APIS
ANTARCTIC PACK ICE SEALS
An international research program coordinated by the SCAR Group of Specialists on Seals

REPORT OF A WORKSHOP TO PRIORITIZE RESEARCH THEMES FOR A MULTI-DISCIPLINARY SEA ICE CRUISE AS PART OF THE APIS PROGRAM

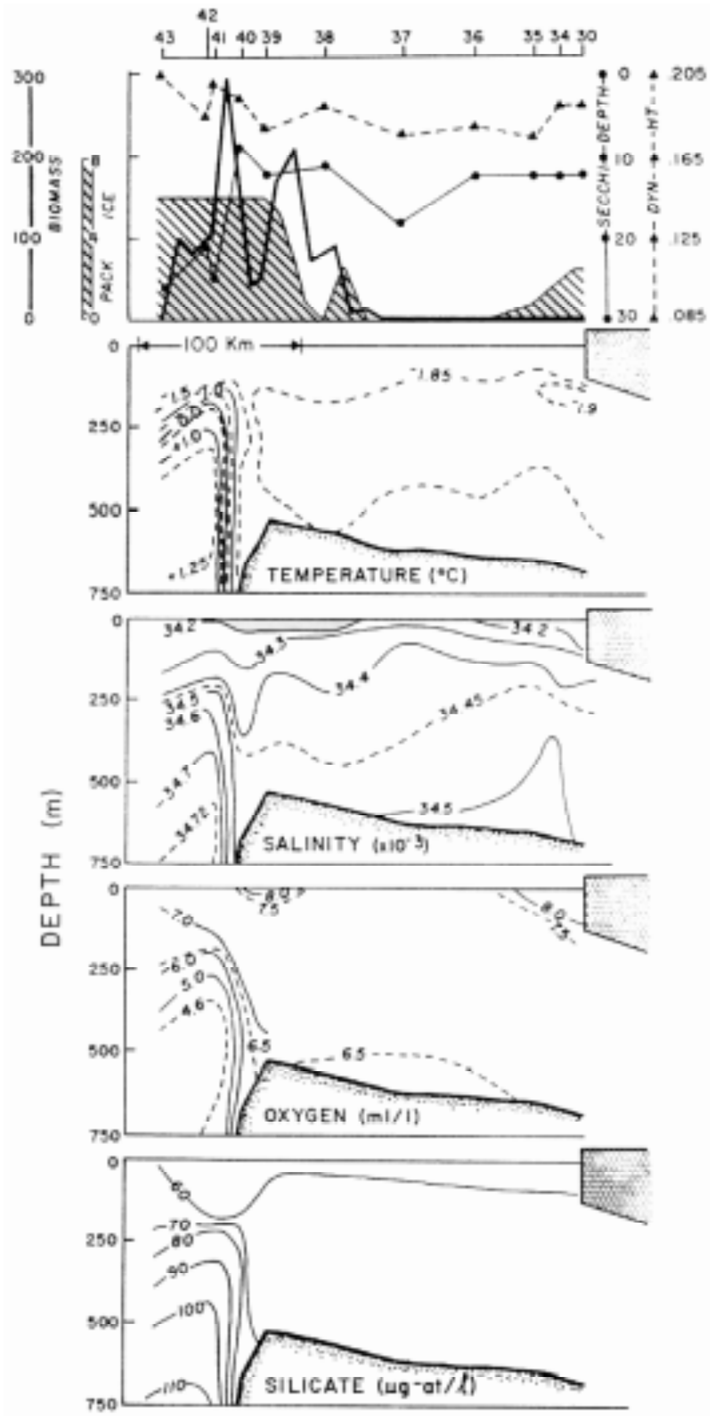
15-16 April 1997, Seattle, WA

Introduction

The pack ice region surrounding Antarctica contains at least 50% of the world's population of seals, comprising about 80% of the world's total pinniped biomass (Laws, 1984). Of the six species of Antarctic pinnipeds, three inhabit the pack ice region year-round: crabeater seals (*Lobodon carcinophagus*), leopard seals (*Hydrurga leptonyx*), and Ross seals (*Ommatophoca rossii*). Weddell seals (*Leptonychotes weddellii*) normally breed on shore-fast ice habitats, but also spend major portions of the year in the pack ice zone. As a group, these seals are among the dominant top predators in Southern Ocean ecosystems and the fluctuations in their abundance, growth patterns, life histories, and behavior (e.g., Bengtson and Laws 1985, Testa *et al.* 1991, Boveng 1993) provide a potential source of information about environmental variability integrated over a wide range of spatial and temporal scales. High abundances of other upper trophic level species such as penguins and flighted seabirds are also present in the Antarctic sea ice zone. Taken together, this considerable biomass of air-breathing predators in the Southern Ocean in relation to the available primary production may be unique in global terms, and suggests unusual ecosystem processes. Variations in top predator distribution, abundance, and features of their behavior and physiology can provide valuable insights into changes in oceanographic features such as the locations of frontal zones and areas of high secondary production.

The Antarctic Pack Ice Seals (APIS) Program was formulated by the SCAR Group of Specialists on Seals to consider the functional significance of ice-breeding seals in the Southern Ocean and to investigate seals' interactions with other top level predators and environmental factors. By encouraging scientists from various national programs to share logistic resources, to collaborate on multi-disciplinary projects, and to identify and utilize centers of specialized analytical expertise, the APIS Program seeks to build a cooperative, multi-national science effort that is not only efficient and cost-effective, but when taken as a whole, will produce scientific opportunities and results that are far greater than the sum of its parts. The APIS Program intends to set ship track lines focused foremost on questions concerning upper level predators and their interactions with biotic and abiotic ecological features. Indeed, to gain a fuller ecological perspective, APIS researchers are seeking full collaboration with scientists from other disciplines. Important sources of complementary data include physical and biological oceanographers, zooplankton researchers, seabird and whale biologists, and specialists in remote sensing technology (e.g., sea ice). In this regard, liaison with other Antarctic research programs such as SO-GLOBEC, EASIZ, and ASPECT will be emphasized.

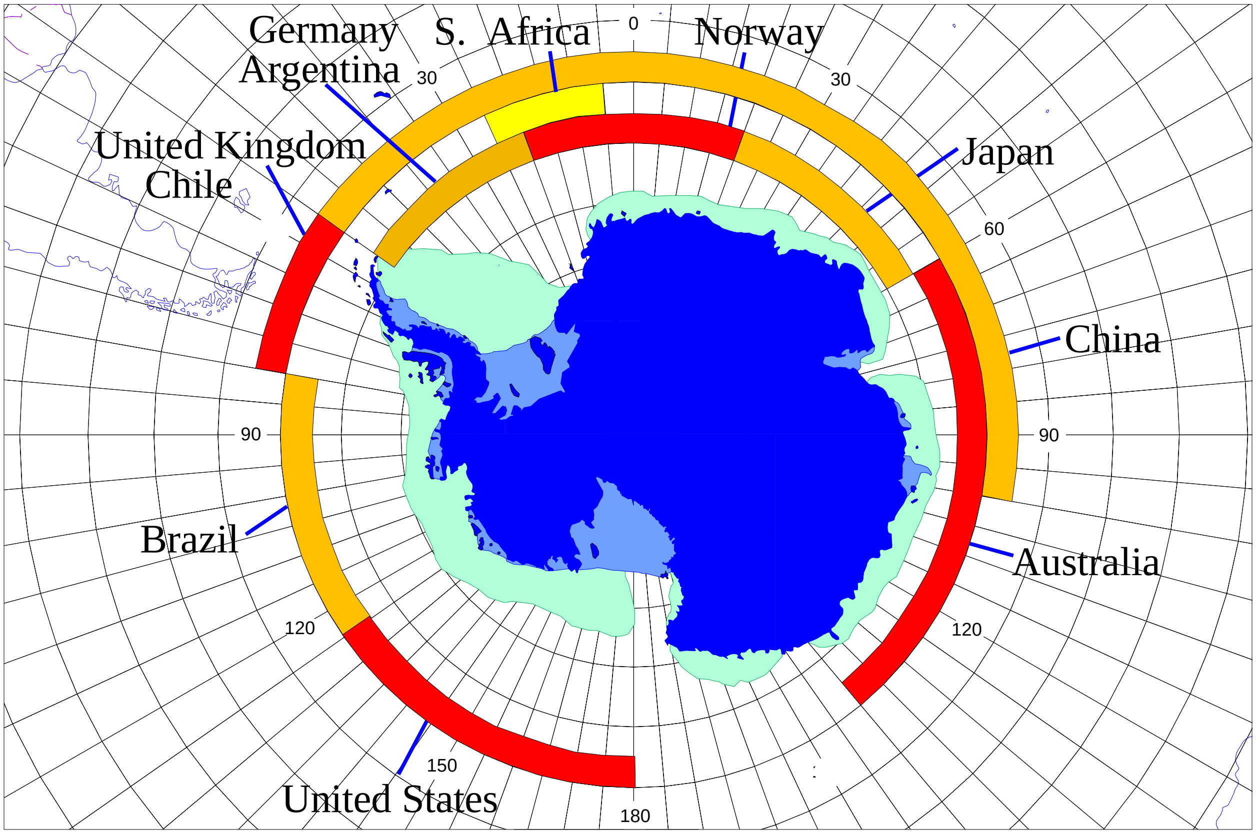
Figure 1. An example of high densities of upper trophic predators (in this case, seabirds) associated with major physical features in the Ross Sea: sea ice cover and the Antarctic Slope Front (after Ainley and Jacobs 1981). The upper panel indicates avian biomass (kg/km^2), pack ice (oktas), Secchi disc depth (m), and dynamic topography of the sea surface (relative to 500 m) along a mostly north/south transect off the Ross Ice Shelf at 170 °W. The lower panels illustrate hydrographic sections constructed from the station along the transect, with the sea floor at bottom and the Ross Ice Shelf at right. The Antarctic Slope Front, as defined by the 0 °C isotherm, was located during the survey period at between 10 and 55 km seaward of the continental shelf break.



One of the general hypotheses being explored by the international APIS Program suggests that there are measurable physical and biological features in the Southern Ocean that result in areas of high biological activity by upper trophic level predators. Meso- and macro-scale environmental features such as the margin of the continental shelf, the physical characteristics of the sea ice, ocean fronts, sea mounts, and icebergs, are thought to produce conditions that lead to high biomass sites within the pack ice region. These sites may provide protection from predators, access to water for foraging activity, and preferred sites for animals to give birth or molt. Moreover, such sites are preferentially chosen, depending upon species' sex, age, physiological condition, and general health characteristics. Preliminary data indicate a strong coupling between biological characteristics of the upper trophic level species and the physical features of the pack ice environment (e.g., Figure 1). However, there have only been rare opportunities to make simultaneous measurements assessing in detail the processes leading to high densities of upper trophic level species associated with such features. Data from all ecosystem levels are needed to allow investigators to begin to understand reasons for the distribution and abundance of upper trophic organisms within the pack ice region during the austral summer.

