MARINE MAMMAL COMM. JUL 1978

WHOI
DOCUMENT
COLLECTION

REVIEW OF INFORMATION REGARDING THE CONSERVATION OF LIVING RESOURCES OF THE ANTARCTIC MARINE ECOSYSTEM

John L. Bengtson

Department of Ecology and Behavioral Biology
University of Minnesota
Minneapolis, Minnesota 55455

July 1978

Final Report to U.S. Marine Mammal Commission
in Fulfillment of Contract MM8AD055

Prepared for

U.S. Marine Mammal Commission
1625 I Street, N.W.
Washington, D.C. 20006

QH
541.5
S3
B4
1978

The views and ideas expressed in this report are those of the author, and do not necessarily
reflect tho ion or
its Committt rine
Mammals.

ng the con-
es :

RETURNED

MBL/WHOI
0 0301 0037668 7

REVIEW OF INFORMATION REGARDING THE CONSERVATION OF LIVING RESOURCES OF THE ANTARCTIC MARINE ECOSYSTEM

John L. Bengtson

Department of Ecology and Behavioral Biology
University of Minnesota
Minneapolis, Minnesota 55455

July 1978

Final Report to U.S. Marine Mammal Commission
in Fulfillment of Contract MM8AD055

Prepared for

U.S. Marine Mammal Commission
1625 I Street, N.W.
Washington, D.C. 20006

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF FIGURES

Page

LIST OF FIGURES (Continued)

I. INTRODUCTION

The Antarctic region has a varied history of geographic exploration, scientific research, and commercial exploitation. The biological richness of the Antarctic marine ecosystem has long been recognized. The magnitude and economic success of Antarctic sealing and whaling attest to the enormous size of the living resources (prior to their devastation) that historically were supported within the Antarctic marine ecosystem.

As it becomes more difficult for world fisheries production to meet demand, people are looking once again to the Antarctic as a source of bountiful, exploitable food resources. Seals, whales, fish, squid and octopus, lobsters and crabs, and krill have been identified as species groups with potential harvest value. Antarctic krill (*Euphausia superba*) is receiving the most attention for a new large-scale fishery (Hardy, 1965; Schaeffer, 1965; Nemoto, 1966; Burukovskii, 1967; Burukovskii and Yaragov, 1967; Il'icher, 1967; Osochenko, 1967; Stasenko, 1967; Sasaki et al., 1968; Marty, 1969; Gulland, 1970; Makarov et al., 1970; Mackintosh, 1970; Moiseev, 1970; Nemoto and Nasu, 1975; and Tomo and Marschoff, 1977).

A. Proposed Krill Surplus

Many proposing the development of an Antarctic krill fishery suggest the existence of a krill surplus within the Antarctic marine ecosystem. They reason: 1) prior to heavy whaling, baleen whales ate enormous quantities of krill annually; 2) the great numbers of whales that have been killed no longer eat krill; 3) since fewer whales eat krill, there must be an unexploited surplus of krill; and 4) an unexploited krill population potentially constitutes a new major fishery. Although the extent of the so-called surplus is uncertain, the economic and social forces for developing a large krill fishery have excited much interest in how to best harvest krill. Unfortunately, the current excitement about krill harvesting seems to have ignored, in many instances, questions of the ecological wisdom of developing a krill fishery.

B. Development of a Krill Fishery

The Soviet Union, Japan, Germany, and Poland, are among the nations interested in developing krill fisheries. The Soviets' interest has been increasing since 1955, and Soviet exploratory expeditions beginning in 1962 have provided information on the biology and distribution of Antarctic krill. Since 1969, Soviet commercial fleets have reported annual catches of marine crustacea (unspecified) from about 7,000 to 17,000 tons (Eddie, 1977). Nakamura (1975) reported that in the early 1970's, a Soviet fishing expedition consisting of 3-4 trawlers caught 5,000 tons in 4 months. Daily catches reached 300 tons (Osochenko, 1967). The Soviets apparently have commercial products available in the form of krill paste for humans and fodder meal for animals.

In the early 1960's, the Japanese (Nasu, 1978) began krill surveys as part of their general oceanographic program. Their vessels and krill catches are listed in Table 1 (Everson, 1977). They have successfully marketed krill products including frozen cooked whole krill, dried whole krill, frozen attrition-peeled tail meats and frozen minced muscle (Eddie, 1977). Krill is also being used in aquaculture research.

The Federal Republic of Germany is also a participant in Antarctic krill harvesting. The results of the 1975-76 expedition of the West German research vessels FFS Walther Herwig and FMS Weser are listed in Table 2. Their largest reported haul was 35 tons in 8 minutes (Everson, 1977). Most West German krill products, including krill mince and krill paste, are still in the experimental stage (Grantham, 1977). Krill mince is being widely tested to replace fish in such preparations as soups, salads, and pie-fillings.

Poland is active in krill harvesting and processing also. The results of their 1975/1976 expedition (Table 2) and 1976/1977 expedition have not been made widely known (Eddie, 1977). A third expedition was planned for 1977/1978. During the 76/77 season, the Poles established a land-based research center on King George Island in the South Shetland Islands to study a variety of scientific topics including krill. Poland has created many palatable products using krill mince as a fish replacement.

Chile, Norway, and Taiwan are among the other countries trying to harvest krill as a food source (Table 2). Of these, the Chileans, who chartered a Spanish trawler, the Arosa VII, to harvest and freeze their catch on board seem to be making the most headway. In 1977, frozen breaded krill sticks were test-marketed domestically and were well accepted. Other krill products have been produced in experimental quantities. The Norwegians harvested some krill in 1976/1977, but their catch was small. Taiwan's early 1977 fishing expedition reported a catch of 130 tons of krill (Eddie, 1977).

Table 1. Exploratory fishing by Japanese vessels (After Everson, 1977).

Vessels	Season	Catch (tons)	Reference
Chiyoda-Maru	72/73	59	Nemoto and Nasu (1975)
Taishin-Maru No. 11	73/74	646	Nemoto and Nasu (1975)
Taishin-Maru and Aso-Maru	74/75	1140 1460	Anon. (1976b)
Exploratory Vessel	75/76	5000	Anon. (1976b)
Planned Catch	76/77	(10000)	Anon. (1976b)

Table 2. Exploratory fishing by other nationalities (After Everson, 1977).

Nationality of Expedition	Season	Catch (tons)	Reference
Chile	74/75 75/76	60	Anon. (1975)
West Germany (2 vessels)	75/76 (77/78)	400	Anon. (1976a)
Poland (2 vessels)	75/76	?	Anon. (1976b)
Other Asian Countries	76/77	?	Anon. (1977b)
Norway	76/77	Small	Anon. (1977a)

C. Purpose of this Paper

The need for a regime to conserve Antarctic marine living resources is apparent. This paper summarizes certain features of the Antarctic marine ecosystem, comments on possible effects of a krill harvest, and discusses the need for an ecosystem approach to managing Antarctic marine living resources. Throughout the paper, the term living resources refers to all living marine organisms, including seabirds, which are an integral part of the structure and function of the Antarctic marine ecosystem.

II. PHYSICAL ATTRIBUTES OF THE ANTARCTIC MARINE ECOSYSTEM

Antarctica is surrounded by the three contiguous basins of the Pacific, Atlantic, and Indian Oceans. These oceans lose their surface identity within the Antarctic Convergence, a region bounded roughly within 60° S. and 55° S. latitude. In this paper, the Antarctic Convergence shall represent the northern limit of the Southern (or Antarctic) Ocean; its southern limit is the Antarctic coast. Figures 1 and 2 are maps of the area and include the statistical zones used by the Food and Agricultural Organization (FAO) for fisheries purposes. Although primarily a surface phenomenon, the Convergence is nevertheless a boundary delineating distinctly different faunal zones.

The deeper ocean layers are continuous with the major ocean basins to the north. The Campbell Plateau south of New Zealand, the Kerguelen Jaussberg Ridge, the Atlantic-Indian Rise, and the Scotia Arc are major topographical regions extending into the Southern Ocean from northern areas. Circulation of Southern Ocean water masses is channeled and constricted by bottom bathymetry and the topography of these features.

A. Major Water Masses and Circulation Patterns

Three major water masses surround the continent: Antarctic Surface Water, Warm Deep Layer, and Antarctic Bottom Water (Figure 3). The Warm Deep Layer is a highly saline, low-oxygenated, water mass which orginates in the major oceans well to the north (Everson, 1977; Gordon and Goldberg, 1970). It flows south and begins to upwell when it nears the continent. As it reaches near-surface layers, it is split into two different water masses due to the sea/air exchange of heat and water. One mass remains near the surface (Antarctic Surface Water); the other sinks to the sea floor contributing to the Antarctic Bottom Water.

Antarctic Surface Water, which also incorporates fresh water from melting ice and snow, flows northerly until it reaches the Antarctic Convergence and sinks beneath the Subantarctic Surface Water (Everson, 1977). This relatively stationary zone rarely deviates more than 160 km north or south. The mixture of Antarctic and subantarctic waters is reflected by temperature changes ranging to 4° C (Kort, 1968). North of the Convergence, the Antarctic Surface Water becomes Subantarctic Intermediate Water, influencing most of the oceans of the southern hemisphere, but eventually returning south when it is altered by heat flux through the sea floor and across thermoclines (Gordon and Goldberg, 1970).

Figure 1. Map of Antarctica and the circumpolar sea showing physical and geographical features, hydrological boundaries and surface water movements (From Marr, 1962).

