4. Elsewhere we have documented the in situ production of alkalinity in lakes. See D. W. Schindler, R. Wagemann, R. B. Cook, T. Ruszczynski, J. Prokopowich, *Can. J. Fish. Aquat. Sci.* **37**, 343 (1980); C. A. Kelly, J. W. M. Rudd, R. B. Cook, D. W. Schindler, *Limnol. Oceanogr.* **27**, 891 (1982); R. B. Cook and D. W. Schindler, *Ecol. Bull.*, R. B. Cook, C. A. Kelly, D. W. Schindler, M. A. Turner, *Limnol. Oceanogr.* **31**, 134 (1986).
5. Acidometric Gran titrations were performed as described in W. Stumm and J. J. Morgan, *Aquatic Chemistry* (Wiley-Interscience, New York, 1970). The equivalence point occurred at *p*H values between 4.5 and 5.0, depending on the inorganic carbon concentration of the sample [D. S. Jeffries, *Can. J. Fish. Aquat. Sci.* **37**, 901 (1980)]. Detailed ionic budgets for terrestrial catchments are given by S. E. Bayley *et al.*, Newbury (in preparation) and S. E. Bayley and D. W. Schindler in (*3*).
6. K. G. Beaty, *Can. Data Rep. Fish. Aquat. Sci. 285* (1981); *ibid. 480* (1984); unpublished data. The long-term residual in the water budget of the lake is approximately 3%.
7. Methods used were described by M. P. Stainton, M. J. Capel, and F. A. J. Armstrong [*Fish. Mar. Serv. Misc. Spec. Publ. 25* (1977)], except that ion chromatography was used for sulfate measurements. Chemical samples were taken weekly from all streams during the ice-free season, which ranged from 25 to 30 weeks. Because streamflows were measured continuously and the records digitized to yield daily values, estimates of stream chemistry for days between weekly sampling were derived by linear interpolation with time. For the elements of concern here, there is little relation between concentration and flow. Combined sampling and analytical errors as a percentage of the mean concentration were as follows: Ca, 0.9; Mg, 2.0; Na, 0.9; K, 3.2; $NH_4$, 6.4; $SO_4$, 2.0; $NO_3$, 4.7; and Cl, 16.0.
8. G. A. Linsey, M. P. Stainton, D. W. Schindler, *Can. J. Fish. Aquat. Sci.* (in press).
9. The average alkalinity of precipitation at ELA is slightly negative. The Northeast Subbasin contains a small *Sphagnum* bog of *p*H 4, which constitutes about one-third of the drainage basin [S. E. Bayley *et al.*, *Can. J. Fish. Aquat. Sci.* (in press)].
10. The East Subbasin contains small amounts of calcareous lacustrine sediments deep in the overburden, apparently originating from glacial Lake Agassiz, which covered part of the area about 10,000 years ago. Such deposits are rare in the drainages of small lakes in the area. Four other streams in the ELA area have been sampled periodically. Only one yielded positive alkalinity [S. E. Bayley and D. W. Schindler, in (*3*)].
11. K. Kennedy, thesis, University of Waterloo, Ontario (1974).
12. If there were no in-lake sources, alkalinity should equal average annual input of alkalinity from precipitation plus terrestrial yield ($49.75 \times 10^9$ μeq) divided by the average outflow ($738 \times 10^6$ liters).
13. Organic acids in Lake 239 are about equally split between weak acids (pKa values >7) and strong acids (pKa's <4), [A. Herczeg, thesis, Columbia University, New York, (1985)]. Although removal of organic anions generates a small amount of alkalinity, their omission does not affect our conclusions.
14. For individual ions, the statistical significance of $\Delta M$ was based on paired $t$ tests of two depth profiles of seven samples each, taken at identical depths in the first and last samplings in the study. The significance of $I - O$ was judged by paired $t$ tests of annual $I$ versus annual $O$ ($n = 3$). The significance level used was $P = 0.05$. Because Gran alkalinity was not measured before 1981, and ion exchange rather than dionex methods were used for sulfate, budgets given here are for 1981–1983 only. Analysis of other ions for the period of record (9 to 13 years) were similar to 1981–1983 values. The significance of the difference between annual alkalinity calculated by Gran titration and ion balance was similarly tested.
15. S. L. Schiff and R. F. Anderson, *Water Air Soil Pollut.*, in press.
16. Although redox conditions are high at the sediment surface, low redox values occur a few millimeters below the sediment-water interface. As a result, sulfate is reduced as it diffuses into sediments, as shown by low porewater sulfate concentrations. High concentrations of iron and manganese also occur in sediment porewaters, but they are reoxidized as they diffuse to the sediment-water interface. On processes affecting alkalinity, see C. A. Kelly, J. W. M. Rudd, R. B. Cook, D. W. Schindler, *Limnol. Oceanogr.* **27**, 868 (1982); C. T. van Breeman, C. Driscoll, J. Mulder, *Nature (London)* **307**, 599 (1984); J. L. Schnoor and W. Stumm, in *Chemical Processes in Lakes*, W. Stumm, Ed. (Wiley, New York, 1985), pp. 322–338.
17. The alkalinity budget of Lake 223 is described by R. B. Cook, C. A. Kelly, D. W. Schindler, M. A. Turner, *Limnol. Oceanogr.* **31**, 134 (1986).
18. Sulfate reduction in ELA lakes is normally limited by the concentration of sulfate and increased as a linear function of sulfate concentration [R. B. Cook and D. W. Schindler, *Ecol. Bull. (Stockholm)* **35**, 115 (1983); D. W. Schindler, in *Chemical Processes in Lakes*, W. Stumm, Ed. (Wiley, New York, 1985).
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21. Sulfate and nitrate reduction in acidified lakes of eastern Ontario and the Adirondacks have been shown to occur at rates similar to those in Lake 223 [J. W. M. Rudd and C. A. Kelly, *Limnol. Oceanogr.* (in press)]. Both processes also occur in *Sphagnum* bogs at *p*H values of 4 or less [H. F. Hemond, *Ecol. Monogr.* **50**, 507 (1980); S. E. Bayley, *et al.*, (in press)]. Work in mesocosms (1 m in diameter) by S. Schiff and R. F. Anderson [*Water Air Soil Pollut.* (in press)] confirms that calcium exchange, nitrate reduction, and sulfate reduction are the most important alkalinity generating processes in ELA lakes. D. W. Schindler [*Water Air Soil Pollut.* (in press)] shows that these processes are important in all acid-sensitive lakes for which input-output balances are available.
22. Supported by the Department of Fisheries and Ocean, Canada. S. E. Bayley and K. G. Beaty assisted in the calculation of terrestrial basin outputs. R. F. Anderson, S. E. Bayley, G. J. Brunskill, P. Campbell, R. E. Hecky, R. Hesslein, and S. Schiff provided helpful discussions or reviewed the manuscript.

