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SPATIAL AND TEMPORAL VARIATION OF DIET WITHIN A PRESUMED METAPOPULATION OF ADÉLIE PENGUINS

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Abstract. We investigated temporal and spatial variability in the diet of chick-provisioning Adélie Penguins (*Pygoscelis adeliae*) breeding at all colonies within one isolated cluster in the southwestern Ross Sea, Antarctica, 1994–2000. We wished to determine if prey quality explained different population growth and emigration rates among colonies. Diet composition was described both by conventional means (stomach samples) and by analysis of stable isotopes in chick tissues (toenails of individuals killed by skuas [*Stercorarius maccormicki*]). Diets were similar among the four study colonies compared to the disparity apparent among 14 widely spaced sites around the continent. Calorimetry indicated that fish are more energetically valuable than krill, implying that if diet varied by colony, diet quality could attract recruits and help to explain differential rates of colony growth. However, a multiple-regression analysis indicated that diet varied as a function of year, time within the year, and percent of foraging area covered by sea ice, but not by colony location. Stable isotopes revealed similarity of diet at one colony where conventional sampling was not possible. We confirmed that sea ice importantly affects diet composition of this species in neritic waters, and found that (1) quality of summer diet cannot explain different population growth rates among colonies, and (2) stable isotope analysis of chick tissues (toenails) is a useful tool to synoptically describe diet in this species over a large area.

Key words: Adélie Penguin, Antarctic, colony choice, diet variation, diet quality, Pygoscelis adeliae, *stable isotope.*

Variación Espacial y Temporal de la Dieta en una Supuesta Metapoblación de *Pygoscelis adeliae*

Resumen. Investigamos la variabilidad temporal y espacial en la dieta de *Pygoscelis adeliae* que se encontraban aprovisionando a sus polluelos en todas las colonias dentro de un grupo aislado en el mar de Ross sud-occidental, Antártica, entre 1994 y 2000. Deseábamos determinar si la calidad de la presa explicaba las diferentes tasas de crecimiento poblacional y emigración entre colonias. La composición de la dieta fue descrita por medios convencionales (muestras estomacales) y por el análisis de isótopos estables en tejidos de los polluelos (uñas de las patas de los individuos matados por *Stercorarius maccormicki*). Las dietas fueron similares entre las 4 colonias estudiadas en relación a la disparidad de la dieta evidente entre 14 sitios dispersos a través del continente. Las análisis de calorimetría indicaron que los peces tienen un mayor valor energético que el krill, sugiriendo que si la dieta varía entre colonias, la calidad de la dieta podría atraer a reclutas y ayudaría a explicar los diferentes índices de crecimiento entre colonias. Sin embargo, un análisis de regresión múltiple indicó que la dieta varió en función del año, de la época dentro de un año, y del porcentaje de área de forrajeo cubierta por el hielo del mar, pero no en función de la localización de la colonia. Los isótopos estables revelaron la semejanza de la dieta en una colonia en que no era posible el muestreo convencional. Confirmamos que el hielo en el mar afecta de manera importante la composición de la dieta de esta especie en aguas neríticas, y encontramos que (1) la calidad de la dieta de verano no puede explicar las diferentes tasas de crecimiento poblacional entre colonias, y que (2) el análisis de isótopos estables de los tejidos de polluelos (uñas de las patas) es una herramienta útil para describir, sinópticamente, la dieta en esta especie a través de un área extensa.

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INTRODUCTION

The concept of a metapopulation (e.g., Hanski and Gilpin 1991), or an assemblage of interacting populations, among colonially breeding seabirds is not well appreciated in current research and management. The vast majority of studies and management practices treat colonies as independent. Recent studies, however, reveal compensatory adjustments among neighboring colonies, a pattern contrary to colony independence. Furness and Birkhead (1984; see also Lewis et al. 2001), studying four seabird species in Britain (Northern Fulmar [*Fulmarus glacialis*], Northern Gannet [*Morus bassanus*], Black-legged Kittiwake [*Rissa tridactyla*], and Atlantic Puffin [*Fratercula arctica*]), showed that size of a given colony is affected inversely by the size of colonies within foraging range of the focus colony, as the large colonies take a proportionate amount of the food resource. To avoid the competition present in the large colony, adjacent colonies need to form (e.g., Gibbs et al. 1987). Another study concluded that the world's largest South Polar Skua (*Stercorarius maccormicki*) colony, in the Ross Sea region, Antarctica, is a ''sink'' (with little successful reproduction) and maintained through immigration of recruits from nearby, smaller colonies (Ainley et al. 1990). Similarly, removal of adults from a large colony of Herring Gulls (*Larus argentatus*) created a ''vacuum'' that was filled by recruits from nearby colonies (Coulson et al. 1982). Finally, the overall Black-legged Kittiwake population in Prince William Sound, Alaska, has not changed much during the past few decades, but several colonies have disappeared or have decreased in size while others have grown accordingly (Suryan and Irons 2001).