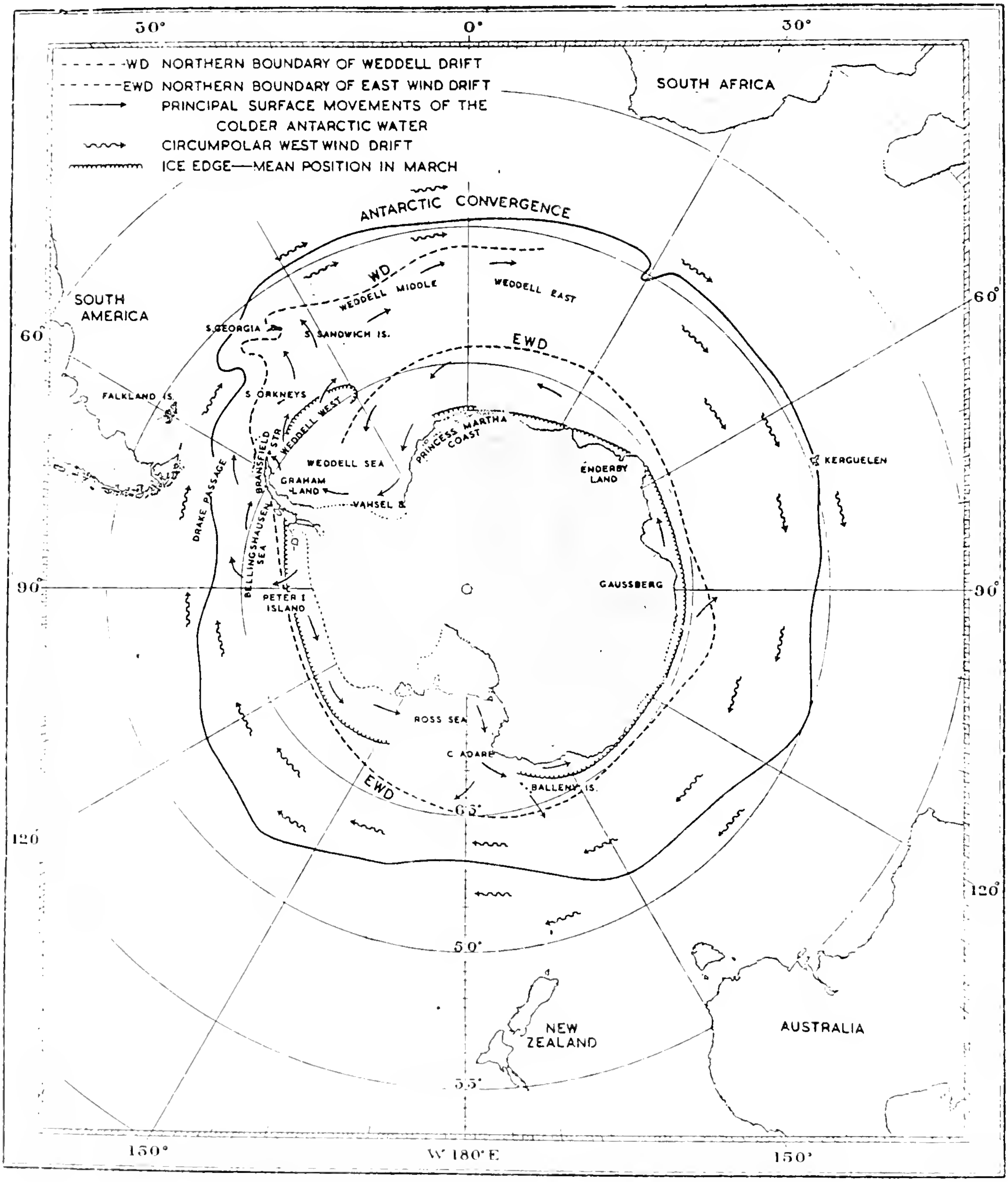
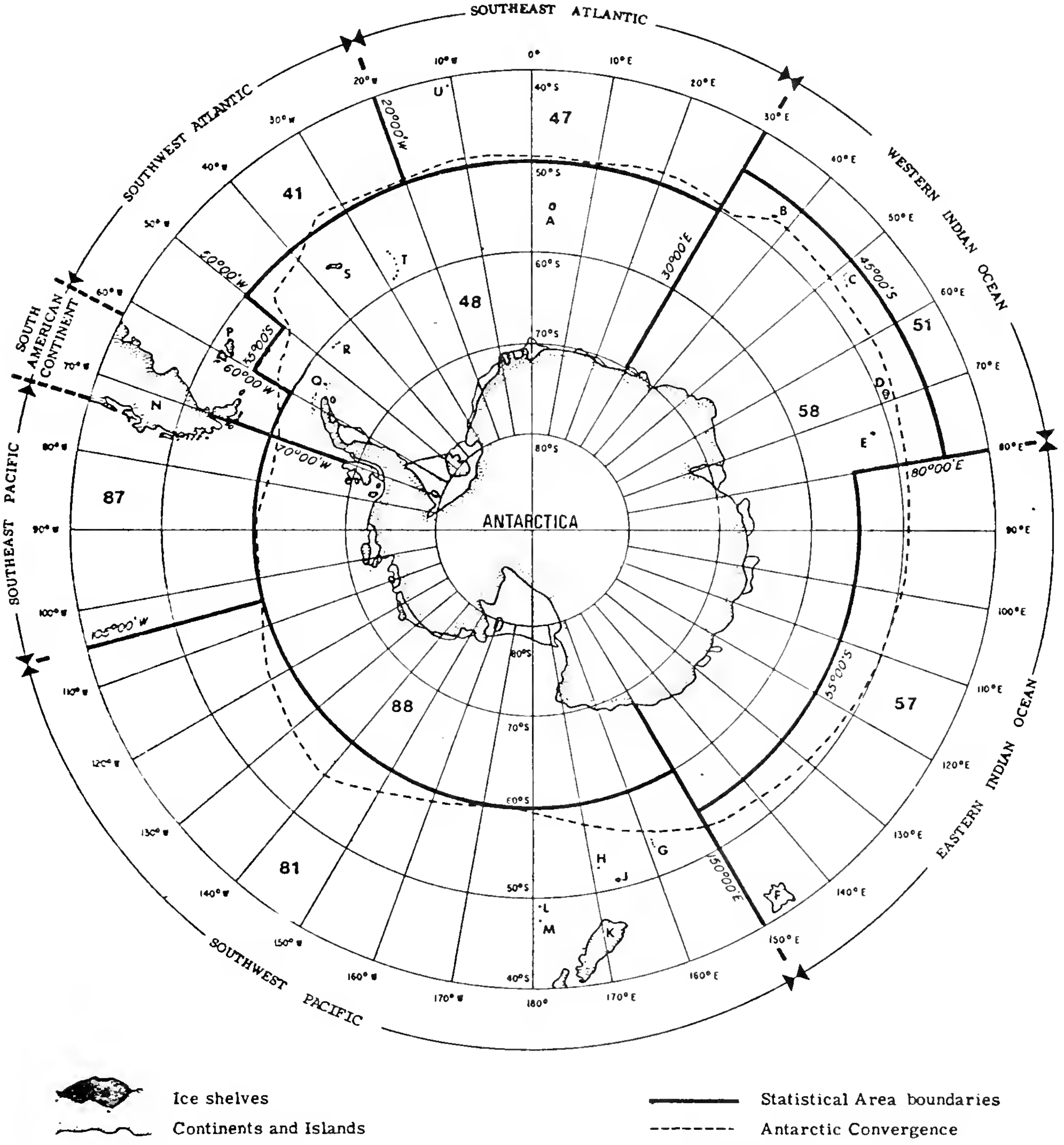
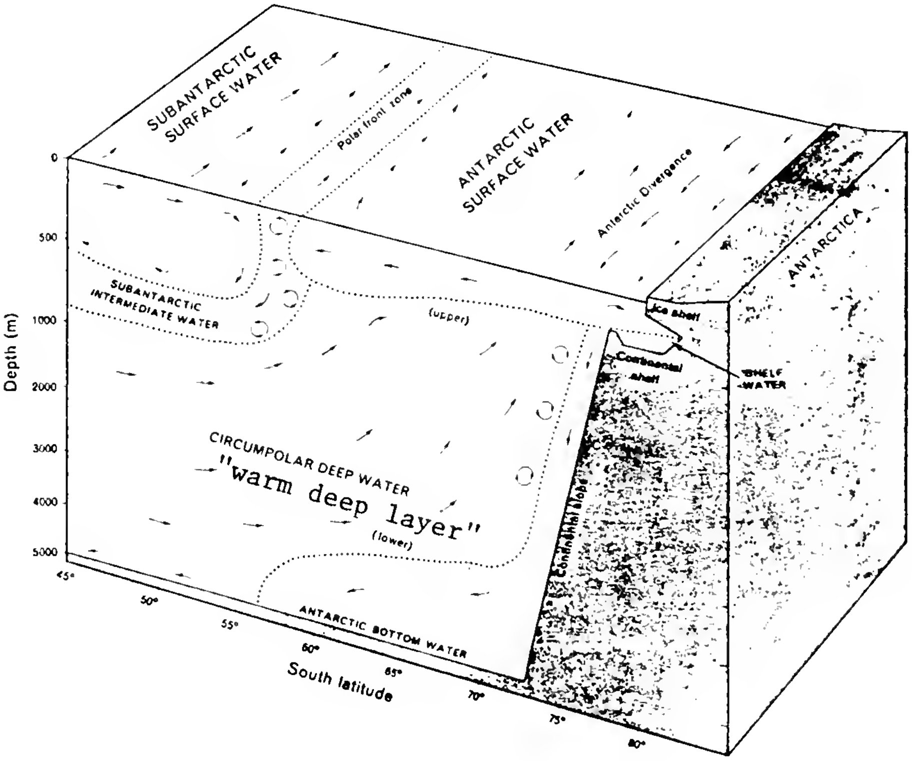


Figure 2. Boundaries of the main statistical regions in the Southern Ocean. Bold-face numbers refer to identity of separate statistical regions (From Everson, 1977).



