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An Apparent Decrease in the Prevalence of "Ross Sea Killer Whales" in the Southern Ross Sea

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Abstract

Killer whales *(Orcinus orca)*, both ecotype-B and -C, are important to the Ross Sea, Antarctic ecosystem. The ecotype-C is referred to as "Ross Sea [RS] killer whale." Herein, we review data on occurrence patterns and diet of RS killer whales and present new information on numbers observed in the southwestern Ross Sea, 2002-2003 to 2008-2009 austral summers. These "resident" whales appear to feed principally on fish, including the large Antarctic toothfish (*Dissostichus mawsoni*). On the basis of sea watches from Cape Crozier, Ross Island, sighting frequency and average group size appears to have decreased; prevalence as indicated by casual observations from helicopter pilots flying over the area on a daily basis has also decreased in nearby McMurdo Sound. Consistent with a decrease in the catch-per-unit-effort of scientific fishing for toothfish in McMurdo Sound, we suggest and review evidence that the change in RS killer whale numbers in the southern Ross Sea is related to an industrial fishery-driven, density-dependent northward contraction of the toothfish stock and not to changes in the physical (and, in turn, biological) environment. We surmise that in this closely coupled foodweb, composed of very abundant penguin, seal, and whale components, loss of the toothfish option for RS killer whales would force more direct competition with other predators for capture of the smaller-fish prey. Therefore, we propose, the RS killer whales have opted to move elsewhere, in a scenario consistent with that of the Pacific coast of Canada, where numbers of resident killer whales have decreased following the loss of large fish as a prey choice.

Key Words: killer whale, *Orcinus orca*, Antarctic toothfish, *Dissostichus mawsoni,* Antarctic silverfish, B15 iceberg, climate change, fish depletion, Ross Sea

Introduction

Based on recent photogrammetric and observational studies, a diminutive form of the killer whale (*Orcinus orca*) has been described for the high latitude of the Southern Ocean (Pitman et al., 2007) and is the form that Pitman & Ensor (2003) referred to as ecotype-C. According to the latter authors, the form that they describe is possibly the same one Russian biologists described as *O. o. glacialis* in the early 20th century, the type specimen for which has been lost; therefore, this taxonomic conundrum likely never will be resolved. Recent genetic work supports ecotype-C as being a separate species—yet to be officially recognized (LeDuc et al., 2008)—and is one of three forms of killer whale that frequent Antarctic waters (see Pitman & Ensor, 2003, for descriptions). R. L. Pitman (pers. comm.) refers to it as the "Ross Sea killer whale" (hereafter, RS killer whale) owing to its high abundance and long history of observation there (beginning with James Clark Ross in the mid-19th century). Herein, we present information on the recent status of this form in the southern Ross Sea.

The RS killer whale, at an average length of 5.6 m for adult males, is 2 to 3 m smaller than ecotype-A; it appears to be smaller, too, than ecotype-B, but further comparison awaits additional work on measurements of ecotype-B (Pitman et al., 2007; R. L. Pitman, pers. comm.). According to Pitman & Ensor (2003), "Type-C [RS] penetrated further into the ice than type-B and regularly occurred in dense pack-ice, along leads in fast ice and in polynyas" (p. 6). These authors further characterized this ecotype as feeding mainly on fish, which is consistent with the lifestyle of the "resident" populations of killer whale that inhabit waters elsewhere (see review in Richlen & Thomas, 2008). Indeed, RS killer whales fitted with satellite transponders in McMurdo Sound (Figure 1) in late January remained in the same general vicinity until mid-March (Andrews et al., 2008). This is quite

