A top–down, multidisciplinary study of the structure and function of the pack-ice ecosystem in the eastern Ross Sea, Antarctica

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ABSTRACT. We used a top–down, multidisciplinary approach to examine the physical and biological environment of the pack ice of the eastern Ross Sea (approximately 125–170°W) during the austral summer of 1999/2000 from RVIB *Nathaniel B. Palmer* and its ship-based helicopters. The approach focused on pack-ice seals while incorporating studies of biotic and abiotic factors that may influence the distribution and abundances of these apex predators in the Ross Sea to yield a holistic understanding of the structure and function of this complex, large marine ecosystem. This research represented the US component of the international Antarctic Pack Ice Seal (APIS) program, which was designed to document the circumpolar distribution and abundance of Antarctic pack-ice seals. The eastern Ross Sea is one of the two major areas in the Southern Ocean where substantial pack ice exists throughout summer. We found that vast multi-year ice floes (>20 km diameter) and smaller floes north of the shore-fast ice front provide a unique habitat for seals and penguins (apex predators) to forage and haul out while molting in late summer. Farther north, more Ross seals were observed than in any previous surveys in the circumpolar pack ice, perhaps because they are attracted to the area in summer to molt on large stable first-year ice floes. Extensive fast ice along the coastline and drifting pack ice in the shelf–slope boundary zone provided haul-out areas for seals and penguins with access to feeding in the coastal shelf region. Distributions of potential prey for seals and penguins varied over the study area, as determined by nets, acoustics, and diving surveys. Antarctic krill (*Euphausia superba*) were found throughout the survey region, overlapping the distributions of two smaller species, *Thysanoëssa macrura* (primarily off-shelf) and

E. crystallorophias (primarily found on-shelf). In some locations, *E. superba* occurred at high densities underneath ice floes, where they foraged on the sea-ice microbial community. Two general fish communities, oceanic and shelf, were distinguished. Off-shelf fishes were members of the classic oceanic midwater fish fauna, whereas on-shelf fishes were Antarctic endemics. The abundance of pelagic fishes was relatively low throughout the study area compared with other Southern Ocean ecosystems. In contrast, benthic fish biomass and diversity on-shelf were high (41 species, 6 families). Hydroacoustic analyses indicated that densities of potential prey were highest in the coastal shelf region where large aggregations of euphausiids (primarily *E. crystallorophias*) and individual juvenile Antarctic silverfish (*Pleuragramma antarcticum*) occurred.

Contents

Introduction

In 1993, the SCAR Group of Specialists on Seals initiated an international program to document the abundance and distribution of the four Antarctic pack-ice seal (APIS) species: crabeater (*Lobodon carcinophaga*), leopard (*Hydrurga leptonyx*), Ross (*Ommatophoca rossii*), and Weddell (*Leptonychotes weddellii*) seals. The authors conducted a major United States component of that study, by icebreaker and helicopters, in the eastern Ross Sea between December 1999 and February 2000. That area consistently retains one of the largest expanses of residual sea ice in summer, when total sea-ice coverage around Antarctica declines to ~20% of its annual maximum (Gloersen and others 1992). Because of the remoteness of the eastern Ross Sea and the high density of multiyear pack ice, which make access and navigation difficult even in summer, studies of the structure and function of biological communities there have been rare and of small geographical scale. Consequently, we planned to maximize the utility of surveys of seal abundance and distribution with a multidisciplinary approach to document additional physical and biological features of the pack-ice environment as explanatory variables. A top–down approach was developed, with the seals, as apex predators, as the key dependent variable, and various physical and biological factors as independent explanatory variables. We hypothesized that the ice-obligate and ice-associated seals would aggregate in pack-ice habitats in mid and late austral summer to forage and molt. The primary objective was to test this hypothesis, with qualifications derived from patterns in explanatory variables, with a second objective to yield a more holistic understanding of the structure and function of the Ross Sea as a large marine ecosystem that has, as yet, been little influenced by human activities.

The results of these studies will be published separately in a variety of specialized scientific journals. However, because of the uniqueness of the research opportunity in this relatively unknown sector of Antarctica, this paper presents a synopsis of the research approach and preliminary results to highlight and integrate the elements of the general multidisciplinary, top–down (apex predator-driven) research approach.

The US Antarctic Pack Ice Seal (APIS) research cruise, 1999/2000

Thirty-one scientists participated in the US APIS 1999/2000 cruise aboard the US RVIB *Nathaniel B. Palmer* to the eastern Ross Sea. The cruise began at Lyttelton, New Zealand, on 20 December 1999 and ended at McMurdo Station, Antarctica, on 10 February 2000 (Fig. 1). We conducted research on the distribution and abundance of seals; seal health and nutrition; seal population and immuno-genetics; penguin ecology; the distribution, abundance, and ecology of fishes; the ecology of krill and other zooplankton; and the physical environment (sea ice and oceanography). Two helicopters and several rubber inflatable boats allowed the various projects to extend the reach of studies beyond just ship-based observations and sampling.

The principal objectives of the research were to 1) document the distribution and abundance of the four species of pack-ice seals, 2) document the biotic and abiotic variables that may govern the distribution of these seals, and 3) investigate the interactions among seals, penguins, fish, krill, and pack ice in the eastern Ross Sea. Three specific questions were focused on:

1. How are the distributions of apex predators and their prey influenced by ecological features and oceanic fronts associated with bathymetry and sea ice?
2. Do biological factors such as prey composition and availability have a stronger, more direct influence on the distribution of apex predators than do physical features such as ice thickness, topography, or floe size?
3. Do apex predators in zones of relatively high density exhibit behavioral and physiological characteristics that are different from predators in areas of lower density?