Code	Name of Islands and Continents	Lat.	Long.	Code	Name of Islands and Continents	Lat.	Long.
A	Bouvet	54 S	5 E	L	Antipodes	49 S	179 E
B	Prince Edward and Marion	46 S	38 E	M	Bounty	47 S	179 E
C	Crozet	46 S	51 E	N	South America		
D	Kerguelen	49 S	70 E	P	Falklands (Malvinas)	51 S	59 W
E	Mc Donald and Heard	53 S	73 E	Q	South Shetland	62 S	58 W
F	Tasmania (Australia)			R	South Orkney	61 S	45 W
G	Macquarie	54 S	159 E	S	South Georgia	54 S	37 W
H	Campbell	52 S	169 E	T	South Sandwich	57 S	26 W
J	Auckland	50 S	166 E	U	Gough	39 S	11 W
K	South Island (New Zealand)						

Figure 3. Schematic representation of water masses and core layers in the Antarctic and subantarctic. (From Gordon and Goldberg, 1970).



Antarctic Bottom Water, characterized by high salinity and high oxygen content, is generally believed to be formed in association with sea ice (Gordon and Goldberg, 1970). As it cools, it moves down the continental shelf and spreads northward along the bottom. The major area of Antarctic Bottom Water formation may be the Weddell Sea and its greatest influence is probably outside the Antarctic zone in the Atlantic (Foster, 1976). The temperature gradient of this water mass is dissipated eventually, and it again cycles southward.

Besides the meridional circulation patterns discussed above, Southern Ocean waters have an equally important longitudinal circulation pattern. A major driving force for Southern Hemisphere currents are the east and west winds generated by the high pressure zones over the Antarctic continent surrounded by low pressure zones at about 65° S. (Foster, 1976). While winds near the continent are predominantly easterly, those north of 60° S. are westerly. Major surface movements follow these patterns, moving west near the continent (East Wind Drift) and east to the north of 60° S. (West Wind Drift) (Knox, 1970; Gordon, 1971).

The East and West Wind Drift interface forms the Antarctic Divergence, an area of upwelling (Knox, 1970; Kort, 1968). At several points along the Divergence, gyres form in areas of atmospheric cyclones. Beklemishev (1961) identified an association between cyclone tracks and whale feeding grounds (and therefore of krill). The most clearly defined gyre is that of the Weddell Sea (referred to as the Weddell Drift). Deacon (1976) pointed out that the maintenance of krill stocks in the Atlantic sector may be contingent on this circulation pattern.

B. Ice Characteristics

An important physical constituent of the Antarctic marine ecosystem is ice. Ice originates from direct freezing of the sea and from precipitation on the continent resulting in glacier and ice shelf formation. Tabular icebergs calving from ice shelves may have a considerable effect on the heat budget of the Southern Ocean as they melt and subsequently cool the immediate waters around them (Everson, 1977).

Equally important is sea ice which fluctuates between approximately 4 and 22 million km^2 between summer and winter (Mackintosh, 1973). Ice prevents wave action and resultant turbulence, and acts as a light and thermal barrier causing a marked seasonality in the sea and primary productivity (Everson, 1977). Sea ice comprising the circumpolar pack ice zone is an important substrate for a variety of creatures, notably seals and penguins. Seasonal fluctuations in pack ice and its movements associated with wind drifts contribute significantly to the distribution and movements of pack ice fauna.

III. MAJOR FAUNAL GROUPS PRESENT IN THE ANTARCTIC MARINE ECOSYSTEM

The following section presents a partial list of Antarctic marine fauna. Admittedly, the list is incomplete and there are many other biotic components within the ecosystem. For example, plankton and benthic invertebrates are not included except for some Euphausiid species. Species and species groups were chosen which were felt to have potential commercial importance in the Southern Ocean or which are known to be important in the overall ecosystem on the basis of the group's large biomass. Hopefully, the list includes representative species which are most critical to discussions of marine ecology and the development of a conservation regime for living resources of the Southern Ocean. The principal sources for this information were Brown et al., 1974 (whales and seals); Watson et al., 1971 (birds); and Everson, 1977 (fish, cephalopods, and Euphausiids).

A. Whales

Baleen whales: Mysticeti

Blue whale	*Balaenoptera musculus*
Pigmy blue whale	*Balaenoptera musculus brevicauda*
Fin whale	*Balaenoptera physalus*
Sei whale	*Balaenoptera borealis*
Minke whale	*Balaenoptera acutorostrata*
Humpback whale	*Megaptera novaeangliae*
Southern right whale	*Eubalaena australis*

Toothed whales: Odontoceti

Sperm whale	*Physeter catodon*
Killer whale	*Orcinus orca*
Hourglass dolphin	*Lagenorhynchus cruciger*
Dusky dolphin	*Lagenorhynchus obscurus*
Peale's dolphin	*Lagenorhynchus australis*
Commerson's dolphin	*Cephalorhynchus commersonii*
Southern right whale dolphin	*Lissodelphis peronii*
Long-finned pilot whale	*Globicephala melaena*
Spectacled porpoise	*Phocoena dioptrica*
Southern bottlenose whale	*Hyperoodon planifrons*
Arnoux's beaked whale	*Berardius arnuxii*

B. Seals

True seals: Phocidae

Crabeater seal	*Lobodon carcinophagus*
Weddell seal	*Leptonychotes weddelli*
Leopard seal	*Hydrurga leptonyx*
Ross seal	*Ommatophoca rossi*
Southern elephant seal	*Mirounga leonina*

Eared seals: Otariidae

Southern fur seals	*Arctocephalus tropicalis* *Arctocephalus gazella* *Arctocephalus forsteri*

C. Birds

Penguins: Spheniscidae

Emperor penguin	*Aptenodytes forsteri*
King penguin	*Aptenodytes patagonicus*
Adelie penguin	*Pygoscelis adeliae*
Chinstrap penguin	*Pygoscelis antarctica*
Gentoo penguin	*Pygoscelis papua*
Macaroni penguin	*Eudyptes chrysolophus*
Rockhopper penguin	*Eudyptes crestatus*

Albatrosses: Diomedeidae

Wandering albatross	*Diomedea exulans*
Black-browed albatross	*Diomedea melanophris*
Grey-headed albatross	*Diomedea chrysostoma*

Fulmars, Prions, Gadfly Petrels, and Shearwaters: Procellariidae

Southern giant fulmar	*Macronectes giganteus*
Southern fulmar	*Fulmarus glacialoides*
Antarctic petrel	*Thalassoica antarcitca*
Cape pigeon	*Daption capense*
Snow petrel	*Pagodroma nivea*
Narrow-billed prion	*Pachyptila belcheri*
Antarctic prion	*Pachyptila desolata*
Fulmar prion	*Pachyptila crassirostris*
Blue petrel	*Halobaena caerulea*
Great-winged petrel	*Pterodroma macroptera*
White-headed petrel	*Pterodroma lessoni*

Kerguelen petrel	*Pterodroma brevirostris*
Soft-plumaged petrel	*Pterodroma mollis*
Mottled petrel	*Pterodroma inexpectata*
Light-mantled sooty albatross	*Phoebetria palpebrata*
White-chinned petrel	*Procellaria aequinoctialis*
Sooty shearwater	*Puffinus griseus*

Storm petrels: Oceanitidea

Wilson's storm petrel	*Oceanitis oceanicus*
Black-bellied storm petrel	*Fregetta tropica*
Gray-backed storm petrel	*Garrodia nureis*

Diving petrels: Pelecanoididae

South Georgia diving petrel	*Pelecanoides georgicus*
Kerguelen diving petrel	*Pelecanoides* (*urinatrix*) *exsul*

Cormorants: Phalacrocoracide

Blue-eyed shag	*Phalacrocorax atriceps*

Skuas: Stercorariidae

South polar skua	*Catharacta maccormick*
Brown skua	*Catharacta lonnbergi*

Terns: Sterninae

Antarctic term	*Sterna vittata*
Arctic tern	*Sterna paradisaea*

Gulls: Laridae

Southern black-backed gull	*Larus dominicanus*

D. *Fish*

Rajidae:

	Raja georgiana
	R. murrayi
	R. eatonii

Gadidae:

Southern blue whiting or Southern poutassou	*Micromesistius australis*

Merluciidae:	
Patagonian hake	*Merluccius hubbsii*
Nototheniidae:	
	Notothenia gibberifrons
	N. coriiceps
Smoothhead Notothenia	*N. neglecta*
	N. rossii rossii
Marbled Notothenia	*N. rossii marmorata*
	N. magellanica
Antarctic tooth fish	*Dissotichus mawsoni*
Patagonian tooth fish	*D. eleginoides*
Antarctic sidestripe	*Pleuragramma antarcticum*
Channichthyidae:	
	Chamsocephalus gunnari
	Channichthys rhinoceratus
	Pseudochaenichthys georgianus
	Chaenocephlalus sp.
	Chionodraco sp.