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# Antarctic Mesopelagic Micronekton: Evidence from Seabirds That Pack Ice Affects Community Structure

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**Through a multidisciplinary project (AMERIEZ), with an unusual complement of components, previously unknown temporal and spatial dimensions to the structure of Antarctic epipelagic and mesopelagic communities were revealed. In late spring, an abundance of crustacean species thought to occur only below 300 meters was detected in ice-covered surface waters. Evident in ice-free waters were the expected occurrence patterns of these normally nonmigratory mesopelagic organisms. Where the pack was consolidated and little light penetrated to depth, primary and secondary production was confined to ice floes, and the physical environment immediately beneath the ice was reminiscent of a mesopelagic one. This suite of characteristics possibly explains why the crustaceans resided at the surface.**

ANTARCTIC PACK ICE COVERS 10 PERcent of the world ocean at its maximal extent during early spring (*1*). Associated with the ice is a distinct biological community, including in-ice living algae and bacteria, epipelagic micro- and macrozooplankton, fishes, birds, and pinnipeds (*2, 3*). As the pack recedes, ultimately to be confined to seven major refugia by early summer (*4*), open-water species, particularly those of upper trophic levels, move southward with the retreating ice edge (*2, 3*). The open-water community takes advantage of its major phytoplankton bloom, which occurs when waters previously shielded by ice are exposed to the long hours of summer sunlight and low density meltwater imparts significant vertical stability to the water column (*5*).