The physical environment

The Ross Sea

The Ross Sea is a large embayment of Antarctica in the Pacific sector of the Southern Ocean. It is defined generally as extending from Victoria Land (170°E) in

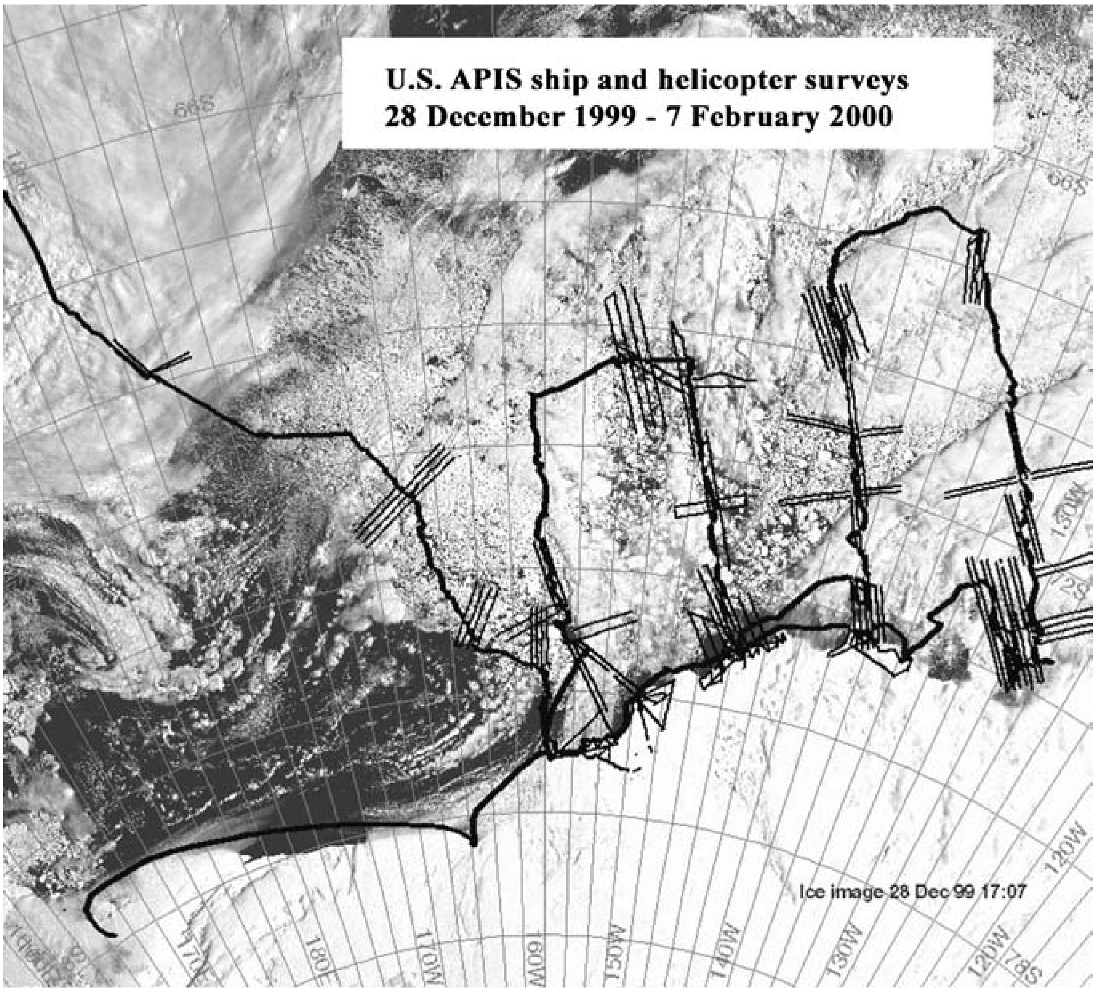

Fig. 1. DMSP visible satellite image (28 December 1999) of the Ross Sea, showing the APIS cruise track (thick lines) and helicopter survey transects (thin lines), conducted between 28 December 1999 and 7 February 2000. The left (western) end point of the cruise line is at McMurdo Station.

the west, eastward to about 125°W, where the Amundsen Sea begins near the King Edward VII Peninsula of Marie Byrd Land (Spezie and Manzella 1999). In the study area in the eastern Ross Sea (east of ~160°W), the continental shelf is relatively narrow, with depths of 500–700 m, and then drops off rapidly to depths exceeding 3000 m. Consequently, the distances between the ice-shelf fronts or fast-ice edge and deep water habitats are often around 30 km or less.

In early summer, just prior to the surveys, the residual pack-ice zone in the eastern Ross Sea was large and highly congested. It consisted mostly of annual ice formed locally, but there was also pack ice that had been advected westward from the Amundsen and Bellingshausen seas, and perhaps from over the continental shelf along the Ross Ice Shelf (http://polar.jpl.nasa.gov/). The seasonal enlargement of the persistent Ross Sea polynya, from a coastal winter location near Ross Island, typically envelops most of the western continental shelf and extends north to just west of 180°W longitude. That open-water pattern leaves three residual sea-ice fronts in summer: (1) the northern edge of the outer pack ice; (2) the western edge of the pack ice along the eastern side of the Ross Sea polynya; and (3) a shore lead near and parallel to the edge of the continent along the southern boundary of the pack ice (Fig. 1). The pack ice that persists through summer in the eastern Ross Sea continues eastward through the Amundsen and Bellingshausen seas.

Sea ice

We divided the study area into five generalized zones, based on pre-cruise knowledge of several physical and biological criteria (Fig. 2). The western edge of the area was known as the Ross Polynya Ice Zone (RPIZ), and the northern edge the Northern Marginal Ice Zone (NMIZ). The southern area over the continental shelf, bounded by fast ice to the south, was divided into the Coastal Polynya Zone (CPZ) and the Ice Covered Shelf Zone (ICSZ). The region between those zones is the Interior Pack Ice Zone (IPIZ).

