

COMPETITION AMONG PENGUINS AND CETACEANS REVEALS TROPHIC CASCADES IN THE WESTERN ROSS SEA, ANTARCTICA

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Abstract. An apparent trophic cascade that appears during summer in the western Ross Sea, Antarctica, explains why the Antarctic silverfish (*Pleuragramma antarcticum*) there becomes cannibalistic; its principal prey, crystal krill (*Euphausia crystallorophias*) becomes scarce; and the diatom community is minimally grazed compared to adjacent areas. The krill is the major grazer of diatoms. On the basis of fieldwork at Ross Island, we suggest that the cascade results from foraging by unusually numerous Adélie Penguins (*Pygoscelis adeliae*), minke whales (*Balaenoptera bonaerensis*), and fish-eating killer whales (*Orcinus orca*). These species and other top predators apparently deplete the krill and silverfish. In drawing our conclusions, we were aided by two “natural experiments.” In one “experiment,” large, grounded icebergs altered the seasonal pattern of change in regional sea-ice cover, but not the seasonal change in penguin diet and foraging behavior that was also detected during the pre-iceberg era. In the other “experiment,” a short-term polynya (opening in the ice) brought penguins and whales together in a confined area, this time altering both penguin diet and foraging behavior. We conclude that the foraging of penguins and whales, and not a formerly hypothesized seasonal decrease in sea-ice cover, explains (1) the annual switch in the penguins’ prey from krill to silverfish, (2) the subsequent lengthening of penguin foraging trips, and (3) a marked decline of cetaceans in the area later in the season. Reduction in the middle-trophic-level prey is expressed in the relaxed grazing pressure on phytoplankton.

Key words: Adélie Penguin; Antarctica; Antarctic silverfish; Antarctic toothfish; crystal krill; killer whale; minke whale; prey availability; Ross Sea; sea ice; trophic cascade; trophic competition.

INTRODUCTION

Trophic cascades are “reciprocal predator–prey effects that alter the abundance, biomass, or productivity of a population, community, or trophic level across more than one link in a food web” (Pace et al. 1999:483). They are recognized and well described in terrestrial, stream, and lake ecosystems (see references in Pace et al. 1999). Despite initial doubts among ecologists, evidence accumulates to indicate their existence, too, in some open-ocean systems (e.g., Verity and Smetacek 1996, Shiomoto et al. 1997, Eiane et al. 2002, Essington et al. 2002, Worm and Myers 2003, Scheffer et al. 2005).

Many trophic cascades formerly linked to top predators in open-ocean ecosystems are not apparent in modern times, owing to the loss of upper trophic levels through overfishing and other factors (Pace et al. 1999, Pauly and Maclean 2003). The waters overlying the Ross Sea continental shelf (72–78° S, 170° E to 158° W along its shelf break), however, encompass an intact marine ecosystem, in contrast to the more northern, pelagic portions of the Southern Ocean, where overfish-

ing has reduced any significant, naturally occurring top-down forcing (cf. Pauly et al. 1998, Ainley 2002a). In the Ross Sea, Ainley et al. (2004) found that large colonies of Adélie Penguins (*Pygoscelis adeliae*) can decrease the availability of prey (crystal krill [*Euphausia crystallorophias*] and Antarctic silverfish [*Pleuragramma antarcticum*]) within the penguins’ foraging range, and they proposed intraspecific interference competition as the cause. Therefore, top predators can importantly influence the prevalence of their prey in the Ross Sea neritic system, as also observed by Testa et al. (1985). On the other hand, providing a bottom-up argument, Ainley et al. (2003) hypothesized that a coincident, seasonal switch in penguin diet from crystal krill to silverfish resulted from a within-season reduction of sea ice, an important habitat of crystal krill.

The arrival and grounding in the Ross Island penguin foraging area of two extremely large icebergs (one being 165 km or >1.5 latitude degrees long!) changed conditions, such that after the austral spring–summer 2000–2001, the sea ice no longer dispersed by mid-season (Arrigo et al. 2002, Ainley et al. 2004). However, the diet switch still occurred, compelling us to reevaluate our hypotheses. In addition, we conducted research to formally evaluate previous observations that penguin foraging behavior seemed to change when cetaceans

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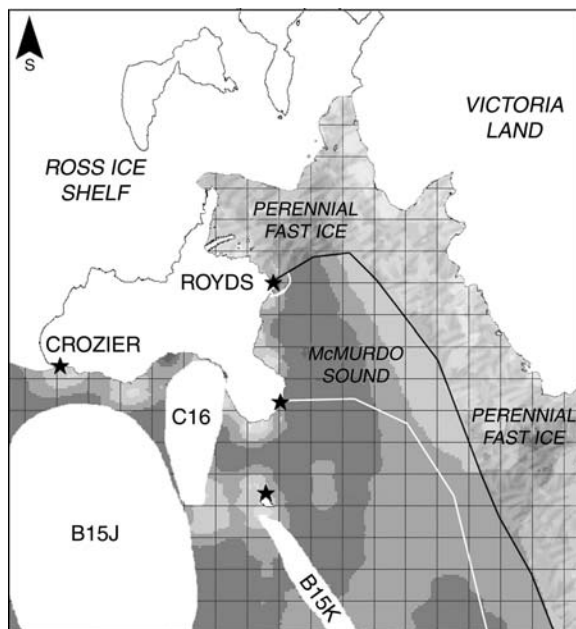


FIG. 1. Southwestern corner of the Ross Sea, an area that encompasses the foraging areas of the various colonies shown by stars (see Ainley et al. 2004). The entire ocean shown was covered in pack ice (divergent, small floes) during the study, except for that covered by the three mega-icebergs (B15J, B15K, C16), that covered by the perennial fast ice (near-continuous sheet of ice), and that covered in 2004 by annual fast ice, which is the area south and west of the long white line. The short white line surrounding the star at Cape Royds is the polynya that developed during January 2005. The depth contour is 100 m (deeper is darker); the grid squares are 10 km.

arrived in the study area. Similar to the penguins, Antarctic minke whales (*Balaenoptera bonaerensis*) feed principally on crystal krill and Antarctic silverfish over the Ross Sea continental shelf (Ichii et al. 1998), but less is known about the diet of type-C killer whales (*Orcinus orca*; Pitman and Ensor 2003). The latter feed on fish, especially Antarctic toothfish (*Dissostichus mawsoni*; see photographs in Thomas et al. 1981, Mastro and Wu 2004; D. G. Ainley, *personal observation*), but also, it is suspected, on the abundant silverfish, in a manner similar to their foraging on abundant, small, schooling fish elsewhere (Similä and Ungarte 1993, Pitman and Ensor 2003; R. L. Pitman, *personal communication*).

We present data on cetacean and penguin foraging behavior and penguin diet changes collected during two “natural experiments”: increased persistence of regional sea ice as a result of blocking by large, grounded icebergs; and the short-term development of a polynya (open water) isolated in one heavily iced area near a colony. Using these data, we: (1) assess the correspondence of changes in penguin and cetacean foraging behavior and penguin diet relative to the sea-ice regime; (2) provide evidence that the penguins and cetaceans all may affect the availability of prey within the foraging range of the penguins; and (3) relate these findings to

more widespread patterns of phytoplankton grazing in the Ross Sea (the prime grazers in the system being the top predators’ prey) and to the observation that the krill-feeding silverfish become seasonally cannibalistic.

