

The structure of upper level pelagic food webs in the Antarctic: Effect of phytoplankton distribution

D.G. Ainley ^a, W.R. Fraser ^a, W.O. Smith Jr. ^b, T.L. Hopkins ^c and J.J. Torres ^c

^a Point Reyes Bird Observatory, Stinson Beach, CA 94970, USA

^b Botany Department and Graduate Program in Ecology, University of Tennessee, Knoxville, TN 37996, USA

^c Department of Marine Sciences, University of South Florida, St. Petersburg, FL 33701, USA

(Received September 9, 1990; revised version accepted February 25, 1991)

ABSTRACT

Ainley, D.G., Fraser, W.R., Smith, W.O., Jr., Hopkins, T.L. and Torres, J.J., 1991. The structure of upper level pelagic food webs in the Antarctic: Effect of phytoplankton distribution. *J. Mar. Syst.*, 2: 111–122.

We investigated diet composition and diversity and the diet overlap between species within the seabird community of the Scotia–Weddell Confluence region, Antarctica, during spring, autumn and winter. Seasonal changes in diet characteristics and overlap among species were viewed in the context of changes in prey availability as a function of vertical distribution in the water column. The latter was in turn affected by where phytoplankton and associated grazers were located. When primary productivity was confined to the pack ice during winter, thus bringing grazers and their predators closer to the surface, micronekton were much more vulnerable to avian predators and the latter were able to select prey on the basis of energetic value. As a consequence the upper food web was much less diffuse than during the other seasons when prey occurred throughout the upper portion of the water column and predators had to be opportunistic. The mobility of micronekton and nekton bring some structure to the upper portion of marine food webs, thereby introducing seasonal variability of trophic relationships within Antarctic food webs.

Introduction

Studies of upper trophic level predators (i.e. birds or mammals) are rare in pelagic waters; the vast majority of data are derived from breeding animals, because then they are concentrated in specific localities. In those situations larger sample sizes can be amassed with a minimum of effort and it can be done more cheaply than by using a ship. The major question, of course, is how representative are the breeding-situation data to the entire annual cycle. When required to remain attached to offspring, predators have to feed on the prey most available to them within foraging range (Pennycuik et al., 1984). In the Antarctic, krill are the major prey fed to offspring (Croxall and Lishman, 1987). Krill are most available along

shelf breaks (Sahrhage, 1988, and references therein) and thus being naturally juxtaposed near to rookeries of land-based predators, krill are the major prey fed to offspring (Croxall and Lishman, 1987). For avian predators independent of the requirements of breeding, however, their diet appears to be much more diverse and less structured (Ainley et al., 1984).

Marine food webs are unstructured; predators eat prey available to them if of suitable size. Two species can even reverse trophic roles as one grows during ontogeny (Steele, 1974). Although ample data are available to show that seabirds generally eat prey on the basis of size (e.g. Ainley et al., 1984), if marine birds can actually select prey on the basis of some other criterion (other than proximity, as discussed above), this would modify the

unstructured characteristic of relationships in the upper trophic levels. Birds can be a model of how highly mobile predators affect food web structure in marine systems. In that regard, what factors control the diversity of diet among pelagic avian predators? Some studies of breeding individuals provide information which indicates that birds may select prey that are energetically most beneficial to them (i.e., "optimum foraging" in its simplest definition; e.g., Chu, 1984; Montevecchi and Piatt, 1984; Vermeer and Devito, 1986). However, researchers have lacked simultaneous information on the relative availability of the various potential prey. In the present study, a part of AMERIEZ (Antarctic Marine Research at the Ice Edge Zone), a multidisciplinary research program, we have investigated prey selection versus prey availability for highly mobile marine predators.

Methods

We made multi-ship cruises as part of AMERIEZ to the Weddell–Scotia Confluence region during November 1983 (spring), March 1986 (autumn) and July–August 1988 (winter) (Fig. 1). During the three cruises we investigated trophodynamic rates and processes and the ecology of the biota of the marginal ice zone. Samples from the 1986 cruise were gathered entirely in Weddell Sea Water (Husby and Muench, 1988). Samples gathered on the other two cruises were gathered in the Weddell–Scotia Confluence, with very few gathered in 100% Weddell Sea or Scotia Sea water (Husby et al., 1989). We confined analysis of all samples to those collected south of 58°S, the approximate Scotia Sea boundary of the Scotia–Weddell Confluence. Specific details of the

