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, Antarctica, ecosystem; the type-C referred to hereafter as "Ross Sea killer whale" (RS killer whale). Herein we review existing data on occurrence patterns and diet of RS killer whales, and present data on numbers observed in the southwestern Ross Sea. These "resident" whales appear to feed principally on fish, including Antarctic toothfish (*Dissostichus mawsoni*). On the basis of sea watches on the outer coast of Ross Island beginning in 2002-03, sighting frequency and average group size began to decrease beginning 2006-07 and thereafter; prevalence also decreased in nearby McMurdo Sound. We discuss trends with respect to environmental change as well as the initiation of industrial fishing for toothfish beginning in 1996-97. Consistent with a decrease in the catch-per-unit-effort of scientific fishing for toothfish in McMurdo Sound, we suggest that the change in Ross Sea killer whale numbers is related to a contraction of the toothfish stock, and not to changes in the physical environment. We surmise that in this closely-coupled foodweb, composed of very abundant penguin, seal and whale components, loss of the toothfish option for Ross Sea killer whales would force more direct competition for the smaller-fish prey. Therefore, the killer whales have opted to move out of the region.

KEY WORDS: ANTARCTIC SILVERFISH, ANTARCTIC TOOTHFISH, B15 ICEBERG, CLIMATE CHANGE, FISH DEPLETION, KILLER WHALE, *ORCINUS ORCA*, ROSS SEA

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INTRODUCTION

Based on recent photogrammatic and observational studies, a diminutive form of the killer whale (*Orcinus orca*) has been described for the high latitude Antarctic (Pitman et al., 2007). This is possibly the same species that Russian biologists described as *O. o. glacialis* in the early 20th century, the type specimen for which was soon lost. Therefore, this question 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 (Pitman and Ensor, 2003). R.L. Pitman (pers. comm.) refers to it as the "Ross Sea killer whale" (hereafter, RS killer whale) owing to its concentration and long history of observation in those waters (beginning with James Clark Ross in the mid-19th century).

The RS killer whale, at an average length of 5.6 m for adult males, is 2-3 m smaller than type-A; comparison with type-B's awaits further work on measurements of the latter; R. Pitman, pers. comm.). According to Pitman and Ensor (p. 6), "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." 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 and 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. This is quite unlike a pod of type-Bs (seal eating, "transient type"; Pitman and 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 (Andrews et al., 2008). Such sites of extensive fast ice would also be occupied by Weddell seals (*Leptonychotes weddelli*), a known prey of type-Bs 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, we present data on changes in relative abundance from 2002 to 2009. We then discuss possible reasons for an apparent decrease in prevalence and apparent group size of this ecotype, a trend not exhibited by type-B, in the southern Ross Sea.

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, and the one in which the most sea ice remains year round (see Gloersen et al., 1992). It mainly has been sighted in the Ross Sea (165° W to 165° E; 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 as far west as Prydz Bay (80° E), but farther to the west (e.g. Weddell, Scotia, Bellingshausen and Amundsen seas) confirmed sightings do not exist, even near to bases where scores of killer whales have been seen and identified (Pitman and Ensor, 2003; R. Pitman, pers. comm.). The easternmost sighting in waters of West Antarctica may be a pod of 24 whales

observed at Cape Colbeck, on the eastern boundary of the Ross Sea in February 1994 (164 ^{o} W; Ainley et al., 2007; while this large group size is indicative of RS killer whale, it is not conclusive: R. Pitman, pers. comm.). An intensive survey of the Amundsen and Bellingshausen seas during February and March 1994 found no killer whales there, although plenty of Antarctic minke whales (*Balaenoptera bonaerensis*) were encountered (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 of the Victoria Land coast and around Ross Island during January-February (Fig. 1); the whales were said to have been observed "near the ship almost every day". Sightings of 50-100 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). The second most abundant cetacean encountered by these expeditions over the Ross Sea shelf was the minke whale.