METHODS

Study area

Observations were conducted at Cape Crozier (77°27' S, 169°12' E), one of the largest of all Adélie Penguin colonies (135 000 pairs), and 75 km away at the much smaller Cape Royds colony, with 3900 pairs (78°33' S, 166°10' E), on opposite sides of Ross Island, southwestern Ross Sea (Fig. 1), during the 2003–2004 and 2004–2005 austral summers (15 November–25 January). Additional information on diet comes from the 1996–1997 to 2002–2003 seasons. Unless written out, e.g., 2003–2004, we designate summers by the initial year, i.e., the spring–summer period November 2003 to February 2004 is the 2003 season.

Data collection

Daily, morning and evening, except at Cape Royds during 2001–2002, we estimated percentage of sea-ice cover within a 180° view of the colonies (Fig. 2). Vantage points were 15 m (Royds) to 115–400 m a.s.l. (Crozier). Large icebergs were considered to be “islands” and not part of the penguin foraging area. Our elevation at Crozier allowed assessment of ice, and the leads between floes, in a radius to 15 km (and whales to ~7 km; the horizon actually being farther). At Royds, we could assess ice cover only to a radius of ~7 km (and whales to ~3 km), beyond which the ice obscured water between floes. These distances were estimated based on mapped points along the adjacent coast. We also monitored large-scale sea-ice cover and iceberg movements by examining 250 m/pixel MODIS Rapid Response System images (*available online*).⁵

Also daily, weather permitting and aided by 8× or 10× binoculars, we logged the number and behavior of cetaceans seen from the same vantage points during 2003–2004 and 2004–2005, unlike the more casual cetacean observations gathered previously (Ballard and Ainley 2005). We observed for at least one hour, 1–3 times per day, with effort directed toward marine mammals (Ainley et al. 2005). We used the maximum count of whales seen at any time during an observation period 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, we could not make true estimates of whale abundance. Rather, differences in counts indexed the relative changes in whale numbers by season and year.

Penguin foraging trip duration (FTD, in hours) was determined using implanted RFID (radio frequency identification) tags (Ainley et al. 1998, Ballard et al.

⁵ (<http://rapidfire.sci.gsfc.nasa.gov/subsets/?RossSea>)

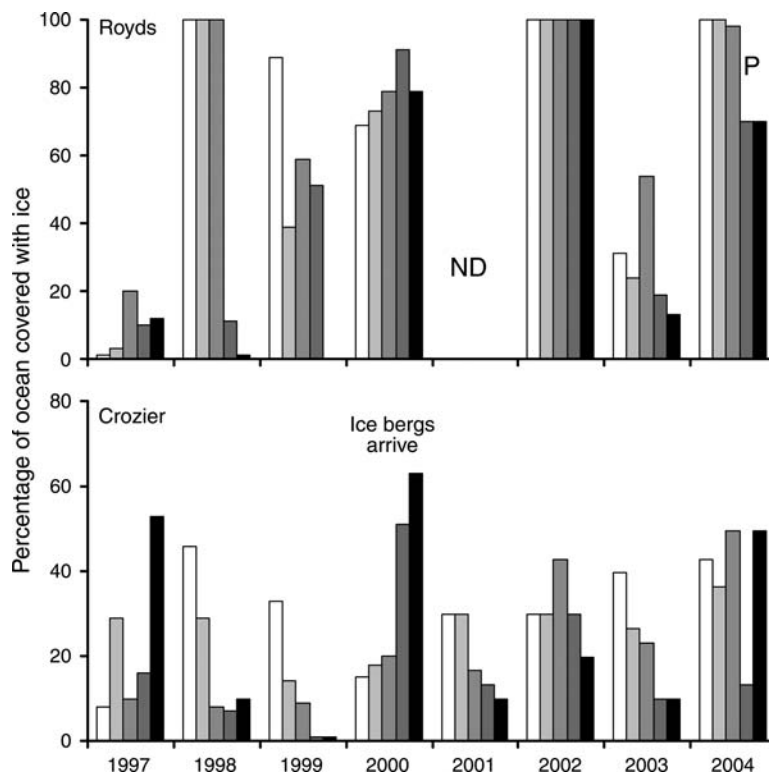


FIG. 2. The percentage of ocean covered by sea ice (average of daily estimates), at Cape Royds and Cape Crozier, by week and year. There were no data (ND) for 2001 at Royds; P indicates a small polynya off Royds. The large icebergs arrived on the scene during the chick-provisioning period in 2000 (see Ainley et al. [2004] for details).

2001). For each individual, the date/time and direction of its travel across a scale were logged in a computer as it passed through an RFID reader upon arriving and departing to feed its chick(s). For all colony-years, we had at least 29 active nests in which at least one member of a pair contained an RFID tag. Between 1996 and 2004, 260 individuals were implanted with tags; each year, the total number of tagged, breeding individuals monitored ranged from 29 to 91. To be considered a breeder, and thus included in analyses during a given breeding season, an individual had to make >4 trips of 6–120 h duration (following Ballard et al. 2001, Dugger et al. 2006). For Royds and Crozier, respectively, our FTD sample included (mean \pm se) 7.6 ± 1.0 and 8.1 ± 0.6 trips per day in 2003–2004 and 4.5 ± 0.6 and 3.5 ± 0.3 trips per day in 2004–2005.

Trip distance (in kilometers) was measured using transmitters (SPOT2, 3, and 4; Wildlife Computers, Redmond, Washington, USA) placed on known parents for 1–2 foraging trips and then switched to new individuals (at least 30 individuals per season per colony, unless otherwise stated). These instruments were configured to transmit at least once every ~ 90 s, 24 hours per day, while “wet”; i.e., when the bird was at the surface of the ocean, but not when it was hauled out on sea ice or in the colony. We filtered ARGOS positions to exclude location class “Z” (“rejected locations”; AR-

GOS 2003), and then used an algorithm to determine “foraging clusters.” Foraging clusters were groups of locations, each having at least two neighbors within 2 km and 4 h. The mean distance of points in the most outward cluster represented the maximum foraging distance for a given trip. Trip duration and distance data collection began at chick hatching and ended about 1 week prior to fledging (~ 15 December–21 January; hatching at Royds was a week later than at Crozier).

Diet was characterized in 2001–2004 by observing food that parents regurgitated to their chicks. Using binoculars, we easily distinguished krill (pink) from fish (gray). Observations were supplemented by spillages around nests and by inspecting stomach contents of chicks killed by skuas. Fish and krill species identity had been established in six previous seasons, 1996–2001, by analyzing samples flushed from stomachs: the diet was composed invariably of crystal krill and/or silverfish (Ainley et al. 2003). Because of diet simplicity, feeding observations provided composition data comparable to samples gained by stomach flushing (D. G. Ainley and G. Ballard, unpublished data).

Data analysis

The percentage of krill in the diet was averaged for all observations by all workers at a given colony by day. Diet in recent years (by observation) was compared to

diet in earlier years (by stomach flushing) by further averaging samples into the 7-d periods used earlier (only weekly samples were taken; see Ainley et al. 1998, 2003): week 1 (with 25 December the midpoint), week 2 (1 January), week 3 (8 January), week 4 (15 January), and week 5 (22 January). We had eight years of data for Crozier (1997–2004) and seven for Royds; during 2001, chicks were too few at Royds to see many feeds. Ice cover and FTD, assessed daily, were averaged for the same 7-d periods. Annual breeding population size was indexed by calculating the mean difference from the 1996 chick count for a given year and colony; 12 subcolonies at Crozier and 13 at Royds were used to develop these figures (Ainley et al. 2004).

