maintenance migrations? *Biology Letters* 8(2): 274-277.
- Dwyer, S.L.; Visser, I.N. (2011). Cookie Cutter Shark (*Isistius* sp.) Bites on Cetaceans, with Particular Reference to Killer Whales (Orca) (*Orcinus orca*). *Aquatic Mammals* 37(2): 111-138.
- Eastman, J.T. (1993). Antarctic fish biology: Evolution in a unique environment. San Diego: Academic Press.
- Eisert, R.; Pinkerton, M.H.; Newsome, S.D.; Oftedal, O.T. (2013). 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. CCAMLR document WG-EMM-13/xx, Hobart, Australia.
- Estes, J.A.; Williams, T.M.; Doak, D.F. (1998). Killer Whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473-475.
- Fenaughty, J.M.; Stevens, D.W.; Hanchet, S.M. (2003). Diet of the Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (subarea 88.1). *Ccamlr Science* 10: 113-123.
- Ford, J.K.B. (2011). Killer whales of the Pacific northwest coast: from pest to paragon. *Journal of the American Cetacean Society* 40(1): 15-23.
- Fuiman, L.A.; Davis, R.W.; Williams, T.M. (2002). Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology* 140(4): 815-822.
- Gill, P.C.; Thiele, D. (1997). A winter sighting of killer whales (*Orcinus orca*) in Antarctic sea ice. *Polar Biology* 17(5): 401-404.
- Graham, B.; Koch, P.; Newsome, S.D.; McMahon, K.; Aurioles, D. (2010). Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: J. West, G. Bowen, T. Dawson, K. Tu, (Eds.) *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping*. Springer-Verlag, Berlin. Pp 299-318.
- Gutt, J. (2002). The Antarctic ice shelf: an extreme habitat for notothenioid fish. *Polar Biology* 25(4): 320-322.
- Guinet, C. (1992). Comportement de chasse des orques (*Orcinus orca*) autour des îles Crozet. *Canadian Journal of Zoology* 70: 1656-1667.
- Guinet, C.; Barrett-Lennard, L.G.; Loyer, B. (2000). Co-ordinated attack behavior and prey sharing by killer whales at Crozet Archipelago: strategies for feeding on negatively-buoyant prey. *Marine Mammal Science* 16: 829-834.

- Guinet, C.; Tixier, P. (2011). Crozet killer whales: A remote but changing environment. *Journal of the American Cetacean Society* 40: 33-38.
- Hanchet, S.M.; Rickard, G.J.; Fenaughty, J.M.; Dunn, A.; Williams, M.J.H. (2008). A hypothetical life cycle for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region. *Ccamlr Science* 15: 35-53.
- Hanchet, S.M.; Mormede, S.; Parker, S.; Dunn, A.; Jo, H.-S. (2012). Results of a CCAMLR-sponsored research survey to monitor abundance of pre-recruit Antarctic toothfish in the southern Ross Sea, February 2012. CCAMLR document WG-FSA-12/41, Hobart, Australia.
- Hazen, E.L.; Friedlaender, A.S.; Thompson, M.A.; Ware, C.R.; Weinrich, M.T.; Halpin, P.N.; Wiley, D.N. (2009). Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology Progress Series* 395: 75-89.
- Hucke-Gaete, R.; Moreno, C.A.; Arata, J.; Blue Whale, C. (2004). Operational interactions of sperm whales and killer whales with the Patagonian toothfish industrial fishery off southern Chile. *CCAMLR Science* 11: 127-140.
- Innes, S.; Lavigne, D.M.; Kovacs, K.M. (1987). Feeding rates of seals and whales. *Journal of Animal Ecology* 56: 115-130.
- Innes, S.; Lavigne, D.M.; Earle, W.M.; Kovacs, K.M. (1986). Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Marine Mammal Science* 2: 227-229.
- Kim, S.L.; Conlan, K.; Malone, D.P.; Lewis, C.V. (2005). Possible food caching and defence in the Weddell seal: observations from McMurdo Sound, Antarctica. *Antarctic Science* 17(1): 71-72.
- Kock, K-H. (1992). Antarctic fish and fisheries. New York: Cambridge University Press.
- Kooyman, G.L.; Ainley, D.G.; Ballard, G.; Ponganis, P.J. (2007). Effects of giant icebergs on two emperor penguin colonies in the Ross Sea, Antarctica. *Antarctic Science* 19(1): 31-38.
- Krahn, M.M.; Pitman, R.L.; Burrows, D.G.; Herman, D.P.; Pearce, R.W. (2008). Use of chemical tracers to assess diet and persistent organic pollutants in Antarctic Type C killer whales. *Marine Mammal Science* 24(3): 643-663.
- Kriete, B. (1995). Bioenergetics in the killer whale, *Orcinus orca*. Ph.D., University of British Columbia.
- Kvadsheim, P.H.; Folkow L.P.; Blix, A.S. (1996). Thermal conductivity of minke whale blubber. *Journal of Thermal Biology* 21(2): 123-128.
- La Mesa, M.; Eastman, J.T. (2012). Antarctic silverfish: life strategies of a key species in the high-Antarctic ecosystem. *Fish and Fisheries* 13(3): 241-266.
- Lauriano, G.; Fortuna, C.M.; Vacchi, M. (2007a). Observation of killer whale (*Orcinus orca*) possibly eating penguins in Terra Nova Bay, Antarctica. *Antarctic Science* 19(1): 95-96.
- Lauriano, G.; Vacchi, M.; Ainley, D.; Ballard, G. (2007b). Observations of top predators foraging on fish in the pack ice of the southern Ross Sea. *Antarctic Science* 19(4): 439-440.