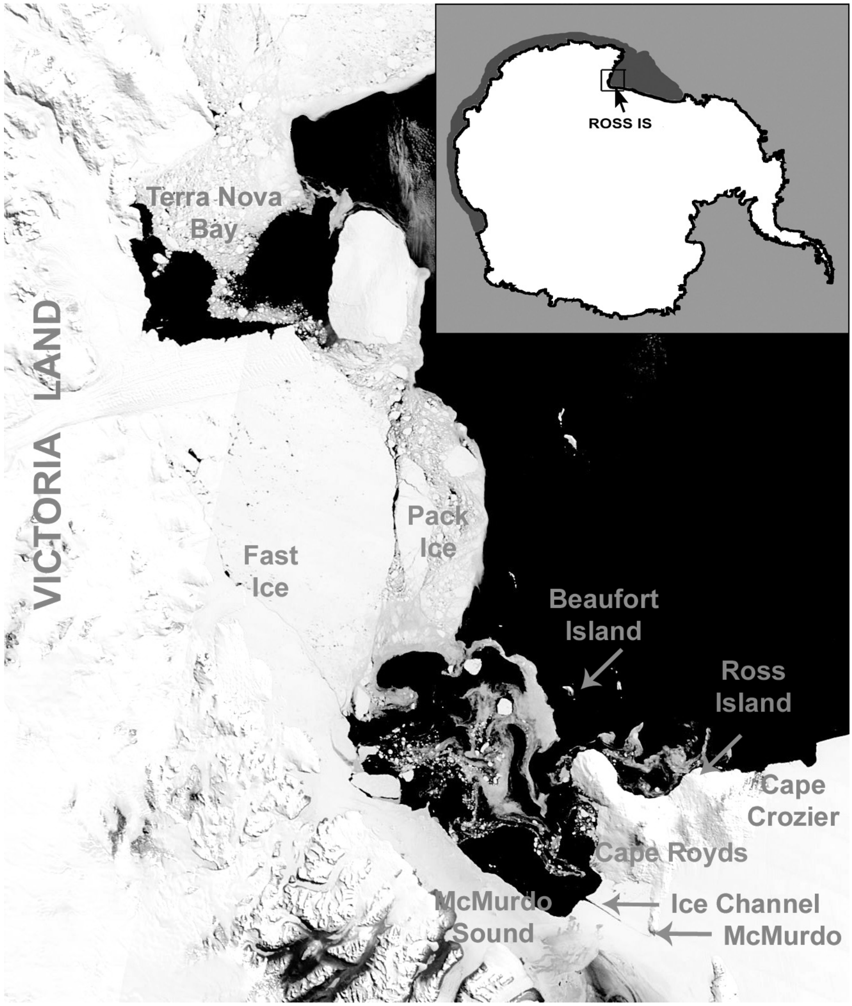

Figure 1. Southwest Ross Sea, showing McMurdo Sound bounded by Ross Island to the east and Victoria Land to the west, the ice channel through fast ice in the southern Sound, and other Ross Sea locations mentioned in the text; the insert shows location of the study area. Darker ocean shading indicates the known area of occurrence of Ross Sea killer whales.

unlike a pod of ecotype-B killer whales (i.e., seal eating, "transient type"; Pitman & Ensor, 2003), which, after marking in the same locality, moved rapidly north in the Ross Sea, pausing briefly at a number of emperor penguin (*Aptenodytes forsteri*) colony sites along Victoria Land. Such sites of extensive fast ice would also be occupied by Weddell seals (*Leptonychotes weddelli*), a known prey of ecotype-B killer whales in the Antarctic (Visser et al., 2008; DGA, pers. obs.).

Herein, after a review of what is known of the ecology of RS killer whales in the Ross Sea, data on variability in relative abundance from 2002-2003 to 2008-2009 are reported for the southern Ross Sea. Possible reasons for an apparent decrease in prevalence and apparent group size of this ecotype are provided; this pattern is not exhibited by ecotype-B killer whales in the study area.

Temporal and Spatial Occurrence Patterns of Ross Sea Killer Whales

Current confirmed sightings indicate that the RS killer whale is concentrated in one quadrat of the Southern Ocean—the one in which the most sea ice remains year round (Gloersen et al., 1992; Figure 1). This form mainly has been sighted in the Ross Sea (waters overlying the continental shelf, 165° W to 165° E; see Ainley, 2009; many hundreds of sightings) and west along the Adélie Land to Wilkes Land (145° E) coasts of East Antarctica. Smaller numbers of confirmed sightings exist farther west to Prydz Bay

(80° E). Further west still (e.g., Weddell, Scotia, Bellingshausen, and Amundsen Seas), confirmed sightings of RS killer whales do not exist, even near to bases where scores of killer whales have been seen and identified (Pitman & Ensor, 2003; R. L. Pitman, pers. comm.).

The easternmost sighting in waters of West Antarctica may be a pod of 24 RS killer whales observed at Cape Colbeck on the eastern boundary of the Ross Sea in February 1994 (164° W; Ainley et al., 2007); while this large group size is suggestive of RS killer whale, it is not conclusive (R. L. Pitman, pers. comm.). An intensive survey of the Amundsen and Bellingshausen Seas during February and March resulted in no killer whales being seen there (Ainley et al., 2007).

Biologists on the British polar expeditions in the first decade of the 20th century categorized the killer whale as "undoubtedly the commonest cetacean in the Ross Sea" (Lillie, 1915, p. 120). The ships that were involved in sightings mainly moved along the pack ice edge near the Victoria Land coast and around Ross Island during January and February (Figure 1); the whales were said to have been observed "near the ship almost every day." Sightings of 50 to 100 whales in the Bay of Whales (170° W) during early expeditions appear to have been RS killer whales by virtue of the numbers and behavior reported (see below). Although his opinion was affected by where these expeditions spend most of their time (i.e., McMurdo Sound and vicinity) Lillie concluded that the second most abundant cetacean encountered over the Ross Sea shelf was the Antarctic minke whale (*Balaenoptera bonaerensis*) (Ainley, 2009).

Killer whales arrive in the southwestern Ross Sea in early December and patrol the receding edge of the fast ice in McMurdo Sound in notable numbers (Ainley et al., 2006a; e.g., 40 and 47, respectively, were counted by helicopter on 14 and 21 January 2008), Terra Nova Bay (Lauriano et al., 2007a, 2007b), and presumably similar habitat elsewhere in the Ross Sea not regularly frequented by humans. Indeed, the whales are largely confined to the marginal ice zone of the Ross Sea Polynya (Ainley, 1985; Karnovsky et al., 2007). The large majority seen in the southwestern perimeter of the polynya (i.e., McMurdo Sound/Terra Nova Bay and vicinity) are RS killer whales, with an occasional small pod of ecotype-B killer whales (Lauriano et al., 2007a). The fact that Lillie (1915) noted a yellow cast to the majority of killer whales that he observed in the Ross Sea suggests this ecotype (or ecotype-B) as well (Pitman & Ensor, 2003). To give some idea about the relative abundance of the two forms in these coastal fast ice areas of the southern Ross Sea, the ratio in numbers of RS killer whales to ecotype-B killer whales on the two dates above was 8:1, although as argued below, that ratio is affected by the decreasing number of RS killer whales visiting the southern Ross Sea during the past few years. Killer whales reach a peak in number in this area between mid-December and mid-January (Ainley et al., 2006a; Appendix 1), which corresponds to the time when fast ice is rapidly disintegrating and, thus, as the edge recedes, unexploited fast ice habitat is exposed that had previously been off-limits due to the finite breath-holding capacity of the whales. The fast ice edge usually lies at about Cape Royds (20 km north of McMurdo Station) during the winter and spring, but by mid-January, it breaks back several kilometers, often as far as the U.S. Antarctic Program's McMurdo Station (site of R. F. Scott's hut; Figure 1). Often, this break-out is facilitated by an icebreaker, which during early January cuts a channel to McMurdo Station. The killer whales use the channel to reach newly exposed prey (see also Jehl et al., 1980; Thomas et al., 1981): RS killer whales seeking fish and ecotype-B killer whales seeking seals. Not long after the channel is made, Weddell seals disappear from the mid-Sound, possibly to avoid predation by ecotype-B killer whales and/or because of increased competition with RS killer whales for fish prey. The killer whales begin to depart this region by late January or early February (Pitman, 2004; Ainley et al., 2006a), with some remaining until the winter darkness in late February-early March (van Dam & Kooyman, 2004).