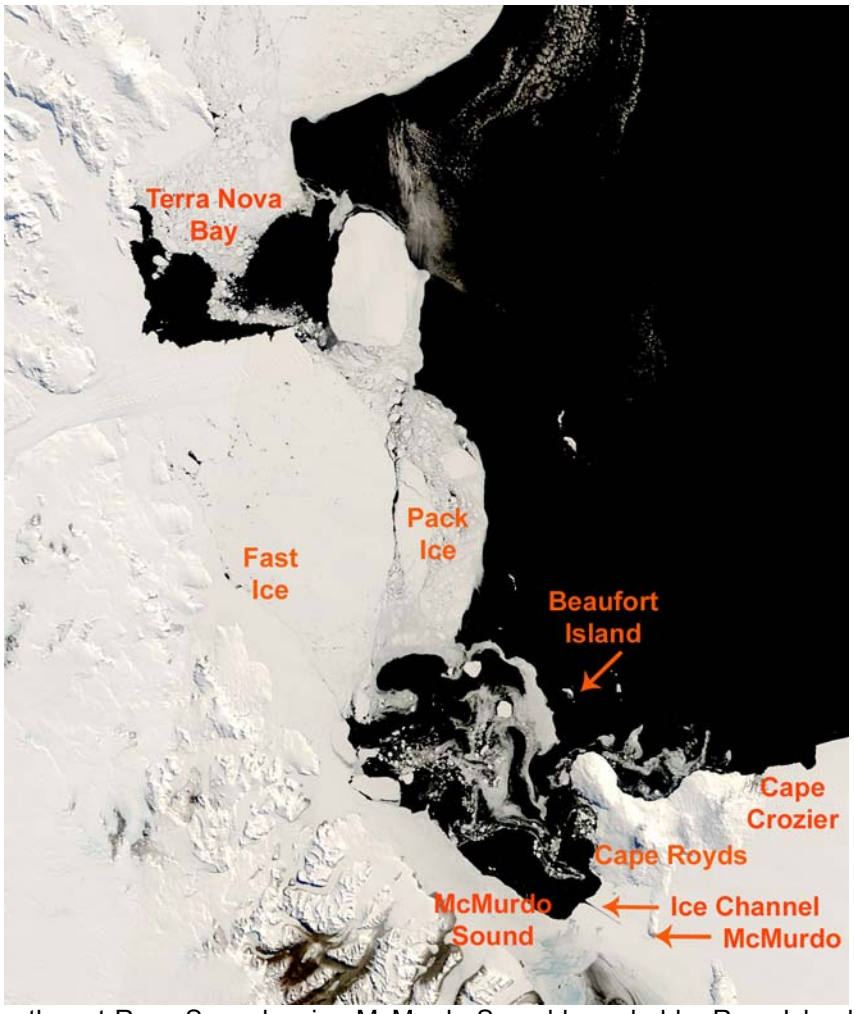

Fig. 1. Southwest Ross Sea, showing McMurdo Sound bounded by Ross Island to the east and Victoria Land to the west, the ice channel through fast ice in the southern Sound, and other Ross Sea locations mentioned in the text.

Killer whales arrive in the southwestern Ross Sea in early December and patrol the receding edge of the fast ice in McMurdo Sound (Ainley et al., 2006a; e.g. 40 and 47, respectively, were counted by air on 14 Jan and 21 January 2008), Terra Nova Bay (this study; Lauriano et al., 2007a, b), and presumably elsewhere. 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 type-Bs (Lauriano et al., 2007a). The fact that Lillie noted a yellow cast to the majority of killer whales that he observed indicates this ecotype (or type-B's), as well (Pitman and Ensor, 2003). The ratio in numbers of RS killer whales to type-B's 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 area 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, exposing unexploited habitat that had previously been off-limits due to the finite breath-holding capacity of the whales. The 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 McMurdo itself (site of R.F. Scott's hut; Figure 1). Often this 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): C's seeking fish and type-B's seeking seals. Not long after the channel is made, Weddell seals disappear from the mid-Sound, possibly to avoid predation by type-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 darkness in late February-early March (van Dam and Kooyman, 2004).