Sea-ice conditions and properties were documented using satellite imagery (for example, Figs 1, 2); airborne

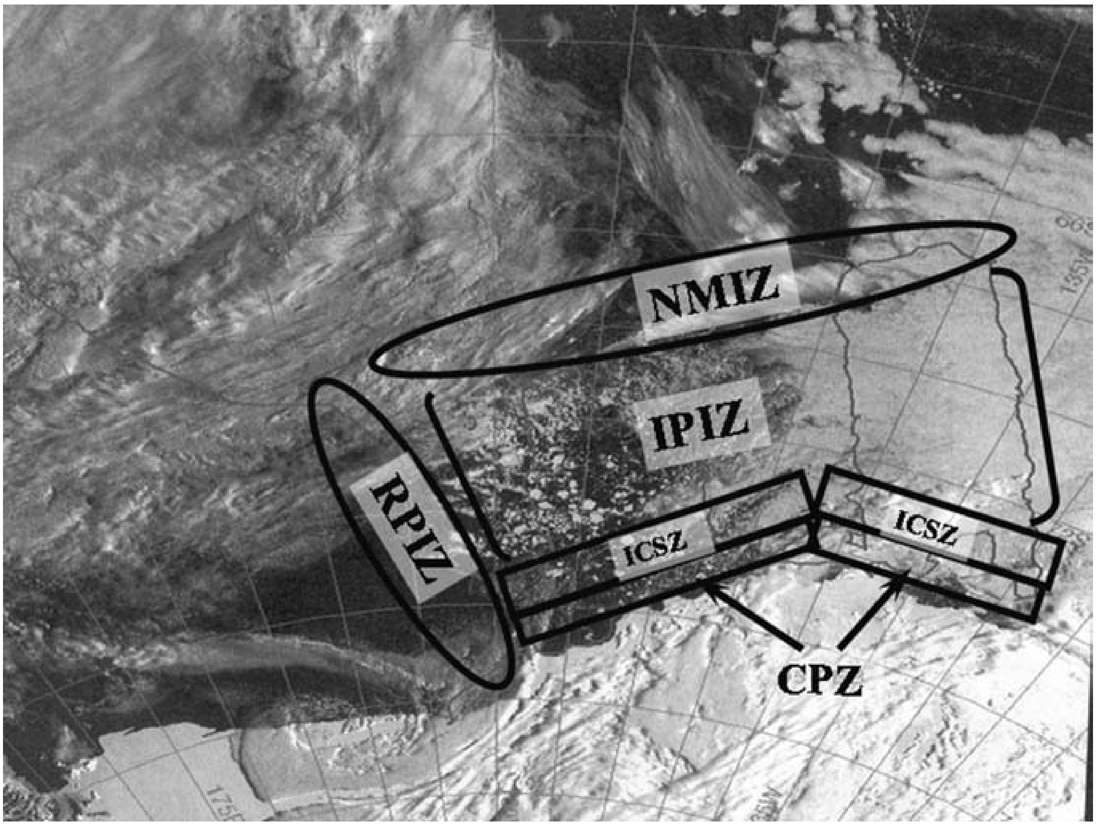

Fig. 2. DMSP visible satellite image taken on 5 February 2000, reflecting sea-ice conditions at the end of the cruise period. Compared to Figure 1, the western and northern boundaries of the sea ice have both retreated. The sea ice is also dispersed, and younger ice has melted leaving mostly the large floes ('floating islands') of multi-year ice visible on the image, particularly in the southern areas of the pack ice. The generalized study zones are: RPIZ = Ross Polynya Ice Zone; NMIZ = Northern Marginal Ice Zone; IPIZ = Interior Pack Ice Zone; ICSZ = Ice Covered Shelf Zone; and CPZ = Coastal Polynya Zone.

digital video recorders on the survey helicopters; shipboard observations of ice thickness, concentration, floe size, and spatial percentage of ridging; and analyses of thickness and other ice properties by direct sampling of ice cores.

The sea ice in the Ross Sea is remarkably complex. Although annual ice dominated the ice habitat in late summer, large ice floes were also scattered about, evidently having broken away from the shore fast ice along the coast. On occasion, icebergs were embedded in those floes. Moreover, multi-year floes, up to several kilometres long, were scattered throughout the area. These floes seem to have originated in the Amundsen Sea, being consolidated into shore fast ice during subsequent winters.

The sea ice retreated in the western and northern parts of the study area throughout the summer (Fig. 2). The ice that was left in the south was dominated mostly by very large, multi-year floes (with at least two surface layers of annual snow), usually longer than 20 km, heavily ridged, and thicker than 3 m. These 'floating sea-ice islands' are rarely found in other pack-ice habitats in the Southern Ocean. We think that these floes originate as shore-fast ice, because of their similarities in surface topography and thickness, and that they then become concentrated along the offshore fast ice front, perhaps remaining there for several years before they eventually break apart and drift north into pack-ice regions. Drifting westward in the interior pack ice, with the prevailing near-continent surface current, those large floes are protected from the physical action of waves and swell by the concentrated pack ice to the north, unlike in other areas where they are quickly eroded and broken (Wadhams and others 1987). Consequently, the large floes in the eastern Ross Sea remain large (that is, >10 km diameter) for some time, and appear to be important platforms for some seals and penguins, until they eventually drift towards the northern reaches of the pack ice. The floes in the two southern zones (CPZ and ICSZ) were indistinguishable, based on thickness of ice and snow cover, and were dominated by thick and substantially ridged multi-year ice (Fig. 3). The sea ice in the NMIZ, IPIZ, and RPIZ was, however, mostly less than a year old, thinner, less ridged, and with less snow cover than the ice in the southern zones. Of those three areas, the ice in the RPIZ was thinnest, owing to its more recent origin in the Ross Sea polynya region in late winter 1999.

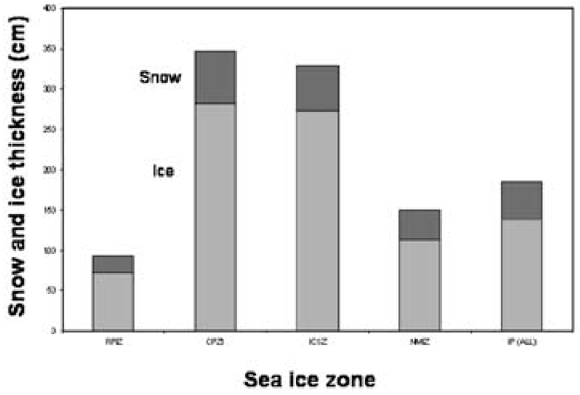

Fig. 3. Snow and sea-ice thicknesses averaged from shipboard ice observations for the zones: Ross Polynya Marginal Ice Zone (RPIZ), Interior Pack Ice Zone (IPIZ), Coastal Polynya Ice Zone (CPIZ), Ice Covered Shelf Zone (ICSZ), and Northern Marginal Ice Zone (NMIZ). The ice thicknesses for the CPIZ and ICSZ are both thick, ridged ice, some multi-year, and are virtually indistinguishable. The other regions are first-year ice dominated with thickness differences probably reflecting degree of ridged ice, less in the RPIZ and somewhat greater in the IPIZ and NMIZ.