Colonies of Adélie Penguins (*Pygoscelis adeliae*) occur in clusters composed of one large colony (or two medium-sized colonies) surrounded by smaller colonies within the greater foraging range of the large colony (the greater foraging range is the area used by breeders as well as nonbreeders, which can forage farther away from the colony; Ainley et al. 1995). Therefore, the pattern of geographic structure is analogous in many respects to those shown by seabirds in Britain (Furness and Birkhead 1984). The locations of the penguin clusters are related to the presence of polynyas (areas of open water within a region covered by sea ice; Ainley 2002), or other phenomena (e.g., local upwelling) that facilitate food acquisition (Fraser and Trivelpiece 1996).

We have been investigating one Adélie Penguin colony cluster in the southwestern Ross Sea, attempting to define the concept of a metapopulation as it applies to this species. The cluster consists of four colonies: a large colony at Cape Crozier (1997 population 135 000 pairs), medium-sized Cape Bird (47 500 pairs in 1997) and Beaufort Island (38 000 pairs when last censused in 1991), and smaller Cape Royds (3900 pairs). Cape Crozier has increased only 17% over the last 27 years, whereas the 2 smaller, regularly censused populations (Bird and Royds) have increased 59% and 156% in that time (Taylor and Wilson 1990, Taylor et al. 1990, Wilson et al. 2001). None of these three colonies are space limited, so ultimately we wish to determine why growth rates differ so greatly among these colonies. Since rates of colony increase, especially at Royds, surpass what can be explained by reproductive success and subsequent chick survival, emigration must be at least one of the factors involved. However, given the broad overlap in the natural history of penguins at these colonies, what may or may not be attractive to recruits at a given colony remains unclear. Penguins at these colonies winter in the same region and arrive at respective colonies at about the same time each spring (Ainley 2002). The foraging ranges of the colonies abut or overlap extensively (30–75%; Ainley et al., in press); banded birds from each colony are often seen at the others (DGA, unpubl. data).

Herein we report our attempt to determine the degree of similarity in diet composition and quality, and the factors that affect diet variation among study colonies, 1994–2000. A diet geographically dissimilar in composition among colonies would lead us to hypothesize that prey availability or quality could differ, which in turn could affect differences in recruitment rates.

METHODS

STUDY AREA

All four study colonies are located in the southwestern corner of the Ross Sea, adjacent to or surrounded by neritic waters (Fig. 1). The cluster, contributing 8% to the world population of this penguin species, is isolated from other clusters in the Ross Sea, where 30% of the world

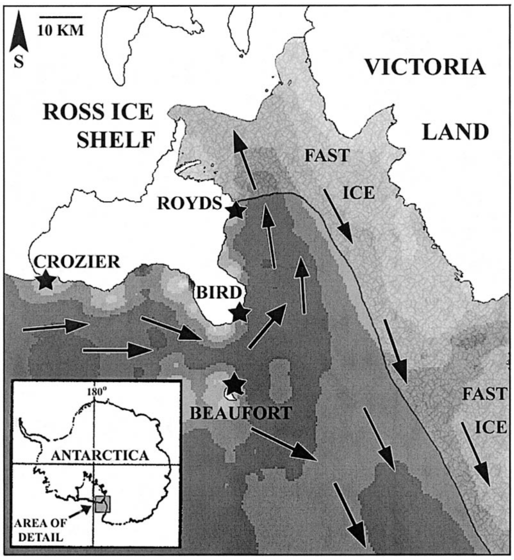

FIGURE 1. The southwestern Ross Sea, showing location of Adélie Penguin colonies on Ross Island sampled in this study. Shades of gray indicate 100-m depth increments, increasing with darkness. Arrows indicate direction of ocean currents. Fast ice is ice that is attached to the mainland.

population nests (Woehler 1993, Ainley et al. 1995). Distance between neighboring colonies ranges from 30–85 km. The maximum foraging range of this species during chick rearing is about 85 km in the southern Ross Sea (Ainley et al., unpubl. data).

All colonies in the cluster are also within the same oceanographic domain. A westward current flows from the eastern Ross Sea continental shelf along the Ross Ice Shelf, passes Cape Crozier, and then turns northward along the Victoria Land coast (Fig. 1). As it turns, the current bifurcates at Beaufort Island, where a minor arm veers southward past Capes Bird and Royds (Jacobs et al. 1970, Barry 1988). Water is >400 m deep throughout the study area, except a bank extending 12 km east from Beaufort Island, owing to isostatic depression of the continental shelf due to the mass of the polar ice cap. Except along shorelines, nowhere is the water shallow enough for the penguins to forage on demersal prey. Knowledge of this oceanographic context is important, as the degree of habitat heterogeneity is known to affect isotope results in studies of colonial birds using stable isotopes of N and C (France 1995, Hobson 1999, Bocher et al. 2000). A detailed isotopic study of the area has not been conducted.