No formal attempt has been made to estimate the numbers of killer whales in the southern Ross Sea using modern techniques (e.g., line transects and the program DISTANCE), but Ainley (1985), using strip transects in a dense coverage of ship tracks criss-crossing the Ross Sea, estimated 3,440 (± SD 2850; all eco-types combined) for the entire shelf and slope during 1976-1981. This was thought to be an overestimate owing to the observed propensity of killer whales to be attracted to ships. Pitman et al. (2007), during a week in mid-January 2005, photographed 252 different individuals (C's) near Beaufort and Ross islands, including McMurdo Sound (an area comprising ~5% of the Ross Sea; Figure 1). A high count in waters off Cape Crozier in December 2002 was 116 (see below), and like what Lillie described (above) on numerous occasions prior to recent years the ships on which we have sailed (DA, GB) in McMurdo/Beaufort vicinity have been literally surrounded by killer whales out toward the horizon.

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 (as discussed also in Ainley et al., 2006b). Not many other persons 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 the year 2000. From this work, photographs of whales with large fish have been published (Thomas et al., 1981: Wu and 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 it (see below). In former years, killer whales with toothfish in their grasp were seen during the first week of the channel chop-in, with that coinciding with the southward disintegration of the fast ice.

Observations of killer whales eating toothfish in the Ross Sea are not confined to McMurdo Sound. In December 1978, while investigating emperor penguins 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 and farther into the Bay. The toothfish were therefore suddenly losing cover and the whales were exploiting the rapidly developing leads.

Lauriano et al. (2007b) provide descriptions of Ross Sea killer whale foraging that was thought to be directed at Antarctic silverfish (*Pleuragramma antarcticum*), but without confirmation. Penguins also foraging in the area were feeding these fish to chicks.

Biochemical observations

Analysis of diet using indirect methods could be of value in this discussion. If the killer whale diet contained a high proportion of toothfish, then one should find whale δN values 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 the fact that killer whale samples were obtained from the outer, non-metabolically active epidermis and outer blubber makes it problematic for closely assessing diet, and can only reveal qualitative information and not proportions of prey species consumed (Krahn et al., 2008). The δN of 13 males averaged 13.2 (range 12.8-14.1) as did that of 15 females (range 12.5-13.7). Four samples exceeded slightly the δN determined for toothfish as reported by Burns et al. (1998; 13.5, range 13.3-13.7) and Bury et al. (2008; 13.9, range 9.0-16.0); a single toothfish sampled by Krahn et al. had a δN of 14.0. Both toothfish and Weddell seals, and presumably killer whales, in the southern Ross Sea feed

heavily on Antarctic silverfish (δN 10.9, range 10.0-11.9) (Burns et al., 1998; see also Ainley et al., 2006b; La Mesa et al., 2004; Ainley and 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 (as noted also Bury et al., 2008).

In contrast with the δN results, the fatty acid analyses revealed little information useful for the present discussion, as results by Krahn et al. (2008) were compared with two fishes that likely are not part of the killer whale diet, *Pagothenia borchgrevinki* and *Trematomus newnesi* (maximum body length ca. 15-20 cm). Both species occur widely dispersed largely in the platelet layer on the underside of ice floes (Koch, 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., 2007; R. Pitman, pers. comm., has observed similar behavior). 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 "substrate" of ice floe undersides. Indeed, all the cetaceans of the Arctic, which feed to a great degree on Arctic cod (*Boreogadus saida*; summarized in Ainley and DeMaster, 1990), a fish that inhabits ice floe undersides, lack dorsal fins altogether and have greatly reduced pectoral fins compared to most other cetaceans.

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 (Fig. 1). 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 one, 2008-09. Unless written out, e.g., 2003–04, we designate spring-summers by the initial year, i.e., the period November 2003 to January 2004 is the 2003 season. During 2003-2005, observations extended from 2 Dec until about 26 January; subsequently, they extended from 15 November until 26 January. These periods corresponded to our presence at Cape Crozier.

