Aquatic Mammals 2012, *38*(2), 153-160, DOI 10.1578/AM.38.2.2012.153

Trophic Interactions and Population Trends of Killer Whales (*Orcinus orca*) in the Southern Ross Sea

David G. Ainley[1] and Grant Ballard[2]

[1]*H.T. Harvey & Associates, 983 University Avenue, Building D, Los Gatos, CA 95032, USA*
E-mail: dainley@penguinscience.com
[2]*PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, USA*

Abstract

Foraging events and related trends in numbers of Type-B and -C killer whales (*Orcinus orca*) are reported for the vicinity of Ross Island, Ross Sea, Antarctica between 2002 and 2010. Updating an earlier report, the frequency of sightings and the number of individuals per sighting of Ross Sea killer whales (Type-C; RSKWs), a fishing-eating ecotype, has continued to decrease in a pattern coincident with a decrease in the number and size of an important prey: Antarctic toothfish (*Dissostichus mawsoni*). Increasingly rare, large fish are much more energetically dense and may also be socially important to the whales, a relationship with potential parallels to that known between well-studied fish-eating killer whales and large Chinook salmon (*Oncorhynchus tshawytscha)* in the northeast Pacific. In contrast, the prevalence of the larger, mammal-eating Type-B killer whales has not changed in the southern Ross Sea study area. Predation events by Type-B killer whales involving Weddell seals (*Leptonychotes weddellii*), interest in large penguins, such as emperors (*Aptenodytes forsteri*), and lack of interest in small penguins, such as Adélies (*Pygoscelis adeliae*), are presented. In the case of both killer whale forms, the progressive seasonal breakup of fast ice in large bays bordering the Ross Sea likely provides reliable, enhanced foraging opportunities as prey are exposed one area at a time during summer. Given the apparent relationship between RSKW prevalence and the availability of large toothfish, we speculate that the current management strategy of Antarctic toothfish in the Ross Sea region threatens current population levels of RSKWs.

Key Words: Antarctic toothfish, *Dissostichus mawsoni*, Ross Sea killer whales, Type-B killer whales, Type-C killer whales, *Orcinus orca*, Weddell seal, *Leptonychotes weddellii*, fish depletion, prey selectivity

Introduction

Two forms of killer whale (*Orcinus orca*) occur regularly over the Ross Sea continental shelf during spring and summer: Type-B and the smaller Type-C or Ross Sea killer whale (Pitman & Ensor, 2003). Morphological, behavioral, and genetic differences strongly suggest that the Ross Sea killer whale (Type-C, hereafter RSKW) is a distinct species (Pitman & Ensor, 2003; Pitman et al., 2007; Morin et al., 2010). The Type-B species in the Ross Sea is considered to be a mammal eater and is known to move rapidly over great distances. This behavior is consistent with their mammal-eating counterparts in other oceans. RSKWs are considered to be fish eaters and exhibit long residency in a given area (Andrews et al., 2008). RSKWs also occupy an identifiable environmental niche that is in contrast to that of Type-Bs, for which an environmental suitability model could not be created due to their more nomadic nature (Ballard et al., 2011). On the basis of relative size, RSKW vs Type-B, we suspect that the Type-Bs of the southern Ross Sea are more similar to the larger Type-Bs (Pack ice killer whale) seen in the Antarctic Peninsula region (see figure in Pitman, 2011, p. 34).

An earlier report (Ainley et al., 2009) described decreasing but not statistically significant trends in the prevalence of RSKWs in the southern Ross Sea, and it hypothesized that the trend could be related to decreasing availability of large Antarctic toothfish (*Dissostichus mawsoni*), a formerly frequent prey. The trend of decreasing fish availability was conjectured to be a function of an industrial fishery for toothfish in the Ross Sea region that began in 1996-1997. The fishery, whose management is problematic (Blight et al., 2010), now includes 15 to 20 vessels that take > 3,000 tons annually. Fishing sites are within 20 km of our study area. Recently, a mark-recapture time series of catch per unit effort and the size of fish caught for 1972 to 2011 has shown that catch and size of fish showed no trend for decades but began to sharply decrease in the study area beginning in 2000 (Ainley et al., 2012b). In the fish study, a vertical steel cable with ~15 hooks spaced a few meters apart was deployed at the same location and checked daily, with rare exception, mid-October to early December. More than 5,500 fish were caught overall.