Total biomass of prey consumed was estimated using the number of breeding and nonbreeding penguins in the colony (based on daily counts of nest plots), the number of chicks fed in those plots, and the number of whales seen. Plot counts for Crozier were compared against known size of the colony in previous years (Ainley et al. 2004; $r^2 = 0.93$); Royds was small enough to be directly counted. Daily whale numbers were estimated by contouring actual counts to fill in for days lacking observations; in-filled numbers were averages of those on bracketing dates. Daily counts were then multiplied by estimates of prey consumption. A minke whale consumes ~250 kg of food/d (Ichii and Kato 1991) compared to about 0.9 kg/d by an Adélie Penguin (reviewed in Ainley 2002b:68). Consumption is not known for the smaller, type-C killer whale but, in captivity, a female A-type killer whale consumes ~125 kg of fish/d (T. Williams, *personal communication*). No other information is available on food consumption by killer whales. A female type-A is smaller than a male type-C, but larger than a female type-C (Pitman and Ensor 2003); therefore, we used the 125 kg/d consumption estimate for all type-C individuals regardless of size. Assuming that whales foraged throughout the penguin foraging areas, we adjusted the estimate of penguin prey consumed by the percentage of their foraging area in which we could detect whales. Thus, with a mean maximum foraging radius of 12 km at Royds (whales seen to 3 km) and 125 km at Crozier (whales seen to 7 km; see *Results*), we judged that we could see whales in 25% of Royds and 6% of the Crozier foraging areas. Therefore, we reduced the daily estimated biomass taken by Royds penguins by 75% and Crozier penguins by 94%.

We used a linear, mixed model procedure (PROC MIXED; SAS Institute 1997) to examine the relationship between the percentage of the penguin diet composed of krill and the FTD, with four explanatory variables: colony (Crozier vs. Royds), week in the chick-provisioning period (1–5), ice cover, and breeding population size. For FTD analysis, the percentage of krill in the diet was also included. Week was treated as a continuous variable in order to assess the importance of a seasonally decreasing trend in krill percentage in the diet. Previously we found that the percentage of krill and

FTD varied by year (Ballard et al. 2001, Ainley et al. 2003). In this study, we were interested in the effect of specific sources of annual diet variation and FTD, so we did not include year as a fixed effect. Rather, we investigated specific effects of the annual amounts of sea ice and population size for each colony. To account for additional annual variation unexplained by ice or population size, year was included as the random effect. An arcsine square-root transformation on the percentage of krill in the diet and the natural log transformation of FTD normalized the residuals. Values reported are means \pm SE.

We used an information-theoretic approach (Burnham and Anderson 2002) to develop model sets to test hypotheses and to select the best models. Model selection included Akaike's Information Criterion corrected for small sample sizes (AIC_c), delta AIC_c (ΔAIC_c), and AIC_c weights. The degree to which 95% confidence intervals for slope coefficients overlapped zero was used to evaluate competing models ($\Delta AIC_c < 2$) and specific explanatory variables.

Our a priori model set for percentage of krill in penguin diets included all single- to four-factor additive-model combinations of our explanatory variables (Table 1). We hypothesized the existence of potentially different relationships between percentage of krill and week, ice, or population size, depending on colony. Thus, we also investigated some two-factor interactions between colony and week, ice, or population. Over the study period, unusual ice conditions meant that ice cover did not necessarily decrease seasonally. In other words, week and ice were not proxies of each other. Thus, we evaluated the idea that the percentage of krill in the diet changed independently of ice conditions by including models with both week and ice as either additive or interactive effects.

The same a priori model set was used to analyze FTD, but because we knew that colony effects would be evident (Ballard et al. 2001), we only included models with colony in our a priori set (Table 2). To this base set, we added more models including the percentage of krill as another additive or interaction effect on FTD (Table 2).

Following Olson et al. (2004), we used changes in the residuals generated by PROC MIXED (SAS Institute 1997) for our best models, compared to the intercept-only model, to determine the amount of variation in krill percentage or FTD explained. The intercept-only models were considered estimates of the total process variance; model variance was estimated as the difference in residual variance of the intercept-only model and the final best model with all specified effects.

Finally, for years in which we had whale data (2003 and 2004), we generated two other data sets. The first contained mean daily FTD and the number of minke whales, killer whales, and both species combined (total whales) using the contoured data previously described. The second contained mean daily percentage of krill in penguin diets and whale numbers, as before. Data

TABLE 1. Models and Akaike values relating (A) mean weekly percentage of krill in penguin diets and (B) foraging trip duration to various factors.

Factors	AIC _c	ΔAIC _c	w _i	k
A) Percentage of krill in diet				
BPS, WK	41.374	0.000	0.252	5
COL, WK	42.122	0.748	0.173	5
COL, BPS, WK	42.772	1.398	0.125	6
BPS, WK, ICE	43.411	2.037	0.091	6
COL, WK, COL × WK	43.484	2.110	0.088	6
WK, ICE	43.734	2.360	0.077	5
WK	43.873	2.499	0.072	4
COL, WK, ICE	44.305	2.931	0.058	6
COL, BPS, ICE	45.182	3.808	0.037	7
WK, ICE, WK × ICE	45.865	4.491	0.027	6
ICE	63.805	22.431	0.000	4
BPS, ICE	65.165	23.791	0.000	5
B) Foraging trip duration (FTD)				
COL, WK, ICE, KRILL, WK × ICE	57.04	0.00	0.367	8
COL, WK, ICE, WK × ICE	57.52	0.49	0.288	7
COL, BPS, WK, KRILL	60.48	3.44	0.066	7
COL, WK, KRILL	61.51	4.47	0.039	6
COL, WK, ICE, KRILL	61.69	4.65	0.036	7
COL, WK, KRILL, COL × KRILL	61.74	4.71	0.035	7
COL, WK, ICE, BPS, KRILL	61.90	4.87	0.032	8
COL, WK, ICE	62.67	5.64	0.022	6
COL, BPS, WK	63.25	6.22	0.016	6
COL, WK	63.32	6.28	0.016	5
COL, WK, KRILL, WK × KRILL	63.94	6.91	0.012	7
COL, BPS, WK, ICE	63.96	6.92	0.012	7

Notes: The 12 best a priori models (of 19 tested for A, 30 for B) were selected using 1997–2004 data. Sample size is $n = 75$ observations for both diet composition and foraging trip duration. Models are ranked according to Akaike's Information Criterion adjusted for small sample sizes (AIC_c); AIC_c, ΔAIC_c, AIC_c weights (w_i), and number of parameters (k) are given for each model. Interaction effects are indicated by "×". Factors are: COL, colony (Royds vs. Crozier); WK, week during the chick-rearing season (weeks 1–5); BPS, breeding population size; ICE, percentage of ocean covered with ice; and KRILL, percentage of krill in the diet.

TABLE 2. Models relating (A) mean foraging trip duration and (B) mean daily percentage of krill in penguin diets to colony (COL), minke whale numbers (MIN), killer whale numbers (KIL), and total whale numbers per day (BOTH).

Factors	AIC _c	ΔAIC _c	w _i	k
A) Foraging trip duration, FTD (n = 92)				
COL, BOTH, COL × BOTH	105.51	0.000	0.226	6
COL, BOTH	105.83	0.323	0.192	5
COL, MIN	106.28	0.776	0.153	5
COL, MIN, COL × MIN	106.99	1.487	0.107	6
COL, MIN, KIL	107.17	1.665	0.098	6
COL, KIL	107.38	1.877	0.088	5
COL, KIL, COL × KIL	107.57	2.066	0.080	6
COL	108.62	3.116	0.048	4
BOTH	114.21	8.700	0.003	4
MIN	114.28	8.779	0.003	4
KIL	115.96	10.455	0.001	4
INTERCEPT ONLY	117.31	11.803	0.001	3
B) Percentage of krill in diet (n = 77)				
COL, MIN	81.54	0.000	0.433	4
COL, MIN, COL × MIN	82.12	0.581	0.324	5
COL, MIN, KIL	83.76	2.214	0.143	5
MIN	84.51	2.962	0.099	3
COL, BOTH	96.59	15.045	0.000	4
BOTH	98.78	17.235	0.000	3
COL, BOTH, COL × BOTH	98.79	17.251	0.000	5
COL, KIL	102.39	20.852	0.000	4
COL	103.46	21.913	0.000	3
KIL	104.36	22.813	0.000	3
COL, KIL, COL × KIL	104.64	23.096	0.000	5
INTERCEPT ONLY	105.38	23.837	0.000	2

Notes: The table shows results for the 12 a priori models tested using 2003–2004 data. Model ranking and column headings are as in Table 1.