No formal attempt has been made to estimate the numbers of killer whales in the southern Ross Sea using modern estimation techniques (e.g., line transects and the program *DISTANCE*), but Ainley (1985), using strip transect methods in a dense coverage of ship tracks criss-crossing the Ross Sea, estimated 3,440 (± SD 2,850; all ecotypes combined) for the entire continental shelf and slope during 1976 to 1981. This was thought to be an overestimate owing to the propensity of killer whales to be attracted to ships. Pitman et al. (2007), during one week in mid-January 2005, photographed 252 different individuals (RS type) near Beaufort and Ross Islands, including McMurdo Sound (an area comprising ~5% of the Ross Sea; Figure 1). A high count of 116 killer whales was reported in waters off Cape Crozier in December 2002, similar to Lillie's (1915) description on numerous occasions early in the 20th century. The ships on which we have sailed (DGA & GB) in the McMurdo/Beaufort vicinity at times in recent years have been literally surrounded by killer whales out toward the horizon.

Materials and Methods

Killer whale counts were made during austral spring-summer at Cape Crozier, Ross Island (77° 27' S, 169° 12' E), which is on the open coast of the southern Ross Sea (Figure 1). We had spent 6 h/d or more gazing at the ocean in 1996 to 2001, radio-tracking foraging penguins (Ainley et al., 2004), but only upon realizing that the presence of killer whales changed the penguins' foraging behavior (Ainley et al., 2006a) did we begin to quantify the number of killer whales present. We counted whales seen offshore beginning with a short trial period in late December 2002 and then each summer season thereafter through the most recently completed 2008-2009 austral summer. Unless written out (e.g., 2003 to 2004), we designate spring-summers by the initial year (i.e., the period November 2003 to January 2004 is the 2003 season). During 2003 to 2005 (and 1996 to 2002), observations extended from 2 December until about 26 January; subsequently, they extended from 15 November until 26 January. These periods corresponded to our presence at a field camp at Cape Crozier.

Sea watches were made from an elevation of 400 m using 8 to 10× binoculars or sometimes a 15 to 32× spotting scope as described by Ainley et al. (2006a). Biologists observed for at least 1 h each, weather permitting, thus accumulating 1 to 3 h/d combined observation time. The numbers of cetaceans seen while working in the penguin colony at Cape Crozier for 4 to 10 h/d was also noted, but such observations lacked the breadth of view available in the sea watches made from higher elevations.

The maximum count of killer whales seen at a single time during a day was used as an index of the number of killer whales present for that day. Due to whale movement through the viewscape (flux) and the relatively small ocean area observed (1 to 2 km out to sea, east and west during sea watch; < 1 km otherwise), we could not make true estimates of whale abundance. Rather, differences in counts provided an index to relative changes in killer whale numbers by season and year. Certainly, our counts are an underestimate of true numbers.

We also counted seals of all species in the Cape Crozier vicinity on a consistent basis, and we present some of those data herein.

Finally, killer whale observations were also made at Terra Nova Bay, but more intermittently because the ice edge (and the whales) is often not in view from the Mario Zucchelli Station where biologists reside. Since 1987 (but mainly 1999 to 2005), 13 sightings were obtained, mostly along the fast ice edge off Cape Washington (northern point of Terra Nova Bay).

Results

Killer whales were seen at Cape Crozier (and Cape Royds in McMurdo Sound) from the last week of November through January in years when observations spanned that period (Figure 2). As noted in Ainley et al. (2006a), the period of peak occurrence occurred from early December to mid-January. The killer whales repeatedly dove over extended periods (hours) under the edge of the Ross Ice Shelf, as well as in leads opening in the fast ice that forms between huge cracks in the shelf.

Overall, the proportion of days on which killer whales were seen from Cape Crozier, the maximum number seen at any single time on a given day, and the mean number seen per sighting all show patterns of decrease during the period of study, especially after 2005 (Table 1). However, considering overall annual trends, the statistical results are as follows—all negative: estimated change per year ± SE for proportion of days seen: $ß = -0.045 \pm 0.027$, $t = -1.69$, $p = 0.15$; max seen per day: $ß = -8.86 \pm 5.35$, $t = -1.66$, $p = 0.16$; mean number per sighting: $ß = -2.65 \pm 1.13$, $t = -2.35$, $p = 0.07$. Similarly, very few killer whales were seen in McMurdo Sound in 2007 and 2008, although the sighting effort there was far less suitable than at Cape Crozier and, therefore, no comparable long-term data series are available. However, helicopter pilots flying between McMurdo Station across McMurdo Sound to Victoria Land (daily) and along the fast ice edge noted the paucity of killer whales especially in 2008 (P. Murphy, pers. comm., 6 February 2009: "As for Orca, somewhat disappointing. I've only seen a few pods; nothing as dramatic as previous years").