E. *Cephalopods*

Onychoteuthidae:	
	Onychoteuthis banksii
	Moroteuthis ingens
	Moroteuthis robsoni
Thysanoteuthidae:	
	Thysanoteuthis rhombus
Ommastrephiade:	
	Nototodarus sloani sloani
	Nototodarus gouldi
	Todarodes sagittatus
	Todarodes filippovae
	Illex argentinus
	Martialia hyadesi
	Symplectoteuthis Oualaniensis
	Dosidicus gigas
	Ommastrephes pteropus
	Ommastrephes bartrami

Histioteuthidae:	*Histioteuthis bonelli*
Architeuthidae:	*Architeuthis sp.*
Gonatidae:	*Gonatus fabricii (antarcticus)*
Loliginidae:	*Loligo sp.*
Octopodinae:	*Pareledone sp.*
F. *Euphausiidae*	
Antarctic krill	*Euphausia crystallorophias* *Euphausia superba* *Euphausia frigida* *Euphausia triacantha* *Euphausia vallentini* *Euphausia longirostris* *Euphausia lucens* *Euphausia similis* *Thyasoessa macrura*

IV. HISTORY OF LIVING RESOURCE EXPLOITATION IN ANTARCTICA

In considering a conservation regime for Antarctic marine life, an historical review of past utilization may offer insight into the overall desirability of various approaches to harvest strategies. Evaluating influential economic, political, and scientific factors in the exploitation of Antarctic seals and whales may suggest policies conducive to management practices in the future.

A. Sealing (Fur Seals and Elephant Seals)

James Cook first crossed the Antarctic Circle in 1773. During the course of several return trips to southern oceans, he recorded seal abundance. Since northern hemispheric sealing was already a profitable and well developed industry, the number of sealers travelling to the Antarctic increased dramatically as word of the vast numbers of seals spread (Stonehouse, 1972).

In 1810 Frederick Hasselborough, an Australian sealer, discovered the subantarctic island of Macquarie and its abundant fur seals (*Arctocephalus fosteri*) and elephant seals (*Mirounga leonina*). He returned the next year with several sealing ships and began harvesting fur seals in earnest. Within only ten years virtually all of the hundreds of thousands of fur seals formerly in that area had been killed. The unrestrained slaughter continued as the sealers then turned to the elephant seal to exploit its blubber for oil. Again, within approximately a decade, all but a few of these seals were killed (Peterson, 1973). Once the seals were no longer abundant enough to exploit economically, sealers departed. However, because few or no fur seals were left, natural migration of fur seals did not reclaim this island until nearly 125 years later. Not until 1955 was a fur seal pup born. Since that time, the residual elephant seal has gradually increased to the present 100,000 or more.

In 1819 a British merchant, blown off course, discovered the South Shetlands and upon its return reported abundant seals. By the 1820-1821 season, 40 ships (British and American) were at the South Shetlands sealing. Within 4 years, 320,000 fur seals were killed, producing 940 tons of oil and leaving the fur seal stock depleted. For the next fifty years, the fur seal population gradually increased until 1870 when the sealers once again wiped out the population (Stonehouse, 1972). This story was repeated many times as the subantarctic islands of South Georgia, Kerguelen, Macquarie, Heard, and South Orkneys were discovered and stripped of seals. By the 1830's, most seal stocks of these islands were depleted or gone altogether (Stonehouse, 1972).

In that era, heavy demands for seal oil, coupled with poor scientific knowledge of individual species, led to maximizing immediate returns instead of trying to ensure the future survival and productivity of these stocks. The problem was accentuated since as many as nine nations simultaneously competed for short-term gains instead of cooperating to support long-term goals. In the end, the sealing industry collapsed due to its own excesses. Even when under the threat of over-harvesting themselves out of business, sealing companies generally resisted changing their harvest approach.

At the turn of the century, when the sealing industry was declining and whaling replacing it as a major source of oil, a first attempt was made at managing a seal population to extend its productivity over a long period. In 1904 an elephant seal population on South Georgia was harvested in limited numbers during a lull period in the local whale harvest. This limited harvest was continued for sixty years and produced a reliable yearly yield without adversely affecting the elephant seal stock.

B. Whaling (Blue, Fin, Humpback, Right, Sei, Sperm, Minke)

Vacant whaling stations such as Grytviken, Leith Harbour, and Husvik on South Georgia -- their beaches strewn with whale bones -- recall the profitable whaling industry in the first half of the century. Within that short 60 year period, the world's whale stocks were reduced by over 85% from 43 million tons to about 6.6 million tons (Laws, 1977a).

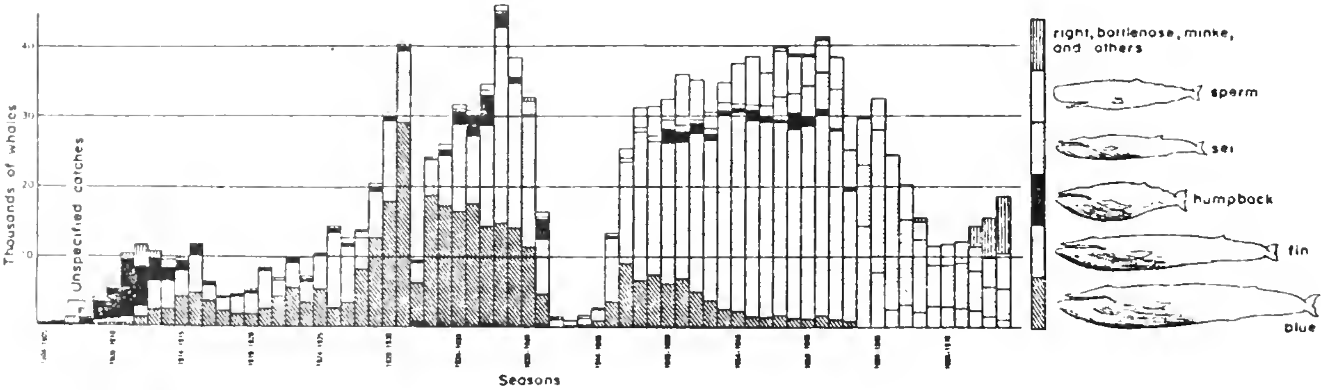
Explorers such as James Clark Ross advertized the abundance of whales in the Antarctic oceans by calling them "a fresh source of national and individual wealth". However, the first few attempts at whaling (1892) in the southern oceans were unsuccessful because of slow, old ships trying to catch fast moving whales (Stonehouse, 1972). In 1904 the first successful whaling station at Grytviken, South Georgia was established. Within a decade a dozen factories or ships (of Norwegian, Chilean, Argentine, and British affiliations) were operable at the South Shetlands; but land-based stations limited flexibility in catch effort. In 1925 steam factory ships were first utilized in the Southern Ocean (Everson, 1977). Their independence and speed, compared to shore stations, allowed a wider hunting range. They were also modified with rear slipways in the hull as well as mechanical strippers and mincers. Rendering capacities allowed ships to catch and process whole whales (Stonehouse, 1972). Unfortunately, because oil was the primary product, the whale was stripped of blubber and bone and the carcass left to rot (not until 1950 was the meat also utilized; Gulland, 1976a).

Whaling records provide valuable scientific data on whale populations. Figure 4 shows catch rates of blue, fin, humpback, sei, sperm, and smaller whales since 1904 (Everson, 1977). Rorqual catch effort over time proceeded along a size gradient; blue whales were first caught, fin whales next, and so forth. Of course, intensive single species harvests had devastating effects on whale stocks. Moreover, efficient whaling fleets were flooding the market with oil, drastically reducing its price. Regulating oil production would also regulate oil prices, so in 1930 Norway and Britian restricted the annual whale kill to a set amount of oil production per year.

Following the decline of whaling during the Second World War, the International Whaling Commission (IWC) was established in 1946 to monitor and regulate whaling efforts. It established the Blue Whale Unit (BWU) and limited the world's annual catch to 16,000 BWU, a limit based on "an inspired guess" (Gulland, 1976a). (One BWU is the equivalent of 2 fin whales, 2.5 humpback whales, or 6 sei whales.) Signatory countries outlined regulations to: 1) regulate the length of the hunting season, 2) establish minimum lengths, 3) protect females with suckling calves, 4) partially protect the humpback whale, and 5) totally protect the southern right whale (by this time no longer an economically attractive target). However, since national quotas were not assigned, whalers sought the biggest whales first - before other nations filled the world quotas. Although total catch was reduced, the quota was too high and the already diminished stocks of blue, fin, and humpback whales continued to decline. National quotas were finally established in 1960. In 1964, a committee of three scientists met to determine optimum catch levels for each species. Based on their efforts in 1965, the IWC established more conservative maximum sustainable yield (MSY) values for each species, regulated quotas by areas within a species' distribution, and provided a means of checking other nations' kill rates.

Today the IWC is a more effective body in scientifically managing whale resources. In the past, even when improved data became available, many of its efforts to conserve whale stocks were unsuccessful due to the political power of the whaling industry. Trying to impose management regulations upon a capital-intensive industry which developed free of such restraints has been demonstrated to be quite difficult. Such examples point to the need for the establishment of conservation and management regimes prior to and during the development of exploitation industries.

Figure 4. Catches of large whales in the Antarctic (From Brown et al., 1974).