In contrast to epipelagic species, the influence of seasonal ice cover and changing day length is poorly known for the deeper-living (100 to 1000 m) mesopelagic component of the Antarctic marine community. In other areas of the world's oceans, a substantial fraction of the mesopelagic fauna migrates from 200- to 500-m daytime depths to or near the surface at dusk, and returns to depth at dawn. These organisms orient to a constant light level or isolume, which moves up and down in the water column with the setting and rising sun (*6*). At night, vertical migrators can make up greater than 70 percent of the micronektonic biomass in the top 100 m (*7*). In the Antarctic, species exhibiting light-oriented movement could have radically different vertical distributions through the austral seasons if light-mediated behavior is maintained throughout the year-

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ly cycle, because diel light-dark regimes differ markedly between winter and summer. Shading of the ocean by pack ice could further complicate vertical distributions during periods of increasing day length, such as austral spring, creating a dichotomy in light levels between the open water and consolidated ice pack.

As part of AMERIEZ, a multidisciplinary, physical-chemical-biological investigation of the Antarctic ice edge zone (*8*), we have been investigating how the advance and retreat of the pack edge affects the pelagic ecosystem. During the austral spring (November) 1983, when the ice edge had just begun to retreat, our stations extended from the ice edge 200 km into the pack ice, reaching the consolidated condition typical of winter, as well as from the edge 600 km into open waters (Fig. 1). Using an array of sampling techniques, not previously combined (*9*), we discovered a pattern in the vertical stratification and movements of micronekton that was undescribed.

Distinct distributional patterns existed at all trophic levels. Phytoplankton chlorophyll a and bacterial standing stocks were extremely low under the pack ice, maximal near the ice edge, and then decreased in ice-free waters northward (Fig. 2) (*5*). Salps, especially *Salpa thompsoni*, were the overwhelmingly dominant organism in the top 500 m of the open water zone. Dominant fishes were *Electrona antarctica*, *Gymnoscopelus braueri* (Myctophidae), and *Notolepsis coatsi* (Paralepididae) and in the lower 500 m were *Bathylagus antarcticus* (Bathylagidae) and *Cyclothone microdon* (Gonostomatidae). There was a clear trend of increasing biomass and diversity in the ichthyofauna (*10*) as well as a change in the seabird fauna moving northward away from the pack ice (*11*). At 58°S (the Weddell-Scotia confluence) a sharp drop in fish biomass and a change in seabird species composition occurred. Vertical migration was the dominant diel distribution pattern exhibited by fish species (*10*).

Amphipods and euphausiids dominated the crustacean catch in open waters south of 59°S. Among these were the large gammarids *Cyphocaris* and *Parandania* and the smaller hyperiids *Vibilia* and *Cyllopus* commonly associated with salps. *Euphausia superba* occurred in surface waters throughout the study area although not in the huge concentrations sometimes encountered elsewhere (*12*). Representatives of the classical midwater crustacean fauna (for example, Pasiphaeidae, Oplophoridae, Mysidacea, Penaeidae, Ostracoda), common in boreal, temperate, and tropical regions, were not captured with any regularity until north of 58°S. No decapods, mysids, or ostracods were captured in trawls reaching less than 310 m anywhere in the open-water transects, day or night.

Consistent with availability, as indicated in the trawl data, the myctophids, *E. antarctica* and *G. braueri*, and the euphausiid, *E. superba*, were the main prey of seabirds in open waters (Fig. 3). Also consistent with trawl data, the amphipods *Vibilia* and *Cyllopus* were most prevalent in seabird diets in the open waters north of 58°S. Most prey were captured when they moved upward into surface waters at "night" as part of their diel cycle (*3*). In the pack ice, trawls could not be used, but assuming that seabird diet still provided a comparable index, they indicated changes in the micronektonic community. In the outer reaches of the pack ice the above prey were consumed less regularly, and deep into the pack, crustacea of the genera *Pasiphaea* and *Eurythenes* replaced myctophids in the seabird diet.

The capture of an occasional pasaphaeid by birds in open water was unexpected because *Pasiphaea longispina* had not been captured in trawls shallower than 310 m, and the birds sampled dive no deeper than 5 m (*3*). An even greater surprise was the dominance of *P. longispina* among prey of the few seabird species that frequented the consolidated pack, principally snow and Antarctic petrels. The fact that two other deep-water forms, the large amphipod *Eurythenes gryllus* and the ostracod *Gygantocypris mulleri*, were also eaten by these pack ice seabirds confirmed that an upward, seasonal displacement of mesopelagic crustacea had occurred. In open water these crustacea behaved according to expectations: they remained at depth and did not exhibit a diel vertical migration.