- LeDuc, R.G.; Robertson, K.M.; Pitman, R.L. (2008). Mitochondrial sequence divergence among Antarctic killer whale ecotypes is consistent with multiple species. *Biology Letters* 4(4): 426-429.
- Lenky, C.; Eisert, R.; Oftedal, O.; Metcalf, V. (2012). Proximate composition and energy density of nototheniid and myctophid fish in McMurdo Sound and the Ross Sea, Antarctica. *Polar Biology* 35(5): 717-724.
- Libralato, S.; Christensen, V.; Pauly, D. (2006). A method for identifying keystone species in food web models. *Ecological Modelling* 195: 153-171.
- Lockyer, C. (1991). Body composition of the sperm whale, *Physeter catodon*, with special reference to the possible functions of fat depots. Report of Marine Research Institute, Reykjavik, Iceland.
- Lorrain, A.; Graham, B.; Menard, F.; Popp, B.; Bouillon, S.; van Breugel, P.; Cherel, Y. (2009). Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. *Marine Ecology Progress Series* 391: 293-306
- MacLeod, C.D.; Reidenberg, J.S.; Weller, M.; Santos, M.B.; Herman, J.; Goold, J.; Pierce, G.J. (2007). Breaking symmetry: The marine environment, prey size, and the evolution of asymmetry in cetacean skulls. *Anatomical Record-Advances in Integrative Anatomy and Evolutionary Biology* 290(6): 539-545.
- Mann, J. (2000). Unraveling the dynamics of social life: Long-term studies and observational methods. In: Mann, J.; Connor, R.C.; Whitehead, H. (eds). *Cetacean Societies: Field studies of dolphins and whales*, pp. 45-64. University of Chicago Press, Chicago and London.
- Mårtensson, P. E., E. S. Nordøy, et al. (1994). Digestibility of krill (*Euphausia superba* and *Thysanoessa* sp.) in minke whales (*Balaenoptera acutorostrata*) and crab-eater seal (*Lobodon carcinophagus*). *British Journal of Nutrition* 72(5): 713-716.
- Matkin, C.; Durban, J. (2011). Killer whales in Alaskan waters. *Journal of the American Cetacean Society* 40(1): 24-29.
- McClelland, J.W.; Montoya, J.P. (2002). Trophic relationships and the nitrogen isotopic composition of amino acids. *Ecology* 83: 2173-2180
- Misund, O.A. (1993). Dynamics of moving masses: variability in packing density, shape, and size among herring, sprat, and saithe schools. *ICES Journal of Marine Science* 50: 145-150.
- Moir Clark, J.; Agnew, D.J. (2010). Estimating the impact of depredation by killer whales and sperm whales on longline fishing for toothfish (*Dissostichus eleginoides*) around South Georgia. *CCAMLR Science* 17: 163-178.
- Moore, J.E. (2012). Management reference points to account for direct and indirect impacts of fishing on marine mammals. *Marine Mammal Science*, in press.
- Morin, P.A.; Archer, F.I.; Foote, A.D.; Vilstrup, J.; Allen, E.E.; Wade, P.; Durban, J.; Parsons, K.; Pitman, R.; Li, L.; Bouffard, P.; Nielsen, S.C.A.; Rasmussen, M.; Willerslev, E.; Gilbert, M.T.P.; Harkins, T. (2010). Complete mitochondrial genome phylogeographic

- analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research* 20(7): 908-916.
- Mormede, S.; Dunn, A.; Hanchet, S. (2013). Development of a spatial population model for Antarctic toothfish in the Ross Sea region. CCAMLR document WG-SAM-13/xx, Hobart, Australia.
- Mormede, S.; Dunn, A.; Hanchet, S.M. (2011). Assessment models for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea for the years 1997–98 to 2010–11. CCAMLR document WG-FSA-11/42, Hobart, Australia.
- Near, T.; Russo, S.; Jones, C.; DeVries, A. (2003). Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (Perciformes: Nototheniidae). *Polar Biology* 26(2): 124-128.
- Noren, D.P. (2011). Estimated field metabolic rates and prey requirements of resident killer whales. *Marine Mammal Science* 27(1): 60-77.
- Nottestad, L.; Simila, T. (2001). Killer whales attacking schooling fish: why force herring from deep water to the surface? *Marine mammal Science*, 17(2): 343-352.
- O'Driscoll, R.L.; Macaulay, G.J.; Gauthier, S.; Pinkerton, M.; Hanchet, S. (2011). Distribution, abundance and acoustic properties of Antarctic silverfish (*Pleuragramma antarcticum*) in the Ross Sea. *Deep-Sea Research Part II-Topical Studies in Oceanography* 58(1-2): 181-195.
- Olson, P. A., P. Ensor, and S. Kuningas. 2012. Observations of killer whales off East Antarctica, 82°-95°E, in 2009. *Journal of Cetacean Research and Management* 12: 61–64.
- Olson, R.J.; Popp, B.N.; Graham, B.S.; López-Ibarra, G.A.; Galván-Magaña, F.; Lennert-Cody, C.E.; Bocanegra-Castillo, N.; Wallsgrove, N.J.; Gier, E.; Alatorre-Ramírez, V.; Ballance, L.T.; Fry, B. (2010). Food web inferences of stable isotope spatial patterns in copepods and yellowfin tuna in the pelagic eastern Pacific Ocean. *Progress in Oceanography* 86: 124-138
- Pimper, L.E.; Baker, C.S.; Goodall, R.N.P.; Olavarria, C.; Remis, M.I. (2010). Mitochondrial DNA variation and population structure of Commerson's dolphins (*Cephalorhynchus commersonii*) in their southernmost distribution. *Conservation Genetics* 11(6): 2157-2168.
- Pinkerton, M.H.; Bradford-Grieve, J.; Hanchet, S. (2010a). A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Science* 17: 1-31.
- Pinkerton, M.H.; Cummings, V.; Bury, S.J.; Brown, J.; Forman, J.S. (2010b). Trophic relationships in the Ross Sea sector of Antarctica: information from stable isotope and gut contents analysis on the CAMLR-IPY survey 2008. *Report to Ministry of Fisheries*. project IPY200701 Obj10.
- Pinkerton, M.H.; Dunn, A.; Hanchet, S. (2007). Ecological risk management and the fishery for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. *CCAMLR document*. WG-EMM-07/24.

- Pinkerton, M.H.; Forman, J.; Bury, S.J.; Brown, J.; Horn, P.; O'Driscoll, R.L. (2013). Diet and trophic niche of Antarctic silverfish *Pleuragramma antarcticum* in the Ross Sea, Antarctica. *Journal of Fish Biology* 82(1): 141-164.
- Pinkerton, M.H.; Dunn, A.; Hanchet, S.M. (2008). Trophic overlap of Weddell seals (*Leptonychotes weddelli*) and Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea, Antarctica. CCAMLR document WG-EMM-08/43, Hobart, Australia.
- Pitman, R.L. (2011). Killer whales: The top, top predator. *Whalewatcher*, 1-67 p.
- Pitman, R.L.; Dutton, P.H. (2004). Killer whale predation on a leatherback turtle in the Northeast Pacific. *Pacific Science* 58: 497-498.
- Pitman, R.L.; Ensor, P. (2003). Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management* 5(2): 131-139.
- Pitman, R.; Durban, J.; Greenfelder, M.; Guinet, C.; Jorgensen, M.; Olson, P.; Plana, J.; Tixier, P.; Towers, J. (2011). Observations of a distinctive morphotype of killer whale (*Orcinus orca*), type D, from subantarctic waters. *Polar Biology* 34(2): 303-306.
- Pitman, R.L.; Perryman, W.L.; LeRoi, D.; Eilers, E. (2007). A dwarf form of killer whale in Antarctica. *Journal of Mammalogy* 88(1): 43-48.
- Place, A.R. (1992). Comparative aspects of lipid digestion and absorption: physiological correlates of wax ester digestion. *American Journal of Physiology* 263(3): R464-R471.
- Post, D.M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83(3): 703-718.
- Ramos, R.; González-Solís, J. (2012). Trace me if you can: The use of intrinsic biogeochemical markers in marine top predators. *Frontiers in Ecology and the Environment* 10: 258-266.
- Raubenheimer, D.; Simpson, S.J.; Mayntz, D. (2009). Nutrition, ecology and nutritional ecology: toward an integrated framework. *Functional Ecology* 23(1): 4-16.
- Raymond, J.A. (1975). Fishing for Antarctica's largest fish, the Antarctic cod. *Marine Technical Science Journal* 9: 32-35.
- Reid, K.; Croxall, J.P.; Briggs, D.R.; Murphy, E.J. (2005). Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES Journal of Marine Science* 62(3): 366-373.
- Richlen, M.F.; Thomas, J.A. (2008). Acoustic behavior of Antarctic killer whales (*Orcinus orca*) recorded near the ice edge of McMurdo Sound, Antarctica. *Aquatic Mammals* 34(4): 448-457.
- Robinson, N.J.; Williams, M.J.M. (2012). Iceberg-induced changes to polynya operation and regional oceanography in the southern Ross Sea, Antarctica. *Antarctic Science* 24(5): 514-526.