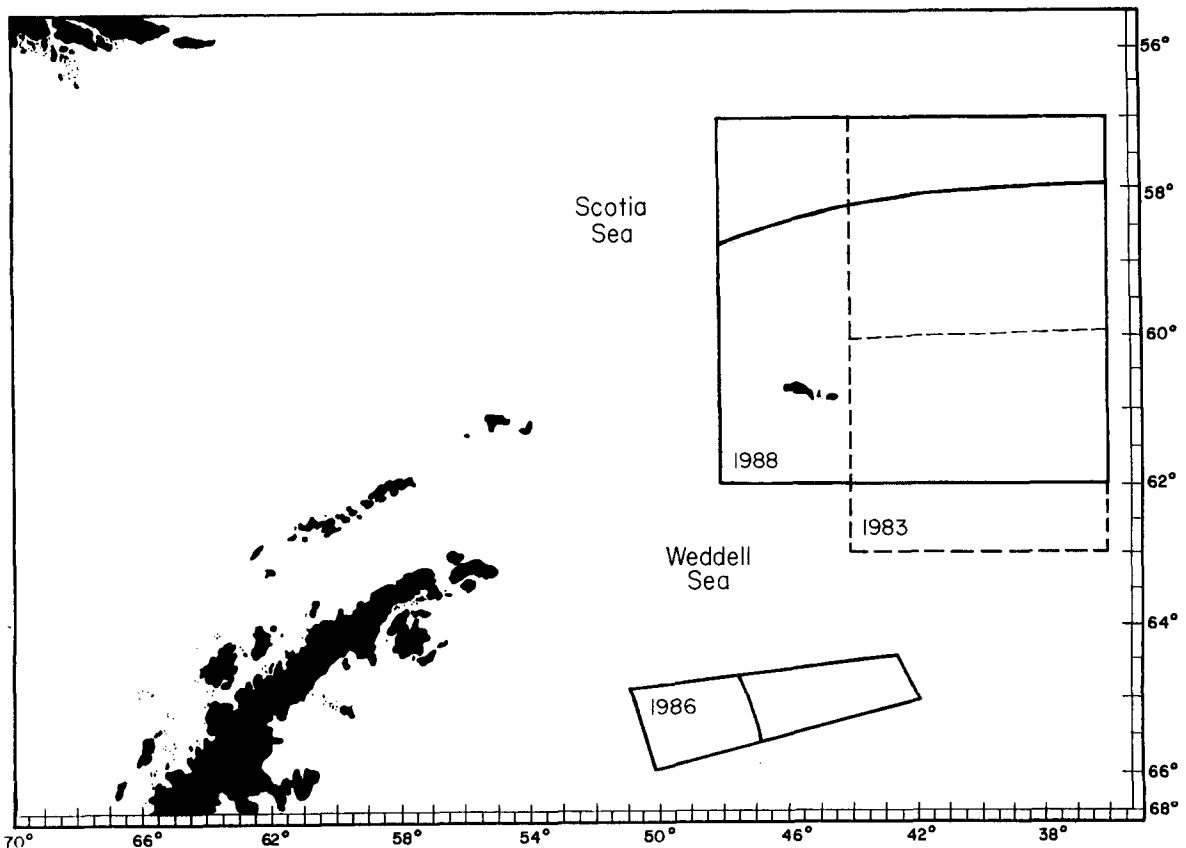


Fig. 1. The southern Scotia and northern Weddell seas showing the boundaries of study areas during three AMERIEZ cruises, November 1983 (spring), March 1986 (autumn) and June–August 1988 (winter). Only diet data gathered south of 57°59'S were used; lines intersecting the three study areas indicate the approximate position of the pack ice edge.

TABLE 1

Scientific names of birds and translations of bird-name codes used in subsequent tables

FUSG	Southern giant fulmar	<i>Macronectes giganteus</i>
FUAN	Antarctic fulmar	<i>Fulmarus antarcticus</i>
PEAN	Antarctic petrel	<i>Thalassoica antarctica</i>
PEBL	Blue petrel	<i>Halobaena coerulea</i>
PETC	Cape petrel	<i>Daption capense</i>
PETS	Snow petrel	<i>Pagodroma nivea</i>
PRAN	Antarctic prion	<i>Pachyptila vitatta</i>
PTKG	Kerguelan petrel	<i>Pterodroma brevirostris</i>
STWI	Wilson's storm-petrel	<i>Oceanites oceanicus</i>
TEAR	Arctic tern	<i>Sterna paradisaea</i>
PENA	Adélie penguin	<i>Pygoscelis adeliae</i>
PENE	Emperor penguin	<i>Aptenodytes forsteri</i>

voyages are contained in Ainley and Sullivan (1984, 1989) and Sullivan and Ainley (1987).

Seabirds were collected by shotgun at 12–15 localities on each cruise. We obtained penguin samples by capturing live birds and pumping their stomachs using the water off-loading technique (Wilson, 1984). No penguin samples were obtained on the 1983 cruise. At each collecting locality, our aim was to collect stomach samples from 5 individuals of each avian species that was present at the locality, with the exception of southern giant fulmars (see Table 1 for scientific names). In pelagic waters of the Ross Sea, this species fed entirely on carrion (Ainley et al., 1984) and the

few individuals collected in the present study confirmed this for the Weddell/Scotia region. We did not sample additional giant fulmars. Collections were made at or near dawn so that prey items would be least digested, as most species feed during twilight or dark (Ainley et al., 1984; Ainley, unpubl.). Due to logistical constraints, we were most successful in timing collections early in the day during the 1983 and 1988 cruises. A total of 645 stomach samples were analyzed for the present study (Table 2).