We did not begin to distinguish between Ross Sea ecotype-C and -B killer whales until 2005 (Appendix 1). In 2005 to 2008, the ratio of ecotype-C to ecotype-B was 50:1, 20:1, 20:1, and 16:1, respectively. This decreasing trend reflected decreasing prevalence of RS killer whales as the apparent abundance of ecotype-B killer whales did not change (*cf*. Appendix 1).

The killer whales at Terra Nova Bay were identified in six sightings—all RS killer whales except for one sighting of ecotype-B individual or pod (Lauriano et al., 2007a), with minimum group size averaging 7.6 ± 1.6 (SE). Seasonally, observations occurred between early-December and mid-January, the same period when RS killer whales are most abundant near Ross Island.

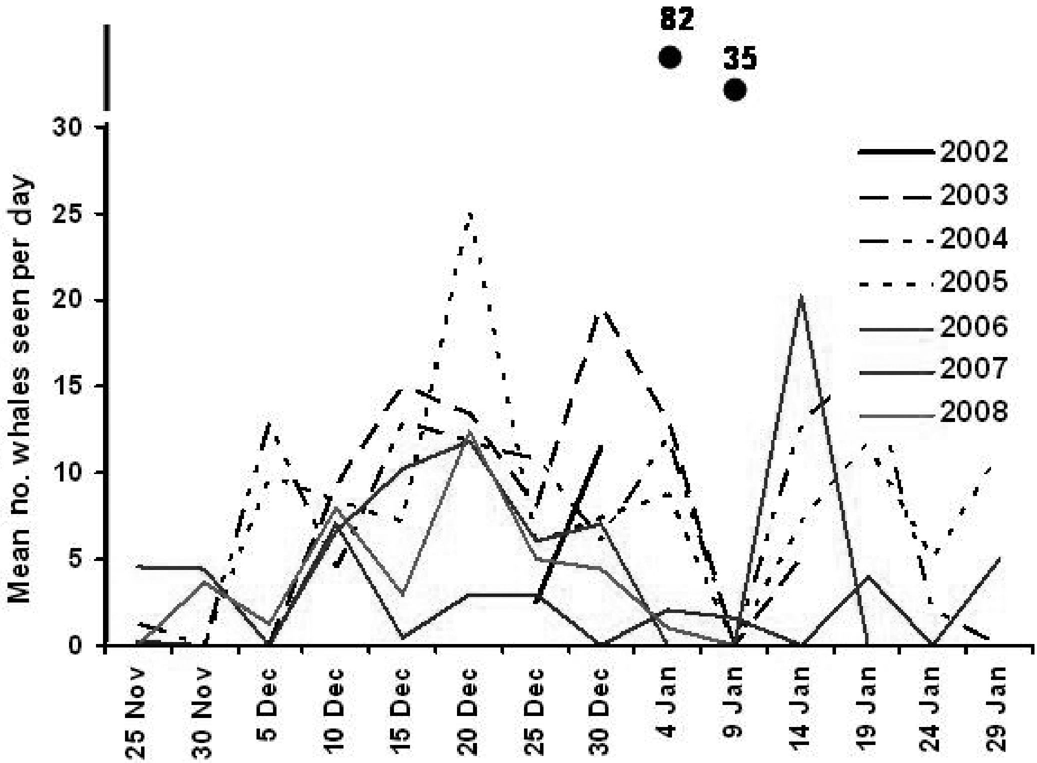

Figure 2. A summary of the number of killer whales seen from a lookout at Cape Crozier, Ross Island; average seen daily for 5-d periods. During 2002, two very high values are presented separately so as to allow the y-axis to expand for the other data points; data for 2004 and 2005 from Ainley et al. (2006b) (see Appendix for details).

Table 1. A summary of observations of killer whales, all ecotypes, at Cape Crozier, during the period 2 December to 26 January each year, 2003 to 2008; some observations also made in 2002 season. Appendix 1 provides a breakdown by ecotype.

Season	No. days seen (proportion)	Maximum no. seen	Mean no. (SE) per sighting
2002-2003	7 of 20 (0.35)	120	36.7 (14.1)
2003-2004	22 of 55 (0.40)	40	18.7 (2.6)
2004-2005	33 of 55 (0.60)	38	15.3 (1.5)
2005-2006	28 of 55 (0.51)	80	18.0 (2.6)
2006-2007	16 of 55 (0.29)	40	17.2 (2.8)
2007-2008	8 of 55 (0.15)	35	14.4 (3.5)
2008-2009	11 of 55 (0.20)	40	14.2 (2.6)

Discussion

Observations of Ross Sea Killer Whale Predation on Fish

Direct Observations—Killer whales have been seen eating toothfish in the southern Ross Sea on several occasions. Each year since 1957, beginning on about 1 January, ice breakers have chopped a channel from the edge of the fast ice (usually near Cape Royds) to McMurdo Station (Figure 1). During the chop-in, sailors on board these vessels have regularly reported killer whales surfacing in the open water astern with large Antarctic toothfish (*Dissostichus mawsoni*) in their mouths, especially in the first week of ice-breaking (as discussed also in Ainley et al., 2006b). Not many other people have spent more than a few minutes in the vicinity of the channel, but those who have done so have seen this phenomenon, including the cetacean research groups who worked in this locality before 2000. From this work, photographs of killer whales with large fish have been published (Thomas et al., 1981; Wu & Mastro, 2004). Therefore, this appears to have been a relatively common observation; however, Pitman et al. (2007), working after 2000 (2002, 2005, 2006), failed to see such predation on fish (see below).