Herein, the inclusion of two additional years of data on killer whale prevalence makes the statistical trend more robust. A continuing significant decrease in numbers of RSKWs is reported, and support for the earlier supposition about a connection to industrial fishing is provided. The Scientific Committee of the Convention for the Conservation of Antarctic Marine Living Resources (SC-CAMLR, 2009) opined that the lack of statistical significance to the trend as earlier reported justified no further attention to the issue (p. 152). In comparison, recent observations confirm the contrasting stable status and foraging behavior of Type-Bs in the study area.

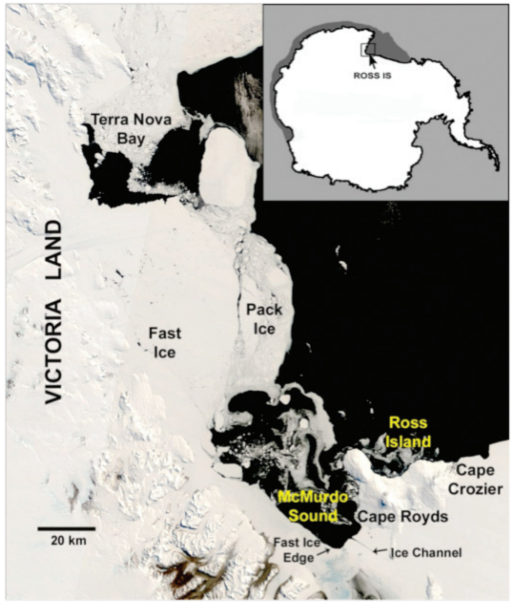

Figure 1. Observation locations at Cape Royds and Cape Crozier and other geography mentioned in the text; photo taken in mid-January 2009; larger scale version available in Ainley et al. (2009). McMurdo Station and Scott Base are located where the ice channel meets the southernmost point of Ross Island. Helicopter surveys went from Cape Royds, and then along the ice edge to where it turned northwest, including the channel when present.

Materials and Methods

Details of data acquisition for cetaceans, specifically, and mammals, in general, have been reported previously (Ainley et al., 2005, 2009). Briefly, daily watches were made each summer season from 2 December through 26 January 2002-2010 (Table 1; see Appendix 1 in Ainley et al., 2009, for actual counts). Aided by binoculars and spotting scopes, daily watches were conducted from high vantage points at both Cape Royds and Cape Crozier, Ross Island (100 and 400 m above sea level, respectively) (Figure 1; see also larger scale view in Ainley et al., 2009). Besides killer whale occurrence, predation on penguins by leopard seals (*Hydrurga leptonyx*) was also documented. In later years, the sighting effort began ~15 November, but to be equivalent to effort in earlier years herein only data acquired after 2 December for all years are considered. Few cetaceans were sighted earlier than 1 December in any case (Ainley et al., 2009, Appendix 1). From both locations, the view was 180° out to at least 2 km. Weather permitting, at least an hour in both the morning and evening were spent looking for killer whales each day. Given that it normally took at least 30 min for a group of killer whales to cross the viewscape, there was little chance that any were missed. In addition, two to five persons conducted penguin observational work for 10 to 12 h daily on the slopes above the Ross Sea shore. Having an unobstructed view of the ocean, that

Table 1. A summary of Ross Sea killer whale (RSKW) sightings from Cape Crozier, 2002-2010

	Days seen in waters off Cape Crozier	Maximum number	Mean (SE) number 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)
2009-2010	8 of 55 (0.15)	18	11.6 (1.5)
2010-2011	14 of 55 (0.25)	26	11.7 (2.0)

effort supplied ancillary information on cetacean presence and behavior. All marine mammals seen were logged along with their behavior and, in the case of killer whales, any long-range-detectable identifying marks were noted. Numbers and the approximate sex/age composition of killer whale groups were estimated. Beginning in late November, weekly surveys by helicopter were conducted along the fast ice edge in McMurdo Sound centered at 77° 30' S, 165° 00' E and running across the Sound from Cape Royds, a known area of concentration for killer whales (Figure 1). Helicopters flew at an altitude of 300 m along a course following the fast ice edge. With three observers, including the pilot, killer whales could easily be seen within 800 m of the edge.