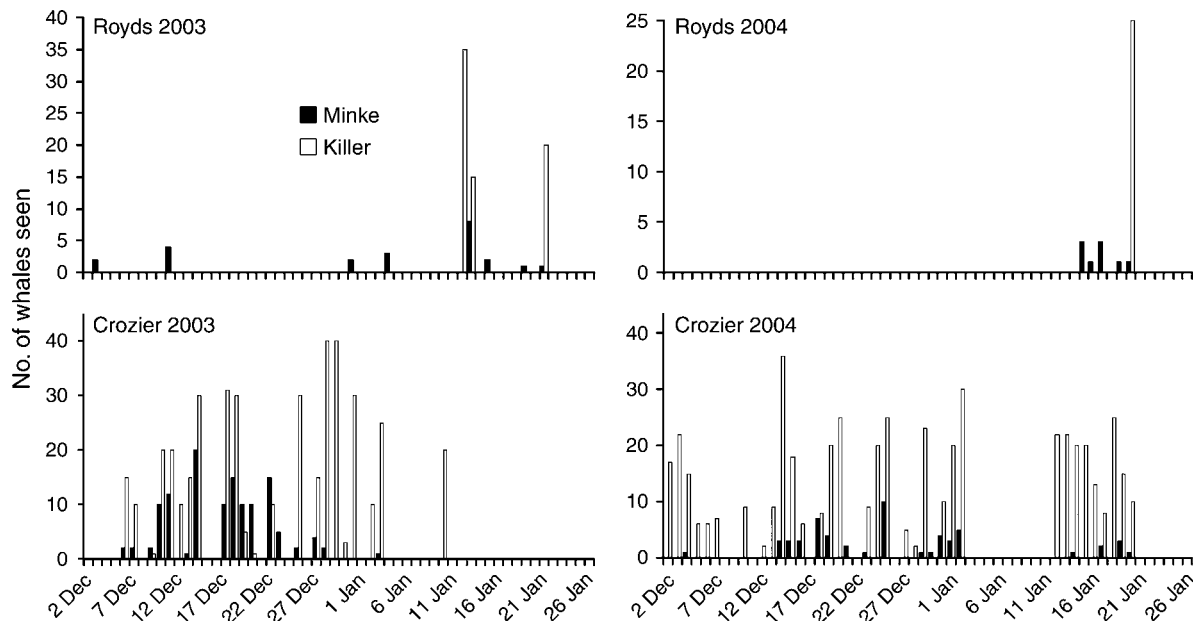


FIG. 3. The number of minke and killer whales seen from vantage points at Cape Royds and Cape Crozier in 2003–2004 and 2004–2005; from mid-November to 25–29 January each year.

corresponded to the period when (1) chicks were being fed and (2) open water was present, because whales could not be present if ice cover were complete. For Cape Crozier, open water occurred before chick-rearing in both years; in 2004, open water at Cape Royds did not occur until January. We used the same linear, mixed-model procedure and information-theoretic approaches, as before, to investigate the relationship between daily FTD and daily diet percentages and whale numbers. The percentage of krill and FTD also were transformed also as before. The a priori model set for both FTD and diet percentages included main effects and interactions of colony, as well as number of minke, killer, and total whales. We included year as a random effect for both FTD and diet percentages to account for annual variation.

RESULTS

Natural experiments: ice cover and penguin–whale interactions

First experiment: changes in large-scale ice, Cape Crozier.—Before the large icebergs arrived, ice cover in view of the colony usually dropped to $\leq 10\%$ by late December or early January (Figs. 1 and 2). After iceberg arrival, more so in 2004, ice cover remained extensive until mid-to-late January. For reasons probably related to larger scale conditions, the penguin spring arrival in 2003 was late and asynchronous, leading to a smaller-than-usual breeding population. In stark contrast was 2004, when arrival was highly synchronous, including young age classes, leading to about a 30% increase in the number of breeders that year.

In 2003–2004, the first whales, two minke and a group of 15 killer whales, appeared on 6 December (Fig. 3). Minke whale numbers peaked at 15–20 whales/d during 14–22 December and then declined; killer whales peaked at 40–50 animals during 14–29 December. In 2004–2005, killer whales appeared on 1 December. Initially, the range was 5–22 animals/d; between 14 December and 2 January there were 5–45 whales/d; and later in January there were 10–35 whales/d. Minke whales were not seen until 14 December and were seen frequently thereafter, with peak numbers through early January. We missed several days in early January due to poor weather, but once we could count whales again, numbers were lower (Fig. 3). Despite continuing observations, no whales were seen after 10 January 2004 or 19 January 2005. We never witnessed any predation of penguins by killer whales (Ballard and Ainley 2005).

Average penguin FTD in 2003–2004 increased from ~ 20 h to 60 h until about 13 January, after which it began to shorten (Fig. 4A). During the period of increase, on 28 December, duration “stepped up” from a range of 20–45 h to 35–60 h. Trip distance increased markedly to >150 km (Fig. 4B), coincident with the highest seasonal abundance of killer whales; distance then briefly declined, followed by another increase coinciding with a spurt in minke whale sightings. In 2004–2005, FTD showed little variation, ranging from 20 to 40 h, until the end of December, after which it increased abruptly, ranging from 30 to 80 h. At that time, numbers of whales began to decrease and many penguins deserted their chicks, taking our instruments with them, foraging far away.