Observations of killer whales eating toothfish in the Ross Sea are not confined to McMurdo Sound. In December 1978, while investigating emperor penguins (*Aptenodytes forsteri*) along the fast ice edge of Terra Nova Bay, G. L. Kooyman (pers. comm.) observed killer whales bringing large toothfish to the surface. At the time, the outer portion of the Terra Nova Bay fast ice was fracturing rapidly to provide leads farther into the bay. The toothfish were therefore suddenly losing cover, and the whales were exploiting the rapidly developing leads.

Lauriano et al. (2007b) described RS killer whales foraging on what was thought to be Antarctic silverfish (*Pleuragramma antarcticum*) but without confirmation. As noted by these authors, penguins that were also foraging in the area were feeding these fish to their chicks.

Biochemical Assessments—Analysis of diet using indirect methods (e.g., stable isotopes, fatty acid signatures) could be of value in characterizing the RS killer whale diet. If the killer whale diet contained a high proportion of toothfish, then the δN stable isotopes of N and C, and fatty acid values of killer whales should be elevated over those of the toothfish. Krahn et al. (2008) analyzed the stable isotopes (N and C) and fatty acids found in RS killer whale skin biopsies obtained in McMurdo Sound at the end of January 2005 and 2006. Skin tissue assays reflect diet over the previous few weeks (Tieszen et al., 1983), but samples were obtained from the outer, non-metabolically active epidermis making it problematic for closely assessing diet; only qualitative information and not proportions of prey species consumed could be revealed (Krahn et al., 2008). The δN of 13 male killer whales averaged 13.2 (range: 12.8 to 14.1) as did that of 15 female killer whales (range: 12.5 to 13.7). Four samples exceeded slightly the δN determined for toothfish as reported by Burns et al. (1998) (13.5, range: 13.3 to 13.7) and by Bury et al. (2008) (13.9, range: 9.0 to 16.0); a single toothfish sampled by Krahn et al. (2008) had a δN of 14.0. In the southern Ross Sea, both toothfish and Weddell seals, and presumably killer whales, feed heavily on Antarctic silverfish (δN 10.9, range: 10.0 to 11.9) (Burns et al., 1998; La Mesa et al., 2004; Ainley et al., 2006b; Ainley & Siniff, 2009). Therefore, close overlap of N and C isotopes is expected. On this basis, RS killer whales, Weddell seals, and Antarctic toothfish are equivalent top-trophic predators in this system (Bury et al., 2008).

In contrast with the δN results, the fatty acid analyses revealed little information useful for the present discussion. Krahn et al. (2008) compared fatty acid levels in two fishes that likely are not part of the killer whale diet: *Pagothenia borchgrevinki* and *Trematomus newnesi* (maximum body length *ca*. 15 to 20 cm). Both fish species are widely dispersed, largely in the platelet layer on the underside of ice floes (Kock, 1992; Eastman, 1993). It is possible that the killer whales could flush these fish, using bubbles, or suck them in while turned upside down, a technique apparently used on the loose-schooling but deeper-living silverfish (Lauriano et al., 2007b; R. L. Pitman, pers. comm.). Such a behavior directed at ice-dwelling fish would require much effort for little value, and otherwise the killer whale's large dorsal and pectoral fins would not be conducive to foraging in the ragged undersides of ice floes. Indeed, all the cetaceans of the Arctic (like beluga [*Delphinapterus leucas*] or narwhal [*Monodon monoceros*]), which feed to a great degree on Arctic cod (*Boreogadus saida*; summarized in Ainley & DeMaster, 1990), a fish that inhabits ice floe undersides, lack dorsal fins altogether, and have greatly reduced pectoral fins compared to most other cetaceans.

Is Consumption of Toothfish Important to Ross Sea Killer Whales?

Keeping in mind the "sliding baseline syndrome" (Pauly, 1995), it is interesting that the group conducting killer whale research in McMurdo Sound after 2000 (Pitman et al., 2007) failed to see toothfish being caught, quite in contrast to the two research groups earlier (three including Terra Nova Bay). The biochemical analysis did not help to elucidate the question of toothfish importance as values for the killer whale and toothfish N and C isotopes, and fatty acids were similar. Had the killer whales been eating a lot of large, adult toothfish, their δN values should have been higher. However, the killer whale tissue samples were gathered at the end of January, a few weeks after the seasonal invasion of the killer whales into southern McMurdo Sound (i.e., after the time when toothfish were regularly once seen in the grasp of whales and a period when humans also find it difficult to catch adult toothfish in those waters compared to earlier in the season) (see above; A. DeVries, pers. comm.). Moreover, those killer whales' tissues were sampled after 2000 when it appears that there were fewer adult toothfish available (DeVries et al., 2008; see below). Given the frequency of observations of toothfish in the grasp of killer whales before 2000 and the fact that this has been observed both in McMurdo Sound and Terra Nova Bay, it seems unlikely that this was a rare phenomenon, although it may have been local and short-lived, and it may be rare now. It would seem that a killer whale would not have much difficulty handling a small, subadult toothfish as pictured in Ponganis & Stockard (2007). Therefore, if small toothfish were now the main age-size class available, not only would the isotope signature be significantly lower (Bury et al., 2008) but it is likely these fish would just be swallowed whole upon being caught.