The international APIS Program is planning a coordinated deployment of multiple research vessels in the pack ice zone around Antarctica during the 1998/99 austral summer (Figure 2), which will offer U.S. researchers a special opportunity to undertake multi-disciplinary ecological research within a circumpolar framework. For U.S. scientists to take full advantage of this opportunity, data from the physical environment and various trophic levels, including sea ice biota, krill, fish, birds, and seals need to be collected simultaneously so that we can begin to understand the coupling that occurs within regional pack ice ecosystems, but considered in a circumpolar perspective. Therefore, to facilitate the participation of U.S. scientists in the APIS Program, a workshop was held in Seattle, Washington, on 15-16 April 1997. The workshop brought together an interdisciplinary group of U.S. scientists to consider possible studies that would provide information on the role of the upper trophic level species in the Antarctic marine ecosystem and to answer questions about factors that influence their distribution and abundance. The workshop's purpose was to prioritize research themes and outline questions that could be considered by an interdisciplinary cruise into the region of pack ice in the eastern Ross/western Amundsen Seas between mid-December and mid-January 1998/99. Such a cruise would be considered as a U.S. contribution to the larger international effort of the APIS Program, and data obtained from this cruise would be integrated with data from other national programs. During the workshop, an overall cruise plan was outlined (see section on "Provisional Cruise Plan"), and several fundamental, unifying questions were posed concerning the relationships among upper trophic predators, lower trophic species, and other physical and biological features within the pack ice zone.

Figure 2. Anticipated participation of Antarctic national programs in the international APIS Program. Plans for APIS cruises are presently in various stages of planning for different programs, from the proposal stage (e.g., U.S.) to confirmed funding and logistic support (e.g., Australia, Germany, Norway).



Unifying Questions

Workshop discussions concerning the distributions and interactions among various physical and biotic components of sea ice ecosystems led to the development of three questions that drew together or unified researchers' interests. The following questions form the foundation upon which U.S. investigators' hypotheses within their respective disciplines will be formulated.

Within the sea ice zone in the eastern Ross/western Amundsen Seas in summer:

1. How is the distribution of upper trophic predators and their prey influenced by meso- and macro-scale oceanic fronts and ecological features associated with bathymetry and sea ice?

2. At the meso-scale, do biotic features have a stronger, direct influence on the distribution of upper trophic predators than do abiotic features (e.g., ice thickness, topography, floe size)?

3. Do upper trophic predators located in zones where their densities are relatively high exhibit behavioral and physiological characteristics that are different than those of predators in low density areas?

Research Topics Addressing the Unifying Questions

Addressing these questions will require an integrated, multi-disciplinary approach. The research disciplines relevant to these questions range from those concerned with abiotic features of the environment to those focusing on lower, intermediate, and upper trophic components of the biota. Complementary research topics from within each of these disciplines are essential if U.S. investigators' plan for an integrated APIS cruise is to succeed. Associated with each research topic are one or more specific hypotheses that can be tested during the APIS cruise; when taken together, the results will help to answer the unifying questions. Because such an integrated approach requires not only conceptual integration, but also close logistical coordination of field sampling efforts, these topics were chosen not only for their inter-disciplinary significance but also for the feasibility of conducting them simultaneously from one research vessel. The research topics and hypotheses, their significance (to the APIS Program as well as the broader scientific community), and the proposed methodological approaches are briefly described below. Component topics of this multi-disciplinary approach include:

1.	Physical oceanography:	frontal systems along the continental shelf break (p. 5),
2.	Sea ice:	characteristics of austral summer pack ice (p. 6),
3.	Krill/ice biota:	distribution and abundance of euphausiids in pack ice (p. 8),
4.	Fish:	species composition and distribution (p. 9)
5.	Seabirds:	foraging behavior and habitat selection of emperor penguins (p. 10),
		distribution and abundance of aerial seabirds (p. 11),
6.	Seals:	distribution and abundance (p. 12),
		environmental influences on seasonal foraging strategies (p. 14),
		multi-dimensional movements in relation to environment (p. 15),
		acoustics (p. 16),
		genetics patterns in relation to life history characteristics (p. 17),
		immunogenetics (p. 19),
		body condition and nutritional physiology (p. 20),
		diving physiology and blood volume (p. 21), and
		disease and pathology (p. 22).

1. <u>Physical oceanography: frontal systems along the continental shelf break</u>

Hypothesis: The Antarctic Slope Front (ASF) plays a strong role during the austral summer in the distribution of pack ice seals and other upper trophic level predators and their prey.

The ASF is a region of relatively high horizontal temperature and salinity gradients, current shear, upwelling deep water and sinking surface and shelf waters (Jacobs 1991). Some investigators (e.g., Ainley and Jacobs 1981, Ainley *et al.* in review) have found that seabirds tended to be more concentrated above the ASF in areas such as the Ross Sea. In contrast, other authors (e.g., Viet and Hunt 1991) did not find as strong a correlation between seabird distribution and the ASF in other Antarctic sectors, but they lacked access to contemporaneous oceanographic data. The ASF frequently occurs adjacent to the continental shelf break and beneath a sea ice edge, which could independently influence biota abundance. Little is known about the ASF's temporal variability, or whether icebergs and other material entrained in its associated slope current are factors in its apparent biological abundance. In addition, the ASF is usually weakly manifested in the thermohaline field of the surface mixed layer, so the apparent food concentrating mechanisms for shallow-diving predator species are unclear.

Significance: Studying the ASF in the context of the APIS cruise would offer new insight into the relationships among the ASF, other environmental features, and biological communities. The ASF, already compared with seabirds, might on this project be correlated with additional species such as krill (Euphausia sp.), fish, and seals that are mobile beneath the sea surface. Such a study may permit the repetition of earlier transects in the region, providing a measure of inter-annual variability of the ASF. It should also allow the establishment of baselines against which future ecosystem-oriented surveys of species abundance and frontal strength can be assessed.

Approach: Conductivity-temperature-depth (CTD) casts would be made wherever the ship can be stopped for an hour or more, profiling to the sea floor on the shelf and slope, or to Circumpolar Deep Water core depths. This work could be done at any time of the day or night, and some of it could be scheduled during daytime seal and bird surveys. Station spacing would vary from 5-10 km near ocean and ice fronts, or where high biomass is observed, to approximately 50 km elsewhere. Water samples could be collected for other projects as needed. The CTD could carry additional sensors (e.g., for fluorometry, currents, and/or light transmission or scattering), that may be useful in analyzing the diving patterns of seals and penguins and their behavioral interactions with prey.

2. <u>Sea ice: characteristics of austral summer pack ice</u>

Hypothesis: The physical characteristics of sea ice (e.g., ice thickness, topography, floe size, coverage) are strongly associated with the distribution patterns of upper trophic level predators in the eastern Ross Sea.

Research questions that are implicit in this hypothesis include: 1) What is the large-scale distribution of sea ice in the region, as described by parameters of ice thickness, floe size, snow thickness, deformation, and ice concentration (among others)? 2) Are there relationships between the distribution and abundance of various animal species and large-scale characteristics and processes of sea ice and snow such as the proximity to open ocean (marginal ice zone), or the presence of large floes with access to open water (near shelf regions), or distances from these physiographic boundaries? 3) Can all systematic differences in the distribution of upper trophic predators be linked to availability of prey irrespective of ice conditions? 4) Are there joint correlations for animal distribution and abundance, such as availability of prey and the presence of ice of particular concentrations (varying from 0 to 100%)? 5) Are there ice associations that directly affect prey distribution and therefore indirectly affect upper trophic predator distribution? 6) Are there other ice associations that override prey considerations in concentrating their predators? 7) Are there ice characteristics that influence behavioral or physiological features of upper trophic predators?

Significance: This hypothesis and related questions relate principally to the 1st and 2nd APIS unifying questions. The simple presence or absence of pack ice may have the largest overall effects on animal distributions on large scales, although important questions still remain, even at these largest scales. It is not clear, for example, whether marginal ice zones are present because of frontal boundaries or whether they create their own frontal boundary. In the first case, the ice is a passive tracer of the ocean circulation which is the principal driver on the environment that shapes the biological response. In the second case, the frontal structure that may be created by the marginal ice zone, which therefore is more actively influencing the biology.

At meso-scales, a pack ice study of topography, thickness, floe size and other characteristics can be regarded as the principal null hypothesis statement of the 2nd APIS unifying question. That is, in order to verify that biotic factors exert the primary influence on upper trophic predators, one should also determine that abiotic factors, such as the ice characteristics do not directly influence the distribution. This can only be achieved by accurate characterization of the ice and rigorous statistical correlations and associations between the biology and the ice. For example, prey availability may be a principal influence on upper trophic predators' distribution, but prey distribution may be driven by direct associations with the ice. If, for example, krill are concentrated in deformed ice regions, possibly because of the increased surface area available for feeding on ice algae, then upper trophic predators may also be associated with deformed ice, but indirectly. It may also be possible for ice to directly affect predator distribution at certain times of the year. For example, large, stable, and/or ridged floes may provide required security for molting birds or newborn seals. Factors affecting predators' sea ice preferences may change with time, since they may be related to seasonal activity or life cycle effects of the animals. Therefore, particular ice characteristics may be correlated not only with the type of animal and its abundance but with particular age classes, sex, health and the physiological state of the animals.

Approach: The sea ice studies outlined here are exclusively interdisciplinary, given that the physical state of the ice environment at all scales and the associations with the biology at large-scale (e.g., abundance and distribution), meso-scale (e.g., species composition), and small-scale (e.g., health and physiology) all need to be correlated. Two levels of ice characterization would be necessary. The first is available from ice observations taken from the ship using protocols for ice characterization derived from a classification scheme currently in use and advocated by SCAR's Antarctic Sea Ice Processes and Climate (ASPECT) Program. These sea ice data would also be made available in standardized format to the ASPECT data base and provide a contribution to the circumpolar ice characterization being undertaken by that program. Hourly observations would be taken while the ship is underway. These observations would be augmented by aerial photography and helicopter reconnaissance during seal abundance surveys. The second level of characterization would be measurements of ice thickness and properties obtained during two to four hour sampling stations. Drilling, coring, and surface measurements (topography, snow depth, snow characteristics) could be conducted jointly during these sampling periods.

3. <u>Krill and sea ice biota: Distribution and abundance of euphausiids in pack ice</u>

Hypotheses: 1) The distribution of euphausiids is strongly influenced by meso- and macro-scale oceanic fronts and ecological features associated with bathymetry and sea ice. 2) At the meso-scale, the distribution of prey (e.g., euphausiids) have a stronger, direct influence on the distribution of upper trophic predators than do abiotic features.

In high latitudes, *Euphausia crystallorophias* (the ice krill) generally occupies the shallow shelf, whereas *E. superba* (Antarctic krill) is usually found near the shelf break or over deep water. However, because the distributions of these two species often overlap to some degree, it would be illuminating to investigate how their horizontal and vertical distribution changes in the eastern Ross Sea in relation to various biotic and abiotic parameters: ice cover (ice edge, unconsolidated or consolidated pack ice), water depth (> 3000 m, shelf break, shelf), and predation pressure (seal and seabird abundances). During the spring and summer one would predict that the need to feed is high (growth and reproduction), and that the euphausiids would be in the region of highest food except under very high predation pressure. Under the ice, one would assume generally that particulate organic matter concentrations in the water column are less than in the ice biota, even in spring and summer.

Significance: *E. superba* and *E. crystallorophias* are the dominant macrozooplanktonic organisms in the pack ice region, and are among the important prey items for seals and seabirds inhabiting the region. However, distributions and abundances of macrozooplankton are virtually unknown in the eastern sector of the Ross Sea. This project would help confirm if the hypothesis of "risk balancing" generated by work west of the Antarctic Peninsula has broader applications--to other species and other seasons. In the winter west of the Antarctic Peninsula, habitat segregation between adult and larval Antarctic krill is likely the result of "risk balancing" between the need to acquire energy and predation (Quetin *et al.* 1996). For adults, the need to feed is less than the need to avoid predation by the vertebrates that use the pack ice as a habitat. As a result, the adults remain relatively deep in the water column where food is scarce but where predation pressure is presumably reduced. The reverse is true for krill larvae, which appear to be obligate inhabitants of the ice-water interface, and which can often be found coupled to the underside of the ice grazing on the ice biota. Quetin *et al.* (1996) postulated that predation on the larvae is minimal given that larvae are smaller than the krill generally found in the diets of seals and seabirds. The balance of the need to feed and the risk of predation may be different in the spring and summer compared to winter, as well as for different species of euphausiids.