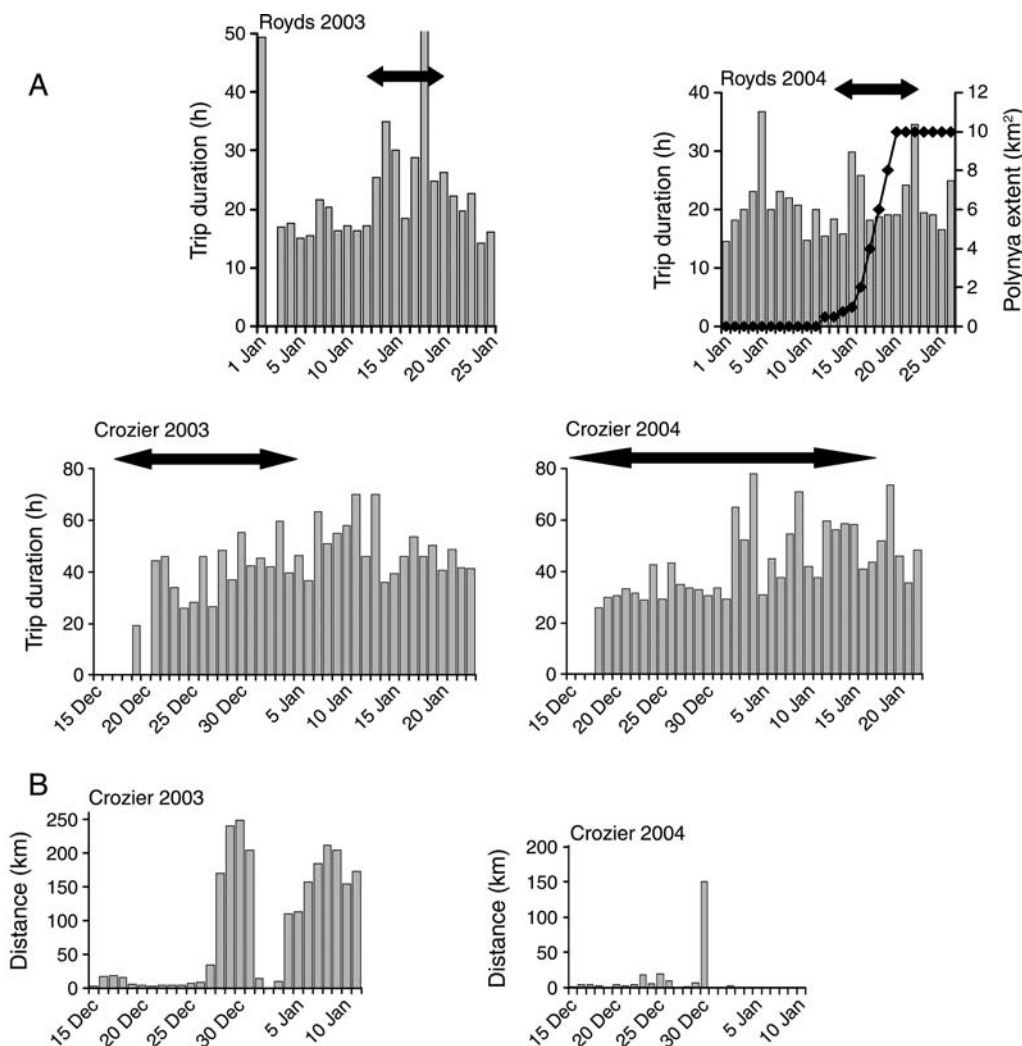


FIG. 4. (A) Penguin foraging trip duration for Royds (top) and Crozier (bottom) in 2003–2004 and 2004–2005, relative to whale presence indicated by arrows (see Fig. 3). At Royds, there were 7.6 ± 1.0 and 4.5 ± 0.6 trips/day (mean \pm SE) for the two years, respectively; at Crozier, there were 8.1 ± 0.6 and 3.5 ± 0.3 trips/day, respectively. The extent of the polynya at Royds (right-hand axis) is indicated by the dark line in 2004–2005. (B) Penguin foraging trip distance at Cape Crozier, December–January 2003–2004 and 2004–2005.

In both years, when penguin hatching began, krill comprised 80–100% of the diet (Fig. 5). Then, on about 28 December 2003, the diet switched largely to fish (20–100%). This was when killer whale numbers peaked, about a week after minke whale numbers peaked, and at about the time that penguin FTD and foraging distance began to increase. During the next season, in the midst of maximum whale abundance but just before minke whales began to disappear, fish prevalence increased from 10% (23 December) to 40% (7 January), after which diet was composed mostly of fish (60–90%). As time passed, in both seasons, penguins continued to feed predominantly on fish (20–100%).

Estimated total mass of prey consumed by cetaceans in 2003–2004 increased rapidly and soon equaled that taken by the reduced population of penguins through 18

December (Fig. 6). The mass of prey taken by whales remained at a lower, but substantial, level until about 4 January. In contrast, estimated prey mass consumed per day by whales was much lower in 2004–2005, but was spread over a longer portion of the penguin season. Prey consumption by whales was greatest from about 30 December to 12 January, the period when penguin FTD grew and nest desertion rate increased.

Second experiment: polynya, Cape Royds.—The 2003 season began with McMurdo Sound free of fast ice to the north of Royds, in stark contrast to 2004, when it was completely covered with fast ice. In both years, the edge of perennial ice extended west from Royds (Figs. 1 and 2). In waters north of the edge, pack-ice cover remained appreciable in 2003–2004, ranging from 10% to 50% (similar to most pre-iceberg years except 1997–

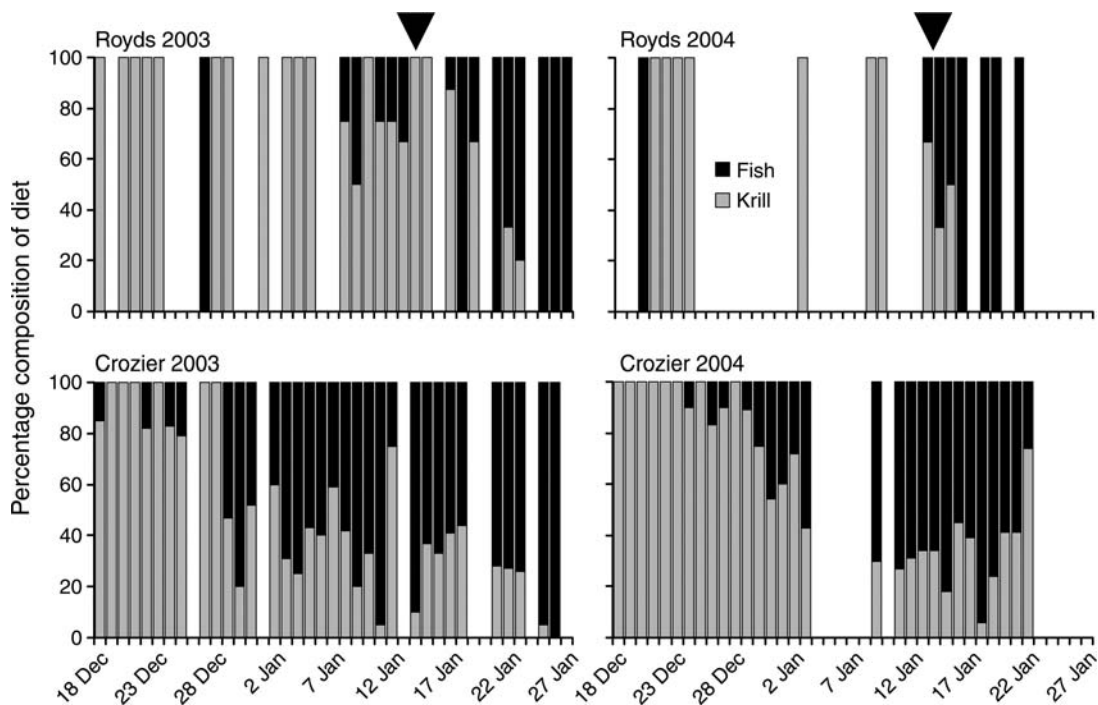


FIG. 5. The percentage of fish and krill in the diet of Adélie Penguins at Cape Royds and Cape Crozier, 2003–2004 and 2004–2005. A blank column indicates that no data were available due to storms or absence of observers for other reasons. At Royds 2003–2004, minke whales were present from mid-December but did not appear in view of Royds until the date indicated by the arrow; in 2004–2005, minke whales were absent from the area until the date indicated. At Crozier 2003–2004, minke and killer whales were present from about 6 December; in 2004–2005, killer whales arrived about 1 December and minke whales about 14 December.

1998), declining to $>30\%$ by early January. Foraging habitat was nearby and breeding success was very high.

In the 2004 season, foraging habitat within 70 km consisted of a few ice cracks, including that between the multiyear fast ice just off Royds and fast ice that had formed only a few months previously. Despite these conditions, the breeding population doubled compared to 2003, but $>90\%$ of nests failed as penguins deserted eggs to replenish fat reserves (*unpublished data*). Successful pairs were those in which *both* mates foraged in ice cracks rather than walking to the annual fast-ice edge; otherwise, nests failed. The average FTD of breeders that eventually succeeded initially averaged 15–23 h (Fig. 4A). Beginning on 3 January 2005 a week-long windstorm transformed the Royds ice crack into a flaw lead, several meters wide; on 15 January it grew suddenly to a polynya that soon reached 10 km² (Figs. 2 and 4A), with overall ice cover in view dropping to $\sim 70\%$. FTD declined to ~ 15 h. At that time the annual fast-ice edge was about 50 km away.