SAMPLE COLLECTION

To quantify diet composition and quality, we used conventional methods (stomach samples), stable-isotope analysis of penguin tissues (ratios of ^{15}N to ^{14}N and ^{13}C to ^{12}C, referred to as $\delta^{15}N$ and $\delta^{13}C$), and calorimetry. We used isotope analysis because, owing to logistical and permitting constraints, we could not obtain a series of conventional diet samples from penguins at the Beaufort Island colony. We were allowed to visit this colony, a Specially Protected Area under the Antarctic Treaty, only at the end of the breeding season and could not do any invasive sampling. We felt that isotope analysis of near-to-fledging chicks would better characterize diet over the entire chick period than would infrequent conventional diet sampling (Hobson et al. 1994).

We knew that we could reconstruct diet from isotope signatures, because previous studies had shown that (1) isotope abundance in bird tissues is determined by the relative proportions of isotopically distinct dietary components (Hobson 1993, 1995); (2) penguin diets in this area are dominated by just two prey species that occur at disparate trophic levels: Antarctic silverfish (*Pleuragramma antarcticum*) and crystal krill (*Euphausia crystallorophias*; Emison 1968, van Heezik 1988, Ainley et al. 1998); and (3) the isotope signatures of these primary prey species differ ($\delta^{15}N$ values are 10.9 for *P. antarcticum* in McMurdo Sound and 5.1 for *E. crystallorophias* from waters off East Antarctica; Burns et al. 1998, Hodum and Hobson 2000). Using a similar approach, seal diets have been isotopically reconstructed within our study area (Burns et al. 1998).

Stomach contents. Stomach-content samples were obtained from breeding adults using the water off-loading technique (Emison 1968, Wilson 1984) each austral summer from 1995–1996 to 2000–2001. (Herein, we designate each summer season by its initial calendar year.) In this operation, using small-diameter tubing, warm water is gently pumped into the penguin which, when it becomes too full, regurgitates upon being tipped upside down. Samples were obtained within 1 day of one another, at each colony (Crozier, Bird, Royds), at 7-day intervals beginning 25 December (the beginning of the chick-

TABLE 1. Numbers of samples of stomach contents and toenails used to assess diet of Adélie Penguins at four colonies in the southwestern Ross Sea. Numbers for stomach-content samples are the number of weeks during which 4–7 individuals were sampled. Weekly means were calculated and used to construct Figure 3. Numbers for toenail samples are the number of individual chicks from which one toenail was analyzed using stable isotopes.

		Year (25 December to 25 January)						
Colony	Type	1994	1995	1996	1997	1998	1999	2000
Beaufort	Stomach							
	Toenails			4	3	7		
Bird	Stomach	5	5	5	5	5	5	5
	Toenails	4	5	4	3	5		
Crozier	Stomach	4	4	5	5	5	5	5
	Toenails	4	5	5	3	7		
Royds	Stomach	1	1	5	5	5	5	5
	Toenails	5	4	5	3	7		

rearing period) and ending about 22 January. Dates closely corresponded among years as well. Sampling was sporadic during the first two years due to logistical problems (Table 1). We did not obtain the complete contents of the stomach; rather we took about one-fourth (about 250 g). Most of the food beneath the upper portion is a soupy mush which cannot be objectively separated by prey species, and taking only the upper portion allowed the parent to provide at least some food to its chick. Parents ordinarily do not feed their entire food load to the chicks (Lishman 1985, Ainley et al. 1998). No data exist that indicate Adélie Penguin parents feed their chicks a diet different from what they eat themselves. Food was collected from 4–7 adults, just after they came ashore, during each sampling session. Each sample was preserved with 70% ethanol and frozen at −10°C for later analysis.

Stable-isotope analysis. We compared the diet of Beaufort Island penguins with that of penguins at other colonies using stable-isotope analyses of chick tissues from all four colonies. At Capes Crozier, Bird, and Royds, one foot was cut from the carcasses of 5–7 near-to-fledging chicks killed by South Polar Skuas each year from 1994–1998 (1996–1998 at Beaufort Island; Table 1). Therefore, samples represented the same period of dietary integration. These chicks were not starving; skuas can easily take chicks at a body mass up to 2 kg (and larger ones if few adults are present for protection; Young 1994). Feet were dried in a laboratory oven set at 100°C for 24 hr (to satisfy importation requirements set by the U.S. Department of Agriculture). Dried feet were then sealed in plastic bags for transport and later analysis.