As noted above, besides toothfish, RS killer whales are thought to also prey on silverfish (Lauriano et al., 2007b). According to Fuiman et al. (2002), silverfish under the ice of McMurdo Sound typically exist in small mid-water shoals in which the fish are spaced 2 to 4 m apart. Although once referred to as "Antarctic herring" or "the anchovy of the Antarctic" on the basis of numbers caught in mid-water trawls (DeWitt & Hopkins, 1977, and references therein), these are the only observations of their schooling behavior. It appears that RS killer whales, presumably when feeding on silverfish, exhibit fish-concentrating behavior reminiscent of that used by killer whales to catch herring (*Clupea* spp.) in northern seas (Lauriano et al., 2007b). Otherwise, it would not be worth a killer whale's energetic cost to pursue single, 20 to 25 g silverfish or any fish available in the southern Ross Sea, other than large toothfish, which do not form schools or shoals.

In that regard, on the basis of fish encounters seen by a critter-cam attached to Weddell seals in McMurdo Sound, the ratio of toothfish to silverfish is 1:100, but in terms of biomass, it is 2.7:1 (summary in Ainley & Siniff, 2009). No other fish sampling data that might accurately represent the relative abundance of both silverfish and toothfish are available anywhere in the Ross Sea (or elsewhere). Therefore, at least on the basis of the Weddell seal video data, it appears to be energetically advantageous for killer whales to take toothfish when they can. Finally, according to Fuiman et al. (2002), both toothfish and silverfish occur much higher in the water column (i.e., almost to the surface) when under the fast ice as opposed to the near-bottom depths inhabited by toothfish in ice-free waters. Such a near-to-surface prevalence would render these fish more vulnerable to killer whale predation or at least make the killer whales' foraging more energy efficient. This phenomenon of otherwise deep-living organisms living close to the surface when under ice is not confined to these fish (Ainley et al., 1986). The risk taken by toothfish of increased predation by occupying shallow waters is not surprising given the richness of prey over the Ross Sea shelf and the need for toothfish to recover there after spawning near sea mounts in low-production waters north of the Ross Sea (*cf.* Fenaughty et al., 2008; Hanchet et al., 2008).

Given the reduced sighting effort, the occurrence of RS killer whales in Terra Nova Bay during periods overlapping occurrence off Ross Island suggests this area is equally important for these top predators. Whether or not the same killer whale pods visit both areas remains to be determined. It appears that outer Terra Nova Bay and its wind-driven polynya are a crucial breeding ground for Antarctic silverfish (Vacchi et al., 2004), and, thus, it is not surprising that top predators, including toothfish, abound in this area. Of pertinence here, presumably, RS killer whales by virtue of their numbers (50 to 100) and conspicuous dorsal fins were responsible for the Bay of Whales, farther east in the Ross Sea, being so named by Shackleton (1909, p. 50; Ainley, 2009). Later, Amundsen (1912, p. 273) commented that the killer whales arrived when the fast ice was breaking up in the Bay of Whales, the location where that explorer built his base camp. These are the conditions seen in McMurdo Sound and Terra Nova Bay when RS killer whales are exploiting the fast ice habitat and foraging on toothfish.

Why Would Ross Sea Killer Whales Be Decreasing in Abundance?

Owing likely to the relatively short number of years during which we derived quantitative indices to the number of killer whales present off Cape Crozier, the decreasing trends we describe beginning especially by 2005 are not "robust," but our sense of the whales' abundance during 1996 to 2001 was that there were "a lot" of them present each summer. Since then, we propose that the commercial toothfish fishery has reduced the prevalence of large fish in the southern Ross Sea, thus reducing foraging options for killer whales. The result appears to be that both group size and relative abundance of RS killer whales (but not abundance of ecotype-B) has been decreasing in those waters (Appendix 1). Presumably, the whales are spending more time elsewhere, where toothfish remain abundant, or where there is less competition for silverfish from other predators. Below we speculate on other factors which could be involved.

In addition to a decades-long increase in the large-scale (Pacific sector) sea ice season and ice extent, as well as increased prevalence of the Ross Sea Polynya (Parkinson, 2002; Zwally et al., 2002) and alteration of Circumpolar Deep Water off the shelf (Jacobs, 2006), two major phenomena have impacted the southern Ross Sea in recent years. The first, beginning in 1996, is a fishery for Antarctic toothfish (Pinkerton et al., 2007; CCAMLR, 2008); previously the Ross Sea fish had been unexploited (Kock, 1992; Ainley, 2009). This fishery is concentrated along the Ross Sea continental slope, although smaller portions of the catch have been taken over the shelf, including near Terra Nova Bay and just east of Ross Island. Adult fish are targeted—the same age-class seen taken by killer whales. Since 2004, when the fishery expanded from 9 to 22 vessels, the catch achieved its allowed level of about 3,500 tonnes per annum. While the catch-per-unit-effort (CPUE) in the fishery along the slope has not shown a downward trend, the CPUE in a mark-recapture study conducted by scientists in McMurdo Sound has declined from 0.0136 fish per hook-hour in 1987, to 0.0075 fish/h-h in 2001, to 0.0006 fish/h-h in 2007 (no scientific fishing subsequently). The 1987 CPUE was considered representative of the catch rate during 1974 to 2000, when 200 to 500 fish per annum were tagged and released during those years in which fishing effort was made (DeVries et al., 2008). One potential explanation is that the toothfish population has contracted in a density-dependent fashion towards its "center" located along the Ross Sea slope, 600 km north of McMurdo Sound, as a result of commercial fishing pressure (DeVries et al., 2008). While no assessment of the size or extent of the toothfish stock has ever been made, the continental slope is where the most fishing effort is expended (72% of fish taken from there; Bury et al., 2008), indicating where the fishing has had the greatest pressure.