In mid-November 2003, beaked whales frequented the fast-ice edge in the middle of the Sound (deduced from the descriptions given by helicopter pilots flying across McMurdo Sound; see Ponganis and Kooyman 1995). A few weeks later, minke whales appeared there, assessed as we flew along a portion of the ice edge during two flights. We saw minke whales infrequently from Royds

beginning about 1 January and did not see cetaceans consistently until 12 January, when a group of 35 type-C killer whales appeared, followed by 15 whales two days later (Fig. 3). Minke whales then increased consistently to 8 whales/d, but were not seen after 21 January. During December and January, we saw type-B killer whales on four occasions, perhaps the same two groups of 5 and 7 animals each seen twice. On one occasion, a group captured at least one Weddell seal (*Leptonychotes weddelli*). The type-Bs never showed any interest in penguins, although they swam and spy-hopped along small ice floes where penguins were resting.

In January 2005, the polynya's appearance brought the first minke whales to waters off Cape Royds (Fig. 3). They arrived by swimming in the 10 m wide lead stretching along the island's shore from the annual (fast) ice edge (50 km to the north). Breathing holes, broken by the whales' sharp rostrum, could be seen in the thin, new ice that encrusted the lead, each of the holes a few hundred meters apart (see photos in Ainley [2004]). Penguins and the whales foraged together under the ice ringing the polynya, often diving simultaneously, the whales submerging longer than the penguins (i.e., 10 min compared to 2 min). On 21 and 29 January, we saw pods of ≥ 20 type-C killer whales.

In 2003–2004, penguins fed within 12 km of the colony, the norm in previous years of light ice cover

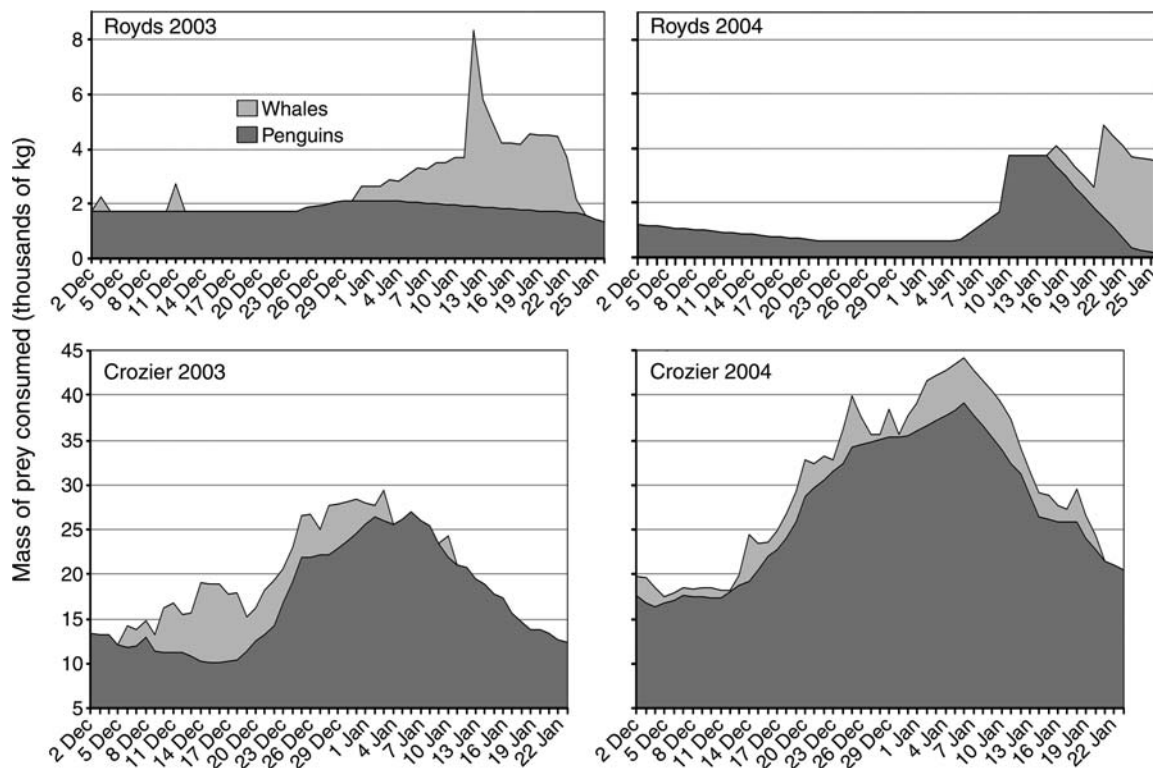


FIG. 6. Estimates of the total mass of prey consumed per day by penguins and cetaceans within the areas in which cetaceans were counted (not the entire foraging area of the penguin colony): number of animals present times average daily consumption rate; Cape Royds and Cape Crozier, 2003–2004 and 2004–2005 seasons. Penguin estimates were reduced to represent the percentage of the foraging area within the cetacean viewing area. Owing to flux in cetacean occurrence and the fact that nonbreeding penguins did not feed every day, patterns shown are likely to be underestimates for cetacean consumption and overestimates for penguin consumption.

(Ainley et al. 2004). FTD, traditionally much shorter than at Crozier (see Ballard et al. 2001, Ainley et al. 2004), remained at ~ 15 h through the first half of January (Fig. 4A). However, corresponding with the highest incidence of whales, it then doubled during 15–23 January; subsequently, coinciding with whale departure, it declined to reach 15 h. During the polynya period of 2004–2005, when whales were visible regularly, penguin FTD increased, including two spurts of particularly long trips (up to 30 h).

During the 2003–2004 and 2004–2005 seasons, krill dominated the penguin diet through 7 and 14 January, respectively (generally 100%; Fig. 5). On 18 January and 15 January, respectively, shortly after minke whales were regularly in view, the penguin diet switched almost entirely to fish (with few exceptions, 60–100%).

Estimated total biomass of prey consumed by penguins and whales increased in late December 2003 with egg-hatching, a week after the appearance of the cetaceans. A large spurt of prey mass was taken in mid-January, when the most cetaceans were present and when penguin diet composition shifted (Fig. 6). In 2004, the estimate of the total prey consumed began at a higher value than in 2003, owing to the greater number of breeding penguins, but it quickly declined as penguins

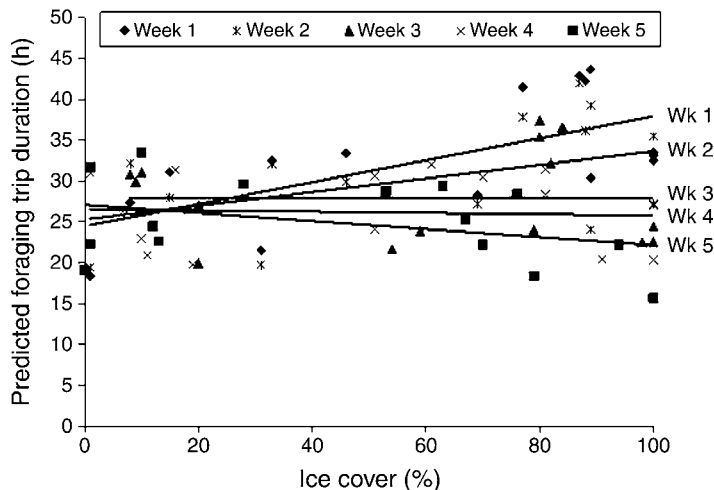
deserted the colony. Prey biomass taken by penguins resurged when the flaw lead developed, encouraging visiting penguins to feed locally rather than returning quickly to the far-distant ice edge. When the polynya developed, cetacean prey consumption made up for the declining penguin population.