Approach: Distributions for the two euphausiids would be determined in relation to oceanic fronts, sea ice structure, bathymetry, biomass of primary producers, and the abundance and distribution of upper trophic predators. Vertical distribution of zooplankton biomass (krill) in the water column will be sampled using acoustics (120 kHz) and SCUBA surveys of the ice/water interface. The biomass and horizontal distribution of krill will be sampled using acoustics, horizontal/vertical net (500 um mesh) tows in ice (note that although oblique tows in ice are being planned, vertical tows would be used if the pack was too thick in some areas to use oblique tows effectively), and SCUBA. Characteristics of euphausiid aggregations (density, size, depth) will be sampled using acoustics and SCUBA. Live euphausiids for measurements of length frequencies, etc. as indicator of prey size available, condition of prey, and reproductive status will be obtained from horizontal/vertical net (500 um mesh) tows in ice. Additional data needed for optimizing a multi-disciplinary approach include identification of fronts using an along-track system (e.g., it may be possible to rig a hose--possibly towed off the stern attached to a weighted line held close to the stern of the ship--with a deck pump that could do along-track sampling); water column structure (Circumpolar Deep Water etc.) using a CTD and fluorometer with chlorophyll as an index of food availability for grazers; ice biota using sucker samples by SCUBA; ice structure and concentration; and predator abundance.

4. Fish: species composition and distribution

Hypotheses: 1) When moving landward from deep ocean stations the fish community composition will show a sharp increase in diversity and biomass at the Antarctic slope front (cf. Jacobs 1991). Landward of the front, there will be increased representation by the Notothenioid fishes, primarily benthic as adults, as the bottom depth decreases. Moving seaward from the front, representatives of the classical midwater families will increasingly predominate until the Notothenioids are absent. At the front itself, the two fish fauna meet and provide a particularly fertile hunting ground for upper trophic predators. 2) Fishes appearing in the diets of upper trophic predators will change with proximity to the Antarctic slope front, but only partially reflecting changes in prey abundance and distribution (predators select prey based on ease of capture and caloric value/item).

Significance: The relative importance of fish to the energetic needs of Antarctic upper trophic predators is currently unclear. Research on the diets of birds and mammals have mainly focused on populations during the breeding season (Ainley *et al.* 1991), where proximity to coastal breeding sites dictates foraging range. In many cases, since krill is the most abundant prey near land-based rookeries where research has been carried out, it is a major prey fed to offspring of birds such as pygoscelid penguins (Croxall and Lishman 1987). Food webs are more complex in the pelagic regions of the Antarctic where the strictures of a limited foraging range are removed. In those cases, fishes, as an energy rich morsel, can and do play a larger role in the diets of upper trophic predators (Ainley *et al.* 1991).

Approach: The proposed APIS broad-scale survey provides an ideal forum for testing hypotheses on the importance of fishes to the diets of apex predators and on the distributions of the fishes themselves. The cruise track crosses the shelf-slope break several times, affording a comparison of fish species presence-absence and fish community structure with respect to bathymetry and physical characteristics of the water column. A combination of vertical and oblique net tows will be the principal method of sampling fish during the cruise. Towing nets in the pack ice has proven successful in the past if steps are taken to tow them immediately behind the vessel (i.e., with the A-frame winch boom positioned forward over the deck) so that the tow cables are protected from ice.

5. Seabirds: foraging behavior and habitat selection of emperor penguins breeding in the Ross Sea

Hypotheses: 1) Most of the foraging emperor penguins (*Aptenodytes forsteri*) sighted during December will be distributed along the Ross Sea shelf break regardless of the distribution of pack ice. 2) In January most emperor penguins sighted will be in areas of heavy pack ice, which meet their requirement for stable ice floes during the molt. 3) Densely distributed birds in the pack ice will be molting, and dispersed birds will be feeding in preparation for the molt.

Significance: The Ross, Amundsen, and Bellingshausen Seas form one connected ocean bordered by the Victoria Land coast in the west and the Antarctic Peninsula in the east. This is possibly the last unexploited frontier on the planet. For that reason alone every aspect of it should be studied in detail. Emperor penguins are presumably a year-round top predator in this environment, and are of special interest for two reasons: 1) this is one of two upper trophic predator species of Ross Sea inhabitants that may, for most of its life cycle, remain entirely within the Ross Sea/Amundsen Sea complex, and 2) it is a highly visible species in which breeding colonies can be censused relatively easily. The population status of this top predator will be an important indicator of trends in fast-ice, pack-ice, and prey species of the Ross and Amundsen Seas (Ainley 1983, Ancel *et al.*, 1992). One conclusion from emperor penguin studies conducted in the Ross Sea since 1983 (Kooyman and Mullins 1990, Kooyman *et al.* 1991, Kooyman 1993, Kooyman 1994) is that the colony sizes seem to have a high degree of variability from one year to the next. One way to get a better idea of the status of the Ross Sea populations is to determine if there are other colonies along the coast of Marie Byrd Land, in addition to the recently surveyed colony at Cape Colbeck. Thus, an assessment of the birds in the pack may provide a clue as to the size of populations that may exist in areas east of the Ross Sea.

Regarding foraging behavior, no studies have been conducted on the pre-molt diving behavior and diet of emperor penguins in offshore pack ice. It is quite likely that the diving behavior at this time will be intense in preparation for the 30 day molting fast. In this period of high sun and abundant food it is impossible to predict the preferred depth and food of the birds. The region is an area of heavy pack ice at a time when the western Ross Sea is relatively depleted of pack ice. The objective during this part of the cycle is to work in the pack ice where the birds are and determine not only the foraging pattern of the birds but the prey type, its relative abundance and depth distribution, and the associated species of other predators.

Approach: The high visibility of emperor penguins, including when they are feeding, may function as a resource indicator for hot spots of biological activity during the cruise. From satellite tracking experiments, the most likely molting areas for the majority of Ross Sea birds are now known (Kooyman, pers. comm.). Therefore, it is proposed to cruise through the heavy pack to these locations to study their distribution and abundance, pre-molt foraging behavior, and the ice conditions and characteristics where the molt actually takes place. In a previous cruise to this region, large numbers of molting birds were noted (Ainley *et al.* 1984), and one would expect to find rich marine resources and stable sea ice. Only two studies of emperor penguins during the pre- or post-molt period have been undertaken (Piatowsky and Putz 1994, Putz 1995). Those researchers took advantage of birds foraging before the molt near the ice edge of their putative colony.

For the APIS cruise, satellite depth recorders (SDR) transmitters will be applied to 10 emperor penguins as they depart Cape Washington for pre-molt feeding to determine diving behavior and its relationship to observed prey distribution. Line transects will be carried out from the ships bow, complemented by helicopter flights to calibrate counting methods in regard to penguin distribution variability relative to the ship and its usual route through the pack. Penguin prey selection will be determined by capturing and lavaging about 10 birds. Assessment of prey distribution and abundance in the area will be determined in collaboration with APIS investigators utilizing acoustic sensors, nets, and divers' under-ice observations.

6. Seabirds: distribution and abundance of aerial seabirds

Hypotheses: 1) Densities of aerial seabirds will be highest at ice edges and fronts associated with the marginal ice zone and the continental slope (i.e., the Antarctic Slope Front). 2) Aerial seabirds will not be distributed uniformly throughout the pack ice zone. Seabird distributions and abundance will be related both to variation in prey populations and to physical environmental features which may affect the accessibility of preferred prey (e.g., ice coverage, presence of open leads). 3) Diet selection by aerial seabirds within the pack ice is flexible, and reflects a balance between energy value of prey and prey accessibility. Thus, diets will vary in relation to physical characteristics of the sea ice that affect access to the water column.

Significance: Aerial seabirds are an important component of Antarctic pack ice ecosystems, but have received relatively little attention compared to their flightless (penguin) counterparts. Because they are so much more mobile than penguins and pinnipeds, they can potentially respond much more quickly to changes in meso-scale patterns in prey availability. This project will examine in detail how sea ice characteristics, hydrographic structure, and prey availability jointly affect the foraging behavior and resulting distributions of these species. Numerous previous studies have identified ice edges (reviewed by Hunt 1991) and oceanic fronts (reviewed by Schneider 1991) as areas of enhanced seabird abundance. Ainley and Jacobs (1981) described concentrations of seabirds near ice edges and the Antarctic Slope Front within the proposed APIS study area. However, the general role of these environmental features in the trophic ecology of seabirds is uncertain because most published studies have been based on only a few transects across the features in question. Studies which have included large samples of transects have revealed that concentrations of seabirds at oceanic fronts and ice-edges are intermittent (Schneider *et al.* 1987, Veit and Hunt 1991). Since it is apparent that fronts and ice edges can be important to seabirds, a more appropriate question is: "*What specific features of fronts and ice edges attract seabirds?*" Most previous studies provided little information with which to address this question because fronts and sea ice have been treated as dichotomous variables (i.e., ice present *vs*. no ice; front *vs*. no front). The continuous environmental sampling of the APIS cruise will provide the details necessary to understand the factors influencing the formation of high densities of seabirds.

Previous studies that focused primarily on the ice edge as a factor in seabird distribution did not afford a detailed investigation of how finer-scale variability in ice cover within the pack ice zone affects seabird distributions and diets. Pack ice is a unique environment in that physical accessibility of food may be an overwhelming constraint, mitigating the importance of absolute variation in prey abundance. Previous workers have concluded that Antarctic seabirds do not select foraging habitat on the basis of prey availability (Ainley *et al.* 1992). However, this conclusion is ambiguous because the pack ice zone was treated as a homogeneous region, and it seems likely that such highly mobile predators will preferentially concentrate in areas within the ice where their preferred prey is most accessible. During the proposed cruise, factors affecting both prey abundance and accessibility will be measured contemporaneously, providing an opportunity to unravel this important potential interaction between prey abundance and accessibility.

Approach: The proposed APIS survey provides an ideal platform for testing hypotheses about environmental determinants of seabird distribution and abundance. The cruise track will cross ice edges and the Antarctic Slope Front multiple times, affording sufficient samples for testing the hypotheses. Previous work in the region by Ainley *et al.* (1984) indicates that Antarctic petrels (*Thalassoica antarctica*) and snow petrels (*Pagodroma nivea*) will likely be the predominant species of flying seabirds in the region at the time of the proposed cruise. These two species
exhibit specialized feeding behaviors for exploiting ice-associated prey (Griffiths 1983, Ainley *et al.* 1984) and will be good subjects for tests of the above hypotheses. Seabirds will be counted from the bridge while the ship is underway, and densities along the cruise track will be computed using standard methods. Diets will be examined by collecting samples of ~5 of each of the two focal species at as many “hotspots” as is feasible. Non-destructive sampling will be employed where possible. Detailed information on hydrography and physical characteristics of the pack ice zone that affect prey accessibility will be available from other APIS investigators. In addition, other investigators will be measuring a variety of characteristics of potential seabird prey populations, including: 1) horizontal and vertical distributions in the water column (hydroacoustics), 2) size, biomass, and species composition (net tows), and 3) characteristics of prey aggregations at the ice-water interface (SCUBA).