The ocean

We documented the thermohaline and dissolved oxygen properties of the upper 1000 m of the water column throughout the study area (Jacobs and others 2002a) and observed a relatively fresh mixed layer (33.5–34.0 in salinity) above shallow summer and deeper (100–400 m) winter pycnoclines (Fig. 4). A temperature-maximum and oxygen-minimum occurred at 200–500 m, and a salinity maximum slightly deeper, typical of Circumpolar Deep Water. The thickness of the surface water layer increased rapidly over the continental rise and slope, and low-salinity water occurred over most of the continental shelf (Fig. 4). That structure is similar to that of the eastern Weddell Sea, which also has an inclined subsurface front between the deep and shelf waters. The thicker layer of low-salinity water near and above the continental shelf results mainly from the melting of sea and glacial ice, and from a net surplus of precipitation over evaporation (Jacobs and others 2002b; Hohmann and others 2002). The measurements of salinity during the cruise helped to substantiate a recent freshening trend at the upper levels of the Ross Gyre, while observations of the underlying temperature maximum indicated continued warming of the deep water in this region (Jacobs and others 2002b).

Air temperatures generally ranged from 0 to -5°C, and wind speeds averaged more than 8 m s^{-1} with a mean northward directional component that would cause sea ice to move slowly away from the coastline. Most of the upper water column appeared to drift slowly westward, with the highest bottom-referenced geostrophic velocities <10 cm s^{-1} over the continental slope, and more eastward velocities on transects near the Amundsen sector.

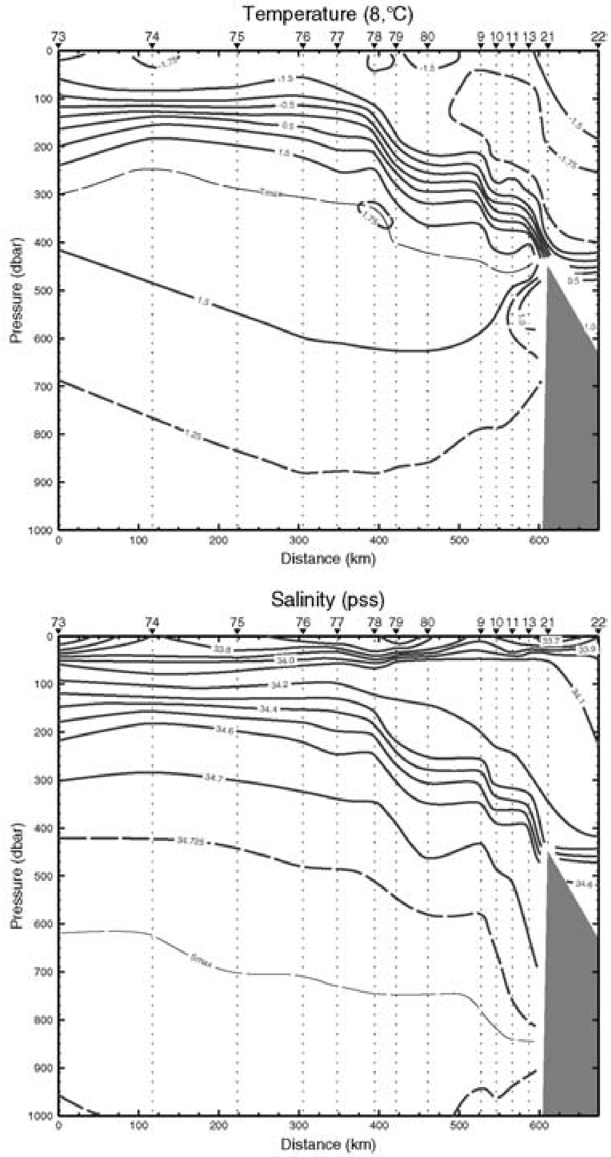

Fig. 4. Temperature and salinity along the transect near 158°W in Figure 1 (north at left). The density field will closely follow salinity, which shows a summer halocline around 40–50 dbar (meters) and a deeper winter halocline/thermocline (pycnocline) descending southward toward the continental shelf break. Contoured from 20-m average data in Jacobs and others (2002b).

Biological productivity is often enhanced near ice edges and above the Antarctic slope front (Ainley and Jacobs 1981; Smith and Nelson 1985; Ainley and others 1998; Buckley and others 1979; Ichii 1990). That front is most developed at depths >200 m and is stronger near the wider continental shelf in the western Ross Sea. Increased productivity in open water areas over the continental slope and shelf is facilitated by eddy and tidal current mixing beneath the mobile pack and fast ice, and by the addition of micronutrients by upwelling and meltwater. Higher turbulence and biomass near the sea floor on the shelf and upper slope may provide attractive resources for seal and penguin predators capable of diving to and foraging in demersal habitats.

The biological environment

Seals

Prior to the APIS cruise, little was known about the distribution and abundance of seals in the interior pack ice of the eastern Ross Sea. Although there had been research cruises in the western Ross Sea, they had not been dedicated to studying seals. Most of those cruises occurred in areas along the shore-lead, the outer fringe of the pack ice, or in late summer and made only anecdotal observations of seals. Historically, the general impression has been that the biomass and productivity of the eastern Ross Sea pack ice is lower than that of other areas of the Antarctic, owing in part to observations of fewer penguin colonies east of Ross Island and lower harvest rates of baleen whales relative to more productive areas elsewhere (such as the Scotia Arc).

During the cruise, we studied seals and penguins by capturing and handling them (for tissue sampling, measurements, and tagging) as well as by counting them from the ship and helicopters. We also qualified and quantified (for example, concentration and size) the types of sea ice that seals and penguins were hauled out on. These observations were used to derive a general picture of factors influencing distribution and abundance in relation to ice habitat, other fauna, and oceanographic observations.