Modeling the change in penguin diet

Krill prevalence in the diet declined by week (see figure in Ainley et al. 2003). Our best model contained the additive effects of week and breeding population size; the next best included colony and week (Table 1A). Only models that contained week as an explanatory variable had any weight; the top three containing week, population size, or colony (or both) had a combined Akaike's weight of 0.55. Relationships between percentage of krill and week, colony, and population size were as hypothesized: krill prevailed in the diet but decreased through chick-rearing ($\beta = -0.13$; 95% CI = -0.16 to -0.09) and with population size ($\beta = -0.21$; 95% CI = -0.32 to -0.03). Penguins at Royds generally ate more krill than those at Cape Crozier ($\beta = 0.14$; 95% CI = 0.01 – 0.26).

The best model containing ice cover was nearly competitive (within $2 \Delta AIC_c$), but the 95% CI on the

FIG. 7. Predicted mean foraging trip duration from the best mixed model, plotted against ice cover, by week, including both Royds and Crozier, 1997–2004. The best model includes the additive effects of colony (COL) and krill (KRILL) and the interaction between week (WK) and ice cover (ICE).



coefficient for ice cover included zero ($\beta = 0.08$; 95% CI = -0.17 to 0.33). Thus, its high rank was related to the effects of week and population size. These results indicate that the ice cover effect was not important, which was not surprising, given that annual ice cover varied significantly due to more extensive cover after iceberg arrival and the strong seasonal decrease of krill in diets. The best mixed-effects model containing week and population size (Table 1A) explained 36% of the variation in the percentage of krill in penguin diets.

Modeling FTD in relation diet, ice, and colony

FTD was longer at Crozier than at Royds (34.0 ± 1.77 h vs. 26.6 ± 2.90 h, mean \pm SE; see also Ballard et al. 2001, Ainley et al. 2004). In addition, FTD increased with decreased krill in the diet and an interaction existed between ice cover and week. The effect of ice cover on FTD increased for weeks 1–3, but was minimal or decreasing during weeks 4 and 5 (Fig. 7). Our two best models contained this ice cover \times week interaction, accounting for 65% of the total model weight (Table 1B). The addition of krill improved model weight, but the confidence interval on the coefficient for krill did include zero ($\beta = -0.30$; 95% CI = -0.61 to 0.01). Thus, this was a weaker effect. No other models were competitive and the two best models without the colony covariate received no support. Therefore, the inclusion of the colony effect in all a priori models was well justified (Table 1B). The best mixed-effects model containing the additive effects of colony and krill, and the interaction between week and ice cover explained 35% of the variation in FTD.

Modeling FTD and diet in relation to whales

For the two years for which we had whale data, we found that FTD increased in relation to total whale numbers at Crozier, but declined slightly at Royds. Given the minimal variation in FTD at Royds, the latter was not a meaningful result. The effects of colony were strong, with higher FTD at Crozier compared to Royds

(similar to results just described), but the effects of total whale numbers were weak. The 95% CI on the coefficient for the interaction between colony and total whale numbers included zero ($\beta = 0.02$; 95% CI = -0.003 to 0.04) and there were many other models within two AIC_c of this top model (Table 2A). The second-best model containing the additive effects of colony and total whale numbers had a covariate estimate for whale numbers that did not include zero ($\beta = 0.007$; 95% CI = 0.001 to 0.013), but the effect was very small.

The percentage of krill in penguin diets varied with minke whale numbers at both colonies (Table 2B). As previously noted, colony was an important effect; during both study years, the effect of minke whale numbers on percentage of krill on the diet was less at Crozier than at Royds. As before, colony was an important effect; during both study years, penguins generally had a higher percentage of krill in the diet at Crozier across all levels of minke whale abundance. Although we included year as a random effect in the diet analysis, it was consistently estimated as zero in all models, suggesting that there was little detectable annual variation in diet over the two years. We ultimately removed year as a random effect from the diet models, and this had no effect on model selection results.

DISCUSSION

Proposed hypothesis

The following summarizes the results from this and other studies and offers the hypothesis that prey depletion caused by penguins and whales, probably with the help of other predators such as seals, silverfish, and toothfish, provides the links among various scenario elements.

1) Adélie Penguins feed on crystal krill beginning in November during the egg stage of the breeding cycle (previously established; references in Ainley 2002b). Silverfish are also feeding largely on crystal krill (DeWitt and Hopkins 1977, Eastman 1985).

2) Minke and killer whales arrive in December and, with the hatching of eggs, penguins begin foraging to provision chicks as well as themselves. Penguins and minke whales feed on krill (Ainley et al. 2003, Ichii et al. 1998); killer whales feed on toothfish and silverfish; and toothfish also feed on silverfish (Eastman 1985).

3) Penguins at the largest colonies (especially in years of large populations), along with minke whales, reduce krill availability to the point that both species, along with the killer whales, must begin to feed on silverfish (Ainley et al. 2003; see Ichii et al. [1998], who only noted whales feeding on silverfish, not a seasonal diet switch). The older age classes of silverfish begin to feed on year-0 silverfish (Eastman 1985), also a prey species of penguins and seals in the area (Ainley et al. 2003, Burns et al. 1998).

4) Responding to predation, silverfish availability declines, forcing penguins at large colonies to expand their foraging area, both horizontally (Ainley et al. 2004) and vertically (i.e., diving deeper; G. Ballard and D. G. Ainley, *unpublished data*), and because the penguins have changing needs (e.g., switching from guard to crèche stage: one vs. two parents foraging simultaneously) and because whales, especially killer whales, arrive or depart the area in groups. Penguins in small colonies can cope with the depleted prey, but the percentage of krill in the diet declines with increased consumption by the predators present.

5) With krill depleted and fish prevalence declining, minke whales depart to forage elsewhere, probably having surpassed the prey energy density needed for efficient foraging (see Brodie et al. 1978, Piatt and Methven 1992). As penguins and killer whales reduce fish density below that needed for efficient foraging, the whales depart the area. As indicated by the observation that penguins sometimes return to shorter foraging trip duration following cetacean departure (e.g., in 2003–2004 at both colonies), interference competition must be playing a role. Indeed, it has been observed elsewhere that krill may be absent at large-scale ice edges, but greatly concentrated well back from the edge, perhaps being “chased” there by air-breathing predators to the limits of their breath-holding capabilities (Brierly et al. 2002). Such a pattern must be the result of interference (as well as exploitative) competition. At other times prey must be truly depleted, as in 2004–2005 at Crozier when penguins at this large colony increased their foraging areas to an even greater extent after whale departure. During pre-iceberg years, the Crozier foraging area reached at least 3700 km² in area during the late chick-provisioning period of years when colony size was large; it grew even larger during the iceberg years (Ainley et al. 2004; G. Ballard and D. G. Ainley, *unpublished data*).