Linear regression of natural log-transformed mean number of whales seen per sighting per year (Table 1) was used to assess statistical significance of trends. Regression on untransformed data was used to translate this to changes in actual numbers of killer whales seen (Figure 2). Qualitatively, we relate trends in killer whales to information on the prevalence (catch per unit effort) and size of toothfish.

Results

Ross Sea Killer Whales (Type-C)

The number of RSKWs seen at Cape Crozier on the northeast coast of Ross Island has continued to decrease (*cf.* Ainley et al., 2009). The linear trend, now with the addition of two more seasons of data, is statistically significant at a rate of 10.1% fewer RSKWs seen per sighting per year (β for ln (n whales seen per sighting) = -0.106 ± 0.026, $p = 0.004$, adjusted $r^2 = 0.67$; Figure 2). Analysis of the untransformed data shows this to translate to an estimated 2.1 fewer whales seen per sighting per year. Analyzed without the perhaps anomalously high first year (2002), the trend remained significant (β for ln [n whales seen per sighting] = -0.099 ± 0.019, $p = 0.01$, adjusted $r^2 = 0.87$).

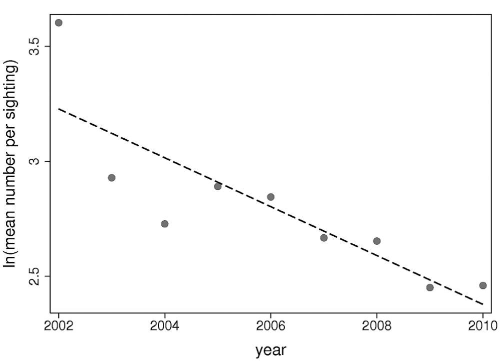

Figure 2. Trend in natural log transformed numbers of Ross Sea killer whales (RSKWs) seen per sighting per year at Cape Crozier, Ross Island, 2002-2010

At Cape Royds on the southwest coast of Ross Island, the time series of killer whale counts is not as long as at Cape Crozier; and at Cape Royds, the RSKWs (unlike Type-B) rarely came close enough to estimate numbers adequately from shore. The RSKWs in this area were presumably hunting deep-dwelling toothfish (depth in area descended quickly to 400 m), while the Type-Bs were hunting seals associated with coastal tide cracks (see below). Therefore, the record for RSKW occurrence is not as complete as for occurrence off Cape Crozier, and so no trends for Cape Royds are reported.

During the last 2 y, approximately weekly flights along the fast ice edge leading across McMurdo Sound from Cape Royds to the mainland coast at Marble Point (Figure 1) were made (Table 2). Most typically, groups of 10 to 20 (usually just one adult male) or no killer whales were evident. The size of the largest groups seen decreased in the second year, consistent with the Cape Crozier trend. In fact, the year earlier, a group of 175 RSKWs was seen by the authors by helicopter flight along the edge to thus emphasize the trend. The groups seen during recent years, judging from near-daily sighting efforts at Cape Royds, appeared to visit for a day or two but often less than a day. They would then be absent for several days. Groups were judged to be the same based on number and age composition as well as a few individuals having easily seen markings (e.g., dorsal fin cut off at top). On an approximate 5- to 7-d schedule the killer whales were seen traveling south by Cape Royds to the fast ice (under which they foraged). A short time later, they would be seen traveling north (see Andrews et al., 2008, for satellite tracks of RSKWs tagged off Cape Royds).

Table 2. A summary of killer whale observations from helicopters flying along the McMurdo Sound ice edge and in the icebreaker channel, late November through January 2010 and 2011; only counts of 20 or more whales are shown.

				Number and frequency of animals seen		
	Dates	Flights	No. orca	Largest number	2nd largest	3rd largest
2009-2010	3 Dec to 27 Jan	9	3 x	150	75	40-50 3x
2010-2011	28 Nov to 24 Jan	11	2 x	50	20-30 3x	--

Type-B Killer Whales

These larger killer whales were seen infrequently in small groups of < 10 individuals (usually 5 to 8). The ratio of RSKW to Type-Bs in most recent years at Cape Crozier has been 16:1, changed from 50:1 10 y ago when RSKWs were more abundant (Ainley et al., 2009; see Appendix 1 of that report for actual count data by day). At Cape Crozier, one and three sightings of Type-Bs, respectively, were logged during our 3-mo presence in 2009-2010 and 2010-2011. This frequency of sighting is consistent with previous years (see Ainley et al., 2009, Appendix 1). A similar frequency of Type-Bs was evident at Cape Royds.