7. <u>Seals: distribution and abundance</u>

Hypotheses: 1) Crabeater, leopard, Ross, and Weddell seals are not uniformly distributed throughout the pack ice zone in the eastern Ross sea. 2) The summer densities of pack ice seals in the eastern Ross Sea are highest along meso- and macro-scale oceanic fronts associated with the continental shelf slope and the ice edge. 3) Densities of pack ice seals in the eastern Ross Sea are higher than in other sectors of the Antarctic because the summer distribution of sea ice allows the seals to remain in and forage within important oceanic frontal zones (i.e., near the continental shelf slope and at the marginal ice edge over deep, off-shelf water) rather than having to migrate to residual ice zones over the continental shelf near the coastline.

Significance: Antarctica's pack ice seals are a numerically and ecologically important group in

Southern Ocean ecosystems. As long-lived, upper trophic level predators with a circumpolar distribution, these seals are a source of information about ecosystem interactions and environmental variability integrated over a wide range of temporal and spatial scales. During the last comprehensive censuses of pack ice seals, conducted in 1983, markedly lower seal densities were observed than levels seen previously in the late 1960s and early 1970s (Erickson *et al.* 1983, Erickson and Hanson 1990). It is presently unknown whether these observations reflected a real decline in seal population abundance, altered distributions of seals, or other factors (e.g., different haulout patterns or census methods) that might have influenced the visibility of the seals during the surveys. Despite their interest scientifically, research on these seals has been hampered by limited logistic opportunities to work in the pack ice zone.

Obtaining data on pack ice seal abundance and distribution would be a major contribution to the collaborative, circumpolar survey planned as part of the international APIS Program. Completion of that APIS goal would, for the first time, produce a continent-wide abundance estimate based on a consistent, statistically sound survey design. That estimate would provide one of the most reliable estimates of the size and distribution of a significant portion of the biomass of air-breathing predators (i.e., seabirds, pinnipeds, cetaceans) in Antarctic marine ecosystems. Estimates of predators' abundance and diet preferences can also provide an independent check on the abundance of lower trophic species, which are even more difficult to estimate than predator abundances (Croxall *et al.* 1985, Foote *et al.* 1990, VanFraneker *et al.* 1997). Associations between the occurrence of seals, other species (especially their prey), and the physical features of the ice and underlying ocean will provide the basis for answering #1 and #2 of the U.S. APIS unifying questions.

Approach: The SCAR Group of Specialists on Seals has recommended that future abundance surveys of pack ice seals should employ line transect methods. Line transect sampling, a form of distance sampling (Buckland *et al.* 1993), can accommodate different types of survey platforms and changing sighting conditions. Although seal densities over modestly-sized areas can be estimated from shipboard line transect surveys, the circumpolar abundance estimate sought by the international APIS Program depends critically on surveying large areas of sea ice habitat by helicopter.

The proposed survey would use a combination of ship and helicopter surveys. The ship's trackline would assure appropriate coverage of several large strata in the Ross Sea study area (Figure 3) and the helicopters would increase the coverage along transects generally perpendicular to the ship's trackline. Based on previous estimates of seal sighting rates and densities, a combination of 1,000 km of ship trackline and 10,500 km of helicopter trackline would be expected to produce an abundance estimate with a CV (coefficient of variation) of 12% for crabeater seals.

A key element of accurate abundance estimates for Antarctic pinnipeds is the proportion of the seal population that is hauled out on the ice, where the seals are counted. Visual counts of seals hauled out on ice within a specific area throughout a day provide estimates of the timing (but not proportion) of seals' haulout patterns (Erickson *et al.* 1989). Studies of Antarctic pack ice seal have shown that this proportion varies with factors such as time of day and the age of the seals, but it can be adequately estimated with modest sample sizes using satellite-linked time-depth recorders (SLTDRs) or similar instruments attached to seals (Matsuki and Testa 1991, Bengtson and Stewart 1992, Bengtson *et al.* 1993, Nordøy *et al*. 1995, Bengtson and Stewart 1997). SLTDRs will be attached to seals of all four species during the APIS cruise. These instruments will provide data for calculating haulout correction factors throughout the cruise while the surveys are being conducted.

8. <u>Seals: environmental influences on seasonal foraging strategies of leopard and crabeater seals</u>

Hypotheses: 1) The mean distance between the shelf slope and the geographic locations of crabeater and leopard seals varies seasonally for crabeater seals, but not for leopard seals. 2) In areas such as the eastern Ross/western Amundsen Seas, where the continental shelf slope remains covered with sea ice year-round, crabeater seals select habitats near the ice edge in summer and near the continental shelf slope in winter. 3) Whereas the mean depth of crabeater seal dives is deeper in winter than in summer, the mean depth of leopard seal dives exhibits no significant seasonal pattern.

Significance: The diets of crabeater and leopard seals contrast strongly. Crabeater seals are specialist krill feeders (though they may be forced to utilize other species in areas away from krill concentrations; e.g., Green and Williams 1986); leopard seals also eat krill, but their diet commonly includes fish, squid, seabirds, and other seals, especially young crabeater seals (e.g., Siniff and Bengtson 1977, Bengtson 1982, Siniff and Stone 1985, Green and Williams 1986, Lowry *et al.* 1988). Thus, crabeater seals feed principally at one trophic level, whereas leopard seals feed at two or more. This species pair, comprising a predator-prey relationship and potentially a competitive relationship, is particularly interesting and important for understanding the upper trophic levels of the pack ice ecosystem and how top-down versus bottom-up forces regulate the food web dynamics (e.g., Fretwell 1987, Hunter and Price 1992). Comparison of diving behaviors and seasonal movements will help to explain prey switching of leopard seals, a phenomenon that may be a factor in dramatic and periodic fluctuations in the age structure of crabeater seals (Bengtson and Laws 1985, Testa *et al.* 1991, Boveng 1993, Boveng and Bengtson *in press*).

If crabeater seals' seasonal movements are influenced primarily by the availability of krill, their principal prey, the seals' movements should reflect the annual migration of adult krill from the continental shelf/slope to the receding ice edge in the spring, and back to the shelf/slope in the autumn (Siegel 1988, 1989). However, the seals' ability to remain in close proximity to these migrating concentrations of krill depends on the presence of pack ice, which adult crabeater seals apparently require as a haulout platform throughout the year. In contrast, because leopard seals' diet is so varied, they are not constrained by the seasonal distribution of a single prey item. In autumn, krill swarms return to the shelf slope from their summer foraging, and are available throughout the winter; in spring, crabeater seal pups are born in this same zone, providing an abundant, energy rich prey source just prior to the leopard seals' own reproductive activities; throughout the summer and into the early autumn, coastally-breeding seabirds such as penguins supplement a diverse diet that may also include fish and cephalopods; and by early autumn,

fledgling penguin chicks are available. This flexibility to switch among prey items may allow leopard seals to remain within a smaller home range associated with coastal areas and the continental shelf slope, and thus exhibit less seasonal movement than crabeater seals.
As specialist krill predators, crabeater seals do not switch their prey seasonally, and are therefore likely to perform deeper foraging dives during the winter than in the summer. This prediction is based on the expectation that the seasonal vertical distribution of adult krill changes from a relatively shallow distribution in summer while grazing phytoplankton to a relatively deeper distribution in ice-covered habitats during winter (e.g., Kawaguchi *et al.* 1986, Quetin and Ross 1991, Gutt and Siegel 1994, Quetin *et al.* 1996, 1994, Torres *et al.* 1994). Because leopard seals, as predators of a wide variety of invertebrate and vertebrate prey, switch prey frequently depending on relative availability (e.g., Siniff and Bengtson 1977, Bengtson 1982, Siniff and Stone 1985, Lowry *et al.* 1988), they are unlikely to exhibit major differences in the mean depth of their diving behavior between winter and summer.

The results of this work will establish broader temporal and spatial contexts within which to interpret the findings obtained during the shipboard portion of the study (austral summer in the eastern Ross Sea). The seasonal movements of crabeater and leopard seals--when considered in light of what is known about prey movements and distribution of abiotic features--will help to explain the nature of ecological associations observed during the summer APIS cruise. The anticipated results, that crabeater seal habitat selection is closely tied to bathymetry and its associated ecological features (e.g., Antarctic Slope Front) would contrast with a commonly accepted notion that crabeater seals preferentially occupy the marginal sea ice zone. For leopard seals, any information about seasonal movements will be novel and will help to develop basic understanding of this poorly-known species.

Approach: The seasonal movements and diving behavior will be measured by satellite-linked time-depth recorders. These instruments will be attached to post-molt crabeater and leopard seals during the APIS cruise, and will provide locations, hourly haulout frequency, and histograms of dive depths and time at depth for up to 12 months. The seals' locations and movements will be analyzed in relation to sea ice distribution (satellite images) and bathymetry. The distributions of dive depths and time at depth will be compared between seasons and between species to test for differences in diving behavior.

9. <u>Seals: multi-dimensional movements in relation to physical and biotic environmental features</u>

Hypothesis: Multi-dimensional (horizontal and vertical) movements of Antarctic pack ice seals are complexly influenced by interactions of prey dynamics, ocean currents, ice characteristics and distribution, wind patterns, water column physics, and varying ecological and reproductive requirements of seals. These factors are sometimes independent variables, sometimes co-dependent variables, and sometimes confounding variables.

Significance: Several models describing animal movements in three dimensional space and time have been developed recently (e.g., Brillinger *in press*, Brillinger and Stewart 1997, *in press* a, *in press* b). Applying such models to muti-disciplinary data sets collected concurrently during the

APIS cruise will identify the key factors that influence seal distribution, abundance, health, and life history parameters. In particular, the horizontal and vertical movements of pack ice seals will be analyzed in relation to meso- and macro-scale characteristics of the biotic and physical Antarctic pack ice environment. It will also provide insight into the likely patterns of change in pack-ice seal ecology that may be expected in response to gradual natural or rapid anthropogenic environmental change.

Approach: This project will collect data on the three dimensional movements of crabeater, Weddell, leopard, and Ross seals directly using satellite-linked time-depth recorders in collaboration with other APIS researchers that are collecting similar types of ecological information. Multi-dimensional movement models will be applied to the recorded trajectories of the seals among other moving and stationary entities and properties of the marine environment (e.g., prey, physical fronts, ice) with the seals' movements structured as ultimate dependent variables. One central feature of these flexible models is their accommodation of the movements of a variety of faunal taxa, their intra- and inter-specific interactions, and their interactions with the environment. They consist of diffusion process and differential equation models that incorporate covariates. The application of these models to the APIS cruise's multi-disciplinary, seal-centered data sets will allow a formal assessment of temporal and spatial aspects to environmental variation and the responses of upper trophic predators.

10. <u>Seals: acoustics</u>

Hypotheses: l) The distribution of Antarctic marine mammals, as determined acoustically, is influenced by meso- and macro-scale oceanic fronts and ecological features associated with bathymetry and sea ice. 2) Pack ice seals located in zones where their densities are relatively high produce sounds at different rates than seals from low density areas. 3) The degree of variation in pack ice seals' vocal repertoires corresponds to the degree to which seal populations are genetically discrete.

Significance: The oceans around Antarctica naturally abound with underwater sounds from biological sources such as seals and whales, and from abiotic sources such as moving and melting ice, wind and wave action, and even anthropogenic noise (Bohne *et al.* 1985). Over the last 20 years, underwater recordings of sounds from Antarctic seals have been made during the austral spring and summer (Green and Burton 1988, Rogers *et al.* 1995, 1996, Stirling and Siniff 1979, Thomas and Kuechle 1982). Killer whales, minke whales, and humpback whales have also been recorded on an opportunistic basis, but little is known about the identifying characteristics and roles of sounds in these social cetaceans (Awbrey *et al.* 1982, Fisher *et al.* 1983, Leatherwood *et al.* 1981, 1982a, 1982b, Thomas *et al.* 1981).