In general, observations from the icebreaker of patterns of abundance and distribution of seals were consistent with the original hypotheses. Densities of seals were greatest along the oceanic fronts of the shelf area and the pack-ice edges. However, the observations differed from some patterns reported earlier for other areas. For example, the average group size of crabeater seals in the Ross Sea was 1.5 seals, compared to 2.2 observed in the Weddell Sea in 1968 (Siniff and others 1970), although it is not yet clear whether these differences are significant. Many weaned crabeater seal pups were seen in both the pack ice and along the continental margin. Although few leopard seals were seen during the cruise, most adult crabeater seals encountered had distinctive scars from previous attacks by leopard seals (Siniff and Bengtson 1977), indicating a relatively high frequency of inter-specific encounters. Some fresh wounds, inflicted by leopard seals, were observed on weaned pup and yearling crabeater seals, although they were less frequent compared with older seals. Because of the low observed abundance of leopard seals, this suggests that some crabeater seals may migrate into the area or perhaps be passively transported there when they haul out on large floes that originate elsewhere.

Seal health, condition, and immunogenetics

The timing of the US APIS cruise coincided with the post-breeding and molt periods for seals. This correlation was reflected in the most common lesions observed (mild dermatopathies, conspecific bite wounds on adults, predator wounds on weaned pups) and in subclinical inflammatory hemograms and serum chemistries (Yochem and others 2001). Bacterial screens for *Salmonella* sp., gastrointestinal tract flora examinations, and skin and wound cultures were performed aboard ship, whereas analyses of more than 150 aerobic bacterial isolates, including standard biochemical testing and fatty acid analysis, and partial DNA sequencing of unusual organisms, were performed later in laboratories in the US. A general scan of fecal enteric bacteria revealed microbes commonly found in fish-eating mammals: *Aeromonas* sp., *Vibrio* sp., *Pasteurella* sp., and *Edwardsiella* sp. (Yochem and others 2001). Serosurveys for evidence of exposure to other infectious diseases are continuing. Two of 75 seals tested to date were suspect-positive for *Brucella* sp., and all seals were negative for morbillivirus (CDV, DMV, PDV, PMV) and *Leptospira* sp. (Yochem and others 2001). Negative test results for CDV from studies during the cruise contrast with the positive tests for crabeater seals found along the Antarctic Peninsula (Bengtson and others 1991).

Decker and others (2001, 2002) examined the genetic variability in each of the four pack-ice seals (n = approximately 400 seals) at the DQ-alpha, DQ-beta, and DO-alpha loci in the major histocompatibility complex (MHC) class II system. Genetic loci in this system are important relative to individual and population responses to infectious disease in mammals as they encode proteins that play key roles in recognizing foreign antigens and subsequently triggering an appropriate and effective immune response (for example, Hedrick and Kim 2000; Kasahara 2000). Preliminary results indicated that leopard seals were monomorphic and homozygous at the DQ-alpha locus, but that crabeater, Weddell, and Ross seals had levels of heterozygosity that equal or exceed that detected, as yet, in other pinnipeds (Decker and others 2001). Moreover, Decker and others (2002) reported that variation at the DO-alpha appears to be maintained by stabilizing selection. Continuing analyses focus on the mechanisms maintaining this genetic diversity (for example, balancing selection, diversifying selection) and the relationships among immunogenetic diversity, detected infectious disease, and population structure and persistence. As yet, no clear patterns have been seen in the prevalence of infectious and non-infectious diseases, nor in the patterns of genetic variability at the important genetic loci of the immune system versus the various physical and biological variables in the eastern Ross Sea.

Leopard seals

Few leopard seals were seen during the cruise, although at the Bay of Whales in the Ross Ice Shelf seven leopard seals were counted along the coast and fast ice in the bay itself, the greatest number seen anywhere in the surveyed area. Periodically throughout the cruise, a hydrophone was used to listen for seal vocalizations. Although a few leopard seals were seen near the coast, their characteristic underwater calls were never heard, suggesting that the breeding season was over (Stirling and Siniff 1979). This observation contrasts with the suggestion that leopard seals may breed as late as January (Siniff and Stone 1985), based on anatomical examinations of seals collected in the Antarctic Peninsula area. Overall, however, both the few observations of leopard seals and the absence of their underwater vocalizations suggest that they were not common in the study area.

Weddell seals

Weddell seals in the eastern Ross Sea, as elsewhere, were common in the coastal fast ice. However, substantial numbers were also found well out into the pack ice (0.1–0.2 seals km^{-2}; and see Stewart and others 2003), even though their relative abundance declined with increasing distance from the coast. Most of those seen offshore were young and non-reproductive, and were seen mostly on large ice floes. Some of these large floes were located over deep water, suggesting the seals were feeding in the water column or possibly on the epontic (sub-ice) community. Since the data from trawls suggested that few fish were located in the first 500 m, it was probably necessary for these seals to dive below this depth to find fish. Young Weddell seals are generally not seen at coastal breeding colony sites until they are sexually mature. Stirling (1969) and Stewart and others (2000, 2001) found that Weddell seal pups from McMurdo Sound migrate north into the pack ice and open water of the polynya in the western Ross Sea. Thus, it seems likely that the pack-ice areas in which substantial numbers of Weddell seals were found represent habitat used by immature animals until they are old enough to return to the breeding colonies (Stewart and others 2001, 2003). Further genetic analysis and use of satellite transmitters to track immature Weddell seals may allow identification of the breeding colonies from which these younger seals originate. Stewart and others (2003) have recently argued, using data from the US APIS cruise and independent studies of the movements of satellite-tagged seals, that the pack ice of the Ross Sea is an important foraging niche for Weddell seals generally.

Several of the fast-ice areas along the coast appeared typical of good breeding habitats for Weddell seals. The shelf was narrow, but the bottom was rich in fish species and various invertebrates, and within the diving abilities and foraging ranges of Weddell seals. However, only in the more stable coastal fast ice, well inside the outer fringe, were old adults characteristic of breeding colonies found.

The largest numbers of adults in post-reproductive condition occurred along cracks in the sea ice at the bottom of large canyon-like crevasses that form in the Ross Ice Shelf as it moves north past Roosevelt Island and fractures before reaching the Bay of Whales. It is likely that some seals live there year-round as the continued movement of the shelf would help to keep the cracks open, even in winter.