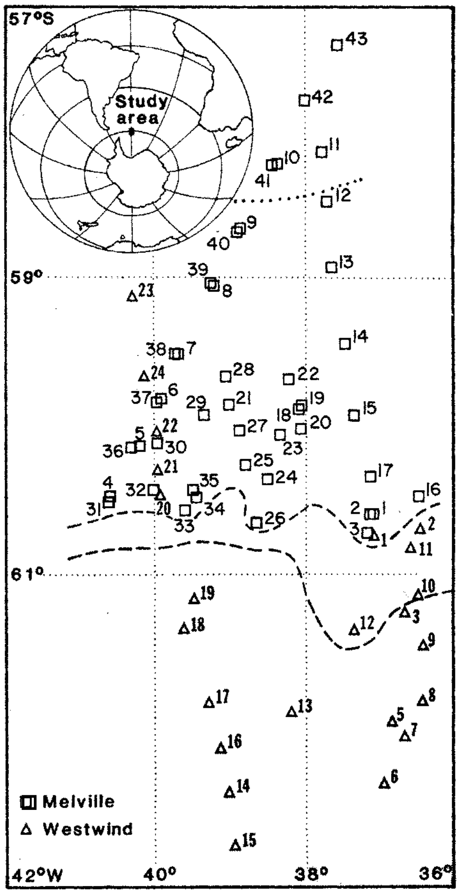

Fig. 1. Positions and pattern of oceanographic stations occupied during AMERIEZ, November 1983. Dotted line indicates Scotia/Weddell Confluence, dashed line indicates pack ice edge, and shading delimits heavy ice and "winter" conditions.

During daylight within the pack, after the overturning of a small iceberg, we noted several live *P. longispina* inhabiting channels in what had been the berg's underside. Later, we noticed this organism, as well as *E. superba*, in ice channels on the underside of old, decaying floes on at least 20 different occasions. Since icebergs occurred in open waters, these observations provided a possible explanation for where birds to the north of the pack may have been finding pasaphaeids. Alternatively, some birds could have captured them in the pack and then flown north, but their fresh condition in bird stomachs indicates that this was unlikely. Furthermore, most pasaphaeids were eaten by seabirds that do not frequent ice-free water (*9*). Thus, at least one, and perhaps more, of the crustacean species eaten by seabirds is entirely mesopelagic in open waters, and is thus unavailable to the birds, but within the pack ice it occurs at the surface (*13*).

Observations of nonmigratory mesopelagic fauna in surface waters are exceedingly rare and have usually been reported as strandings in regions of strong upwelling (*14*). A similar explanation is not possible here, because data on salinity and temperature as a function of depth showed the deepest mixed layer to be 130 m (*15*). Thus, we must conclude that the presence of these organisms at the surface was behaviorally mediated.

Our understanding of communities beneath ice-covered seas is limited by difficulties with wintertime and under-ice sampling. Nevertheless, the surface residence of the three mesopelagic organisms is enigmatic. Because most of the non-krill zooplankton biomass reportedly sinks below 500 m to overwinter (*16*), it seems possible that a fertile feeding ground would exist within the species' normal (300 to 1000 m) depth range.

A likely explanation for these species' presence at the surface in ice-covered but not ice-free water is the combination of factors present during the austral spring and observed during AMERIEZ. For the pack ice zone, temperature variability was less than 3.0°C in the top 1000 m (*15*). In waters free of ice, primary production extended to a depth of about 100 m (0.1 percent of surface light) as part of the ice-edge bloom (*5*), but as we moved into more concentrated ice, phytoplankton chlorophyll a became increasingly restricted to the surface until it was confined to the ice itself with extremely low concentrations in the waters beneath. Thus, the most important cues associated with vertical movement in the oceanic water column were severely damped or absent in the consolidated ice pack, and significant productivity occurred only within the ice. As a consequence, the environment near to the ice was strongly reminiscent of the mesopelagic one, perhaps encouraging *P. longispina* and other species to reside at the surface.