Sea watches were made from an elevation of 400 m using 8-10X binoculars or sometimes a 15-32X spotting scope, as described by Ainley et al. (2006a). Each biologist observed for at least one hour weather permitting, thus accumulating 1–3 h/d. We also noted numbers of cetaceans seen while working in the penguin colony for 4 -10 h/d, but such observations lacked the breadth of view available in the sea watches made from higher elevations.

We used the maximum count of whales seen at a single time during a day to index the number of whales present for that day. Due to whale movement through the viewscape (flux) and the relatively small ocean area observed (1-2 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 indexed

the relative changes in whale numbers by season and year. Certainly our counts are an underestimate of true numbers.

RESULTS

Killer whales were seen from the last week of November through January in years when our observations spanned that period (Fig. 2). As noted in Ainley et al. (2006a), the period of peak occurrence occurred from early December to mid-January. The whales often dove for long periods 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.

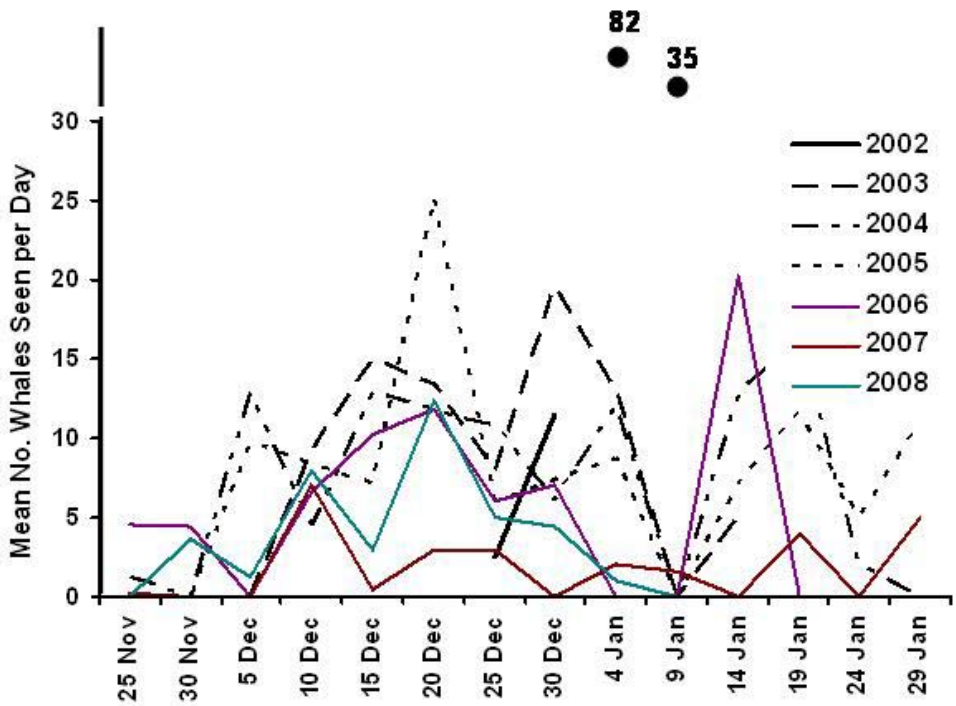

Fig. 2. A summary of the number of pygmy killer whales seen from a lookout at Cape Crozier, Ross Island: average seen daily for 5-d periods. During 2002, two very high values are presented separately so as to allow the y-axis to expand for the other data points; data for 2004 and 2005 from Ainley et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

Overall, the proportion of days on which killer whales were seen at Crozier, the maximum number seen on a single day, and the mean number seen per sighting all decreased during the period of study, especially after 2005 (Table 1). Similarly, very few were seen in McMurdo Sound in 2007 and 2008, although the sighting effort there is 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 Feb 2009: ”As for Orca, somewhat disappointing. I've only seen a few pods nothing as dramatic as previous years.”).