V. SUMMARY OF AVAILABLE DATA ON MAJOR ANIMAL GROUPS

Both the sealing and whaling industries had at least one important aspect in common: attention was only directed to the species. No consideration was paid to the environment, and in the case of the seals, no *bona fide* management or conservation efforts were made until it was too late. Although nations did attempt to develop policies to conserve whales, many feel that these efforts failed to prevent over-harvesting until it was virtually too late. Conservation strategies were conceived as single species actions without consideration for ecological aspects of the whales' biotic and physical environment.

Moreover, there are other aspects of the ecosystem in general which were not considered with this sort of single species management. For example, ecosystem features such as nutrient cycling, energy flow, and species interactions such as competition and predation ought to be incorporated into management plans. These features must be considered today in recognition of their values to the entire ecosystem and their potential impact on both consumptive and non-consumptive uses of resources. Alternative priorities to direct resource exploitation include scientific research, tourism, aesthetic values, and maintaining ecosystem viability.

Although it is likely that many factors were responsible for the mismanagement and consequent over-fishing of whales, the single species approach was probably a major shortcoming. Consideration of the diverse features of the target species' ecosystem is better adapted to flexible, conservative management. An ecosystem approach to krill management is, therefore, imperative in light of krill's central role in the ecosystem. In an effort to understand how various forms of Antarctic marine life may interact, available information on several major Antarctic faunal groups will be reviewed. These groups are important both because of their central role in the ecosystem and the possible associated impacts on these groups resulting from future harvest of living resources.

A. Antarctic Krill

Central to this discussion of Antarctic living resources is *Euphausia superba*, known as Antarctic krill. Much of the recent krill literature pertains to potential new fisheries on its sizeable stocks present in the Southern Ocean. However, research on the biology and ecology of krill is scant, and much remains to be learned about krill's natural history. Several comprehensive works regarding krill and Euphausiids in general include the work of Fraser (1936), Bargmann (1945), Marr (1962), Nemoto (1966), Mauchline and Fisher (1969), Mackintosh (1970, 1972b, 1973, 1974), Ivanov (1970), and Everson (1976). Everson's (1977) excellent review of living resources in the Southern Ocean summarizes much of the information on krill and is heavily drawn upon in the following discussion.

1. Distribution

Krill are found in a circumpolar band around Antarctica and are thought to be swept generally northward by surface currents (Baker, 1954; Marr, 1962; Mackintosh, 1973; Everson, 1976) (Figure 5). Although several species of the genus *Euphausia* exist south of the Antarctic Convergence, *Euphausia superba* dominates. Figure 6, illustrating the relative distribution of Euphausiid and vertebrate species on a north/south latitudinal gradient, shows that *Euphausia superba* has a wide distributional range south of the Convergence. Although krill have a circumpolar distribution, there are areas of variable densities. Traditional areas of high krill concentrations include the East Wind Drift, the Scotia Sea, and South Georgia area (Beklemishev, 1960, 1961; Marr, 1962; Nemoto, 1968; Mackintosh, 1973). Brinton (1976) suggested that two major factors, current eddys and nutrient upwelling a different locations around Antarctica, contribute to the large scale distribution patterns of krill. Voronina (1966b) stated that in addition to the effects of currents, large krill concentrations may be due to prespawning accumulations.

Everson (1977) discusses various theories about krill distribution and movements. Perhaps the two main hypotheses about krill distribution are that 1) krill populations for the most part stay in one spot and 2) krill are distributed in a large circulation pattern. Some authors feel that krill remain in the same general area throughout their life, and that this might be accomplished by swimming in the opposite direction of currents and drift (Marr, 1962; Semenov, 1969; Mackintosh, 1972b). Although krill appear able to swim against currents up to speeds of .33 knots, resisting currents for sustained periods seems energetically unfeasible. Krill might also stay in one area by migrating through different water layers with opposing currents (Chevtsov and Makarov, 1969). Krill could ride the currents in one direction, and then, by making a relatively short vertical migration, enter the adjacent water mass and be carried back towards the starting point. Physical barriers, caused either by a temperature gradient or currents due to upwelling patterns, might also limit krill distribution to one area (Khvatskiy, 1972; Makarov, 1972; Fisher, 1976).

Ruud (1932) felt that krill may be swept over wide distances by major circulation patterns, and the Weddell Sea gyre with its associated high krill concentrations is offered as an example of

Figure 5. Principal concentrations of Antarctic krill. Arrows indicate major water currents (From Marr, 1962).

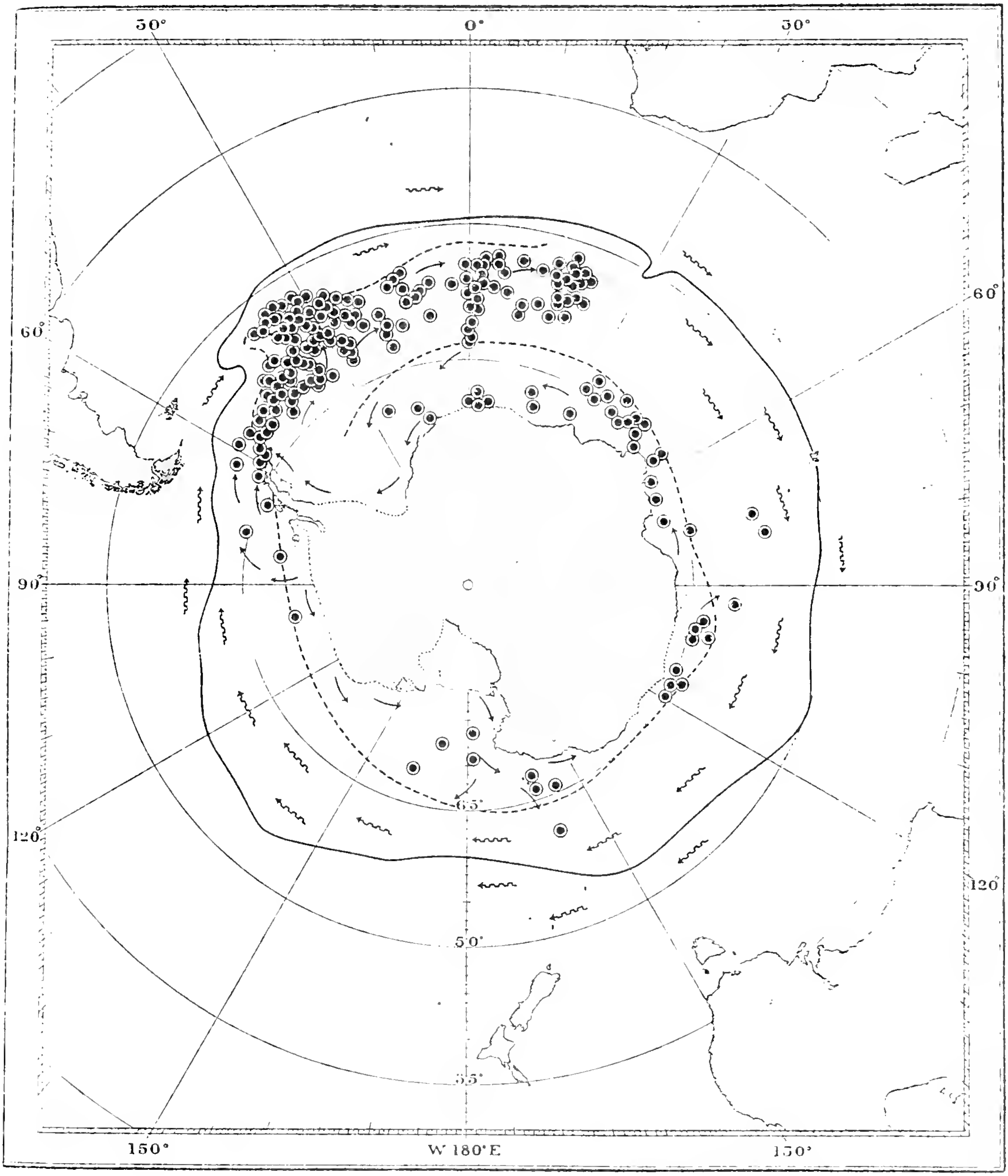
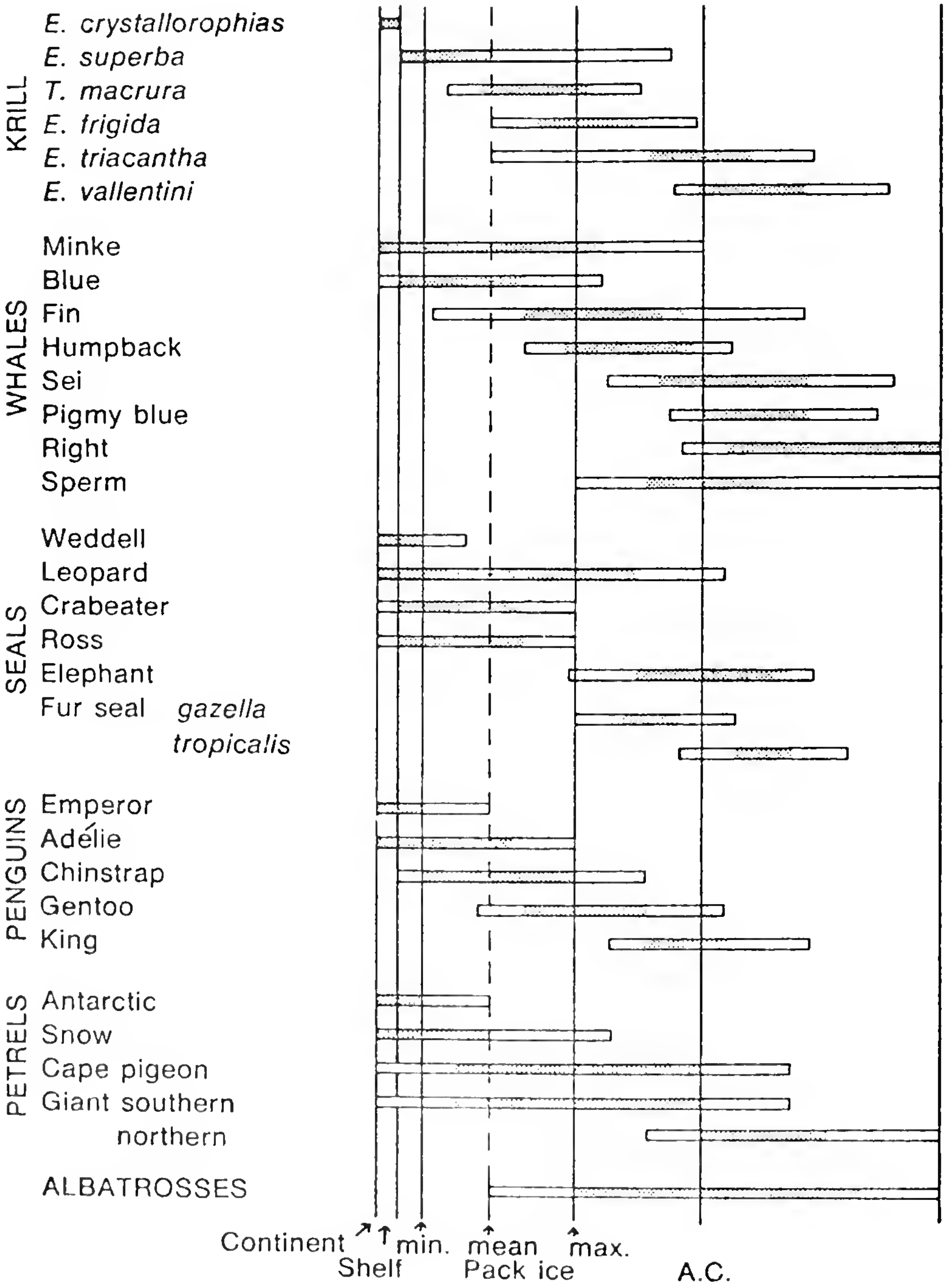