Crabeater seals

In general, crabeater seals have been found to be substantially more abundant in the pack ice than any other seal. Indeed, of the 21,414 seals observed, 16,231 were identified as crabeater seals. Their densities varied among habitats, as did those of other seals. The greatest densities were at or near the continental shelf break, and the lowest densities in the pelagic areas farther north (RPIZ, shelf and shelf break = 0.74 seals km^{-2}; ICSZ = 0.62 seals km^{-2}; CPZ = 0.50 seals km^{-2}; IPIZ = 0.39 seals km^{-2}; NIMIZ = 0.31 seals km^{-2}. The crabeater seals seem to be attracted to the shelf slope and shelf break areas because of greater biological productivity and concentrations of krill there. As krill is the primary prey of crabeater seals, its geographic availability is probably the key factor affecting seal distribution during the non-breeding season. Oceanic frontal structures near the shelf slope may create conditions favorable for krill foraging success and consequently good foraging conditions for crabeater seals in late summer. The densities of crabeater seals were 19–48% higher in the two marginal ice zones (RPIZ and MNIZ) than in adjacent waters near the continental slope (CPZ and ICSZ) or in deeper offshore waters (IPIZ). The relatively higher densities in the RPIZ and MNIZ may be more related to concentrating effects of shrinking haulout habitat as the actively melting and receding ice rather than to active selection of those areas as foraging habitats by crabeater seals.

Ross seals

Ross seals rarely have been encountered by research vessels in the Southern Ocean. Consequently most knowledge of their biology and behavior derives from a few opportunistic and anecdotal observations. Prior to the cruise, most observations of Ross seals were from heavy pack-ice areas near the South African Antarctic continental base, SANAE (Condy 1977). During the cruise, 79 Ross seals were sighted from the ship and others were located during helicopter surveys. Forty-two were handled for measurements and specimen collection. Many of them were hauled out toward the central areas of large first-year floes in the IPIZ where the ice cover was 8–9/10ths. Most seals were in various stages of molt and appeared to be sedentary and fasting, as evidenced by few tracks in the snow around them and little fecal matter near them. Blood samples taken also showed all but one of 40 Ross seals had not fed in the last few hours. These observations alone are not unusual for seals or definitive for fasting behavior, but are at least consistent with fasting. Underwater recordings in the heavy pack in December and early January, similar to that reported by Watkins and Ray (1985), indicated substantial vocal activity and suggests that some seals were still mating. This is later than the timing of mating for the other pack-ice seals.

We think that prior inferences about the rarity of this species may be mostly due to the few surveys made into the interior pack ice at appropriate times of the year, when they are hauled out to give birth or molt. Moreover, Ross seals appear to be pelagic at most other times of the year, similar to southern elephant seals. The timing and route of the cruise evidently correlated with the peak of molting,

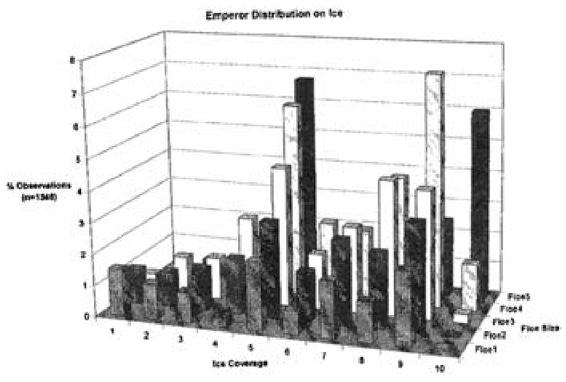

Fig. 5. Observations of emperor penguins as seen from shipboard observations, as a function of ice coverage in tenths and floe sizes. (Floe 1 = 20–100 m diameter; floe 2 = 100–500 m diameter; floe 3 = 500 m–1 km diameter; floe 4 = 1–2 km diameter; floe 5 > 2 km diameter). Floes >2 km are generally the large multi-year floes referred to in the text, where numbers of emperor penguins were found.

for some age classes at least, before seals stopped using the pack ice for hauling out and moved north into open water.

Emperor penguins

Kooyman and others (2000) recently found that some emperor penguins breeding at colonies along the coast of Victoria Land later travel to and molt in interior pack-ice habitats in the eastern Ross Sea in summer. The movements of penguins within those areas suggested that the birds were drifting on pack-ice floes for several weeks in late December and January, coincident with the molting season. Observations in the Weddell Sea pack ice during the same season also indicated many molting birds on large, presumably more stable, pack-ice floes. The authors confirmed that this area of the eastern Ross Sea is a key habitat for molting emperor penguins. We counted more than 11,000 emperor penguins there during ship and aerial surveys. They evidently fast while molting, as indicated by measurements of body mass and diet of some birds. The greatest number of emperor penguins were recorded on larger floes (Fig. 5), particularly those with ice ridging. The penguins evidently use those ridges for shelter from the wind. The large size of the floes, and extensive ridging, probably make them more likely to persist until molting is complete. Many birds were also seen on fast ice, particularly on the heavily ridged outer fringes, that might also be the source of the 'floating island' floes.

Fish

Fish were sampled using three types of nets and a 120/38 kHz echo-sounder that was operated in tandem with most of the net tows. Forty-seven tows were completed, 22 with a 4 m^2 MOCNESS, 14 with a 10 m^2 Tucker trawl, and 11 with a 15 m fish trawl. Six of the 11 tows with the fish trawl were on the bottom in the shelf region that defined the southern end of the study area (the CPZ and ICSZ). Trawling effort was distributed evenly along the APIS transect lines.

We collected 2681 fishes, representing 46 species and 10 families. Most (2574 individuals, 41 species, six families) were collected on the bottom during six tows that were made on the shelf. The others were collected in the midwater, on and off the shelf.

Hydroacoustic analyses of 38 kHz and 120 kHz frequencies for fishes and other potential seal and penguin prey indicated that acoustic targets occurred throughout the upper 500 m of the water column over the study area, with the coastal shelf region having 5- to 15-fold higher densities than the overall average for the study area. This coastal area was characterized by dense aggregations of *E. crystallorophias* plus individual targets, which net tows suggest may have been juvenile *P. antarcticum*.