We assessed sea-ice extent (percent of sea surface covered within each colony's respective foraging area) and distance from colonies to nearest pack ice using weekly satellite images (AVHRR and DMSP) archived by the U.S. Antarctic Program and the Arctic and Antarctic Research Center (University of California San Diego). Image analyses were performed with ArcView 3.2 (ESRI 2000). Image resolution varied from 0.5 to 1.5 km per pixel. Foraging area was determined by radio-telemetry for each season, 1996–2000 (Ainley et al., unpubl. data).

Prey sampling for calorimetry. We used four samples of krill and four samples of fish. The fish were collected by trawls in the study area by other researchers during the chick period in 1996–1998. The krill were extremely fresh, undigested samples from penguin diet. Samples were dried in an oven and weighed before analysis.

SAMPLE ANALYSES

Calorimetry. We compared the energetic value of *P. antarcticum* and *E. crystallorophias* obtained from the southern Ross Sea during summer. Any difference would indicate the importance of assessing colony-related differences in diet composition. We used a bomb calorimeter consisting of a hollow steel container lined with platinum and filled with pure oxygen. A dried, weighed sample was placed inside and ignited with an electric fuse. The heat produced was measured by a sensitive thermocouple and was displayed on a galvanometer. From the galvanometer reading, the calories liberated from the sample were calculated. Benzoic acid was used for calibration in order to establish the relationship between the galvanometer reading and the amount of heat released by the combusted sample.

Conventional comparison of diet. Diet samples were sorted and prey species identified and weighed immediately following the breeding season (within 5 days of the last sample collected). Before weighing, most of the liquid was squeezed from piles of prey using light pressure. Results are reported herein as percent composition by wet mass. We calculated the average composition of the 4–7 samples at each colony on each sample date. Preliminary results for the first three years were presented in Ainley et al. (1998).

Samples were compared by colony and year using Morisita's index of similarity (Horn 1966), which has been used previously in this application (Ainley et al. 1984, 1992): $C = 2\Sigma xy/(\Sigma x^2 + \Sigma y^2)$, where x and y are a prey species' proportions in the two diets being compared. The index can vary between 0.0 and 1.0 (or 0% to 100%). We also used this index to compare results from this study with quantitative studies of this species' diet conducted elsewhere in Antarctica during the chick-provisioning period. In that comparison, to be more equivalent to the other Antarctic studies, which were not conducted in the same or adjacent years, we did not include same-year values from the present study (e.g., Royds 1996 vs. Crozier 1996).

Stable isotopes. The middle (primary) toenail was clipped from each sampled chick foot, submerged briefly in a 10% HCl solution, and placed in a 55°C oven for several days until dry. The distal 4 mm of each nail (nails averaged 16.7 ± 0.3 mm from cuticle to tip; $n = 50$) was ground to a powder and analyzed for relative $\delta^{13}C$ and $\delta^{15}N$ using the procedure of Rau et al. (1990), where δ values increase as the heavier isotope increases relative to the lighter isotope of either C or N. Units are in parts per thousand (per mil, ‰) with an analytical precision typically of ± 0.2‰ and 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Initially, we wanted to see if the isotopic variability encountered could be explained by changes in the relative contribution of the primary dietary items of the penguins, *P. antarcticum* and *E. crystallorophias*. We examined this by determining the correlation between isotope abundances and seasonally averaged percent fish in stomach contents. The $\delta^{13}C$ and $\delta^{15}N$ measurements subsequently were used to statistically test for differences in diet among the colonies and years sampled.

STATISTICAL ANALYSES

In addition to the calculation of Morisita's Index (above) to compare diet similarity, we also used linear models to identify the importance of different factors that might affect diet variation (Neter et al. 1990, StataCorp 1999). The dependent variable was percent fish in an individual's diet; explanatory variables were year, week within year, colony, and percent of foraging area covered by sea ice. We summarized the ice data into four even categories based on distribution of the data: 1 = 0–7%, 2 = 8–20%, 3 = 20–33%, and 4 = 33–77%. We used arcsine-square root transformations of the percent fish in order to normalize the data to meet the assumptions of linear models (Zar 1999). We tested each of these main terms independently with one-way models and, finding them each significant independently, combined all in a 4-way model in which each term was compared with all others in the model. In two separate 3-way models, we tested the effect of ice or week combined with year and colony to get further insights to their individual impacts on diet, because we suspected they might effectively be proxies for each other (ice was measured on a weekly basis). We tested each potentially meaningful two-way interaction (year × ice, year × week, year × colony, week × colony, ice × colony).

We also used linear regression to relate transformed percent fish in the diet to values of $\delta^{13}C$ and $\delta^{15}N$, and compared similarity in diet among colonies, as determined from $\delta^{15}N$ values (all colonies, by year, including Beaufort Island) using Pearson correlation. Finally, we used ANOVA to compare the difference in calorimetric values for four samples each of krill and fish collected in the region during our study.