Given that Pitman & Durban (2010) reported predatory behavior, including prey choice, among Type-B killer whales in Marguerite Bay, Antarctic Peninsula (see also Visser et al., 2008), it is appropriate to offer analogous Ross Sea sightings in order to expand this knowledge.

On two occasions in January 2011, the authors witnessed groups of Type-Bs swimming parallel to the shore at Cape Crozier and literally through thousands of penguins coming and going to the colony (~500,000 penguins present). Single killer whale individuals (adult female sized) would break out of the groups and chase penguins with vigorous surges and then rejoin the group. Since these individuals never paused to consume a penguin, which would involve skinning it and picking at the breast meat (see Pitman & Durban, 2010), we conclude that none of these efforts was successful. If there were bits of penguin appearing in the water, a flock of skuas (*Stercorarius maccormicki*) would have appeared as they do with leopard seal kills of penguins around Ross Island (Ainley et al., 2005).

On 20 November 2008, an entire group of seven Type-Bs chased a flock of nine emperor penguins (*Aptenodytes forsteri*) onto the fast ice at Cape Royds. Apparent interest in these larger penguins is consistent with the report of Andrews et al. (2008) who noted that satellite-tracked Type-Bs visited emperor penguin colony locations along their routes. Also, G. Kooyman (pers. comm.) reported killer whales patrolling the fast ice edge at which emperor penguins are congregated at Cape Washington in the Ross Sea. Emperor penguins are five times the mass of an Adélie and, thus, the effort to pursue this larger prey would have much higher energetic cost-benefit. During our observations at Cape Royds, the Type-Bs milled about for a few hours just off the ice while the penguins stood just back from the ice edge. Unfortunately, researchers could not watch this interaction continuously owing to competing duties. The last view occurred when the killer whales were departing, tail-slapping as they left, but no emperor penguins could be seen. Whether the killer whales were ultimately successful in their strategy to take these penguins is unknown.

Washing of seals off ice floes by Type-Bs, a behavior typical among groups in waters along the western shore of the Antarctic Peninsula (Visser et al., 2008; Pitman & Durban, 2011), has not been seen in our study area. There is, however, a report of a group of Type-Bs that vigorously splashed tourists in an inflatable boat in the southern Ross Sea (Pitman & Durban, 2011). Whether that incident is analogous to washing seals from ice floes is unknown. In our study area, Type-Bs spy hop along floes breaking away from the fast ice. The killer whales ignored small penguins on these floes.

On one occasion (16 December 2010), nine Type-Bs took a Weddell seal (*Leptonychotes weddellii*) juvenile (weaned within the month) from beneath the ice cracks that form along Cape Royds and along which the seals typically haul out. This group of a few dozen Weddell seals was spread between 20 and 100 m from the fast ice edge. After the predation event, all the remaining seals moved 2 km farther in from the edge and presumably out of breath-holding range of killer whales. On another occasion off Cape Royds (27 January 2004), seven Type-Bs took a recently weaned Weddell seal in a lead within the fast ice. In both cases, the killer whales swam at maximum speed toward the ice and the seals from several hundred meters away and were likely responding to seal vocalizations (R. Pitman, pers. comm.) given under water. We know of two reports of killer whales during the past 2 y, presumably Type-Bs, taking Weddell seals from small polynyas that form late in the season near McMurdo Station and Scott Base (southernmost point of Ross Island; Figure 1). Several hundred seals, mostly Weddell but including crabeater seals (*Lobodon carcinophagus*), usually frequent the ice in the vicinity of those polynyas during January-February. Access there by the killer whales is facilitated by the ice channel broken by icebreakers through the fast ice so that supply ships can provision McMurdo Station/Scott Base (Figure 1). The strategy invoked by the killer whales in this type of foraging seems to be one of surprise, hunting for seals lounging in the water just beneath their breathing holes or ice cracks. The killer whales appear suddenly after long periods of absence, especially as the fast ice is breaking up. This would represent a time when the seals were less knowledgeable about safe haul-out locations and naïve about paying attention to possible danger.