The rate of underwater sounds in pinnipeds can provide useful information on the species composition in an area, the relative abundance of a particular species, the diel haulout pattern (Green and Burton 1988, Thomas and DeMaster 1982, 1983), and the onset of breeding (Thomas *et al.* 1983, 1989). Weddell seals drastically decrease the rate of underwater sounds when upper trophic predators, such as killer whales and leopard seals move into an area (Thomas *et al.* 1987).

Comparison of acoustic properties of cetacean and pinniped sounds show that each species exhibits an "acoustic niche." They partition the frequency and time domain characteristics of their sounds to avoid masking and to optimize information content. Data on a captive leopard seal indicate they produce sounds in the ultrasonic range up to 100 kHz, but no recordings at this frequency range have been made in the wild (Thomas *et al.* 1982).

Antarctic pack ice seals exhibit a variety of underwater sounds that reflect their mating system (Thomas 1996). As the degree of social interactions increase, so does the types of sounds. For example, the monogamous crabeater seal has a single sound. The promiscuous leopard seal has nine sounds, and the polygynous Weddell seal has 34 sounds. Investigators working at three ocean basins around Antarctica (i.e., near McMurdo Sound, Antarctic Peninsula, and Prydz Bay) examined geographic variations in the underwater repertoire of Antarctic seals. Crabeater seals showed no variation in the single sound by location. In contrast, Weddell seals (Thomas and Stirling 1983, Thomas *et al*. 1988) and leopard seals (Thomas and Golladay 1995) had variations and unique sounds at each site. Sound repertoire data can be used in conjunction with genetic samples collected for each species to indicate discrete breeding populations around Antarctica.

Approach: Acoustic surveys will document the distribution of upper tropic predators, such as whales and seals in relation to physical and biotic features in the pack ice. An important objective of this research is to document features about underwater sounds from biotic and abiotic sources that correlate with the abundance of pack ice seals during the austral summer in the Ross Sea. Passive acoustics provide a non-invasive method for collecting data on both biotic and abiotic sounds. Acoustic studies are ideal for helicopter and ship surveys because data can be collected opportunistically without interference to other research activities. During helicopter surveys, personnel will be left on a remote ice floe and record underwater sounds using hydrophones and battery-operated recorders. In addition, a calibrated B & K sound pressure level meter adapted for a hydrophone will collect ambient noise profiles. An ANABAT II bat detector adapted with a hydrophone will collect sounds in the ultrasonic range. During ship surveys, sonobuoys will be deployed and underwater sounds telemetered to the ship as it moves away. Onboard and post-cruise analysis of recordings will be conducted using a RTS real time sonogram analyzer and SIGNAL power spectrum and oscillogram analyzers. A LeCroy digital oscilloscope will provide average power spectra and FFT of recordings. Special emphasis will be placed on examining the spectral characteristics of ambient noise in the presence and absence of various biota, such as seals, whales, fish, birds, and krill. Similarly, spectral characteristics of ambient noise at locations with different ice cover, thickness, and topography and at different water depths will be examined.

11. <u>Seals: genetics patterns in relation to life history characteristics</u>

Hypothesis: The degree of heterozygosity demonstrated by the four species of Antarctic pack ice seals corresponds to their characteristic life histories as demonstrated by aspects such as dispersal and distribution patterns, habitat selection, social system, and degree of philopatry.

Significance: Although each of the four species of Antarctic pack ice seals has a circumpolar distribution in the sea ice zone, they have very different life histories, which have led to ecological partitioning. This partitioning is reflected in measures such as foraging behavior, prey preferences, habitat selection, and geographic distribution and movements. Based on these differences, the genetic heterozygosity of Antarctic pack ice seals can be expected to vary widely among species from Weddell seals (relatively low), through leopard and Ross seals, to crabeater seals (relatively high).

The Weddell seal population is estimated at approximately 800,000; adults are found primarily in coastal areas where they breed and give birth annually on early season fast ice (Siniff *et al*. 1977). The Weddell seal population near McMurdo Station, Antarctica has been the subject of extensive research, which demonstrated these seals' strong tendency to return to their natal area to breed (Siniff *et al*. 1969, 1977, Stirling 1969, 1971, Testa 1987, Testa and Siniff 1987). This degree of philopatry is greater than that known for any other pack ice seal and thus, the Weddell seal is predicted to show the lowest level of heterozygosity among the four species.

Crabeater seals are estimated to number between 15 and 30 million, and they feed almost exclusively on krill (e.g., Laws 1984). This species uses drifting ice floes for breeding and pupping, demonstrating no known tendency for philopatry. Moreover, recent satellite telemetry data revealed that individuals can travel at least one third the distance around the Antarctic continent during a period as short as 11 months (Bengtson, pers. comm.). These demographic and ecological features suggest that crabeater seals should have the greatest level of genetic heterozygosity.

The leopard seal population is estimated at between 100,000 - 200,000 (Reeves *et al*. 1992), and individuals are known to feed on a wide variety of prey including seals, birds, fish, cephalopods, and krill (Siniff and Bengtson, 1977, Bengtson, 1982, Siniff and Stone 1985, Lowry *et al.* 1988). Although little is known of leopard seal movements, the same individual seals have been observed returning annually to forage near penguin and fur seal colonies (Hiruki *et al*. in prep). This behavior is consistent with utilizing traditional, well known hunting areas, which would presumably be advantageous to predators of advanced prey like penguins and seals. Therefore, leopard seal heterozygosity is expected to fall somewhere between Weddell and crabeater seals.

Ross seals are rarely observed but are usually seen as solitary seals in areas of consolidated pack ice over deep water (Erickson and Hanson 1990, Bengtson *et al*. 1995, Bester *et al*. 1995). They are known to forage on pelagic fish and cephalopods in the upper 200 m of the water column (Øritsland 1977, Skinner and Klages 1994, Bengtson and Stewart 1997). It is difficult to postulate where the Ross seal may fall on a population genetics continuum because so little is known of its overall life history pattern. However, it is expected that Ross seals exhibit levels of heterozygosity somewhere between that of crabeater and leopard seals due to the habitat they occupy.

The overall population genetics patterns of the four species of Antarctic pack ice seals are particularly important when considering the future impacts that climate change and increasing human presence may have on Antarctic marine ecosystems. Obtaining information on genetic patterns and relating it to individual life history characteristics is a crucial step in beginning to understand how natural selection operated to develop the ecological partitioning observed today. Furthermore, knowledge of genetic patterns around the continent will be essential for considering management issues such as the size and location of protected areas, distribution of fishing, or mitigation of other human-related impacts within marine ecosystems.

Approach: During the APIS cruise into the Ross sea, tissue samples will be collected from all seals captured and handled. These samples will be combined for analyses with samples taken by investigators from other cruises in the international APIS Program to create a comprehensive sample from all areas surrounding the Antarctic continent. It is expected that curation and analyses of all samples will be coordinated through the genetics laboratory of Dr. Curtis Strobeck, at the University of Alberta, Canada, which has been designated as a genetics center for the international APIS Program. Analyses will involve microsatellite DNA fingerprinting procedures using a suite of primers already developed and found to occur in Weddell, crabeater and leopard seals. No samples of Ross seals have yet been tested but they are expected to have similarly promising results.

12. <u>Seals: immunogenetics</u>

Hypotheses: 1) Antarctic pack ice seals are immunogenetically depauperate because they lack selective factors (e.g., disease) that would normally promote genetic variability at immunologically relevant loci (i.e., major histocompatibility complex loci). 2) Consequently, any variability at these loci is related to non-selective factors (e.g., genetic drift) and the geographic patterns of genetic distance within species reflect reproductive isolation of local populations, effective population size, migration patterns, demographic histories, and meta-population dynamics. 3) Homogeneity at these immunogenetic loci reflects a pathogenically "benign marine environment" (Slade 1992). The demographic, physiological, and medical consequences of this immunogenetic vulnerability to new pathogenic threats will be expressed as regional variability in average health conditions of individuals in regional populations and will covary with the physical and biotic features of the environment that determine regional biological productivity. 4) Similar patterns of variability at major histocompatibility complex (MHC) loci and microsatellite (MS) loci will be found within each of the four pack ice seal species due to non-selective factors on the former and neutrality in the latter.

Significance: The relationships between individual and population fitness (i.e., reproduction, health, and survival), probabilities of population persistence under environmental stress, and immunogenetic persistence are poorly known. One way to determine whether selection is important in structuring MHC loci is to compare, from the same individuals, loci where nucleotide variation is influenced by non-selective vs. selective mechanisms (i.e., at MS vs. MHC loci). Nucleotide variation at MS loci is thought to be influenced primarily by non-selective factors and is typically high owing to higher mutation rates, a large number of unlinked loci, and co-dominance (e.g., Ashley and Dow 1994, Queller *et al.* 1994, Slatkin 1995a, 1995b). Nucleotide variation at loci in the MHC region is important in resistance or immune system response to disease (e.g., Hedrick 1994) and is thought generally to be maintained by some sort of balancing selection, particularly driven by mechanisms of pathogen resistance, negative assortative matings, and maternal-fetal interactions. These comparisons should improve our understanding of the roles played by particular genetic loci in immunological responses to direct (disease) and indirect (environmental) stressors in wildlife populations. This work may also provide some indication of the vulnerability of populations to changes in physical and environmental conditions that occur gradually or relatively rapidly (e.g., global climate change) and allow predictions of their influences on the seals' meso- and macro-scale patterns of health, abundance, and distribution.

Approach: Tissue and blood samples will be collected from all Antarctic pack ice seals captured and handled during the APIS cruise. Samples will also be acquired from collaborators in other national programs participating in the international APIS Program in other Antarctic sectors. Nucleotide variation will be examined at selected MS and MHC loci to determine meso- and macro-scale genetic variability in each seal species. By comparing genetic variation in both systems in the same individuals we will evaluate the neutral and selective forces that influence genetic variation at the MHC site directly by testing the hypothesis that proportions of alleles at each do not differ from Hardy-Weinberg expectations. An excess of heterozygotes at MHC loci may indicate balancing selection in response to infectious disease, whereas a simultaneous evaluation of MS (neutral) loci will provide a check on whether other factors may have contributed to skewed genotype ratios. If these factors vary with respect to variation in biotic and abiotic characteristics of the Antarctic environment then the patterns of genetic variation at the MHC loci should vary geographically in concordance with patterns of environmental heterogeneity.

13. <u>Seals: body condition and nutritional physiology</u>

Hypotheses: 1) The body condition and physiology of upper trophic level predators differs between sites of high and low predator density. 2) There are nutritional, metabolic, and body condition differences between Antarctic pack ice seals that feed on different prey items or that are nutritionally compromised.

Significance: It should be possible to differentiate among groups of seals that are nutritionally, biochemically or metabolically compromised. Several populations of seals and sea lions in Alaska are in severe population decline. The extent to which body condition and nutritional physiology may be involved in this decline has been examined by assessing the population health and body condition of these species (Castellini *et al*. 1993, Rea 1995). These studies included blood chemistry surveys for lipid, protein and carbohydrate metabolic disturbances, as well as assays for responses to metal contamination, generalized immune function, and water balance. In addition, body morphometric studies and blubber biochemistry and morphology were examined (Castellini and Calkins 1993, Fadely *et al*. 1997). Because the population of Weddell seals in McMurdo Sound is a healthy and well known stock, this group was used from 1992 through 1994 as a "healthy" control for many of the same biomarkers (Testa *et al*. 1993, Castellini *et al*. 1994). In those studies, health and condition indices were used to characterize several hundred weaned Weddell seal pups, whose fate is currently being monitored as they recruit into the adult population.