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

	Days Seen	Maximum Number	Mean (SE) No. per Sighting
2002-03	7 of 20 (0.35)	120	36.7 (14.1)
2003-04	22 of 55 (0.40)	40	18.7 (2.6)
2004-05	33 of 55 (0.60)	38	15.3 (1.5)
2005-06	28 of 55 (0.51)	80	18.0 (2.6)
2006-07	16 of 55 (0.29)	40	17.2 (2.8)
2007-08	8 of 55 (0.15)	35	14.4 (3.5)
2008-09	11 of 55 (0.20)	40	14.2 (2.6)

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

Killer whale observations have been done intermittently at Terra Nova Bay, in part because the ice edge is often not in view from the Mario Zucchelli Station where biologists reside. Since 1987 (but mainly 1999-2005), 13 sightings have been obtained, mostly along the fast ice edge off Cape Washington (northern point of Terra Nova Bay). The whales were identified in 6 sightings, all RS killer whale except for one sighting of type-B (Lauriano et al. 2007a), with minimum group size averaging 7.6 (SE 1.6). Seasonally, observations occurred between early-December and mid-January, the same period when RS killer whales are most abundant near Ross Island.

DISCUSSION

Is consumption of toothfish important to killer whales?

Curiously, and being aware of the "sliding baseline syndrome" (Pauly,1995), 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, as values for the whales and toothfish were similar. Had the whales been eating a lot of toothfish their δN values should have been higher. However, the whale tissue samples were gathered at the end of January, a few weeks after the seasonal invasion of the whales into southern McMurdo Sound, i.e. after the time when toothfish were once seen in the grasp of whales and a period when humans also find it harder to catch toothfish in those waters compared to earlier in the season (A. DeVries, pers. comm.). Moreover, those whales' tissues were sampled after 2000, when we believe there were fewer toothfish available. 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 and Stockard (2007). Therefore, if small toothfish were now the main age-size class available, not only would isotope signature be significantly lower (Bury et al., 2008) but likely these fish would just be swallowed whole upon being caught.

Besides toothfish, as noted above, RS killer whales are thought to also prey on silverfish (see 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 2-4 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 (see DeWitt and 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 to catch herring (*Clupea* spp.) in northern seas (see Lauriano et al., 2007b). Otherwise, it would not be worth a killer whale's energetic cost to pursue single, 20-25 g silverfish or any fish available in the southern Ross Sea, other than large toothfish, that 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(see summary in Ainley and Siniff, 2009). No other fish sampling data that would 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 seal 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 these fish in ice-free waters. Such a nearer-to-surface prevalence would render these fish more vulnerable to killer whale predation, or at least make the 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 (see Ainley et al., 1986).

The occurrence of RS killer whales in Terra Nova Bay during periods overlapping occurrence off Ross Island suggest this area to be equally important for these top predators. Whether or not the same pods are involved remains to be determined. It appears that Terra Nova Bay and its wind driven polynya are a crucial Antarctic silverfish breeding ground (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 (50-100) and conspicuous dorsal fins, were responsible for the Bay of Whales, farther east in the Ross Sea, being so named by Shackleton (1911, p. 50). Later, Amundsen (1912, p. 273) commented that the whales showed up 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 the decreasing abundance of Ross Sea killer whales?

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 is that both group size and abundance of RS killer whales (but not type-Bs) has been decreasing in those waters. 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 what other factors could be involved.

In addition to a gradual, 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 (Koch, 1992). 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 3500 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 success during 1974-2000, when 200-500 fish per annum were tagged during those years in which fishing effort was made (DeVries et al., 2008). The latter authors proposed that, as a result of commercial fishing pressure, 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. While no assessment of the size or extent of the toothfish stock has ever been made, in any case, 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 spring, 2001-2005. 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, indicates 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 and Siniff, 2009), were depressed during the iceberg years. The population, though, immediately and completely rebounded 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 seal counts at Cape Crozier (Appendix 2). As well, 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., unpubl. data). A similar scenario, i.e. mean longer foraging trips and lower mean adult weights, was observed in Terra Nova Bay colonies (Olmastroni et al., 2004). In both localities once the iceberg departed, penguin patterns returned to normal, i.e. in 2006 and following (Ainley et al., unpubl. 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, b; Lauriano et al., 2007b; Ainley et al., unpubl. data).