Means are given ± SE unless otherwise specified. We assumed statistical significance when $P \leq 0.05$. Residuals from all regression analyses were normally distributed as evaluated by a formal test for skewness and kurtosis and confirmed by visual inspection.

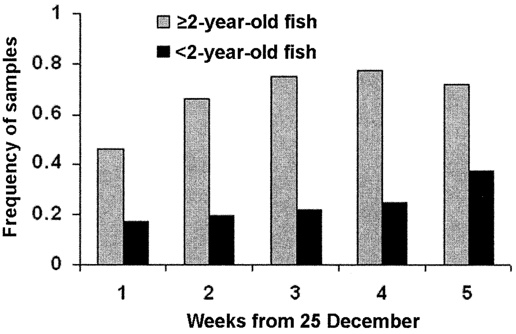

FIGURE 2. Changes during the summer in prevalence of two age classes of the Antarctic silverfish (*Pleuragramma antarcticum*) in the diet of Adélie Penguins breeding on Ross Island. Data are averaged over 1994–1998 from three colonies in the Ross Sea.

RESULTS

ENERGETIC VALUE OF PREY

The energetic value of *P. antarcticum* subadults of the size eaten by the penguins (Fig. 2), averaged 5.20 ± 0.16 kcal g^{-1} ($n = 4$). This was the age (size) class most prevalent in the samples. *E. crystallorophias* adults averaged 4.62 ± 0.11 kcal g^{-1} ($n = 4$). The difference between these mean values was statistically significant ($F_{1,6} = 34.7$, $P = 0.001$). Therefore, differences in diet composition within and between colonies, as reviewed below, are important with respect to prey quality.

CONVENTIONAL DIET SAMPLES

Ross Sea colonies. Regardless of colony, year, or week within year, better than 95% of the diet, by mass, was composed of *P. antarcticum* and *E. crystallorophias* (Fig. 3). Contributing slightly (<5%) on occasion were amphipods and pelecypods. As the summer progressed, prevalence of fish usually increased and krill decreased. Among the fish consumed, prevalence of juveniles increased also as summer passed (Fig. 2). The juveniles consumed were of two size classes centering around 70 and 120 mm standard length (Fig. 2); the smaller were at least one year of age and none were adults (J. Torres, pers. comm.). The euphausiids consumed included subadults (17–22 mm) and adults (25–35 mm).

Statistical models relating percent fish consumed to year, week within year, and percent ice cover confirmed these patterns. Testing each explanatory variable separately, percent fish consumed varied most with ice ($F_{1,60} = 28.1$, $r^2 = 0.32$, $P < 0.001$), but also varied with week ($F_{1,92} = 15.6$, $r^2 = 0.15$, $P < 0.001$), year ($F_{6,87} = 2.7$, $r^2 = 0.15$, $P = 0.02$), and colony ($F_{2,91}$

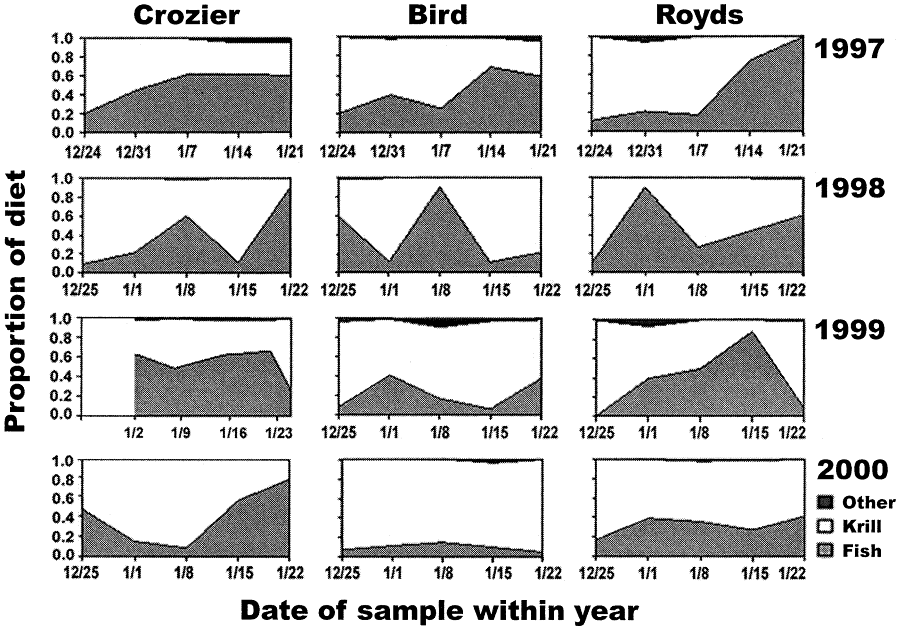

FIGURE 3. Weekly and yearly variation in diet composition of Adélie Penguins nesting at the Cape Crozier, Bird, and Royds colonies, 1997–2000 (see Ainley et al. 1998 for 1994–1996).