On the basis of these projects in both the north and south polar regions, a suite of critical biomarkers has been developed that can be used to distinguish among stocks of pinnipeds in differing regions and stocks that may be food or health stressed (Castellini *et al*. 1993, Zenteno-Savin and Castellini 1997). Through chemical composition profiles, the types prey consumed by seals can also be identified if representative prey samples are collected nearby (Iverson *et al*. 1997). These methods will allow testing the idea that groupings of seals in different densities or regions around the Antarctic continent differ by indices of health, body condition and biochemistry.

Approach: In collaboration with teams assessing prey selection and medical status of seals (i.e., parasitology, bacteriology, and clinical health), it should be possible to determine if there are differences in the basic biology of seals that congregate within regional "hot spots" of biological activity. Seals will be sampled inside and outside of regions of high concentration while they are hauled out on the sea ice. Blood and blubber biopsy samples will be collected from every seal captured and handled during the APIS cruise. Body morphometric values (length, girth, mass), blubber thickness and whole body water state (using bio-electrical impedance techniques) can also be collected from animals that are appropriately sedated. Samples of prey items from the same region will be collected for chemical signature identification (stable isotopes of carbon and nitrogen and for lipid fatty acid profiles) through collaboration with other investigators on the APIS cruise. Collaborators will also provide measurements of seal density, ice and oceanographic conditions, prey type and seal bioenergetics (diving and haul-out patterns).

14. <u>Seals: diving physiology and blood volume</u>

Hypothesis: 1) Inter-individual and inter-species variations of total and sequestered red cell mass correlate with the ability to execute frequent and/or prolonged dives in Antarctic pack ice seals. 2) Within an Antarctic pack ice seal species, the fraction and quantity of splenic red cell sequestration increase as juveniles become adults.

Significance: Physiological mechanisms have developed in certain seal species permitting prolonged periods of apnea. Oxyhemoglobin in circulating and sequestered red blood cells provides an important source of oxygen for vital tissues such as the brain and heart during prolonged breath holding. The blood hematocrit of Weddell seals increases by nearly 50% during the first 10-12 minutes of a dive (Kooyman et al. 1980, Qvist et al. 1986). Indirect and direct evidence support the importance of splenic sequestration of erythrocytes in permitting prolonged periods of apnea. In relationship to body mass, Weddell seals have very large spleens which contract during diving and after the intravenous administration of epinephrine (Castellini and Castellini 1993, Hurford et al. 1996). The circulating hematocrit markedly increases subsequent to splenic contraction. It has been estimated that over 20 liters of red blood cells could be stored in the Weddell seal spleen during periods of rest and injected into the central circulation during diving bouts.

The overall importance of splenic contraction in permitting prolonged breath-holding is uncertain. Evidence based on autopsy specimens suggests that the spleens of deep diving seals comprise a greater fraction of body mass than that of shallow diving seals. Studies are proposed to examine the importance of this mechanism of controlling circulating blood volume by directly correlating
its extent with diving behavior. Seals that tolerate prolonged periods of apnea, such as Weddell seals, are hypothesized to have a greater change of blood volume with splenic contraction than those that do not. In addition, it is likely that juvenile seals of each species, which should have a shorter apneic tolerance time, have less red cell mass and a reduced sequestered blood volume compared to adults of the same species. These studies will lend support to the importance of this mechanism for permitting extensive and repetitive diving. Our understanding of blood volume, red cell mass, and splenic sequestration will also be extended to pack ice dwellers such as crabeater and leopard seals.

Approach: Weddell, crabeater, and leopard seals of various ages (juvenile and adult) will be captured and anesthetized. Body morphometrics will be measured and a double lumen catheter will be placed into a vein in the extradural venous plexus. Measurements of hemoglobin concentration, hematocrit, plasma epinephrine and norepinephrine concentrations, and plasma volume (determined by two independent methods: indocyanine green dilution and hydroxyl starch
dilution) will be initially performed while the seal is anesthetized. Anesthesia should allow near maximal splenic sequestration and a reduced circulating red cell mass. Following these baseline measurements, epinephrine be injected intravenously to simulate sympathetic stimulation. Hemoglobin concentration and hematocrit will be measured serially following the epinephrine injection. Subsequently, a satellite-linked time-depth recorder (SLTDR) will be placed, antibiotics will be administered, the cannula will be removed, and the seal directly observed until it fully recovers. Data from the SLTDRs will be used to establish the diving patterns for each seal.

Determination of plasma volume (which does not change significantly with splenic contraction) and baseline (anesthetized) and epinephrine-stimulated hematocrit will be used to calculate circulating blood volume during rest and with stimulation. The difference between these two values can be considered to represent sequestered blood volume. Analysis of variation and correlation analyses will be performed to determine if the circulating and sequestered blood volume vary significantly with the species or age of the seals, plasma catecholamine levels, or with diving behavior.

15. <u>Seals: disease and pathology</u>

Hypothesis: 1) Health and pathogen seroprevalence of Antarctic pack ice seals in locations where their densities are relatively high differ from those of seals in low density areas. 2) Health status accounts for some of the observed variability in the seals' athletic performance (e.g., diving ability, migratory behavior).

Significance: Current health status and historical pathogen exposure are likely to account for some of the observed variability in reproductive and survival rates of Antarctic pack ice seals (e.g., Bengtson *et al*. 1991). Specifically, such exposures may help to explain why selected life history parameters in pack ice seals appear to fluctuate in a periodic fashion (e.g., Bengtson and Laws 1985, Testa *et al*. 1991, Boveng 1993) or why population parameters and observed densities of seals have changed over the past 30 years (e.g., Erickson *et al*. 1983, Erickson and Hanson 1990). Establishing a biomedical database (including standard hematological and serum biochemical profiles, thyroid and adrenal hormone analyses, reproductive hormone assays, microbiological surveys, and pathogen seroprevalence) for Antarctic pack ice seals will help to elucidate these issues. The hypotheses can be tested by comparing health and pathogen seroprevalence among species and among locations, as well as analyzing geographic patterns of pathogen exposure in Antarctic pack ice seals, particularly in relation to immunologically relevant (e.g., major histocompatibility complex) genetic diversity.

Approach: 1) Samples will be collected from Antarctic pack ice seals in high density and low density areas along the survey track of the APIS cruise. The following biomedical samples will be collected: blood, feces, and urine (opportunistically); swabs of nares, vagina, anus, and any wounds/lesions observed; skin scrapings of any dermatological lesions observed; and ectoparasites when observed. Samples from other investigators participating in the international APIS Program in other sectors of the Antarctic will be compared with samples from this APIS cruise, allowing evaluation of geographic variation in pathogen seroprevalence and serum biochemistries. Physical exams will be performed to: a) evaluate posture, locomotion, rate/character of respiration and heart rate, b) examine integument for evidence of molt, wounds, abscesses or other lesions, and ectoparasites, c) palpate for musculoskeletal abnormalities such as fractures or muscle atrophy, d) inspect eyes, ears, nares and oral cavity for hydration status and abnormalities such as corneal ulcers, conjunctivitis, fractured teeth, and e) evaluate, where possible, the nature (e.g., color and consistency) of urine, feces, and vaginal discharge.

Provisional Cruise Plan

The multi-disciplinary cruise that is outlined above would best be undertaken during the January to February time frame. At present, prospective investigators are aware that the research icebreaker *R/V Nathanial B. Palmer* (equipped with helicopters) could be made available for a cruise as outlined here from mid-December 1998 to mid-January 1999. That period would suit most of the logistic criteria associated with the projects outlined here.

The area of greatest interest to U.S. APIS investigators during the 1998/99 austral summer is the eastern Ross Sea and western Amundsen Sea. That area has the dual advantages of encompassing the features of sea ice and bathymetry that will allow investigators to test APIS hypotheses, as well as also contributing to the international APIS Program by conducting surveys in an important zone that would not otherwise be covered by other national programs (i.e., 125°W to 180°). Undertaking the proposed U.S. cruise in that sector will allow the coordinated research efforts of the international APIS Program to achieve nearly complete circumpolar coverage. Figure 3 presents a provisional cruise track for the APIS cruise.

This cruise track is based on approximately 29 days of active research in the pack ice and two days in transit between the survey are and McMurdo Station. The conceptual design of the cruise plan was based on the following considerations:

1. Deploying the ship in pack ice areas that will allow testing hypotheses derived from the three APIS unifying questions,

2. The need to ensure efficient deployment of helicopters so that all representative sectors of the pack ice study area can be sampled by aerial surveys to complement the sampling conducted from the ship, and

3. Selecting an area that would coordinate and complement the sampling efforts of research undertaken by other Antarctic national programs participating in the international APIS Program (i.e., coordinating with Brazil so that the entire Amundsen/Bellingshausen Seas and the eastern Ross Sea are surveyed).

It is estimated that this cruise track would provide sampling opportunities along approximately 1,500 km of ship-based observations and 10,500 km of linear aerial survey transects from helicopters. Three sampling strata have been identified within the study area, which will allow testing APIS hypotheses: I. on-shelf and off-shelf ice edge/shelf slope, II. ice-covered coastal

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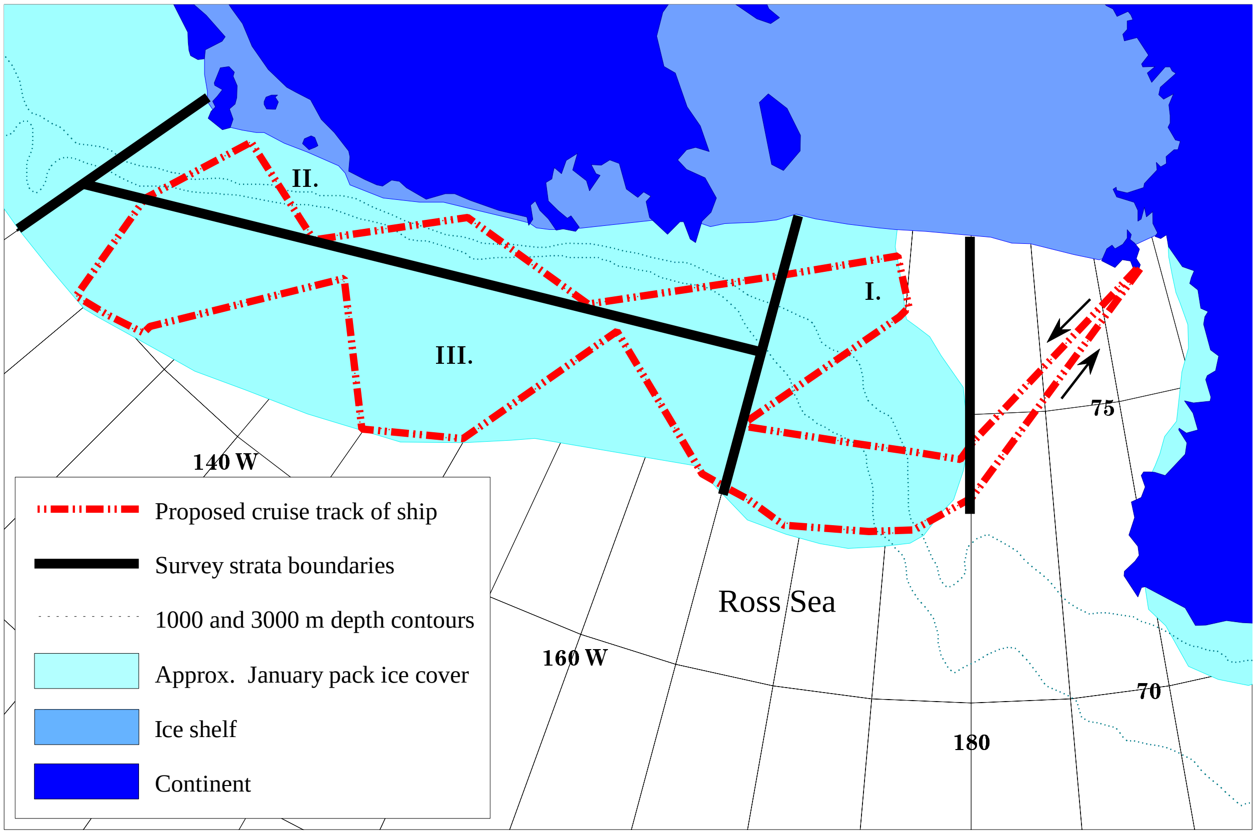
Figure 3. Provisional cruise track for the proposed 1998/99 U.S. APIS cruise. This cruise track assumes that the R/V Nathanial B. Palmer will start and end its cruise at McMurdo Station.



and shelf slope habitats, and III. off-shelf ice edge and ice-covered habitats. This level of sampling would meet the recommended effort levels for this sector of the international APIS Program's circumpolar abundance survey for pack ice seals, which seeks to develop an abundance estimate with a CV of 10% or less. In addition, this cruise track would allow a sufficient sampling effort to detect differences in seal density of approximately 0.2 seals/km^2 between sampling strata (i.e., bathymetric or ice coverage) with 90% probability.