The midwater fish fauna of the oceanic region of the study area was similar to that found at lower latitudes. Myctophids were dominant, although the bathylagid squid *Bathylagus antarcticus* and the gonostomatid squid *Cyclothone* were also present at low densities. At the slope, the oceanic fishes largely disappeared to be replaced by the nototheniid *Pleuragramma antarcticum*. On the shelf, the oceanic species were absent: the dominant fish in the water column was *antarcticum*. Thus, a distinct on-shore gradient in faunal composition with a break at the slope was found, as also reported by DeWitt (1970).

The series of tows on the bottom revealed that diversity and biomass were enormous relative to the water column. For those species that have access to it (capable of 500 m dives), the ocean floor appears to be a prime foraging habitat.

Biomass of midwater fishes in the APIS study area was quite low relative to the other Southern Ocean sea-ice ecosystems (Hopkins and Torres 1989; Hopkins and others 1993; White and Piatkowski 1993; Geiger and others 2000; Plotz and others 2001). For example, data from a variety of seasons in the Weddell Sea region (Lancraft and others 1989, 1991) indicated that the fish biomass in the upper 1000 m of the Weddell Sea was four to six times that in the current study area in the Ross Sea. Midwater fishes were absent from the upper 200 m in the Ross Sea during this survey, but were present at those depths in the Scotia and Weddell seas during all seasons. The absence of fishes from the upper 200 m in the Ross Sea may be due to the lower temperature (–1.8°C) and 24 h of daylight in the Ross Sea in summer.

Euphausiids

Three methods were used to study the three species of euphausiids (*Euphausia superba*, *Euphausia crystallorophias*, and *Thysanoëssa macrura)* living in the summer pack ice: net tows, simultaneous hydroacoustic transects, and scuba diving under the ice. Both *Euphausia* species are potential prey of seals (Laws 1977). In general, *E. superba* was found throughout the eastern

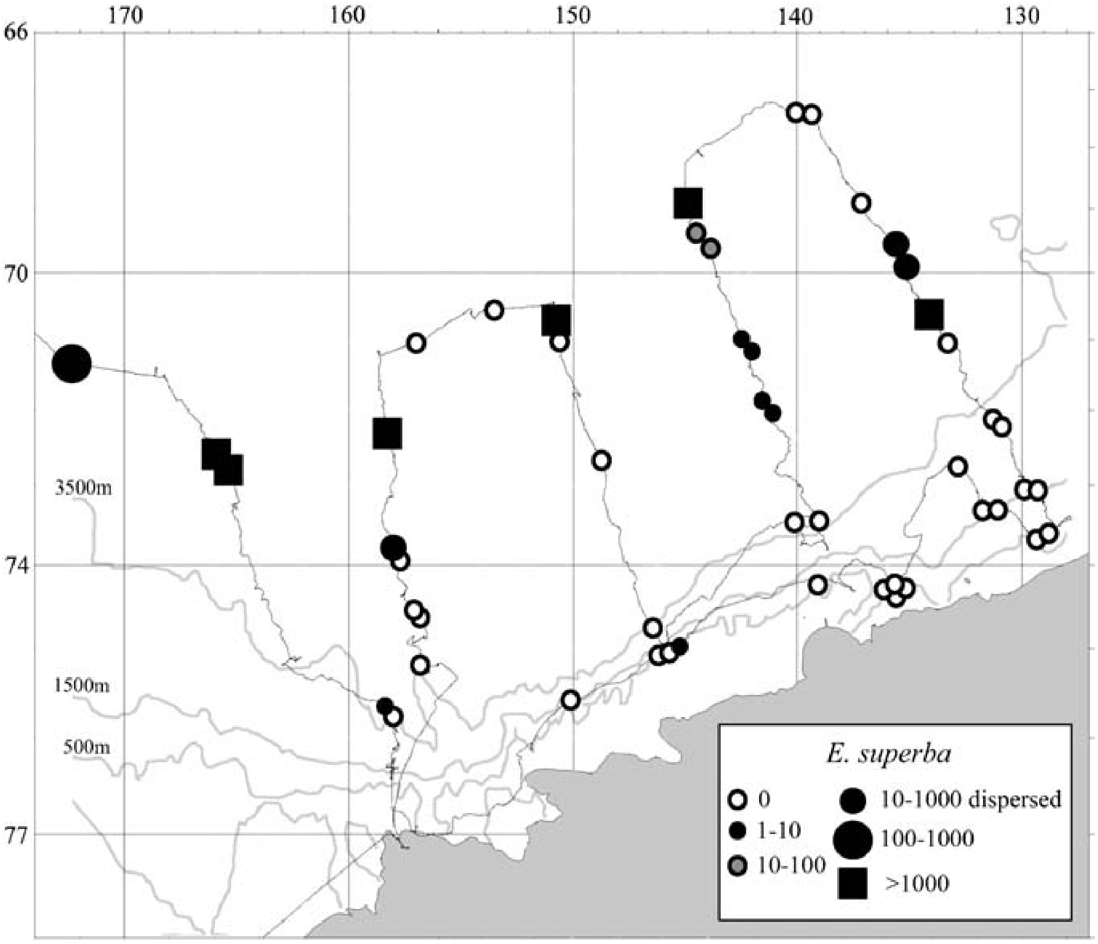

Fig. 6. *E. superba* densities from dive observations. Numbers are the number of individuals seen in a survey of a ~350 m^2 area under the ice.