After each collection, stomach samples were roughly sorted soon after our return to the ship. Whole prey items were measured and certain parts of incomplete prey were either measured immediately or saved for future measurement. For crustaceans, we measured total length, or the largest diameter of their eyes if the specimen was partial. We measured the standard length of fish and the mantle length of cephalopods. We did not include prey items from the gizzard (i.e. otoliths, squid beaks, exoskeletons) unless there were soft parts in the stomach, unless otoliths and squid beaks showed no sign of corrosion or abrasion, or in the case of crustaceans, if the exoskeleton was mostly whole (Duffy and Jackson, 1986). All lengths of fish and squid were estimated from regressions based on the largest diameter of otoliths or the length of the lower beak in cephalopods, respectively. As weights of delicate

TABLE 2

Number of birds inspected and proportion with empty stomachs, Scotia–Weddell confluence region

	1983		1986		1988	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
FUSG	2	0.0	1	0.0	1	0.0
FUAN	27	25.9	18	33.3	11	9.1
PEAN	19	0.0	52	9.6	30	3.3
PEBL	19	0.0	17	0.0	8	0.0
PETC	39	5.1	16	31.3	12	16.7
PETS	69	8.7	40	0.0	46	4.3
PRAN	40	7.5	15	6.7	–	–
PTKG	–	–	23	4.3	1	0.0
STWI	36	22.2	15	20.0	–	–
TEAR	10	0.0	12	25.0	–	–
PENA	–	–	11	0.0	29	17.2
PENE	–	–	18	0.0	8	0.0

items are difficult to determine at sea, and preservation reduces the wet weight, we used regressions based on otolith or beak length, or in a few cases based on body length, to determine the weight of fish and cephalopods. Even with these strictures, the relative importance of cephalopods may be slightly overestimated (Wilson et al., 1985). We used regressions on body length or eye diameter to determine crustacean weights. Some of these regressions are available from the literature (e.g., Clark, 1986; Hecht, 1987; Ainley et al., 1988), but many are unpublished and will be reported elsewhere. For squid, when a regression on beak size indicated an item in excess of the weight of the fullest stomach for that avian predator that we encountered in this study, we assumed that the prey had been found dead and scavenged (in many cases the squid was bigger than the bird). In this case, the weight of that item in the diet was considered to be equal to the average stomach weight of non-empty stomachs for that species (averages determined for the sample from all cruises combined).

The stomach content of fish eaten by birds was determined during 1988 for 34 fish in the stomachs of 21 different birds. For collected birds, we also gathered other information, such as natural isotope ratios and flight morphology, and this information will also be reported elsewhere. All avian specimens were donated to major museums in the U.S., most notably the Los Angeles County Museum of Natural History.

In the present report we refer to characteristics of the horizontal and vertical distribution of chlorophyll *a* and the vertical distribution of prey in the water column. Details of sampling techniques for these aspects of the present study can be found in Lancraft et al. (1989), Hopkins and Torres (1989) and Cota et al. (1990). The data for comparing chlorophyll embedded in the pack ice and that in the water column were summarized from Kottmeier and Sullivan (1990) and Sullivan et al. (1990). The discrete-depth midwater trawls during 1988 were done within the pack ice, whereas in the other two years they were done only in open water near the ice edge. Surface tows (i.e., 0 through 100 m) were conducted at night (2 in 1983, 3 in 1986 and 8 in 1988); 1983 and 1986 data were com-

bined in the present analysis (after Lancraft et al., unpubl.). The degree to which results from "surface" tows were biased during 1988, due to techniques to avoid catching ice floes, is unknown (see Discussion).

Diet diversity was determined using the Shannon-Weiner formula (Hurtubia, 1973). Diet overlap among predators was determined using Morisita's Index (Horn, 1966), where 0 equals no overlap and 1 equals total overlap. For comparisons, we chose an index value > 0.844 to denote diet similarity on the basis of a frequency distribution. That is, for an interval from 0.00–0.19, 68 species comparisons occurred; for 0.20–0.34, 5 comparisons; 0.35–0.49, 7; 0.50–0.69, 13; 0.70–0.84, 6; and 0.85–1.0, 37. The number of comparisons in the last interval increased noticeably from the immediately previous interval and, therefore, we took this discontinuity as the interval to demarcate diet similarity (see also: Diamond, 1983; Ainley et al., 1984).

Results

Productivity in lower trophic levels

As the seasons progressed from spring to autumn to winter, the importance of algal and microorganismic communities in the pack ice as sources of food for grazers increased relative to the contribution of communities in the water column. Moreover, the amount and distribution of phytoplankton in the water column (indicated by chlorophyll *a* concentrations) and level of production differed dramatically among the three seasons (Fig. 2), which was not unexpected (Smith, 1987). Chlorophyll concentrations were about $3 \mu\text{g}/\text{l}^{-1}$ in the upper 60 m during spring, but during

TABLE 3

Vertical distribution of chlorophyll *a* ($\mu\text{g}/\text{l}^{-1}$), summarized by location in the water column or in the pack ice overlying it

	1983 Spring	1986 Autumn	1988 Winter
Pack Ice	3.69	4.12	13.8
Water Column	1.60	0.18	0.10
Ratio	2	23	138

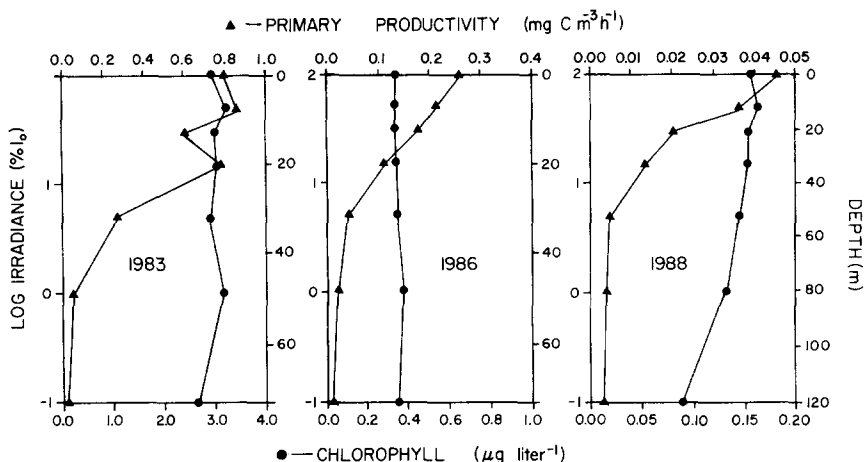


Fig. 2. The vertical distribution of chlorophyll *a* in the water column integrated for the entire cruise during spring 1983, autumn 1986 and winter 1988; note change in depth scale for 1988.