Program Coordination

For a multi-disciplinary program of the type described herein to succeed, it is vital that effective coordination be maintained among investigators. Therefore, U.S. investigators in the APIS Program are planning the following meetings and workshops:

1. Pre-cruise meeting (April-June 1998),
2. Post-cruise data workshop among U.S. investigators (September-November 1999), and
3. Participation in an international data workshop with APIS investigators from other national programs (June-August 2000). This workshop is likely to be scheduled in association with XXVI SCAR, which is to be held in Japan.

In addition, once the National Science Foundation has determined the extent to which the proposed APIS cruise will be supported, a U.S. APIS steering committee will be formed to promote communication and coordination among investigators.

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Literature Cited

Ainley, D.G. 1983. Biomass of birds and mammals in the Ross Sea. Pp. 498-515 *in* Antarctic nutrient cycles and food webs (Siegfried, W.R., Condy, P.R., and Laws, R.M., eds). Springer-Verlag: Berlin.

Ainley, D.G. and S. Jacobs. 1981. Sea-bird affinities for ocean and ice boundaries in the Antarctic, Deep-Sea Res., 28:1173-1185.

Ainley, D.G., Fraser, W.R., Smith, W.O., Hopkins, and T.L., 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.

Ainley, D.G., S. Jacobs, C. Ribic and I. Gaffney. (in review) Seabirds, sea ice and ocean fronts in the Amundsen and Southern Bellingshausen Seas, late summer - early autumn, 1994.

Ainley, D.G., E.F. O'Connor, and R.J. Boekelheide. 1984. The marine ecology of birds in the Ross Sea, Antarctica. Ornithological Monograph, Am. Ornithol. Union, 32:17-91.

Ainley, D.G., C.A. Ribic, and W.R. Fraser. 1992. Does prey preference affect habitat choice in Antarctic seabirds? Mar. Ecol. Prog. Ser., 90:207-221.

Ancel, A., G. Kooyman, P.J. Ponganis, J.-P. Gendner, J. Lignon, X. Mestre, N. Huin, P.H. Thorson, P. Robisson, Y. Le Maho. 1992. Foraging behaviour of emperor penguins as a resource detector in winter and summer. Nature, 360:336-339.

Ashley, M.V. and B.D. Dow. 1994. The use of microsatellite analysis in population biology: background, methods, and potential applications. Pp. 185-201 *in* Molecular Ecology and Evolution: Approaches and Application (B. Sherwater, B. Strait, G.P. Wagner, and R. DeSalle, eds.). Birkhauser Verlag: Basel.

Awbrey, F.T., J.A. Thomas, W.E. Evans, and J.S. Leatherwood. 1982. Ross sea killer whale vocalizations: preliminary description and comparison with those of some northern hemisphere killer whales. Rep. Int. Whal. Commn., 32: 667-670.

Bengtson, J.L. 1982. Reproductive ecology of crabeater and leopard seals along the Antarctic Peninsula. U.S. Ant. J., 17:185.

Bengtson, J.L. and R.M. Laws. 1985. Trends in crabeater seal age at sexual maturity: an insight into Antarctic marine interactions. Pp. 667-675 *in* Antarctic nutrient cycles and food webs (Siegfried, W.R., Condy, P.R., and Laws, R.M., eds). Springer-Verlag: Berlin.

Bengtson, J.L. and B.S. Stewart. 1992. Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. Polar Biol., 12:635-644.

Bengtson, J.L. and B.S. Stewart. 1997. Diving patterns of a Ross seal (*Ommatophoca rossii*) near the eastern coast of the Antarctic Peninsula. Polar Biol., 17:000-000.

Bengtson, J.L., P.L. Boveng, U. Franzen, P. Have, M.-P. Heide-Jørgensen, and T.J. Härkönen. 1991. Antibodies to canine distempter virus in Antarctic seals. Mar. Mammal. Sci., 7:85-87.

Bengtson, J.L., A.S. Blix, I.L. Boyd, M.F. Cameron, M.B. Hanson, and J.L. Laake. 1995. Antarctic pack ice seal research, February-March 1995. U.S. Ant. J., 30:191-193.

Bengtson, J.L., R.D. Hill, and S.E. Hill. 1993. Using satellite telemetry to study the ecology and behavior of Antarctic seals. Korean J. Polar Res., 4:109-115.

Bester, M.N., A.W. Erickson, and J.W.H. Ferguson. 1995. Seasonal change in the distribution and density of seals in the pack ice off Princess Martha Coast, Antarctica. Ant. Sci., 7:357-364.

Bohne, B. A., J.A. Thomas, E. Yohe, and S. Stone. 1985. Examination of potential hearing damage in Weddell seals in McMurdo Sound, Antarctica. U.S. Ant. J., 19:174-176.

Boveng, P.L. 1993. Variability in a crabeater seal population and the marine ecosystem near the Antarctic Peninsula. Ph.D. Dissertation, Montana State University, 110 pp.

Boveng, P.L. and J.L. Bengtson. *In press.* Crabeater seal cohort variation: demographic signal or statistical noise? *In* Antarctic Communities (B. Battaglia, J. Valencia, and D.W.H. Walton (eds.). Cambridge University Press: Cambridge.

Brillinger, D. R. *In press*. A particle migrating randomly on a sphere. J. Theoretical Probability.

Brillinger, D. R. and B. S. Stewart. 1997. Elephant seal movements: dive types and their sequences. In: Modelling longitudinal and Spatially Correlated Data: Methods, Applications, and Future Directions (T. G. Gregoire *et al.*, eds.). Lecture Notes in Statistics, Vol. 122, Springer: New York.

Brillinger, D. R. and B. S. Stewart. *In press* a. Elephant seal movements: some frequency based studies. Braz. J. Probability and Statistics.

Brillinger, D. R. and B. S. Stewart. *In press* b. Elephant seal movements: modelling migrations. Can. J. Statistics.

Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall: London. 446p.

Castellini, M. and D. Calkins. 1993. Mass estimates using body morphology in Steller sea lions. Mar. Mammal Sci., 9:48-54.

Castellini, J.M. and M.A. Castellini. 1993. Estimation of splenic volume and its relationship to long-duration apnea in seals. Physiol. Zool., 66:619-627.

Castellini, M.A., R.W. Davis, T.R. Loughlin and T.M. Williams. 1993. Blood chemistries and body condition of Steller sea lion pups at Marmot Island, Alaska. Mar. Mammal Sci., 2:202-208.

Castellini, M.A., J.W. Testa, L.D. Rea, J.M. Moss and K.K. Hastings. 1994. Diving development and survivorship in Weddell seals pups. U.S. Ant. J., 29:171-172.

Croxall, J.P. and G.S. Lishman. 1987. The food and feeding ecology of penguins. Pp. 101-134 *in* Seabirds: Feeding Ecology and Role in Marine Ecosystems (J.P. Croxall, ed.). Cambridge University Press: Cambridge.

Croxall, J.P., P.A. Prince, and C. Ricketts. 1985. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. Pp. 516-533 *in* Antarctic Nutrient Cycles and Food Webs (W.R. Siegfried, P.R. Condy, and R.M. Laws, eds.). Springer-Verlag: Berlin.

Erickson, A.W. and M.B. Hanson. 1990. Continental estimates and population trends of Antarctic ice seals. Pp. 253-264 *in* Antarctic Ecosystems: Ecological Change and Conservation (K.R. Kerry and G. Hempel, eds). Springer-Verlag: Berlin.

Erickson, A.W., L.J. Bledsoe, and M.B. Hanson. 1989. Bootstrap correction for diurnal activity cycle in census data for Antarctic seals. Mar. Mammal Sci., 5:29-56.
Erickson, A.W., M.B. Hanson, and D.M. Kehoe. 1983. Population densities of seals and whales observed during the 1983 circumnavigation of Antarctica by USCGC POLAR STAR. U.S. Ant. J., 18:163-166.

Fadely, B.S, J.M. Castellini and M.A. Castellini. 1997. Recovery of harbor seals from EVOS: condition and health status. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration project 96001), University of Alaska, Fairbanks.

Fisher, S.R., L.M. Ferm, and J.A. Thomas. 1983. Circumpolar acoustic surveys for marine mammals using a towed array of hydrophones. U.S. Ant. J., 17:171-173.

Foote, K.G., I. Everson, J.L. Watkins, and D.G. Bone. 1990. Target strengths of Antarctic krill (*Euphausia superba*) at 38 and 120 kHZ. J. Acoust. Soc. Am., 87:16-24.

Fretwell, S.D. 1987. Food chain dynamics: the central theory of ecology? Oikos, 50:291-301.

Green, K. and H. Burton. 1988. Annual and diurnal variations in the underwater vocalizations of Weddell seals. Pol. Biol., 8:161-164.

Green, K. and R. Williams. 1986. Observations on food remains in faeces of elephant, leopard, and crabeater seals. Pol. Biol., 6:43-45.

Griffiths, A.M. 1983. Factors affecting the distributiom of the Snow Petrel (*Pagodroma nivea*) and the Antarctic Petrel (*Thalassoica antarctica*). Ardea, 71:145-150.

Gutt, J. and V. Siegel. 1994. Benthopelagic aggregations of krill *(Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic). Deep-Sea Res., 41:169-178.

Hedrick P.W. 1994. Evolutionary genetics of the major histocompatibility complex. Am. Nat., 143:945-964.

Hiruki, L.M., M.K. Schwartz, and P.L. Boveng. *In prep*. Hunting and social behavior of leopard seals (*Hydrurga leptonyx*) at Seal Island, South Shetland Islands, Antarctica.

Hunt, G. L., Jr. 1991. Marine birds and ice-influenced environments of polar oceans. J. Mar. Syst., 2:233-240.

Hunter, M.D. and P.W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology, 73:724-732.

Hurford, W.E., P. Hochachka, R.C. Schneider, G.P. Guyton, K.S. Stanek, D.G. Zapol, G.C. Liggins, and W.M. Zapol. 1996. Splenic contraction, catecholamine release, and blood volume redistribution during diving in the Weddell seal. J. Appl. Physiol., 80:298-306.

Iverson, S.J., K.J. Frost, and L.F. Lowry. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Marine Ecology Progress Series.

Jacobs, S. 1991. On the nature and significance of the Antarctic slope front. Mar. Chem., 35:9-24.