Weddell seals are direct competitors with RS killer whales for both toothfish and silverfish. However, the decreasing numbers of RS killer whales seen at Crozier during the last few years, if indeed this is related to decreased prevalence of toothfish, could not be due to increased foraging pressure by the seals, because the temporary surplus of seals at Crozier departed before the decreasing trends in killer whales became evident. Moreover, numbers of Ross Sea killer whales decreased 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 seals and whales. Therefore, once the sea ice regime returned to normal, there should have been a spike in foraging success on toothfish.

CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) has a goal of reducing the Ross Sea toothfish stock to 50% of its pre-fished biomass by 2020; by 2006, without any independent biomass estimates, it was thought, 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. Roche and 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 seals can dive much deeper (600 vs 300-400 m) and hold their breath much longer than the whales (~80 vs ~10 min), and can live in extensive ice where only ice cracks allow air access. Therefore, the 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 seals and killer whales may have forced these fish to seek deeper waters or change their movement patterns (see discussion in 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 and Barry, 2002).

Ultimately, 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 the minke whales and penguins, to deplete the supply of their prey, euphausiids, in the region (see review 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. In this region 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 a respectable number of minke whales, it has been shown by “natural experiments”” that changes in one predator population immediately causes changes in others, e.g. penguins versus minke and killer whales (Ainley et al., 2006a; Ainley, 2007). Without the benefit of eating toothfish, the option for killer whales is to move out of the foraging ambits of the more physiographically constrained predators, the Weddell seals and penguins. If killer whales can not find food elsewhere, then a reduction in calf production seemingly would become evident and eventually population decline.