autumn and winter, maximum concentrations were only about 0.35 and 0.15 $\mu\text{g}/\text{l}^{-1}$, respectively, and were over eight times lower in autumn than during spring. Chlorophyll concentrations of algal com-

munities (an index of microbial biomass also) in the pack ice varied little among the seasons (Table 3). During spring, water column concentrations rivaled those in the ice, but during autumn ice concentrations were 23 times greater than in the water column and during the winter 138 times greater.

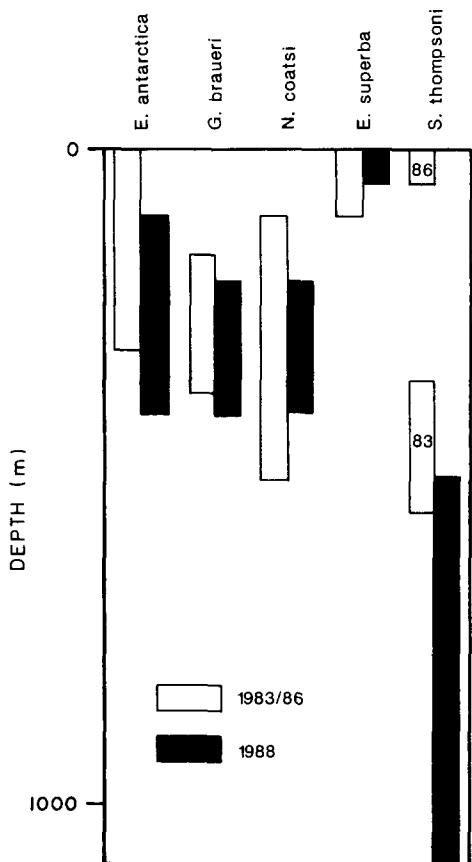


Fig. 3. Depth intervals at which five seabird prey were captured in discrete depth trawls, 1983/1986 and 1988.

Vertical distribution of seabird prey

The results of discrete-depth trawls indicated that krill (*Euphausia superba*), a grazer, were closer to the surface during winter (1988) compared to spring and autumn (1983 and 1986; Fig. 3). During winter, krill were found principally shallower than 40 m; during the other two seasons they occurred from the surface through 80 m. Results for important fish prey (i.e., *Electrona antarctica*, *Gymnoscopelus braueri* and *Notolepis coatsi*), however, showed the opposite pattern. These fish were caught in numbers deeper than 150 m, with only *E. antarctica* reaching as shallow as 90 m during winter. During 1983/86, *E. antarctica* reached the surface and *N. coatsi* to 90 m. According to trawl data, *E. antarctica* reached the surface during spring and autumn.

Seabird diets

In no season was there a disproportionate prevalence of birds having empty stomachs; thus, all

TABLE 6

Percentage composition by weight of seabirds in the Scotia–Weddell confluence region during winter 1988; only items contributing $\geq 0.1\%$ are included

	FUAN	PEAN	PEBL	PETC	PETS	PTKG	PENA	PENE	FUSG
Crustaceans									
<i>Cylopus lucasii</i>							2.0		
<i>Euphausia superba</i>		1.0					4.6		
<i>Gnathophausia gigas</i>	2.0			5.1					
<i>Pasiphaea scotia</i>	2.9				3.0				
<i>Thysanoessa macrura</i>							1.7		
Fish									
<i>Electrona antarctica</i>	91.6	62.0	100	71.0	94.3	100		1.0	
<i>Gymnoscopelus braueri</i>		6.0		3.7	2.1				
<i>Notolepis coatsi</i>				10.7	2.0				
<i>Protomyctophum bolini</i>		1.0			1.0				
Cephalopods									
<i>Galiteuthis glacialis</i>								13.4	
<i>Gonatus antarctica</i>								1.6	
<i>Kondakovia longimana</i>							73.9	45.5	
<i>Psychroteuthis glacialis</i>		26.9		9.3			17.6	38.6	
Other									
Carrion									100

exception of the southern giant fulmar, fed almost exclusively on *E. antarctica*. In all years we assumed that giant fulmars fed on carrion (seal or bird parts) and that emperor penguins fed on squid. The Adélie penguins fed on krill during spring and squid during winter. Large crustaceans, such as *Eurythenes gryllus*, *Pasiphaea scotia* and

Gnathophausia gigas, were not important as food items during autumn, perhaps because their abundance decreased away from the Scotia–Weddell Confluence.