The other major event impacting the southern Ross Sea recently was the grounding of two immense icebergs, C16 and B15A (175 km long), which prevented the outward excursion of sea ice from the region during the springs of 2001 to 2005. As a result of the increased shading, and perhaps changed circulation (conjecture only), the extent of phytoplankton blooms and primary productivity in the southwestern Ross Sea was depressed (Arrigo et al., 2002). Direct information on whether this affected the foodweb is not available; as it is, much of the algal production sinks to the benthos, regardless, in any year (Smith et al., 2007).

Indirect evidence, however, indicated that the foodweb was not seriously affected, at least judging from the response of air-breathing predators excluded physically from the area by the extensive fast ice. Owing to the thick, persistent ice in McMurdo Sound (and a density-dependent response to fewer ice cracks), numbers of Weddell seals, another toothfish/silverfish predator (Ainley & Siniff, 2009), were depressed during the iceberg years. The population immediately and completely rebounded, though, after the icebergs departed in July 2006, with the sea ice regime returning to its usual seasonal pattern (Siniff et al., 2008). It is thought that the seals, therefore, frequented areas peripheral to the heavy McMurdo Sound sea ice—for instance, at Cape Crozier and Beaufort Island. Indeed, this is shown in Weddell seal counts at Cape Crozier (Appendix 2). As well, the breeding success of Adélie penguins (*Pygoscelis adeliae*) at Cape Crozier was depressed during the iceberg years, but the cause is thought to be longer foraging trips owing to the more extensive ice and presence of the iceberg occupying part of the usual foraging area (Ainley et al., unpub. data). A similar scenario (i.e., mean, longer foraging trips and lower mean adult weights) was observed in the Terra Nova Bay Adélie penguin colonies (Olmastroni et al., 2004). In both localities, once the iceberg departed, penguin population dynamics returned to previous patterns (i.e., in 2006 and following) (Ainley et al., unpub. data; Pezzo et al., 2007). The penguins feed on krill and silverfish (Ainley et al., 2006b). Minke whale numbers in the area have shown no negative trends; this species, too, feeds on krill and silverfish (Ainley et al., 2006a, 2006b, unpub. data; Lauriano et al., 2007b).

Weddell seals are direct competitors with RS killer whales for both toothfish and silverfish. However, any decreases in numbers of RS killer whales seen nearby Cape Crozier during the last few years, if indeed related to decreased prevalence of toothfish, does not seem to be due to increased foraging pressure by the seals because the temporary surplus of Weddell seals at Cape Crozier departed while RS killer whale numbers seen from Cape Crozier were still relatively high. Moreover, numbers of RS killer whales appear to be decreasing both off Cape Crozier and in McMurdo Sound. Seemingly, despite potentially depressed primary productivity, the portion of the toothfish stock that resided under the more extensive sea ice would have been better protected from predation from both the Weddell seals and killer whales. Therefore, once the sea ice regime returned to normal, there should have been a spike in foraging success on toothfish.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has a goal of reducing the Ross Sea toothfish stock to 50% of its pre-fished biomass by ~2025. In 2006, without any independent biomass estimates, it was determined by modeling that one-third of that goal had been achieved (Pinkerton et al., 2007). Whether or not, or when, in a depressed state of the fish stock, killer whales in the Ross Sea resort to taking toothfish from longlines, as they do elsewhere (e.g., Kock et al., 2006; Roche & Guinet, 2007), remains to be seen. R. L. Pitman (pers. comm.) believes that killer whales would actually prefer to take toothfish caught on longlines as the effort required would be much less than catching free-swimming fish.

Also remaining to be seen with further depression of the fish stock is a decrease in Weddell seal numbers in the region. Logically, this should occur after any effects are evident among killer whales as the Weddell seals can dive much deeper (600 vs

300 to 400 m) and hold their breath much longer than the whales (~80 vs ~10 min), and they can live in extensive fast ice where only ice cracks allow air access. Therefore, the Weddell seals can exploit a much greater volume of potential prey habitat, both temporally and physically. Indeed, toothfish are rarely encountered by the fishery over the Ross Sea banks, large sections of which are shallower than 600 m (to 50 m). Like formerly numerous, large nototheniid fish on the Scotia Shelf, the foraging by Weddell seals and killer whales may have forced these fish to seek deeper waters or change their movement patterns (Everson, 1970). A photograph of a large toothfish taken on one of these banks, without a sea ice canopy overhead, shows it hiding (from predators and/or from prey?) among the large sponges and other benthic invertebrates (Eastman & Barry, 2002).

Ultimately, with respect to the needs of whales and seals, removing toothfish should not be compensated by an increase in silverfish (toothfish prey) as the latter already are dense enough that they must resort to cannibalism in the late season when they have helped, with minke whales and penguins, to deplete the supply of their euphasiid prey in the region (reviewed in Ainley et al., 2006a). Moreover, removing toothfish would force more direct competition between killer whales, Weddell seals, and the smaller predators for silverfish in a foodweb that is already delicately balanced (Ainley, 2007). In the southern Ross Sea, which has 10% of the world population of Adélie penguins and 15% of emperor penguins, as well as the largest concentration anywhere of Weddell seals and notable numbers of minke whales (Ainley, 2009), it has been shown by "natural experiments" that changes in one predator population immediately cause changes in others (e.g., penguins vs minke and killer whales) (Ainley et al., 2006a; Ainley, 2007). Without the benefit of eating large toothfish, the option for killer whales is to move out of the foraging ambits of their more physiographically constrained and densely populated competitors, the Weddell seals and penguins. If killer whales cannot find large fish elsewhere, then a reduction in calf production seemingly would become evident and eventually true population decline would ensue. This is the scenario that has been documented off the Pacific coast of Canada, where the disappearance of large-bodied chinook salmon (*Oncorhynchus tshawytscha*) has, in part, led to a noticeable decrease in the resident killer whale population (Ford & Ellis, 2006).