Kawaguchi, S., K. Ishikawa, and O. Matsuda. 1986. The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Lutzow-Holm Bay, Antarctica. Mem. Natl. Inst. Polar Res., Spec. Issue, 44:67-85.

Kooyman, G.L. 1993. Breeding habitats of emperor penguins in the western Ross Sea. Ant. Sci., 5:143-148.

Kooyman, G.L. 1994. Natural history of emperor penguin colonies of the Ross Sea, 1993. U.S. Ant. J., 29:170-171

Kooyman, G.L. and J.L. Mullins. 1990. Ross Sea emperor penguin breeding populations estimated by arial photography. Pp. 161-176 *in* Antarctic Ecosystems: Ecological Change and Conservation (K.R. Kerry and G. Hempel, eds.). Springer-Verlag: Berlin.

Kooyman, G.L., P.J. Ponganis, P.H.Thorson. 1991. Natural history of Ross Sea emperor penguin colonies. U.S. Ant. J., 26:181-182.

Kooyman, G.L., E.A. Wahrenbrock, M.A. Castellini, R.W. Davis, and E.E. Sinnett. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. J. Comp. Physiol., 138:335-346.

Laws, R.M. 1984. Seals. Pp. 621-715 *in* Antarctic Ecology, Vol. 2 (R.M. Laws, ed.). Academic Press: London.

Leatherwood, J.S., F.T. Awbrey, and J.A. Thomas. 1982a. Minke whale response to transiting survey vessel in the Antarctic. Rep. Int. Whal. Comm., 32:795-802.

Leatherwood, J.S., J.A. Thomas, and F.T. Awbrey. 1981. Minke whales off northwestern Ross Island. U.S. Ant. J., 16:154-156.

Leatherwood, J. S., F.S.Todd, J.A. Thomas, and F.T. Awbrey. 1982b. Incidental records of cetaceans in southern seas January and February 1981. Rep. Int. Whal. Comm., 32:515-520.

Lowry, L.L., J.W. Testa, and W. Calvert. 1988. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. Pol. Biol., 8:475-478.

Matsuki, M. and J.W. Testa. 1991. Population ecology and satellite telemetry of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound. U.S. Ant. J., 26:185-186.

Nordøy, E.S., L. Folkow, and A.S. Blix. 1995. Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. Pol. Biol., 15:261-268.

Piatkowski, U. and K. Putz. 1994. Squid diet of emperor penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica during late summer. Ant. Sci., 6:241-247.

Putz, K. 1995. The post-moult diet of Emperor Penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica. Pol. Biol., 15:457-463.

Øritsland, T. 1977. Food consumption of seals in the Antarctic pack ice. Pp. 749-768 *in* Adaptations within Antarctic Ecosystems (G.L. Llano, ed.). Smithsonian Institution: Washington, D.C.

Queller, D.C., J.E. Straussmann, and C.R. Hughes. 1994. Microsatellites and kinship. Trends Ecol. Evol., 8:285-288.

Quetin, L.B. and R.M. Ross. 1991. Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. Am. Zool., 31:49-63.

Quetin, L.B., R.M. Ross, and A. Clarke. 1994. Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. Pp. 165-184 *in* Southern Ocean Ecology: the BIOMASS Perspective (S.Z. El-Sayed, ed.). Cambridge Univ. Press: Cambridge.

Quetin, L.B., R.M. Ross, T.K. Frazer, and K.L. Haberman. 1996. Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba*. Pp. 357-371 *in* Foundations for Ecological Research West of the Antarctic Peninsula, Antarctic Research Series, Volume 70.

Qvist, J., R.D. Hill, R.C. Schneider, K.J. Falke, G.C. Liggins, M. Guppy R. Elliott, P.W. Hochachka, and W.M. Zapol. 1986. Hemoglobin concentrations and blood gas tensions of free-diving Weddell seals. J. Appl. Physiol., 61:1560-1569.

Rea, L.D. 1995. Prolonged fasting in pinnipeds. Ph.D. thesis. University of Alaska, Fairbanks.

Reeves, R.R., B.S. Stewart, and S. Leatherwood. 1992. The Sierra Club handbook of seals and sirenians. Sierra Club: San Francisco.

Rogers, T.L., D.H. Cato, and M. M. Bryden. 1995. Underwater vocal repertoire of the leopard seal in Prydz Bay. Pp. 223-236 *in* Sensory Systems in Aquatic Mammals (R.A. Kastelein, J.A. Thomas, and P.E. Nachtigall, eds.). DeSpil: Amsterdam.

Rogers, T.L., D.H. Cato, and M.M. Bryden. 1996. Behavioral significance of underwater vocalizations of captive leopard seals, *Hydruruga leptonyx*. Mar. Mammal Sci., 12:414-427.

Schneider, D.C. 1991. The role of fluid dynamics in the ecology of marine birds. Oceanogr. Mar. Biol. Ann. Rev., 29:487-521.

Schneider, D., N.M. Harrison, and G.L. Hunt. 1987. Variation in the occurrence of marine birds at fronts in the Bering Sea. Est. Coast. Shelf Sci., 25:135-141.

Siegel, V. 1988. A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula. Pp. 219-230 *in* Antarctic Ocean and Resources Variability (D. Sahrhage, ed.). Springer-Verlag: Berlin/Heidelberg.

Siegel, V. 1989. Winter and spring distribution and status of the krill stock in Antarctic Peninsula waters. Arch. Fisch-Wiss., 39:45-72.

Siniff, D.B. and J.L. Bengtson. 1977. Observations and hypotheses concerning the interactions among crabeater seals, leopard seals, and killer whales. J. Mammal., 58:414-416.

Siniff, D.B. and S. Stone. 1985. The role of the leopard seal in the tropho-dynamics of the Antarctic marine ecosystem. Pp. 561-565 *in* Antarctic Nutrient Cycles and Food Webs (W.R. Siegried, P.R. Condy, and R.M. Laws, eds.). Springer-Verlag: Berlin/Heidelberg.

Siniff, D.B., D.P. DeMaster, R.J. Hofman, and L.L. Eberhardt. 1977. An analysis of the dynamics of a Weddell seal population. Ecol. Monographs, 47:319-335.

Siniff, D.B., I. Stirling, J.L. Bengtson, and R.A. Reichle. 1979. Social and reproductive behavior of crabeater seals (*Lobodon carcinophagus*) during the austral spring. Can. J. Zool., 57:2243-2255.

Siniff, D.B., J.R. Tester, and V.B. Kuechle. 1969. Seal population densities in the Weddell Sea. Pp. 376-394 *in* Antarctic Ecology, Vol. I (M.W. Holdgate, ed.). Academic Press: New York.

Skinner, J.D. and N.T.W. Klages. 1994. On some aspects of the biology of the Ross seal *Ommatophoca rossii* from King Haakon VII Sea, Antarctica. Pol. Biol., 14:467-472.

Slade, R.W. 1992. Limited MHC polymorphism in the southern elephant seal: implications for MHC evolution and marine population biology. Proc. Royal Soc. London B, 249:163-171.

Slatkin, M. 1995a. A measure of populatino subdivision based on microsatellite allele frequencies. Genetics, 139:457-462.

Slatkin, M. 1995b. Hitchhiking and associative overdominance at a microsatellite locus. Mol. Biol. Evol., 12:473-480.

Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. Ecol., 50:573-586.

Stirling, I. 1971. Population dynamics of the Weddell seal (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica, 1966-68. Ant. Res. Ser., 18:141-161.

Stirling, I. and D.B. Siniff. 1979. Underwater vocalizations of leopard seals and crabeater seals near the South Shetland Islands, Antarctica. Can. J. Zool., 57:1244-1248.

Testa, J.W. 1987. Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddelli*). Can. J. Zool., 65:1091-1099.

Testa, J.W., and D.B. Siniff. 1987. Population dynamics of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica. Ecol. Monogr., 57:149-165.

Testa, J.W., M.A. Castellini and L.D. Rea. 1993. Physiological and behavioral ecology of juvenile Weddell seals. U.S. Ant. J., 28:155-156.

Testa, J.W., G. Oehlert, D.B. Ainley, J.L. Bengtson, D.B. Siniff, R.M. Laws, and D. Rounsevell. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in phocid seal populations. Can J. Fish. Aquat. Sci., 48:631-639.

Thomas, J.A. 1996. The sounds of seal societies. *In* Critical Strategies for Academic Thinking and Writing (M. Kiniry and M. Rose, eds.).

Thomas, J.A. and D.P. DeMaster. 1982. An acoustic technique for determining haulout pattern in leopard and crabeater seals. Can. J. Zool., 60:2028-2031.

Thomas, J.A., and D.P. DeMaster. 1983. Diel haulout patterns of Weddell seals females and their pups. Can. J. Zool., 61:2080-2086.

Thomas, J.A. and C.L. Golladay. 1995. Analysis of underwater vocalizations of leopard seals (*Hydruga leptonyx*). In Sensory Systems of Aquatic Mammals (R.A. Kastelein, J.A. Thomas, and P.E. Nachtigall, eds.). DeSpil: Amsterdam.

Thomas, J.A. and V.B. Kuechle. 1982. Quantitative analysis of the underwater repertoire of the Weddell seal. J. Acoust. Soc. Am, 72:1730-1738.

Thomas, J.A. and I. Stirling. 1983. Geographic variation in Weddell seal vocalizations between Palmer Peninsula and McMurdo Sound, Antarctica. Can. J. Zool., 61:2203-2210.

Thomas, J.A., D.P. DeMaster, S. Stone, and D. Andriashek. 1979. Observations of a newborn Ross seal pup near the Antarctic Peninsula. Can. J. Zool., 58:2156-2158.

Thomas, J.A., L.M. Ferm, and V.B. Kuechle. 1987. Silence as an antipredation strategy by Weddell seals. U.S. Ant. J., 22:232-234.

Thomas, J.A., L.M. Ferm, and K.E. Zinnel. 1989. Underwater vocalization patterns of Weddell seals during the breeding season. U.S. Ant. J., 23:146-148.

Thomas, J.A., S.R. Fisher, W.E. Evans, and F.T. Awbrey. 1982. Leopard seals produce ultrasonic sounds. U.S. Ant. J., 16:185.

Thomas, J.A., J.S. Leatherwood, W.E. Evans, and J. Jehl, Jr. 1981. Ross Sea killer whale distribution, behavior, color pattern, and vocalizations. U.S. Ant. J., 16:157-158.

Thomas, J.A., R. Puddicome, M. George, and D. Lewis. 1988. Variations in underwater vocalizations of Weddell seals at the Vestfold Hills as a measure of breeding population discreetness. Hydrobiologia, 165:279-284.

Thomas, J.A., K. Zinnel, and L.M. Ferm. 1983. Investigation of Weddell seal underwater calls using playback techniques. Can. J. Zool., 61:1448-1456.

Torres, J.J., A.V. Aarset, J. Donnelly, T.L. Hopkins, T.M. Lancraft, and D.G. Ainley. 1994. Metabolism of Antarctic micronektonic Crustacea as a function of depth of occurrence and season. Mar. Ecol. Prog. Ser., 113:207-219.

VanFraneker, J.A., U.V. Bathmann, and S. Mathot. 1997. Carbon fluxes to Antarctic top predators. Deep-Sea Res. II, 44:435-455.

Viet, R. and G. Hunt. 1991. Broadscale density and aggregation of pelagic birds from a circumnavigational survey of the Antarctic ocean. Auk, 108:790-800.

Zenteno-Savin, T. and M.A. Castellini. 1997. Plasma angiotensin II, arginine vasopressin and atrial natriuretic peptide in free ranging and captive seals and sea lions. Comparative Biochem. and Physiology.

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