Figure 6. Comparison of the zones occupied by selected species of krill, marine mammals, and birds from the Antarctic continent northward. The relative area of the shelf; the minimum, mean, and maximum area of pack ice; and the area south of the Antarctic Convergence (A.C.) are indicated (Mackintosh, 1973). Each species has a circumpolar distribution, and the range indicated is the approximate average latitudinal range, the gray part indicating the higher densities. (Euphausiid distributions are from Mackintosh (1960) (From Laws, 1977b).



this hypothesis. The basic idea is that krill are swept around in cyclonic gyres with new individuals entering but few leaving (Beklemishev, 1960; Makarov, 1972; Treshnikov, 1971).

2. Movements

In addition to the horizontal movements that may occur as previously suggested, krill are known to make localized horizontal movements into high density patches or swarms (Hardy and Gunther, 1935; Gunther, 1949; Peters, 1955; Marr, 1962; Komaki, 1967). These patches vary in size and sex ratio and sometimes may be composed of individuals of the same age class (Marr, 1962). Figure 7 illustrates the general dimensions of several observed krill swarms. Mackintosh (1966) described swarms made up of juvenile and adult krill densely concentrated in the surface layer. In the summer, swarms mostly remain out of sight beneath the surface in darker waters by day while rising to upper waters strata to feed in the evening.

Marr (1962) stated that dense krill concentrations are likely to occur in the top 100 meters of the water column with the top ten meters being the depth most frequently used. He also described diurnal vertical migration patterns. His observations were supported by Shevtsov and Makarov (1969) as well as Pavlov (1969, 1974) who observed diurnal vertical migrations within the top 80 meters of the surface water. The authors associated these extensive daily movements with feeding. Apparently krill ascend as a swarm to reach the feeding areas where they disperse to feed and eventually regroup before descending.

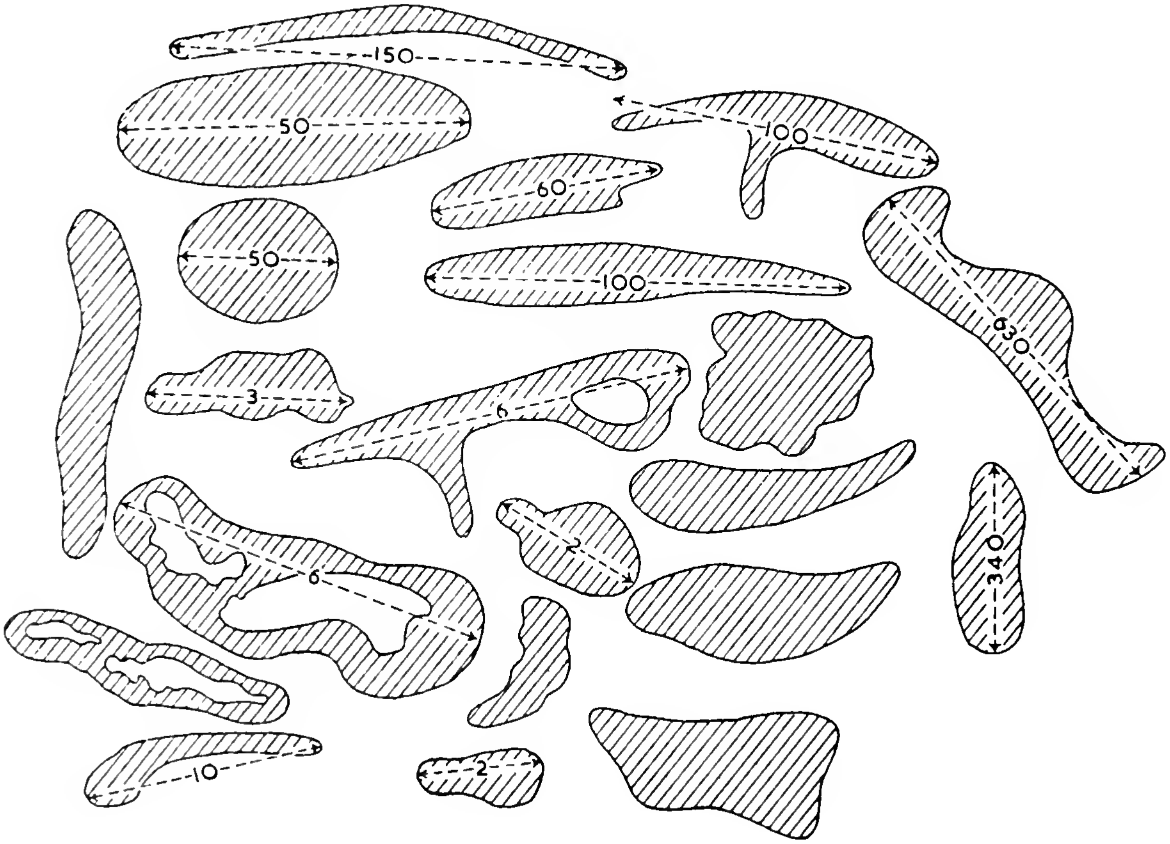
3. Stock Identification

It is not known if separate stocks of krill exist. Clearly the existence of races or stocks would critically influence management plans for a krill fishery. Nemoto et al. (1971) demonstrated the development of clines in North Pacific Euphausiids. Makarov (1974) and Mackintosh (1973), suggested that there may indeed be separate Antarctic krill stocks. They feel stocks might develop due to limited horizontal mixing of the gene pool. Recent work by McWhinnie and Denys (pers. comm.), based on repeated sampling in two different areas (the east Bellingshausen Sea and the Bransfield Strait), also suggests the possibility of separate krill stocks in the greater Antarctic Peninsula area. Although preliminary analyses of biometric measurements indicate possible stock differences, their findings are tentative, and further electrophoretic analyses are planned.

4. Standing Stock

Estimating krill standing stock is difficult due to widely variable krill densities caused locally by swarming. Techniques

Figure 7. Rough sketches of krill patches made by the late E.R. Gunther, Weddell Sea, January to February 1931, the approximate dimensions of some of them being given in yards. Illustration spacing has no relation to natural spacing (From Marr, 1962).



employed to estimate krill abundance have included trawling, acoustic sounders, estimating amounts consumed by predators, and estimating phytoplankton availability. In spite of these efforts, there are no reliable estimates of krill standing stock. Table 3, in presenting several biomass estimates, highlights the inherent uncertainties, evidenced by the wide range of values. Standing stock estimates are as much as several orders of magnitude apart, and estimates of annual production also vary widely (Table 4).

5. Reproduction

Although there are several studies on Euphausiid reproduction, (Marr, 1962; Mackintosh, 1972b; Makarov, 1974), the nature of Antarctic krill's breeding and reproduction is poorly understood. Good general reviews on Euphausiid reproductive biology are provided by Fraser (1936), Bargmann (1937), and Mauchline and Fisher (1969).