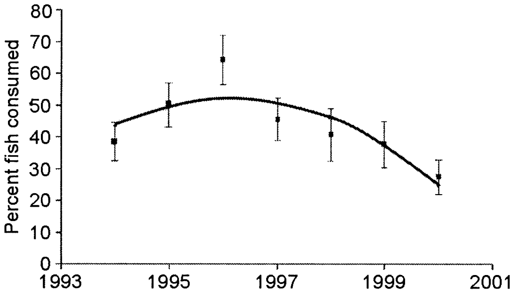

FIGURE 4. Annual change in the average percentage of fish (±95% CI) in the diet of Adélie Penguins breeding at Capes Bird, Crozier, and Royds, Ross Island, 1994–2000.

TABLE 2. Results of regression analysis (4-way linear model) to assess the relationship between percentage of fish (arcsine transformed) in Adélie Penguin diet and year, week within year, percentage of ice cover in the foraging area, and colony. All 2-way interactions were also tested, but none were significant. The model indicated significant effects of year (as a categorical term), week (as a linear term), and ice cover.

Term	β (95% CI)	F	P
Year		2.4	0.04
Colony		2.5	0.09
Week	6.3 (1.1 to 11.5)	5.9	0.02
% Ice cover	−12.7 (−20.8 to −4.5)	4.4	0.003

$= 4.3$, $r^2 = 0.09$, $P = 0.02$). For year, the quadratic term was also significant, reflecting unusually high proportions of fish in 1996 and a marked decrease in 2000 (Fig. 4). When all were combined in a 4-way model, these variables accounted for approximately 48% of the variance in percent fish in the diet ($F_{10,51} = 6.7$, adjusted $r^2 = 0.48$, $P < 0.001$; Table 2). Colony was the only variable not contributing significantly while controlling for the effects of the other terms (Table 2). Most significantly, percent fish varied with the percent of the foraging area covered with pack ice ($F_{1,51} = 9.7$, $r^2 = 0.08$, $P < 0.01$; Table 2). There was less fish in the diet during sampling intervals with higher pack-ice cover. The percent fish was also related to year ($F_{6,51} = 2.4$, $r^2 = 0.12$, $P = 0.04$; Table 2) and increased within year (by week, $F_{1,51} = 5.9$, $r^2 = 0.05$, $P = 0.02$; Table 2). Results were similar when we tested ice and week separately in 3-way models with colony and year; both were significant and in the same direction as in the 4-way model (for 3-way ice model, $F_{9,52} = 6.2$, adjusted $r^2 = 0.43$, $P < 0.001$, for week, $F_{9,84} = 6.0$, adjusted $r^2 = 0.33$, $P < 0.001$). None of the interaction terms were significant (all $P > 0.3$), indicating that these results were consistent across years and colonies.

A comparison of diet using average values of all samples collected at each colony by year, and Morisita's index, also indicated a very high level of similarity among colonies (Fig. 5). The large majority of comparisons produced index values >85%, a value construed as similarity in other Antarctic studies of bird diet (Ainley et al. 1984, 1992). Similarity was >85% in better than 80% of comparisons.

Antarctic-wide colonies. Diet of the Adélie Penguin has been described at 21 localities in 25

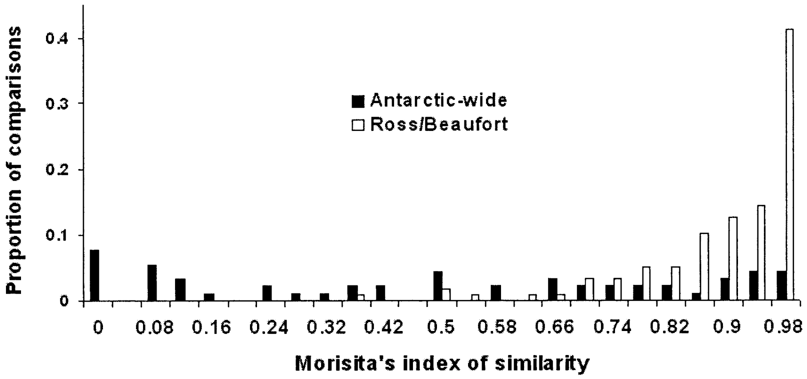

FIGURE 5. Frequency distribution of values derived using Morisita's index of similarity, comparing two sets of data describing Adélie Penguin diet: results of studies spread Antarctic-wide, and those of the present study, which includes three colonies confined geographically to Ross/Beaufort Islands. Morisita's index can range from 0.0 (no overlap in diet) to 1.0 (complete overlap).

published studies (summarized in table 2.1 of Ainley 2002). In virtually all studies, results usually have been reported as summaries (averages) for the sampling period, which usually occurred during the chick-rearing phase, usually of one year (see below), and considered to describe the species' diet during the chick period. At localities near pelagic waters (deep ocean or continental slope), *E. superba* dominated the diet. When penguins foraged in neritic waters (continental shelf, i.e., present study), *E. crystallorophias* or *P. antarcticum* dominated the diet. At some localities both neritic and pelagic waters were accessible to the penguins and diet varied accordingly.