Discussion

The apparent decrease detected in RSKWs seems most likely to be a function of a reduction in local residence time, which means less opportunity for observers to detect them. This is evident in the decreasing number of days on which they have been seen at Cape Crozier (Table 1). The increasingly ephemeral nature of killer whale presence and especially of the large RSKW aggregations during the past 2 y along the McMurdo Sound fast ice edge was consistent with the Crozier pattern (Table 2). This was not typical of their behavior only a short number of years earlier. In that earlier period, dozens of killer whales, often in groups exceeding 100 animals, remained in the area for weeks (*cf.* Andrews et al., 2008; Ainley et al., 2009, Appendix 1; Ainley & Ballard, pers. obs.).

Another factor involved in the decreasing presence of RSKWs would be a lessened tendency for smaller groups to coalesce into larger groups. Both of these factors could have resulted from a need to increase search effort for food, including searching over a wider area. As it is, a number of areas exist around the Ross Sea, similar to McMurdo Sound, where the fast ice breaks out late in the summer thus opening new foraging areas. Whether the same or different groups of RSKW sequentially frequent these areas remains to be determined.

Why would greater search effort be needed by RSKWs? The answer might lie in them having more difficulty in finding prey. Indeed, analysis of the 39-y toothfish fishing effort in McMurdo Sound revealed a dramatic drop in the number of fish caught and their size beginning in 2000 (Ainley et al., 2012b). These decreases corresponded to the initiation of an industrial fishery in 1996-1997 that targets the biggest fish. Fishing takes place within 20 to 50 km north and east of Ross Island as well as off Terra Nova Bay (Pinkerton et al., 2007; Ainley et al., 2012a, 2012b).

The toothfish trends (fewer fish, especially large ones) could well be responsible for the apparent decrease of RSKWs in the region. Near the Crozet Islands, killer whales that depend heavily on Patagonian toothfish (*D. eleginoides*) also have exhibited a decline in numbers. In that case, it is thought that fishermen's outright killing of killer whales, which take fish from the long lines, was largely responsible (Guinet & Tixier, 2011). Nothing indicates that direct killing by fishermen is involved in the Ross Sea decrease. No reports of killer whales depredating long lines in the Ross Sea region have been made as of yet.

The trends in prey and predator interactions in the southern Ross Sea seem to be similar to a scenario at play in the northeast Pacific. Fish-eating killer whales there have decreased in numbers in recent decades, a trend related to the disappearance of large Chinook salmon (*Oncorhynchus tshawytscha*). This decrease has occurred despite smaller salmon remaining in abundance (Ford & Ellis, 2006; Ford et al., 2010). The northeast Pacific killer whale study began well after Chinook salmon began to decrease. It seems logical that an increased search effort by killer whales would precede any actual decrease in their numbers as prey decrease as is occurring in killer whales in the northeast Pacific.

Sightings of RSKWs with large toothfish in their grasp were once common (10 or more years ago) along the fast ice edge and in the ice channel from the edge into McMurdo Station (reviewed in Ainley et al., 2009; ice channel shown in Figure 1). Researchers and personnel on icebreakers during virtually every chop-in reported seeing this. A photo of an RSKW at the surface with a large toothfish is seen in Thomas et al. (1981) as is another in Wu & Mastro (2004). Such a phenomenon has not been reported for the past several years, although icebreakers have continued their presence, and the authors actually placed a "bounty" before the crews asking for any sightings or photos of killer whales with fish. Despite an increase in the time spent observing killer whales in the channel by researchers in recent years, including hundreds of hours by Andrews et al. (2008) and hundreds by a BBC film crew photographing killer whales during the filming of *Frozen Planet* in December-January 2010, no reports of killer whales with fish have been forthcoming. Killer whales with large fish were once seen in the Terra Nova Bay area as well, 100 km north (G. Kooyman as cited in Ainley et al., 2009).

The largest Chinook salmon are somewhat smaller than the largest Antarctic toothfish (1.5 vs 2.0 m). Adults of both fish species have much higher fat content than smaller ones, and they are probably attractive to killer whales for that reason. Small (< 100 cm) subadult toothfish do not have high fat content and remain near the bottom owing to a lack of buoyancy (Near et al., 2003; Ainley et al., 2012a, 2012b). This lack of buoyancy means that small toothfish are generally out of reach of killer whales since bottom depths are ≥ 400 m in most of the study region. Such a depth is within diving range of Weddell seals, and although the vertical set line failed to catch these small fish (Ainley et al., 2012b), the Weddell seals were successful in doing so (Ponganis & Stockard, 2007). Small toothfish are still present in McMurdo Sound (Ainley et al., 2012b).