When diet was analyzed on the basis of numerical composition the importance of krill and other small crustaceans to the diet became dispro-

TABLE 7

Indices of overlap in the diets of seabirds in the Scotia–Weddell confluence region during 1983; composition of diet by number (lower left) and weight (italics; upper right)

	FUSG	FUAN	PEAN	PEBL	PETC	PETS	PRAN	STWI	TEAR
FUSG	–	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
FUAN	0.000	–	0.526	0.528	0.541	0.563	0.535	0.515	0.468
PEAN	0.000	0.903	–	0.745	0.767	0.879	0.772	0.753	0.703
PEBL	0.000	0.926	0.978	–	0.972	0.963	0.996	0.963	0.963
PETC	0.000	0.984	0.982	0.975	–	0.961	0.982	0.970	0.948
PETS	0.000	0.918	0.983	0.994	0.966	–	0.975	0.958	0.938
PRAN	0.000	0.986	0.946	0.909	0.963	0.911	–	0.980	0.966
STWI	0.000	0.987	0.944	0.903	0.963	0.905	0.999	–	0.960
TEAR	0.000	0.957	0.982	0.974	0.978	0.978	0.957	0.952	–

Note: an index value of 1.0 indicates complete overlap and 0.000 indicates no overlap.

TABLE 8

Indices of overlap in the diets of seabirds in the Scotia–Weddell confluence region during 1986; composition of diet by number (lower left) and weight (*italics*; upper right)

	FUSG	FUAN	PEAN	PEBL	PETC	PETS	PRAN	PTKG	STWI	TEAR	PENA	PENE
FUSG	–	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>
FUAN	0.000	–	<i>0.111</i>	<i>0.156</i>	<i>0.983</i>	<i>0.157</i>	<i>0.156</i>	<i>0.457</i>	<i>0.158</i>	<i>0.021</i>	<i>0.091</i>	<i>0.209</i>
PEAK	0.000	1.000	–	<i>0.649</i>	<i>0.047</i>	<i>0.675</i>	<i>0.334</i>	<i>0.665</i>	<i>0.331</i>	<i>0.108</i>	<i>0.452</i>	<i>0.237</i>
PEBL	0.000	0.651	0.658	–	<i>0.000</i>	<i>0.994</i>	<i>0.991</i>	<i>0.581</i>	<i>0.997</i>	<i>0.002</i>	<i>0.455</i>	<i>0.006</i>
PETC	0.000	0.999	0.999	0.642	–	<i>0.002</i>	<i>0.000</i>	<i>0.358</i>	<i>0.003</i>	<i>0.040</i>	<i>0.035</i>	<i>0.011</i>
PETS	0.000	0.657	0.654	0.980	0.646	–	<i>0.000</i>	<i>0.606</i>	<i>0.993</i>	<i>0.003</i>	<i>0.462</i>	<i>0.022</i>
PRAN	0.000	0.883	0.880	0.914	0.877	0.925	–	<i>0.599</i>	<i>0.991</i>	<i>0.006</i>	<i>0.463</i>	<i>0.006</i>
PTKG	0.000	0.970	0.968	0.757	0.970	0.757	0.945	–	<i>0.395</i>	<i>0.007</i>	<i>0.320</i>	<i>0.005</i>
STWI	0.000	0.994	0.994	0.717	0.993	0.725	0.926	0.984	–	<i>0.066</i>	<i>0.511</i>	<i>0.006</i>
TEAR	0.000	0.999	0.999	0.629	0.998	0.636	0.867	0.960	0.990	–	<i>0.844</i>	<i>0.000</i>
PENA	0.000	0.999	1.000	0.630	0.998	0.637	0.867	0.961	0.990	1.000	–	<i>0.003</i>
PENE	0.000	0.199	0.186	0.287	0.194	0.289	0.266	0.249	0.206	0.180	0.180	–

Note: an index of 1.0 indicates complete overlap and 0.000 indicates no overlap.

portionate relative to their energetic value and diet overlap was generally high in all seasons except winter (Tables 7–9). The energetic value of a single crustacean smaller or equal to krill in size is miniscule compared to large crustacea (e.g. pasaphaeids) or fish and squid (Croxall and Prince, 1982; Croxall and Lishman 1987; J.J. Torres, unpubl.). Thus, we do not emphasize analyses on the basis of numerical proportion in the present contribution because of the low nutritional value of small crustaceans. Comparisons of diet diversity support these patterns (Table 10). Diets based on

numerical composition usually show a higher diversity, because small crustaceans are relatively more important.

On the basis of weight, diet overlap was far greater during winter, when 71% of species had the same diet, compared to only 44% during spring (Table 11; not including penguins, which were not sampled in 1983; arcsin transformation of percentages, $t = 2.017$, $p < 0.05$). If only the six species sampled during both winter and spring are included, then the proportion of overlapping diets shows even greater divergence, 67% winter and

TABLE 9

Indices of overlap in the diets of seabirds in the Scotia–Weddell confluence region during 1988; composition of diet by number (lower left) and weight (*italics*; upper right)