In studies at 11 sites, diet during the chick-rearing period was sufficiently quantified to allow comparison using Morisita's index (Fig. 5): Signy Island, 1980–1981 (Lishman 1985); King George Island, 1977 (Volkman et al. 1980); Hukuro Cove, 1989–1990, and Cape Hinode, 1991 (Watanuki et al. 1994); Shirley Island, 1992 (Kent et al. 1998); Prydz Bay, 1992 (Watanuki et al. 1997); Wilkes Land and Adélie Land, 1995 (Weinecke et al. 2000); Franklin, Beaufort Island, and Cape Crozier, 1966 (Emison 1968). In order to consider just the chick-provisioning period we did not use van Heezik (1985) nor Puddicome and Johnstone (1988).

In general, the composition of diets Antarctic-wide proved to be quite disparate. This result is not surprising given the wide geographic and temporal spread among the studies. Otherwise, the few loci of similarity occurred where *E. superba* dominated exclusively, for instance where insular shelves (S. Orkney, S. Shetland) and continental shelves were narrow (Hukuro, Hinode, Prydz Bay); or where colonies were in close proximity (Hukuro and Hinode; Ross Island colonies). The similarity in diet among closely spaced colonies is the subject treated further in this paper.

STABLE-ISOTOPE ANALYSIS OF DIET

Annual proportion of fish in the diet samples at each colony was correlated (though not significantly) with δ^{15}N values from corresponding toenail samples (t = 2.1, r^2 = 0.22; P = 0.06). When the last diet sample collected in a year was excluded from annual averages (i.e., a "modified" average) the relationship became significant (t = 2.2, r^2 = 0.24; P = 0.05; Fig. 6A). These results are consistent with diet changing seasonally (see above) and the fact that the last diet sample and the feet were collected at about the same time; therefore, prey-derived nutrients at the end of the period were less likely to have been incorporated into chick toenail tissues (hence exclusion of the last diet sample). No relationship was apparent between proportion fish and δ^{13}C values (Fig. 6B), probably reflecting lack of significant isotopic carbon difference between fish and krill (e.g., Rau et al. 1991, 1992, Burns et al. 1998).

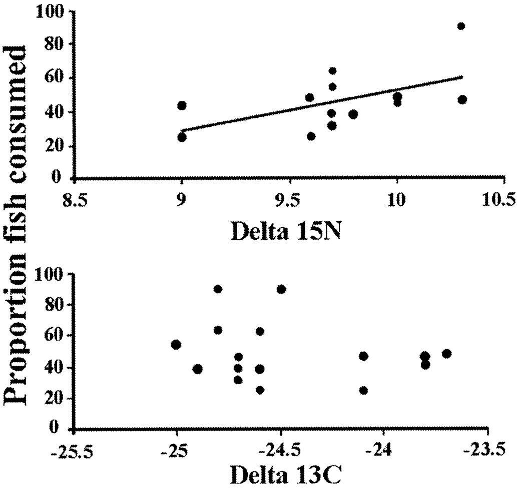

FIGURE 6. Proportion of fish (excluding last weekly diet sample each year) in the diet of Adélie Penguins from colonies on Ross and Beaufort Islands, 1994–1998, compared to (top) δ^{15}N values (significant correlation) and (bottom) δ^{13}C values (not significant).

Finally, using stable isotope signatures, it appeared that diet composition at Beaufort Island was most similar to diet composition at Cape Bird and did not significantly differ from the other Ross Island colonies (Table 3, $F_{3,14}$ = 0.93, P = 0.45). The similarity between Bird and Beaufort is not surprising because the two colonies are closer together (30 km) than they are to other colonies (Fig. 1). The least correspondence was between Crozier and Royds (the most distant colonies). On the basis of the results presented above, these differences probably relate to the amount of pack ice present.

DISCUSSION

As with most studies of seabirds (or other colonial birds), our study has been limited by difficulties in the independent sampling of prey availability. Determining prey availability even

TABLE 3. Values of $\delta^{15}N$ (± SD) from tissues of Adélie Penguins from four colonies in the southwestern Ross Sea, and Pearson's correlation coefficients for average yearly $\delta^{15}N$ values between colony pairs ($n = 6$ per comparison).