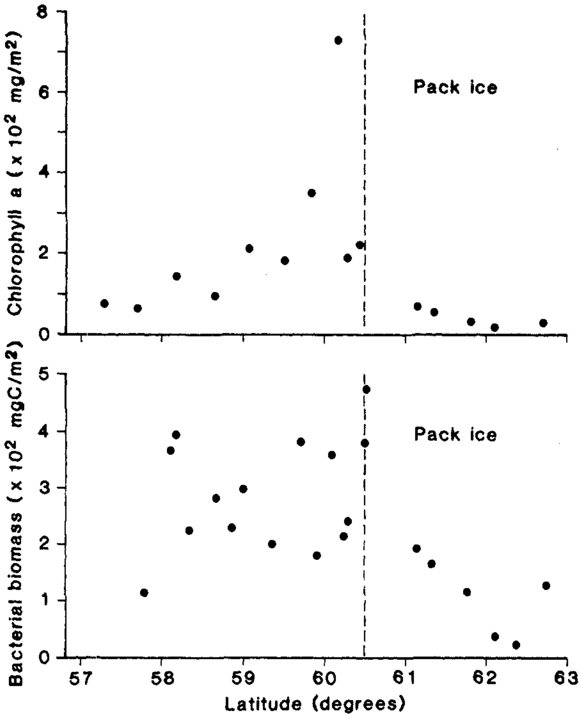

Fig. 2. Chlorophyll a (top) and bacterial biomass (bottom) integrated through the upper 150 m of the water column; data from stations along western edge of AMERIEZ study area: *Melville* stations 33–43 and *Westwind* stations 15–24 (see Fig. 1).

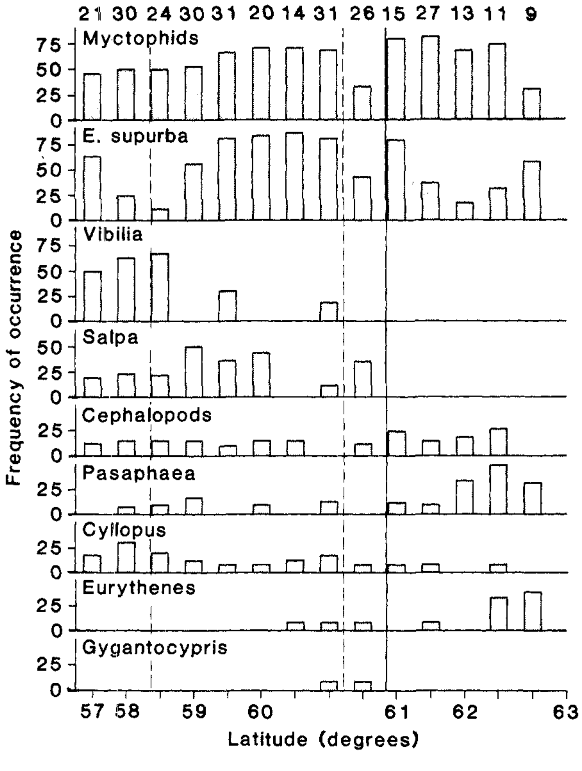

Fig. 3. Frequency of occurrence of major prey items in diets of seabirds, by longitude (sample sizes at top). Dashed vertical line at 58°30′ indicates Scotia/Weddell Confluence, dashed line at 60°30′ indicates northern edge of pack ice, and line at 60°45′ indicates boundary of consolidated pack.

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8. AMERIEZ stands for Antarctic marine ecosystem research at the ice edge zone.
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13. Pasaphaeids were eaten rarely by seabirds in the Ross Sea pack ice (*3*), and have been preyed upon heavily by surface feeding birds in pack ice around Anvers Island (65°S, 64°W) (W. R. Fraser, in preparation); *Eurythenes* was eaten by surface feeding birds in the Bellingshausen Sea pack ice, September 1985 (D. G. Ainley and W. R. Fraser, unpublished observations).
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17. We appreciate the efforts of captains and crews of R/V *Melville* and USCGC *Westwind*. Logistic arrangements were made largely by ITT Antarctic Services, Inc. The research and logistics were funded by NSF's Division of Polar Programs. We thank M. Dunbar and an anonymous reviewer for critical comments on the manuscript.

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