	FUSG	FUAN	PEAN	PEBL	PETC	PETS	PTKG	PENA	PENE
FUSG	–	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>	<i>0.000</i>
FUAN	0.000	–	<i>0.874</i>	<i>0.995</i>	<i>0.952</i>	<i>0.999</i>	<i>0.995</i>	<i>0.000</i>	<i>0.008</i>
PEAN	0.000	0.409	–	<i>0.849</i>	<i>0.945</i>	<i>0.867</i>	<i>0.917</i>	<i>0.091</i>	<i>0.257</i>
PEBL	0.000	0.964	0.289	–	<i>0.929</i>	<i>0.997</i>	<i>1.000</i>	<i>0.000</i>	<i>0.007</i>
PETC	0.000	0.681	0.925	0.557	–	<i>0.948</i>	<i>0.929</i>	<i>0.030</i>	<i>0.088</i>
PETS	0.000	0.978	0.548	0.925	0.793	–	<i>0.997</i>	<i>0.000</i>	<i>0.008</i>
PTKG	0.000	0.953	0.285	0.997	0.545	0.909	–	<i>0.000</i>	<i>0.000</i>
PENA	0.000	0.117	0.934	0.001	0.749	0.266	0.000	–	<i>0.847</i>
PENE	0.000	0.094	0.075	0.085	0.107	0.086	0.083	0.027	–

Note: an index value of 1.0 indicates complete overlap and 0.000 indicates no overlap.

TABLE 10

Diversity indices for the diets of seabirds in the Scotia–Weddell confluence region

	1983		1986		1988	
	Number	Weight	Number	Weight	Number	Weight
FUAN	-1.21	-1.60	-0.19	-0.47	-0.92	-0.38
PEAN	-1.39	-1.11	-0.15	-1.56	-0.95	-0.99
PEBL	-1.16	-0.94	-1.16	-0.20	-0.22	0.00
PETC	-1.13	-0.93	-0.24	-0.46	-0.16	-0.99
PETS	-1.12	-0.99	-0.97	-0.45	-1.04	-0.39
PRAN	-0.86	-0.79	-0.71	-0.36	-	-
PTKG	-	-	-0.94	-1.53	0.00	0.00
STWI	-0.91	-0.75	-0.31	-0.23	-	-
TEAR	-0.92	-0.07	0.00	0.00	-	-
PENA	-	-	-0.01	-0.65	-0.68	-0.82
PENE	-	-	-1.57	-1.18	-1.53	-1.13
$\bar{x} \pm SE^a$	-1.20	-1.11	-0.54	-0.63	-0.86	-0.55
	± 0.05	± 0.13	± 0.22	± 0.24	± 0.16	± 0.19

^a Only for the five species common to all years.

27% spring ($t = 2.259$, $p < 0.03$). Overlap was lowest during autumn (Table 8), but we did not sample waters of the Scotia–Weddell Confluence in that season. Therefore, comparison with the other two seasons may not be valid, because the Weddell Sea is depauperate in potential prey species. Even so, if only the six winter-occurring species are compared the proportion with overlapping diets in autumn is similar to that in spring (13%; $t = 0.973$). Penguin diets overlapped little with the other species, but only during winter were the diets of the two penguin species similar. Diet diversity during autumn and winter was half that of spring, regardless of whether it was calculated on the basis of number or weight.

Diets of fish prey during winter

Fish were fresh enough in the stomach contents of 21 birds during winter to determine their diets

TABLE 11

Proportion of seabird species having the same diet, a summary of Tables 7–9 (no penguins included)

1983	1986	1988
Spring	Autumn	Winter
58%	13%	71%
$n = 36$ comparisons	$n = 45$	$n = 21$

($n = 45$). Four individuals of *G. braueri* had eaten adult krill; 33 individuals of *E. antarctica* had eaten adult krill, one had eaten larval krill, 2 had eaten the amphipod, *Cylopus*, and 5 had eaten the amphipod, *Vibillia*. The dominance of krill in the diet of these fish is marked (84.4%).

Discussion

During spring, when food for grazers (the potential prey of seabirds) was dispersed throughout the water column, avian diets were diverse as determined by diet composition and diversity. During this season energetically less valuable prey (largely as a function of size) comprised an important component of the diet. In such conditions, avian predators apparently were forced to be opportunistic and ate whatever prey were available: fish, squid, or crustaceans of several kinds. Their diets even included salps, which are mostly composed of water (> 96% of wet weight; Huntley et al., 1989) and large numbers of small amphipods (≤ 20 mm).

Seabird diets during winter were dramatically different. The birds ate only the most energetically valuable prey, such as lanternfish on the part of aerial species and squid on the part of penguins. During winter the birds were selective and apparently ignored small prey such as krill, which

had relatively little food value. Apparently, fish and squid ate krill, the aerial birds ate fish and the diving species ate squid. This is the pattern one would expect if prey versus predator size was the overriding factor that structures marine food webs. During winter, krill occurred closer to the surface, which was where their only feeding opportunity lay: on the undersides of ice floes (Daly, 1990). Presumably, the fish and squid eaten by birds had strayed to the surface at night in pursuit of krill, thus exposing themselves to predation (Torres and Ainley, unpubl.).

The length of winter nights also likely increased the advantage of the avian predators, which feed mostly at night (with the exception of deep-diving penguins; Ainley et al., 1984). The fact that relatively shallow-diving Adélie penguins (Kooyman and Davis, 1987) ignored the poorly nutritious krill during winter to prey on squid suggests that squid, too, were moving closer to the surface (to prey on fish and krill). During autumn, only the very deep-diving emperor penguin captured large quantities of squid, which, because prey of squid were distributed deep in the water column, were out of the diving range of the Adélies (which had to feed on the shallow krill, or so we might argue).