Roche, C.; Guinet, C.; Gasco, N.; Duhamel, G. (2007). Marine mammals and demersal longline fishery interactions in Crozet and Kerguelen Exclusive Economic Zones: An assessment of depredation levels. *CCAMLR Science* 14: 67-82.

Schulman-Janiger, A.; Black, N.; Ternullo, R. (2011). Killer whales of California. *Journal of the American Cetacean Society* 40(1): 46-47.

Seibel, B.A.; Dierssen, H.M. (2003). Cascading trophic impacts of reduced biomass in the Ross Sea, Antarctica: Just the tip of the iceberg? *Biological Bulletin* 205(2): 93-97.

Sharp, B.R.; Watters, G.M. (2011). Marine Protected Area planning by New Zealand and the United States in the Ross Sea region. CCAMLR document WS-MPA-11/25, Hobart, Australia.

Sigurjonsson, J.; Vikingsson, G.A. (1997). Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. *Journal of Northwest Atlantic Fishery Science* 22: 271-287.

Simila, T.; Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology* 71: 1494-1499.

Springer, A.M.; Estes, J.A.; van Vliet, G.B.; Williams, T.M.; Doak, D.F.; Danner, E.M.; Forney, K.A.; Pfister, B. (2003). Sequential megafauna collapse in the North Pacific: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Science* 100(21): 12223-12228.

Stevens, D.W.; Dunn, M.R.; Pinkerton, M.H.; Forman, J.S. (2012). Diet of Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea region, Antarctica. CCAMLR document. WG-FSA-12/52.

Stevenson, M.L.; Hanchet, S.M.; Mormede, S.; Dunn, A. (2012). A characterisation of the toothfish fishery in Subareas 88.1 and 88.2 from 1997/98 to 2011/12. CCAMLR document WG-FSA-12/42, Hobart, Australia.

Sweeting, C.J.; Barry, J.; Barnes, C.; Polunin, N.V.C.; Jennings, S. (2007). Effects of body size and environment on diet-tissue  $\delta^{15}\text{N}$  fractionation in fishes. *Journal of Experimental Marine Biology and Ecology* 340, 1–10.

Tixier, P.; Gasco, N.; Duhamel, G.; Viviant, M.; Authier, M.; Guinet, C. (2010). Interactions of Patagonian toothfish fisheries with killer and sperm whales in the Crozet Islands exclusive economic zone: an assessment of depredation levels and insights on possible mitigation strategies. *CCAMLR Science* 17: 179-195.

Trites, A.W. (2003). Food webs in the ocean: who eats whom and how much? In: Responsible Fisheries in the Marine Ecosystem, M. Sinclair; G. Valdimarsson (eds.), FAO, 125-141.

Ulanowicz, R.E.; Puccia, C.J. (1990). Mixed trophic impacts in ecosystems. *Coenoses* 5: 7-16.

Van dam, R.P.; Kooyman, G.L. (2004). Latitudinal distribution of penguins, seals and whales observed during a late autumn transect through the Ross Sea. *Antarctic Science* 16(3): 313:318.

Williams, T.M.; Estes, J.A.; Doak, D.F.; Springer, A.M. (2004). Killer appetites: Assessing the role of predators in ecological communities. *Ecology* 85(12): 3373-3384.

Yeon, I.; Jo, H.S.; Lim, C.; Hanchet, S.; Lee, D.W.; Kang, C.K. (2012). Fatty acid analysis to infer diet of Antarctic toothfish caught in February 2012 in the southern Ross Sea. *CCAMLR document*. WG-FSA-12/61.

Yukhov, V.L. (1971). The range of *Dissostichus mawsoni* Norman and some features of its biology. *Journal of Ichthyology* 11: 8-18.

Zhao, L.Y.; Castellini, M.A.; Mau, T.L.; Trumble, S.J. (2004). Trophic interactions of Antarctic seals as determined by stable isotope signatures. *Polar Biology* 27(6): 368-373.