	Beaufort	Royds	Bird	Crozier
$\delta^{15}N$ values:				
1996	9.3 ± 0.7	9.4 ± 0.8	8.8 ± 0.7	9.2 ± 0.4
1997	9.5 ± 0.3	8.9 ± 1.4	9.5 ± 0.4	9.5 ± 0.6
1998	10.0 ± 0.3	10.3 ± 0.4	10.0 ± 0.3	9.6 ± 0.4
Correlation coefficients:				
Royds	0.80			
Bird	0.94	0.56		
Crozier	0.87	0.39	0.98	

at one site, let alone multiple sites, is a huge task. Furness and Birkhead (1984) and Lewis et al. (2001) assumed that prey were evenly available within foraging range of all colonies in their analyses. Studies of the geographic structure of heron, swallow, and corvid colonies, like our study, also have resorted to deducing relationships relative to prey-resource quality rather than availability (e.g., Brown and Brown 1996, Gibbs et al. 1987, Griffin and Thomas 2000). Only in the case of kittiwake colonies in Prince William Sound (Suryan and Irons 2001) did subsequent study support the assumption that prey distribution was homogeneous (Ainley et al. 2003).

Viewed Antarctic-wide, diet composition of the Adélie Penguin during the chick-provisioning period has been well studied and appears to be heterogeneous, being a mix of various species of fish and euphausiids depending on foraging habitat. This result confirms that the Adélie Penguin cannot be classified as a ‘‘krill predator,’’ a statement common in the Antarctic bird literature (e.g., Croxall et al. 2002). Results from the few studies of geographically close sites, including the present study, indicate that diet might well be similar among closely spaced colonies elsewhere. The homogeneous ocean habitat sampled by penguins at neighboring colonies compared to the variety of foraging habitats possible among widely spaced colonies helps to explain the result (see also Ainley 2002). Even among years, the diet of closely spaced colonies does not vary as much as among widely spaced ones. Therefore, diet quality should be similar among penguins at clustered colonies and should not play a role in the process accounting for multiple colonies in a cluster.

The similarity of diet among colonies in the present study, indicated by both conventional results and $\delta^{15}N$ values, is important given that the fish consumed was of higher energetic value than the euphausiid. In regard to dietary $\delta^{13}C$, similarity of values was further testimony that penguins from all colonies were exploiting the same neritic habitat, bathed by the same ocean current, and penguins were not foraging in pelagic or slope waters (e.g., Hodum and Hobson 2000). Given the similarity in diet composition, there appears to be no advantage to breeding in one colony or another based on energetic value of prey. Prey availability, however, was not directly addressed in our study. Results reported herein agree with those of our previous work showing a change in diet as the chick-provisioning period advanced and indicating that distance to nearest pack ice can strongly affect the foraging effort and success of Adélie Penguins (Ainley et al. 1998).

There was a temporal shift in both diet and percentage of sea-ice cover: penguins tended to eat more fish as sea ice declined later in the season. This pattern begs the question of whether the dietary switch was due to a change in availability (perhaps related to the decline of sea ice) or a preference for more energetically valuable prey (fish) as chicks grew older. The present study has contributed information toward answering these questions, at least in part, thanks to a natural experiment brought by the grounding of a huge iceberg (designated B15A, 175 × 54 km in size). Prior to the 2000 penguin nesting season, this iceberg lodged against the Ross Island shore, jutting northward and obstructing the flow of the coastal current (Krajick 2001, Perkins 2001). As a result, sea ice was trapped in the southwestern Ross Sea and did not dissipate seasonally to the normal degree (Arrigo et al. 2002). We propose that the longer residence of sea ice was the factor that explained the unusually high prevalence of *E. crystallorophias* (krill) and the low prevalence of *P. antarcticum* (fish) in the diet during 2000. On the other hand, the degree to which the availability of fish was affected also remains unknown. Regardless, on a diet dominated by less energetically rich prey, the penguins successfully raised the usual number of robust chicks (Ainley et al., in press).

From a practical perspective, our results indicate that a geographically broad (or narrow) survey of diet among Adélie Penguin colonies could be accomplished quickly (i.e., synoptically) using toenails of chicks found dead (which are easy to find in this species), even after the nesting season has finished. Often, being able to collect data in late summer or autumn alleviates demand among researchers for limited logistical resources during spring and midsummer. The use of chick tissues to accomplish study goals is possible because the choices of prey appear to be narrow depending on the geographic scale of the study. To be sure, other easily acquired tissues (e.g., blood, feathers; Hobson 1995, Cherel et al. 2000, Hodum and Hobson 2000) could be used as well but would require a little more effort, more logistic support, as well as more permits, and may not be possible in special areas. We made a start toward use of this method, but recommend that researchers use larger samples of tissues than did we. Also, it would be valuable to study the C and N isotopic fractionation factors between diet and toenails, and also the change in isotope ratios as a function of section of the nail analyzed, as has been done for whale baleen. Such information would improve our understanding of results.

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