The trawl data partially support the above interpretation. Discrete depth trawls indicated that krill were concentrated closer to the surface during winter than during spring or autumn (Fig. 3). If the trawls could have scraped the undersurface of ice floes, they likely would have caught even more krill. The trawl data, however, do not support the above interpretation as to whether the fish had to swim to the surface to feed. The trawl data also do not confirm the trophic interaction between fish and krill, because even though fish stomachs were full of krill, the vertical distributions of fish and krill in the trawl data do not overlap during winter as in other seasons (Fig. 3).

Squid can not be further addressed in the present analysis because the penguins, which ate most of the squid, can feed anywhere in the upper water column (to 100 m or more deep; Kooyman and Davis, 1987) and no squid were caught by the trawls. Squid predation, however, may provide insight into the difference between what the aerial, surface-feeding birds caught and what the trawls

collected. The squid eaten by cape petrels and Antarctic fulmars were obviously scavenged because of the large size of the squid eaten. Most of those eaten by Antarctic petrels, however, were likely caught directly. The Antarctic petrel is a heavy-bodied bird that has to fly quickly to stay aloft (Ainley, unpubl.). In accord with heavy wing-loading, it is one of only two Antarctic species that can feed by pursuit plunging (i.e., at near full speed they fly right into the water and beneath its surface without pausing to alight first and remain submerged for 3–5 s; Ainley et al., 1984). This indicates that it is a fast predator capable of capturing highly mobile prey.

Trawls designed to sample a diversity of macrozooplankton and micronekton may misrepresent the contribution of the faster organisms. Antarctic birds are noted for their ability to capture prey not observed in trawls (Ainley et al., 1986). The micronekton may be present but because of net avoidance they are not captured by the trawls due to speed or perception of the net on the part of the micronekton. Another possibility is that the organisms are present in a density great enough to satisfy relatively uncommon, upper-trophic-level predators but one too low to be captured by trawls that are even more uncommon. The fish *Notolepis coatsi* is a pelagic predator that eats other fish and, therefore, it too is likely a fast swimmer; only by virtue of its presence in the stomachs of Antarctic seabirds, first revealed in the present study, however, is it known to occur in surface waters. Because it is an upper-trophic-level predator, it is also much rarer than the smaller fish such as the myctophids, on which it preys. Its rarity and mobility may preclude it, too, from being adequately sampled by trawls. Another possibility is that the ship, which is pulling the trawl, displaces highly mobile organisms much more readily than small crustaceans (krill size and smaller). This becomes a concern particularly when the trawl is pulled near the surface in the ship's wake, which is necessary when towing in ice.

In summary, if the fish eaten by seabirds during winter also were feeding (which they were), they would have had to enter the surface layers to find krill and other suitably sized prey. The fact that their stomachs were full of crustaceans

(mainly krill) and that the trawls detected krill concentrations only near the surface is strong evidence for this. By approaching the surface, the fish increased their vulnerability to predation by mobile carnivores. However, myctophids are not known to be adapted to avoid freezing, a concern when temperatures are low enough for seawater to freeze (as during the winter cruise), but the problem has not been much studied in this group either (J.J. Torres, unpubl.). Nevertheless, the trophic interactions and food-web structure in the upper trophic levels of Antarctic pelagic waters appear to be a function of the vertical distribution of phytoplankton and their grazers, as well as perhaps the mobility of the predators. When all prey are equally available, i.e. for aerial predators, in a near-to-surface "smorgasbord", predators actually select prey of higher energetic value. The feeding relationships appear to be more structured during winter, indicating less trophic opportunism, than during spring. We would expect interactions to be even more opportunistic in the midst of the summer phytoplankton bloom.

Acknowledgments

For logistical support we thank the U.S. Antarctic Program, ITT-Antarctic Services and personnel of the *R/V Melville*, *M/V Polar Duke*, *USCGC Westwind* and *USCGC Glacier*. Assistance in the field was provided by J. Donnelly, R. Ferris, T. Lancraft, E. O'Connor, R. Pitman, L. Spear and G. Wallace. The research was supported by grants DPP 8304815 and 8419894 to DGA and DPP grants to the other authors. The comments of A.G. Carey improved the ms. This is contribution no. 484 of Point Reyes Bird Observatory.