Authors differ on essential criteria for breeding sites. The main question is: can krill breed in pelagic oceanic areas or must they depend on continental shelf areas? Eggs, shed up to 500 meters below the water surface (Mauchline and Fisher, 1969), sink to depths of approximately 2,000 meters before hatching. In areas less than 2,000 meters deep, the eggs come to rest on the bottom. After hatching, the larvae slowly rise in the water column maturing as they ascend (Figure 8). In areas deeper than 2,000 meters, it was thought that perhaps eggs would sink so deeply as to prevent ascending larvae from reaching the surface by the time they require rich phytoplankton on which to feed. Hence shelf areas were thought to be important for proper development of eggs (Fraser, 1936). However, evidence now seems to suggest that the increased water density encountered at the Antarctic Bottom Water interface may preclude sinking beyond this point. Voronina (1974) related krill distribution to the relative densities of water over which eggs are spawned. He considered the density structure of the water column in different areas an important factor in limiting the range where krill eggs can develop to the optimal stage prior to ascending.

6. Food Habits

Food habits of krill have been studied by Barkley (1940), Hustedt (1958), Marr (1962), Nemoto (1968), and Kawamura (1978). Although there are differences in the authors' conclusions, there seems to be general agreement that diatoms make up a major portion of krill's food. Kawamura (1978) stated that krill feed almost exclusively on phytoplankton -- predominantly diatoms, and he found a high correlation between krill distribution and waters which had relatively small sized diatoms. Areas in which

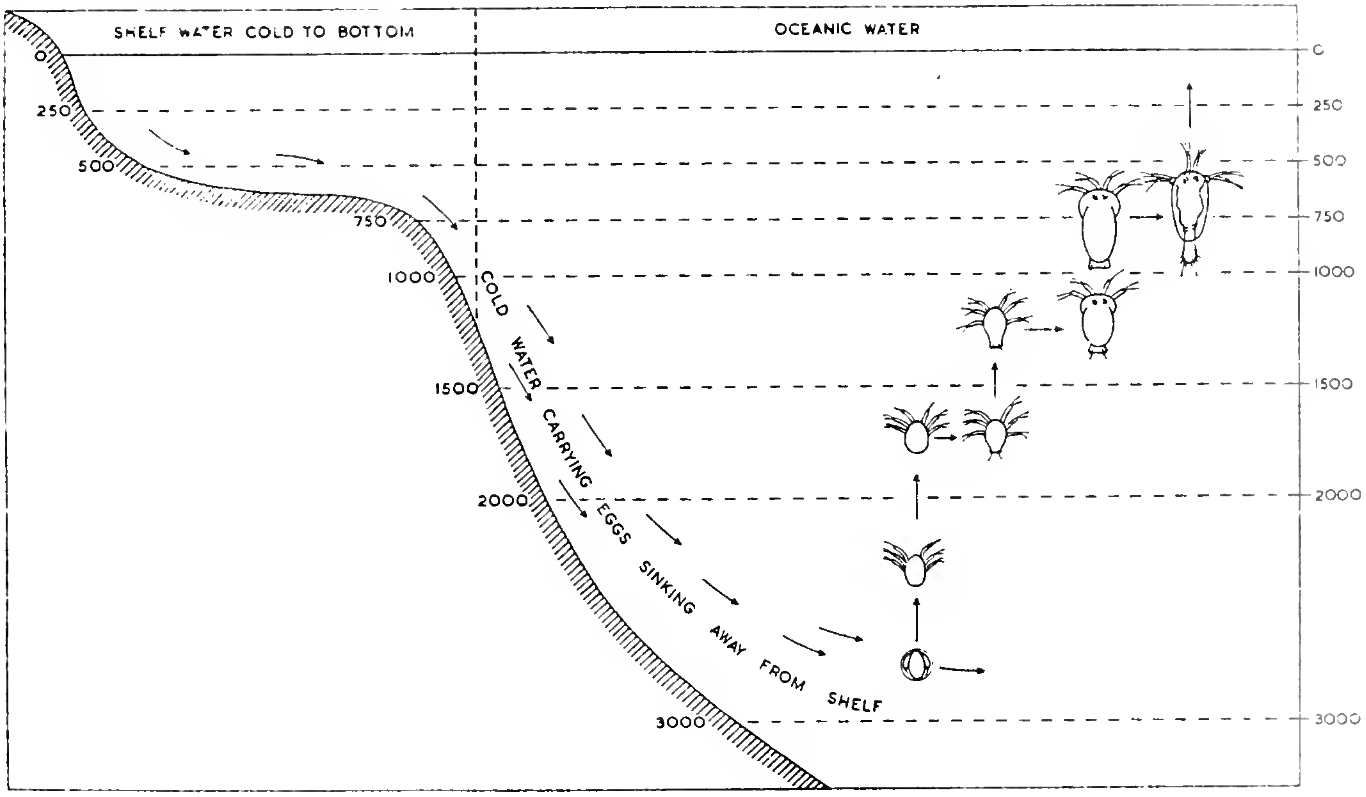
Table 3. Krill biomass estimates

Biomass (million metric tons)	Source
44.5-521	Marr, 1962
750	Gulland, 1970
5000-7500	Moiseev, 1970
953-1350	Makarov and Shevtsov, 1972
800	Lyubimova et al., 1973

Table 4. Estimates of krill annual production

Production (million metric tons)	Source
110	Foxton, 1956
50-500	Gulland, 1970
153	Mackintosh, 1970
1500-2250	Moiseev, 1970
25-50	Lyubimova et al., 1973

Figure 8. Supposed influence of the sinking shelf water on liberated krill eggs (From Marr, 1962).



larger diatoms were present were mostly devoid of krill. Therefore, Kawamura suggested that krill move to reach or remain in areas where preferred foods are located. Pavlov (1971, 1974) has shown that krill can feed on detritus, allowing them to feed throughout the year.

B. Antarctic Whales

Southern Ocean whale stocks, once abundant and diverse, supported the world's largest whale fishery eventually leading to their marked decline. As large-scale fisheries for other Southern Ocean living resources are considered, the role of whales is again central to discussions regarding ecosystem interactions. Several reviews of Southern Ocean whales have been published (Mackintosh, 1970, 1972a; Gambell, 1973, 1976e; Laws, 1977a, 1977b; Nishiwaki, 1977). A great deal is known about the great whales because of their commercial importance. Moreover, because of their large individual and population biomass, their role in the trophodynamics of the marine ecosystem and their direct relationship to krill are of major significance. Hence, the following comments deal principally with baleen species including: sei, fin, blue, humpback, and minke whales. Sperm whales and some of the smaller odontocetes will be mentioned when available information is appropriate to the discussion. The following section reviews information on the distribution, movements, standing stock, stock identification, and food habits of the whales of the Southern Ocean, both before and after major exploitation earlier in this century.

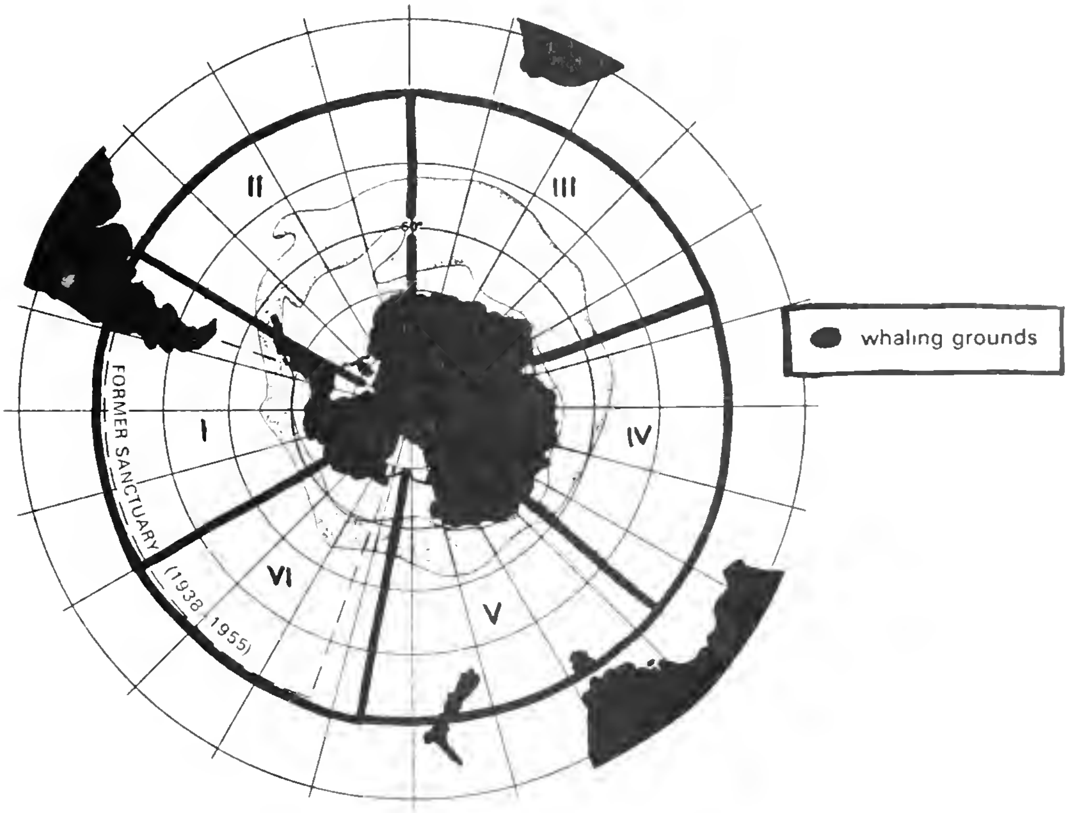
1. Baleen Whales

a. Distribution

Mackintosh (1973) investigated seasonal variations in the location of Antarctic whaling grounds. Figure 9 shows the principal summer feeding areas for Antarctic baleen whales. The relationship between Euphausiid and vertebrate species distribution in the Antarctic is shown in Figure 6.