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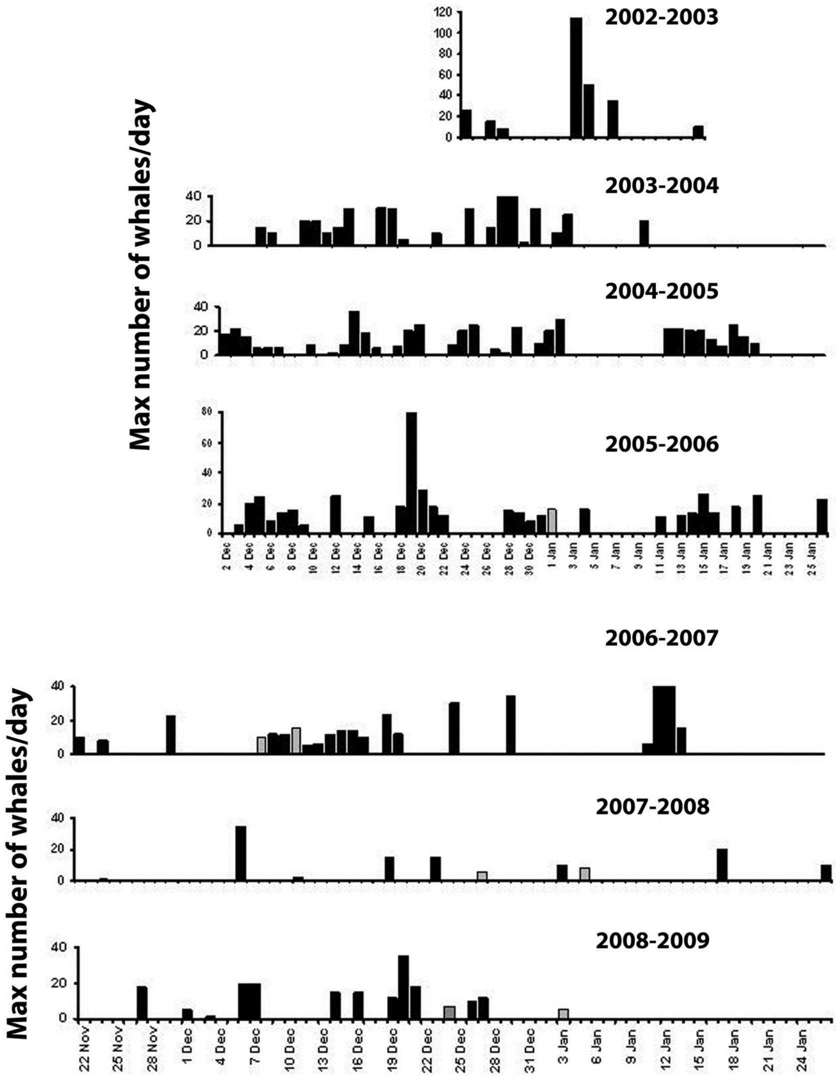
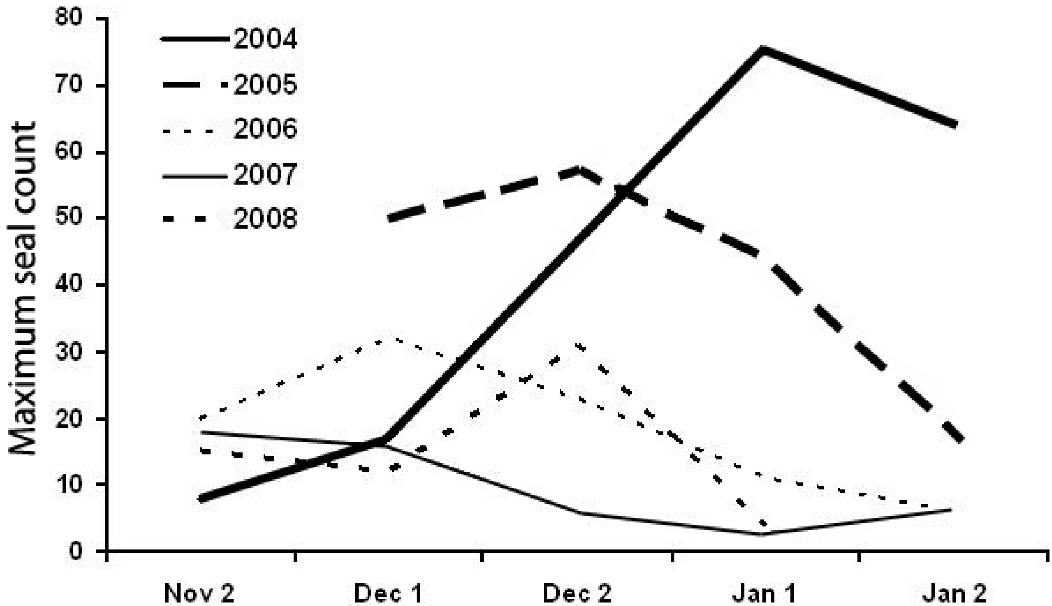


Appendix 1. Records of maximum number of killer whales seen per day at Cape Crozier, 2002 to 2008; days on which ecotype-B killer whales were seen are indicated by light shading (beginning in 2005). Included for "probable" ecotype-B is only one confirmed sighting when the pod came very close to shore and was photographed.



Appendix 2. Maximum daily count of Weddell seals at Cape Crozier within 2-wk periods, 2004 to 2008; lower numbers after 2005 most likely are related to a return of animals to McMurdo Sound following the disappearance of the large icebergs in 2006.