References

- Ainley, D.G., Fraser, W.R. and Daly, K.L., 1988. Effects of pack ice on the composition of micronektonic communities in the Weddell Sea. In: D. Sahrhage (Editor), *Antarctic Ocean and Resources Variability*, Springer, Berlin, pp. 140–146.
- Ainley, D.G., Fraser, W.R., Sullivan, C.W., Torres, J.J., Hopkins, T.L. and Smith, W.O., 1986. Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure. *Science*, 232: 847–849.
- Ainley, D.G., O'Connor, E.F. and Boekelheide, R.J., 1984. The Marine Ecology of Birds in the Ross Sea, Antarctica. Am. Ornithol. Union, Washington, D.C., 97 pp.
- Ainley, D.G. and Sullivan, C.W., 1984. AMERIEZ 1983: a summary of activities on board *R/V Melville* and *USCGC Westwind*. *Antarct. J. U.S.*, 19(5): 100–102.
- Ainley, D.G. and Sullivan C.W., 1989. A summary of a winter cruise of the Weddell and Scotia seas on *Polar Duke*. *Antarct. J. U.S.*, 24(5): 144–147.
- Chu, E.W., 1984. Sooty shearwaters off California: diet and energy gain. In: D.N. Nettleship, G.A. Sanger and P.F. Springer (Editors), *Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships*. Minister Supply Serv. Can., Ottawa, pp. 64–71.
- Cota, G.F., Kottmeier, S.R., Robinson, D.H., Smith, Jr., W.O. and Sullivan, C.W., 1990. Bacterioplankton in the marginal ice zone of the Weddell Sea: biomass production and metabolic activities during austral autumn. *Deep-Sea Res.*, 37: 1145–1167.
- Clarke, M.R., 1986. *A Handbook for the Identification of Cephalopod Beaks*. Clarendon Press, Oxford, 273 pp.
- Croxall, J.P. and Lishman, G.S., 1987. The food and feeding ecology of penguins. In: J.P. Croxall (Editor), *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge Univ. Press, Cambridge, pp. 101–134.
- Croxall, J.P. and Prince, P.A., 1982. A preliminary assessment of the impacts of seabirds on marine resources at South Georgia. *Com. Natl. Fr. Rech. Antarct.* 51: 501–509.
- Daly, K., 1990. Overwintering development, growth and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. *Limnol. Oceanogr.*, 35: 1564–1576.
- Diamond, A.W., 1983. Feeding overlap in some tropical and temperate seabird communities. *Stud. Avian Biol.*, 8: 24–46.
- Duffy, D.C. and Jackson, S., 1986. Diet studies of seabirds: a review of methods. *Colon. Waterbirds*, 9: 1–17.
- Hecht, T., 1987. A guide to the otoliths of southern ocean fishes. *S. Afr. J. Antarct. Res.*, 17: 1–87.
- Hopkins, T.L. and Torres, J.J., 1989. Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. *Deep-Sea Res.*, 36: 543–560.
- Horn, H.S. 1966. Measurement of "overlap" in comparative ecological studies. *Am. Nat.*, 100: 419–424.
- Huntley, M.E., Sykes, P.F. and Marin, V., 1989. Biometry and trophodynamics of *Salpa thompsoni* Foxton (Tunicata: Thalicacea) near the Antarctic Peninsula in austral summer, 1983–1984. *Polar Biol.*, 10: 59–70.
- Hurtubia, J., 1973. Trophic diversity measurements in sympatric predatory species. *Ecology* 54: 885–890.
- Husby, D.M. and Muench, R.D., 1988. Hydrographic Observations in the Northwestern Weddell Sea Marginal Ice Zone during March 1986. U.S. Natl. Ocean. Atmos. Admin., Tech. Memo. No. NOAA-TM-NMFS-SWFC-106, La Jolla, Calif., 33 pp.

- Husby, D.M., Muench, R.D. and Gunn, J.T., 1989. Oceanographic Observations in the Scotia Sea Marginal Ice Zone, June–August 1988. U.S. Natl. Ocean. Atmos. Admin., Tech. Memo. No. NOAA-TM-NMFS-SWFC-127, La Jolla, Calif., 64 pp.
- Kooyman, G.L. and Davis, R.W., 1987. Diving behavior and performance, with special reference to penguins. In: Seabirds: Feeding Ecology and Role in Marine Ecosystems, J.P. Croxall (Editor), Cambridge Univ. Press, Cambridge, pp. 63–76.
- Kottmeier, S.T. and Sullivan, C.W., 1990. Bacterial biomass and production in pack ice of Antarctic marginal ice edge zones. *Deep-Sea Res.*, 37: 1311–1330.
- Lancraft, T.M., Torres, J.J. and Hopkins, T.L., 1989. Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). *Polar Biol.*, 9: 225–233.
- Montevecchi, W.A. and Piatt, J., 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. *Comp. Biochem. Physiol.*, 78A: 15–20.
- Pennycuik, C.J., Croxall, J.P. and Prince, P.A., 1984. Scaling of foraging radius and growth rate in petrels and albatrosses. *Ornis Scand.*, 15: 145–154.
- Sahrhage, D. (Editor), 1988. Antarctic Ocean and Resources Variability. Springer, Berlin, 344 pp.
- Smith, W.O., Jr., 1987. Phytoplankton dynamics in marginal ice zones. *Oceanogr. Mar. Biol. Ann. Rev.*, 25, 11–38.
- Steele, J., 1974. *The Structure of Marine Ecosystems*. Harvard Univ. Press, Cambridge, Mass., 310 pp.
- Sullivan, C.W. and Ainley, D.G., 1987. AMERIEZ 1986: a summary of activities on board the *R/V Melville* and *USCGC Glacier*. *Antarct. J. U.S.*, 22(5): 167–169.
- Sullivan, C.W., Cota, G.F., Krempin, D.W. and Smith, Jr., W.O., 1990. The distribution and activity of bacterioplankton in the marginal ice zone of the Scotia–Weddell sea during austral spring. *Mar. Ecol. Progr. Ser.*, 63: 239–252.
- Vermeer, K. and Devito, D., 1986. Size, caloric content, and association of prey fishes in meals of nestling Rhinoceros Auklets. *Murrelet*, 67: 1–9.
- Wilson, R.P., 1984. An improved stomach pump for penguins and other seabirds. *J. Field Ornithol.*, 55: 109–112.
- Wilson, R.P., La Cock, G.D., Wilson, M.-P. and F. Mollagee, 1985. Differential digestion of fish and squid in Jackass Penguins *Spheniscus demersus*. *Ornis Scand.*, 16: 77–79.