Other factors could also contribute to why RSKWs might find large toothfish preferable to small ones. An underwater photo taken by Norbert Wu in 1999 (Wu & Mastro, 2004) in McMurdo Sound shows a large toothfish being carried by a male RSKW. The fish was somewhat ravaged from being passed back and forth among individual killer whales. The fact that RSKW once regularly brought large toothfish to the surface, as the eastern Pacific killer whales do with salmon, is further indication that more than just satisfying hunger is involved. According to Ford et al. (2010), prey sharing is an important social function, and the "fixed behavioral traditions" (p. 141) in prey selection among killer whales impedes any facility in prey switching when the primary prey becomes less available. Perhaps these factors are also now operating in the case of the RSKWs, though at a stage where actual population size has yet to be affected.

The agency responsible for managing Southern Ocean fishery resources, CCAMLR, is allowing the spawning biomass of Antarctic toothfish in the Ross Sea sector (FAO/CCAMLR Area 88) to be reduced by 50% within 35 y (beginning in 1996-1997) (Constable et al., 2000; Pinkerton et al., 2007). This level of fishing is in contrast to that of species deemed to be prey (e.g., krill) and not a predator. For "prey" or forage species, the rule of thumb is fishing to 75% pre-fishing spawning biomass. This is summarized in Constable et al. (2000): "For example, Patagonian toothfish [*D. eleginoides*], as a large predator, is unlikely to constitute much of the diet of seals and birds (SC-CAMLR 1997). Therefore, the species is considered in a single-species context and the second criterion is applied at the 50% level rather than at the 75% level" (p. 785). The fishery exercises this strategy in the Ross Sea region by taking the largest fish, size having decreased in the fishery in recent years (Ainley et al., 2012a). Such a fishing strategy is necessitated in part by the economically expensive, 2,000 km distance to the nearest port. Vessels must fill holds quickly before foul weather and advancing sea ice forces them out of the Ross Sea. The open water season in the Ross Sea lasts only a few months and is rapidly decreasing (Stammerjohn et al., 2012). During the fishing season in the Ross Sea, January and February, when vessels take advantage of minimal ice cover, these large fish apparently remain near the bottom in deep waters (1,000 to 2,000 m), especially along the continental slope where the fishery expends its greatest effort (SC-CAMLR, 2010). The authors' conclusion from the data presently available is that the current abundance of the RSKW population in the southern Ross Sea will be a casualty of the CCAMLR toothfish fishery management strategy.

It could be argued that observational evidence of the type presented here is not sufficient to link the decreasing presence of RSKWs with the decreasing availability of toothfish, a position purportedly supported by a biochemical study of the killer whale diet (Krahn et al., 2008). In that study, stable isotopes were evaluated in samples of RSKW epidermis taken in 2005 and 2006, several years after large toothfish had mostly disappeared from the southern Ross Sea (Ainley et al., 2012a). The Krahn study and isotopic studies of the Weddell seal diet conducted earlier (Burns et al., 1998) indicate that the seals and killer whales feed at the same trophic level in McMurdo Sound. Results were not comparable because the seal analysis was performed using blood (indicating day-to-day diet) taken from individuals occurring in a portion of McMurdo Sound (Erebus Bay) where no toothfish occur (Testa et al., 1985). Krahn et al. (2008) concluded that RSKWs feed largely on fish but otherwise had little more to say about the relative importance of toothfish in the RSKW diet.