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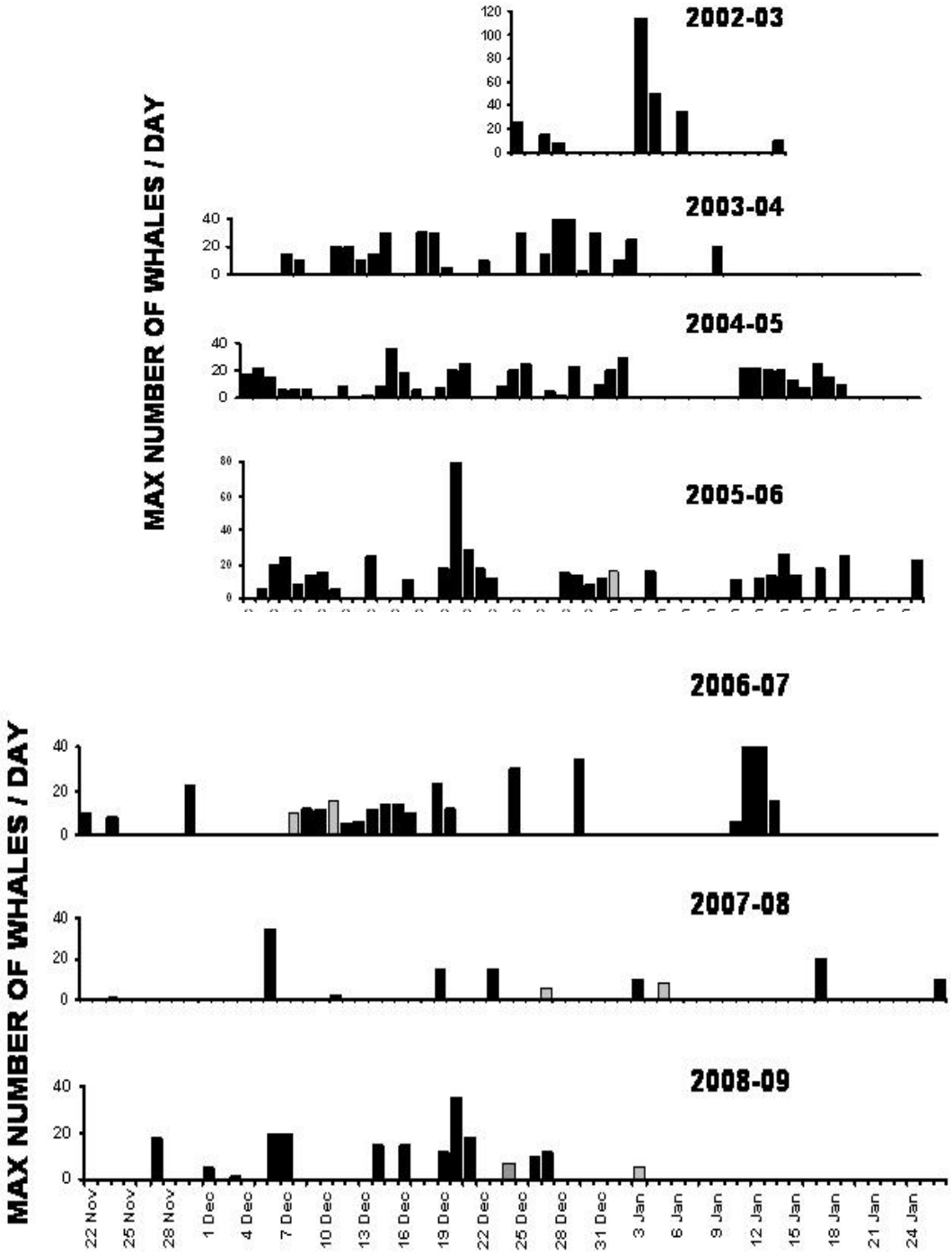
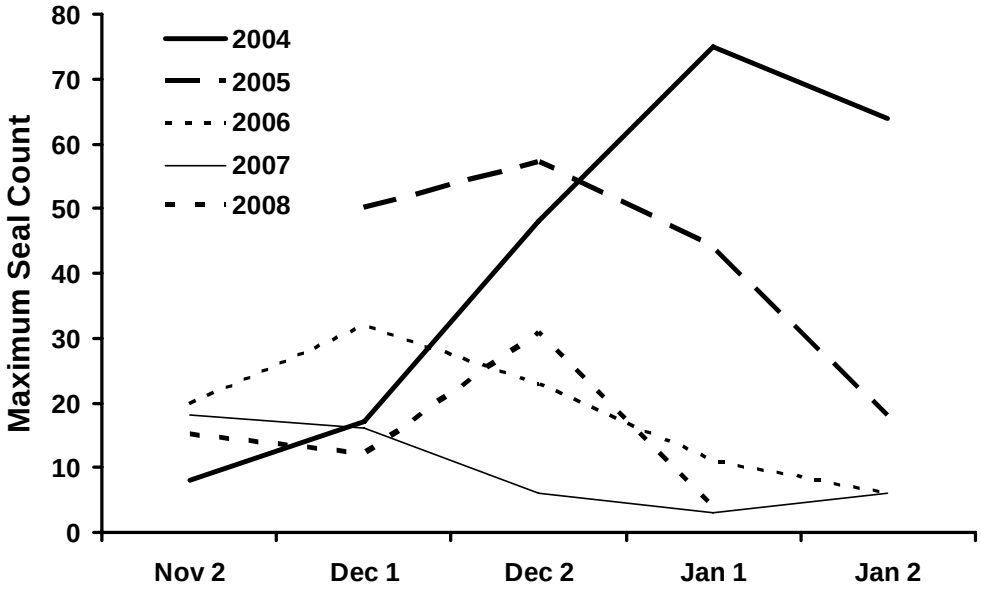


Appendix 1. Records of maximum number of killer whales seen per day at Cape Crozier, 2002-2008; days on which type-B's were seen indicated by light shading (beginning in 2005). Included for are "probable" type-B's, only one sighting of which at Crozier is known for sure since the pod came very close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



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