A number of other observations support the hypothesis that these predators are depleting or altering the availability of their prey in the western Ross Sea. First, the body condition of minke whales is lower than in adjacent waters off George V Coast (Ichii et al. 1998), where Adélie Penguins (and other penguins) are mostly

absent (only a few very small colonies; Woehler 1993). Second, Adélie Penguins are very abundant in the Ross Sea, where 17 penguin colonies totaling 38% of the world population (~3 million individuals, including nonbreeders) breed along its western shores (Woehler 1993). Minke and killer whales are also abundant, particularly within the pack ice of the western Ross Sea (Thomas et al. 1981, Ainley 1985; see also Ichii et al. 1998, Pitman 2004). Ainley (1985) estimated ~14,000 minke whales, well within the limits of the more statistically sophisticated estimate by Branch and Butterworth (2001: Area V-ES in their analysis), and estimated ~3,400 killer whales in this area during the early 1980s. These numbers are equivalent to more current estimates (cf. Branch and Butterworth 2001). Third, Arrigo et al. (2003) noted that the diatom community of the western Ross Sea is ungrazed (in contrast to the northeastern Ross Sea), a pattern consistent with the removal of the grazers (krill especially) by the dense concentration of penguin, cetacean, and piscine predators. Indeed, crystal krill is the most important consumer of phytoplankton in Antarctic neritic waters (Pakhomov and Perissinotto 1997). Few penguins, but many minke whales and surface-feeding petrels, occur in the northeastern Ross Sea, particularly over the slope (Ainley 1985, Ichii et al. 1998) where yet-to-recover blue whales (*Balaenoptera musculus*) are now absent (see the map of whale extractions in Tynan [1998]). Finally, in the southwest Ross Sea (our study area), silverfish turn to cannibalism during late summer, when elsewhere at that time they are still major predators of crystal krill (DeWitt and Hopkins 1977, Eastman 1985).

We are aware that the observations reported here were gathered at the mesoscale or less, that we were unable to estimate the entire cetacean population within the penguin foraging grounds, and that the presence of the icebergs may have further constrained the food available to top predators in the southwestern Ross Sea (see Arrigo et al. 2002). Moreover, we have no concurrent measure of absolute prey abundance and its change over time. On the other hand, reduced diatom grazing pressure, as observed by Arrigo et al. (2003) prior to the icebergs, and cannibalism on the part of silverfish, indicate that vast reduction of the grazers by top predators may be more than conjecture. We therefore hypothesize that what we have reported here is relevant to understanding the forcing factors operating in the Ross Sea neritic food web.

Consideration of other hypotheses

We hypothesize that the variable “week” in our statistical model for penguin diet is a surrogate for progressive predation pressure and/or prey depletion involving krill and forage fish. The results of additional analyses relating FTD to diet and whale numbers are in direct support of this conclusion. They include the increase in FTD as penguin foraging switched from krill

to fish and an increase (decrease) in FTD when total whale numbers increased (decreased) in number. The pressure apparently increases with time, first, owing to the rising effort required of penguin parents (egg-hatching proceeding to steadily growing chicks) and, second, owing to the arrival and increasing abundance of cetaceans. Finally, we found that Royds penguins are more likely to have lots of krill available, but the presence of minke whales has a bigger impact. At Crozier, because there is so much competition just among penguins, the effect of a few whales does not appear to be as great. At least two alternative hypotheses, however, could explain the results.

One alternative hypothesis is that the diet shift could be due to seasonal, climatic changes in sea-ice cover, which influences the availability of crystal krill (Ainley et al. 2003). The name "crystal krill," in fact, comes from this species' association with sea ice. The fact that sea-ice cover remained extensive during the most recent years of this study, due to blockage by the icebergs (Arrigo et al. 2002), compared to pre-iceberg years when the ice gradually disappeared with time, argues against this hypothesis. In addition, no statistical support was evident for a direct relationship between seasonal diet shift and ice cover. Finally, the effect of ice cover on FTD was minimal or decreasing later in the season (Fig. 7), probably because, due to prey depletion, penguins foraged beyond any sea ice that was visible from our observation points, irrespective of ice cover. Before the icebergs, as the diet switched, sea ice declined from as high as 100% cover in October–November (see Ainley and LeResche 1973: Figs. 3 and 5) to as low as 0%. After the icebergs arrived, fast ice never broke out of southern McMurdo Sound (boundary at Cape Royds) until after the penguin season, if at all, and other portions of the Sound always had appreciable pack ice. At Cape Crozier, ice cover also remained much higher than it had previously (Fig. 2).

A second alternative hypothesis is that the demands of growing chicks could compel parents to ignore krill and prey on silverfish, which are of higher caloric value (Ainley et al. 2003). Perhaps the fish also supply other nutrients (e.g., calcium). The argument against this hypothesis is that Adélie Penguins successfully fledge robust chicks elsewhere on a diet composed entirely of krill (Salihoglu et al. 2001). In fact, in some areas Adélie Penguin parents switch foraging areas to feed on krill instead of fish in order to recover their own body condition while trying to provision chicks (Clarke 2001, Clarke et al. 2002). Thus, the switch probably has to do with prey availability, and we do not favor this hypothesis.

*Penguin and whale competition leading
to trophic cascades in the Ross Sea*

We previously presented evidence (Ainley et al. 2004) that penguins at high densities alter the availability of their prey, and our results continue to support this

conclusion. We observed the prey switch in all previous seasons (seven seasons; Ainley et al. 1998, 2003), even when foraging areas were not reduced by large icebergs or fast ice. Our current modeling supports the strength of this pattern, regardless of ice conditions. Given the temporal–spatial correspondence of foraging by these penguins, with cetaceans feeding on the same prey, and the supporting statistical results, it is reasonable to conclude that cetaceans also play a role in this alteration of prey availability.

In attempting to extrapolate the influence of whales on the depletion of prey near penguin colonies, we note that we have been able to deduce only seasonal changes in relative cetacean abundance. Nevertheless, as indicated by our estimates of prey consumption (Fig. 6), the amount of prey taken by the whales appears to be significant relative to the penguins' needs. At the scale of the Ross Sea, given consumption rates and the populations of penguins and minke whales as previously enumerated, the whales would consume 33% more food than the penguins. Most of this activity would take place in the western Ross Sea where, as noted before, most Ross Sea whales and penguins reside during summer (cf. Thomas et al. 1981, Ainley 1985).

It has long been known that zooplankton abundance is generally low in the western Ross Sea (e.g., Hopkins 1987). Tagliabue and Arrigo (2003), providing a "bottom-up" perspective, proposed that phytoplankton there bloom and decline so rapidly that zooplankton have little time to take advantage before the phytoplankton sink to the benthos. This is indicated by the balance between particulate organic carbon (POC) and CO₂ deficits in surface waters, especially in the vicinity of Ross Island (Arrigo et al. 2000: plate 7D), meaning that there is little evidence of substantial grazing. If grazing were high there would be large CO₂ deficits, but not much POC, and this is not the case. On the basis of our study, we offer a top-down interpretation; at the least, top-down zooplankton grazing, especially on the single most important phytoplankton grazer in coastal waters (crystal krill), would exacerbate already low zooplankton abundance. If zooplankton were intrinsically low in this system, why then would such high populations of predators be present?

Therefore, we hypothesize that the Adélie Penguin, minke whale, and type-C killer whale are key species in a trophic cascade evident in the western Ross Sea (see Pace et al. 1999, Soulé et al. 2005). Other predators of silverfish, such as Antarctic toothfish and Weddell seals, are likely to be involved as well. In the absence of data on the temporal and spatial distribution of silverfish and crystal krill collected simultaneously with our observations, our conclusions for the present must remain conservative. On the other hand, elsewhere on the globe, including the pelagic Southern Ocean, where the upper levels of food webs have long been lost (e.g., Pauly et al. 1998, Pace et al. 1999, Jackson et al. 2002, Pauly and McLean 2003), these sorts of species interactions can

only be the subject of theoretical discussion (e.g., Schindler et al. 2002, Springer et al. 2003, Williams et al. 2004, Scheffer et al. 2005). With continued research and protection of this area from depletion of top predators by humans, however, it may still be possible in the Ross Sea to directly investigate the sorts of trophic cascades, competition, and other interactions related to top-trophic species that once characterized the entire world ocean (see discussion in Pace et al. 1999; Ainley 2002a, 2004).

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