Three issues impede further discussion of the fishery vs killer whale prey question. First, sampling of diet thus far has been inadequate among certain Ross Sea predators. Second, accepting currently available isotope data (i.e., isotope signature of RSKW in 2005-2006) as representative of the past is a refusal to acknowledge the "shifting baseline syndrome" (Pauly, 1995, p. 430) precipitated especially by the fishery. Finally, in dealing with highly evolved animals, many nonconsumptive factors exist in food web relationships. For example, "fixed behavioral traditions" (Ford et al., 2010, p. 141; see also Heithaus et al., 2007) confound attempts to quantify or model trophic relationships. A dramatic example of nonconsumptive issues in the case of the RSKW was evident in January 2009 when a polynya formed off Cape Royds about 15 km inside the fast ice sheet covering all of McMurdo Sound at that time. Within 2 d, a group of RSKWs (and two minke whales [*Balaenoptera bonaerensis*]) appeared within the polynya. To have done this, they had to use narrow, along-shore cracks as breathing avenues to find their way into the polynya and its yet-to-be-exploited fish resources. Apparently, the possession of "local" knowledge facilitated the whales' decision and ability to do this. As the sea ice "dissolved" and the polynya formed, there was a "fizzing" sound audible to the authors even a few kilometers away. Likely, given the amplification of sound in water, the whales heard this noise, too, and knew what it represented. To say the least, such cultural aspects of cetacean foraging dynamics are very difficult to model.

The authors do not propose that RSKWs prey exclusively on large Antarctic toothfish but, rather, that their availability is important to this species. Krahn et al. (2008) concluded that further research is needed before biochemical analyses can contribute to the discussion about the specific diet of RSKWs. Included in future research should be the biochemical signature of toothfish of different sizes and ages given that diet and presumably isotope signature changes with growth in size (Fenaughty et al., 2003). All things being equal, the sorts of mark-recapture, photo-ID studies described in Pitman (2011) would no doubt be helpful as well to monitor killer whale prevalence in the Ross Sea.

Acknowledgments

Collection of cetacean data and preparation of this paper was funded by National Science Foundation grants ANT-0440463 and ANT-0944411. We thank S. Jennings, A. Lescroël, M. Massaro, J. Pennycook, A. Pollard, and L. Porzig for participating in observations for the past two seasons. The toothfish data referred to were gathered by A. L. DeVries and C. W. Evans under grants funded by NSF. The U.S. Antarctic Program amply provided all logistical support. R. L. Pitman and two anonymous reviewers provided thoughtful, constructive comments, thus immensely helping to improve an earlier draft of the paper. The views expressed herein do not necessarily represent those of the NSF. PRBO contribution #1862.

Literature Cited

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), 335-347.

Ainley, D. G., Ballard, G., Karl, B. J., & Dugger, K. T. (2005). Leopard seal predation rates at penguin colonies of different size. *Antarctic Science*, *17*, 335-340.

Ainley, D. G., Brooks, C. M., Eastman, J. T., & Massaro, M. (2012a, in press). Unnatural selection of Antarctic toothfish in the Ross Sea, Antarctica. In F. Huettmann (Ed.), *Protection of the three poles* (pp. 35-71). Tokyo: Springer Japan.

Ainley, D. G., Nur, N., Eastman, J., Ballard, G., Parkinson, C. L., Evans, C., & DeVries, A. L. (2012b, in press). Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972-2011. *Fish and Fisheries*.

Andrews, R. D., Pitman, R. L., & Ballance, L. T. (2008). Satellite tracking reveals distinct movement patterns for type B and type C killer whales in the southern Ross Sea, Antarctica. *Polar Biology*, *31*, 1461-1468.

Ballard, G., Jongsomjit, D., Veloz, S. D., & Ainley, D. G. (2011, published online). Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. *Biological Conservation*. http://dx.doi.org/10.1016/j.biocon.2011.11.017

Blight, L. K., Ainley, D. G., Ackley, S. F., Ballard, G., Ballerini, T., Brownell, R. L., Jr., . . . Woehler, E. J. (2010). Fishing for data in the Ross Sea. *Science*, *330*, 1316.

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*, 272-282.

Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I., & Miller, D. (2000). Managing fisheries to conserve the Antarctic marine ecosystem: Practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES Journal of Marine Science*, *57*, 778-791.

Fenaughty, J. M., Stevens, D. W., & Hanchet, S. M. (2003). Diet of the Antarctic toothfish (*Dissostichus mawsoni*) from the Ross Sea, Antarctica (CCAMLR Statistical Subarea 88.1). *CCAMLR Science*, *10*, 1-11.

Ford, J. K. B., & Ellis, G. M. (2006). Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Marine Ecology Progress Series*, *316*, 185-199.