Ross Sea, but the distributions of the other two species were more limited and mutually exclusive, correlating with hydrography and bottom topography. *E. superba* was coupled to the under-surface of the sea ice (Fig. 6), and in the water column (nets and hydroacoustically detected aggregations). In some cases *E. superba* occurred in high densities feeding on the under-ice microbial community. Highest numbers of *E. superba*, whether found in the water column or coupled to the under-ice habitat, were found in the marginal ice zones at both the northern and western edges of the study area, and at a few stations within the coastal shelf zones. *E. superba* were detected by at least one of the sampling methods at virtually all stations, although the estimates of abundance varied considerably among the sampling methods. We think that combinations of these sampling methods are needed to document the distribution of this species completely. *E. crystallorophias*, as documented by nets, was restricted to the coastal shelf zones and a few stations in deeper water (Fig. 7). The deep-water stations with *E. crystallorophias* may be associated with water-mass effects where frontal boundary waters have extended beyond the shelf–slope boundary. *E. cystallorophias* was collected by nets at all stations in the coastal shelf zones, but only seen by scuba divers at about half of the dive stations in the coastal shelf zone. *Thysanoëssa macrura* was restricted to the deeper pelagic waters, and was most abundant in the IPIZ and NMIZ. All three species were found together at only three of the 44 stations. Acoustically detected aggregations in the top 120 m, identified as one of the three euphausiids species by aggregation characteristics, were concentrated along the coast and in the NMIZ, but aggregations were also seen in the IPIZ. The demography, reproductive status, and condition of the euphausiids also showed distinct differences, reflecting the complex interactions of species-specific life cycles with food availability, predation pressure, and sea ice.

Primary production

Phytoplankton biomass was extremely patchy in the eastern Ross Sea. Occasional plankton blooms were usually small (10–15 km across) and separated by large areas of low biomass. It is not yet clear whether such patterns in primary production in the water column below pack ice are typical of most regions of the Antarctic pack ice. Superimposed on this patchy pattern was a trend of increasing biomass through late summer.

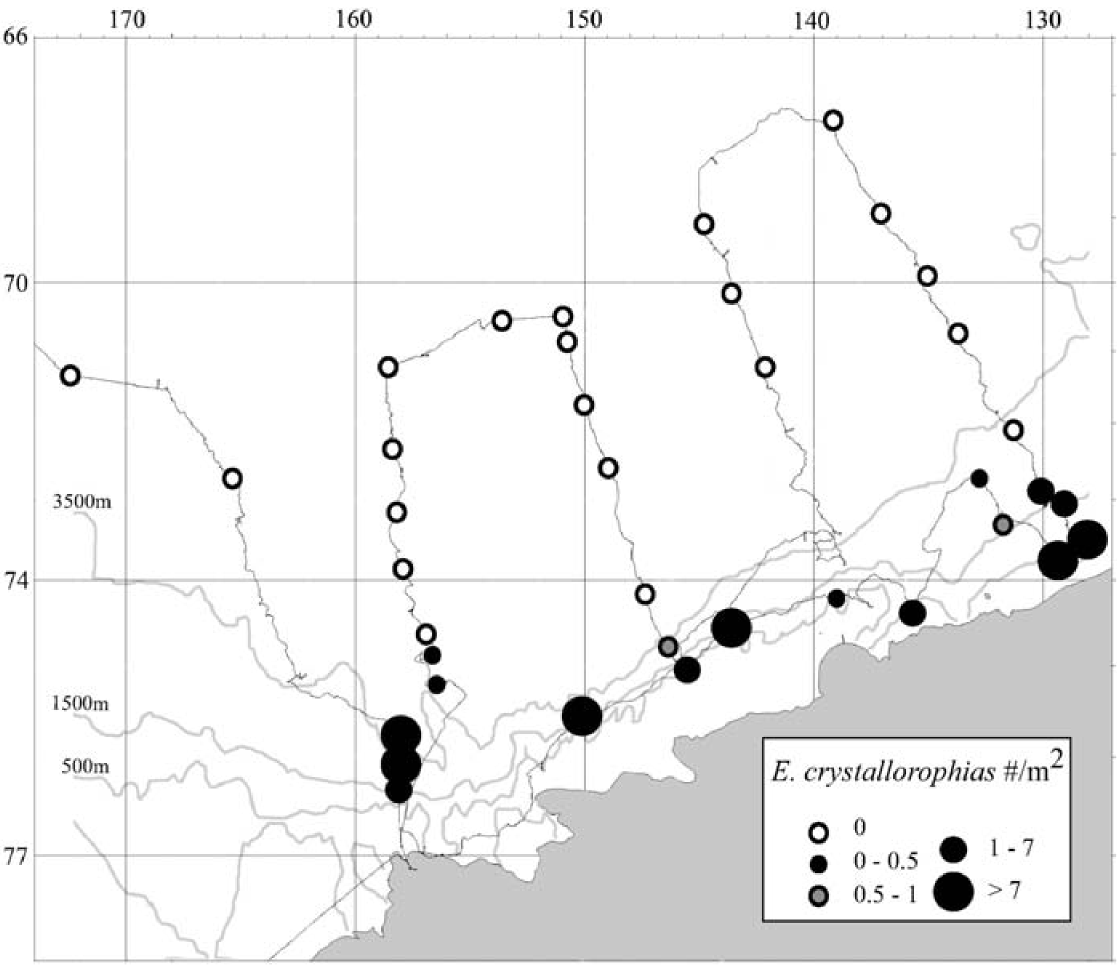

Fig. 7. *E. crystallorophias* densities (number of individuals per 1000 m^3) from net tows.

Conclusions

The eastern Ross Sea appears to be a key habitat for apex seal and penguin predators, evidently owing to the year-round persistence, diversity, and complexity of sea-ice habitats and marginal ice zones in this large marine ecosystem. Crabeater seals were encountered throughout the pack ice of the eastern Ross Sea, where they were the most numerous of the pack-ice seals, although they were less common than in other areas of pack ice. More Ross seals and fewer leopard seals were observed than expected. Weddell seals occurred mostly in association with 'floating islands' of heavily deformed sea ice, which appeared to have broken away periodically from the shore-fast ice. Emperor penguins use this area for molting, especially the 'floating islands.' The distributions of peak areas of phytoplankton biomass and krill were patchy. There were few fish in the upper 500 m of the water column, but fish and invertebrates were relatively abundant at those depths along the continental shelf, especially near the sea floor.

The pack-ice ecosystem of the Ross Sea appears to be a key area in summer as substrate to support molting by crabeater, Weddell, and Ross seals and emperor penguins, and also as a foraging habitat for seals and penguins once they finish molting. These areas may also be refugia from predation by leopard seals, which we found living primarily in near-shore habitats. Analyses of oceanographic and ice data, in relation to data on primary productivity, krill, and other prey species, should provide greater detail of the structure and function of this large marine ecosystem in the Ross Sea and the factors that influence the distribution and high abundance of both seals and penguins there.

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