Ford, J. K. B., Ellis, G. M., Olesiuk, P. F., & Balcomb, K. C. (2010). Linking killer whale survival and prey abundance: Food limitation in the oceans' apex predator? *Biology Letters*, *6*, 139-142.

Guinet, C., & Tixier, P. (2011). Crozet killer whales: A remote but changing environment. *Journal of the American Cetacean Society*, *40*, 33-38.

Heithaus, M. R., Frid, A., Wirsing, A. J., Dill, L. M., Fourqurean, J. W., Burkholder, D., . . . Bejder, L. (2007). State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology*, *76*, 837-844.

Krahn, M. K., 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*, 643-663.

Morin, P. A., Archer, F. I., Foote, A. D., Vilstrup, J., Allen, E. E., Wade, P., . . . Harkins, T. (2010). Complete mitochondrial genome phylogenetic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research*, *20*, 908-916. http://dx.doi.org/10.1101/gr.102954.109

Near, T. J., Russo, S. E., Jones, C. D., & DeVries, A. L. (2003). Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (Perciformes: Nototheniidae). *Polar Biology*, *26*, 124-128.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome in fisheries. *Trends in Ecology and Evolution*, *10*, 430.

Pinkerton, M., Hanchet, S., & Bradford-Grieve, J. (2007). Finding the role of Antarctic toothfish in the Ross Sea ecosystem. *Water and Atmosphere*, *15*, 20-21.

Pitman, R. L. (Ed.). (2011). Killer whales: The top, top predator. *Whale Watcher*, *40*, 1-67.

Pitman, R. L., & Durban, J. (2010). Killer whale predation on penguins in Antarctica. *Polar Biology*, *33*, 1589-1594. http://dx.doi.org/10.1007/s00300-010-0853-5

Pitman, R. L., & Durban, J. (2011, first published online). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal*

Science, *28*(1), 16-36. http://dx.doi.org/10.1111/j.1748-7692.2010.00453.x

Pitman, R. L., & Ensor, P. (2003). Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management*, *5*, 1-9.

Pitman, R. L., Perryman, W. L., Leroi, D., & Eilers, E. (2007). A dwarf form of killer whale in Antarctica. *Journal of Mammalogy*, *88*, 43-48.

Ponganis, P. J., & Stockard, T. K. (2007). The Antarctic toothfish: How common a prey for Weddell seals? *Antarctic Science*, *19*, 441-442.

Scientific Committee of the Convention for the Conservation of Antarctic Marine Living Resources (SC-CAMLR). (1997). *Report of the sixteenth meeting of the Scientifc Committee.* Hobart: CCAMLR. Retrieved 26 April 2012 from www.ccamlr.org/pu/e/e_pubs/sr/97/all.pdf.

SC-CAMLR. (2009). *Report of the twenty-eighth meeting of the Scientific Committee*. Hobart: CCAMLR. Retrieved 24 April 2012 from www.ccamlr.org/pu/e/e_pubs/sr/09/toc.htm.

SC-CAMLR. (2010). *Report of the Scientific Committee, Appendix K*. Retrieved 24 April 2012 from www.ccamlr.org/pu/e/e_pubs/sr/10/toc.htm.

Stammerjohn, S. E., Massom, R., Rind, D., & Martinson, D. G. (2012). Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. *Journal of Geophysical Research*, *39*, L06501. http://dx.doi.org/10.1029/2012GL050874

Testa, J. W., Siniff, D. B., Ross, M. J., & Winter, J. D. (1985). Weddell seal-Antarctic cod interactions in McMurdo Sound, Antarctica. In W. R. Seigfried, P. R. Condy, & R. M. Laws (Eds.), *Antarctic nutrient cycles and food webs* (pp. 561-565). Berlin: Springer.

Thomas, J. A., Leatherwood, S., Evans, W. E., Jehl, J. R., Jr., & Awbrey, F. T. (1981). Ross Sea killer whale distribution, behavior, color patterns, and vocalizations. *Antarctic Journal of the United States*, *16*, 157-158.

Visser, I. N., Smith T. G., Bullock, I. D., Green, G. D., Carlsson, O. G. L., & Imberti, S. (2008). Antarctic Peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Marine Mammal Science*, *24*, 225-234.

Wu, N., & Mastro, J. (2004). *Under Antarctic ice: The photographs of Norbert Wu*. San Diego: University of California Press.