Although baleen whales generally have a circumpolar distribution, latitudinal differences between species exist since some whales travel farther south to feed than others. For example, blue whales and minke whales concentrate between 60° S. and 70° S., fin whales are most highly concentrated while feeding from 50° S. to 60° S., sei whales are mostly found from 40° S. to 50° S., pigmy blue whales rarely are found south of 54° S., and southern right whales mostly inhabit subantarctic waters between 30° S. and 50° S. year-around (Taylor, 1957; Ichihara, 1966; Ohsumi et al., 1970; Laws, 1977a). In addition to partitioning feeding grounds by species, whales also demonstrate

Figure 9. Map of whaling statistical areas and whaling grounds (From Brown, et al., 1974). High whale harvests were undertaken in areas II and III.



latitudinal and longitudinal segregation within species between age classes and sexes (Laws, 1960a, 1961, 1977b; Mackintosh 1965; Dawbin, 1966). Older individuals appear to occupy more southerly areas in locations of dense zooplankton concentrations, and pregnant or lactating females arrive at different times depending on their particular reproductive status. Laws (1977a) proposed that these segregation patterns may have been the result of competition for food, implying that food availability may have been limiting to the whale populations prior to major whaling and commercial exploitation.

Gulland (1974), suggested that cetacean distribution is related to the basic productivity of various oceanic areas. Although whale abundance and primary productivity levels did not necessarily correlate well, he showed very good correlations between baleen whale and zooplankton densities (particularly krill). Baleen whales are more confined to areas of high zooplankton biomass than are sperm whales which feed on secondary consumers such as squid. Gulland also examined the relative catch levels of whales in the different statistical areas (Figure 9), and found that Sections II and III had much higher total catch levels than other areas. Section IV had a moderately high catch level. While these figures suggest that Sections II, III, and IV were more productive than areas I, V, or VI, Gulland cautioned that since most whaling was concentrated in these areas, the catch figures may have a strong bias.

b. Movements

Every year, whales migrate from their northerly breeding grounds to the cold Antarctic waters primarily to feed on krill and other zooplankton (Mackintosh, 1970, 1972a) (Figure 10). Whale concentrations feed in a narrow circumpolar band along the pack ice edge as it moves south in the summer (Mackintosh, 1973). As the pack ice begins to move north in the fall, the whales return north to their tropical and subtropical breeding grounds (Mackintosh, 1972a). Figure 11 outlines the movements of female fin whales in relation to time of year, reproductive status, and pack ice distribution as well as their annual intensive 3 to 5 month feeding periods. Figure 12 presents information on principal movements between breeding and feeding grounds obtained from marked sei, humpback, and fin whales.

Movements of Southern Ocean baleen whales, particularly those that migrate long distances, appear to have regular features. Dawbin (1966) stated that migrations of blue, fin, humpback, and sei whales are staggered. Blue whales are the first to arrive in the feeding grounds, fin and humpback whales coming second, and sei whales generally arriving last (Laws, 1977b). Southern right whales do not appear very migratory and rarely penetrate polar waters (Laws, 1977b). Whereas north-south

Figure 10. Schematic diagram of general migration patterns of great whales (From Mackintosh, 1965).

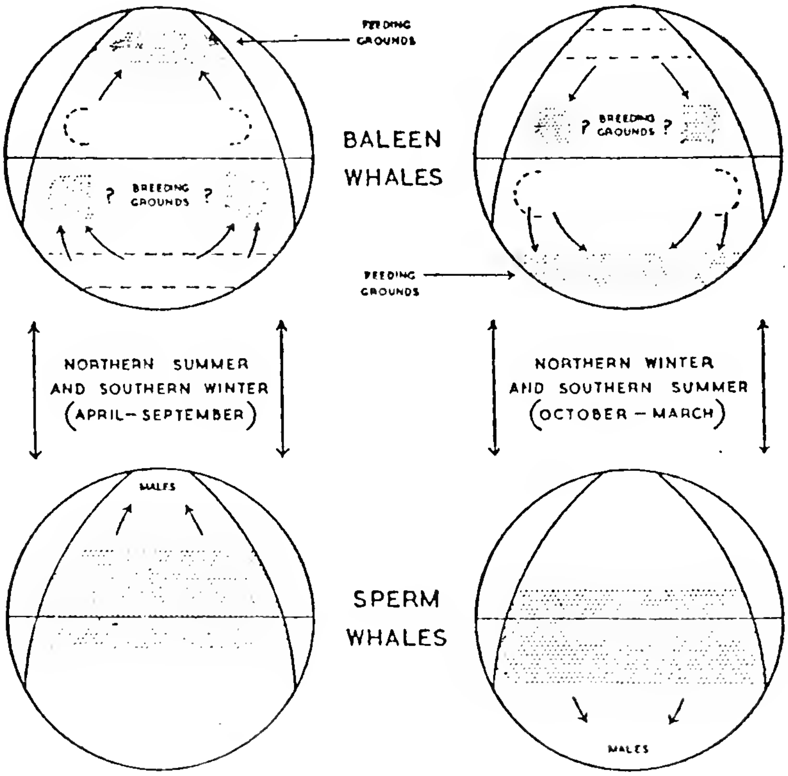


Figure 11. The seasonal cycle in southern fin whales. Upper part: migrations of a typical adult female, by latitude and time. Lower part: lactation, etc., apply to the thicker curves; thinner curves are for a female in the opposite phase of the 2-year cycle. Continuous lines are based on relatively firm evidence, and broken lines are tentative. Lightly dotted lines are the probable envelope of most migrations (From Mackintosh, 1972d).

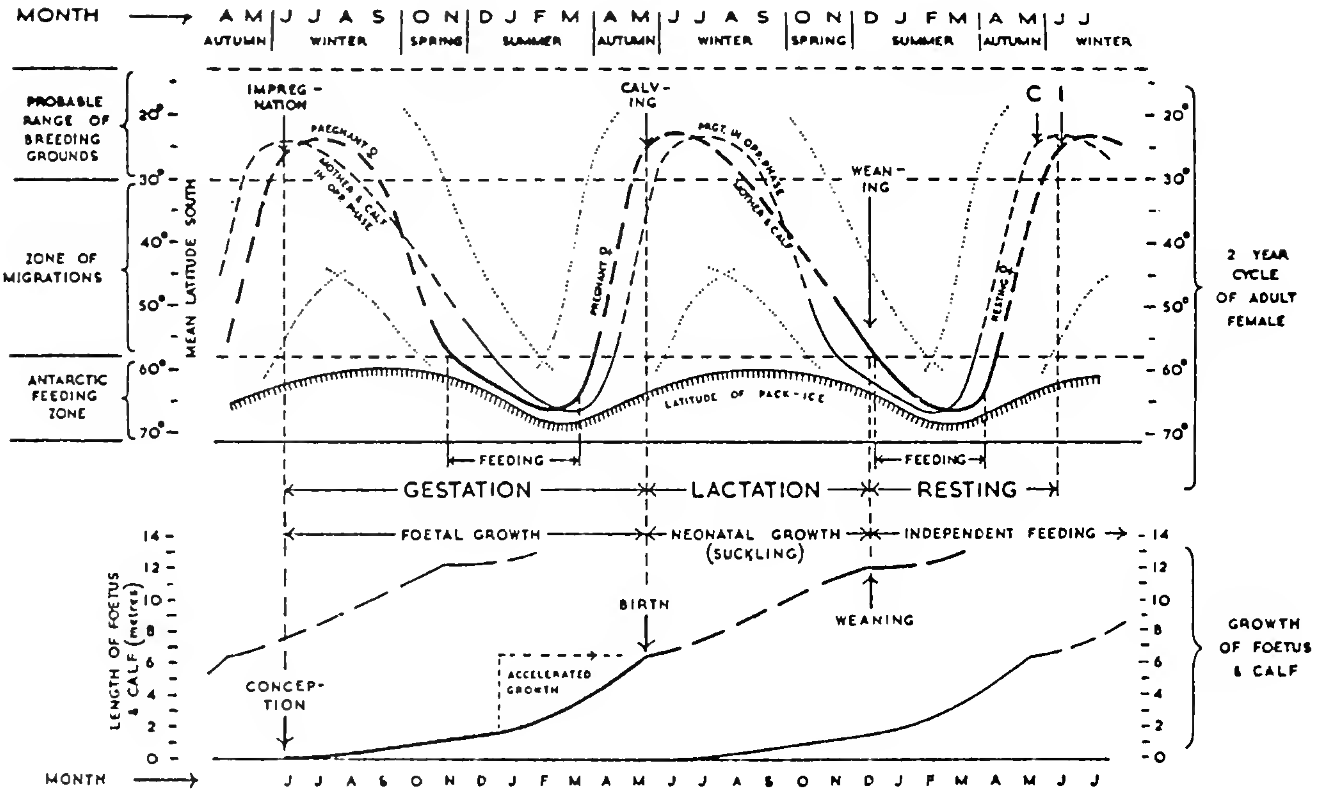
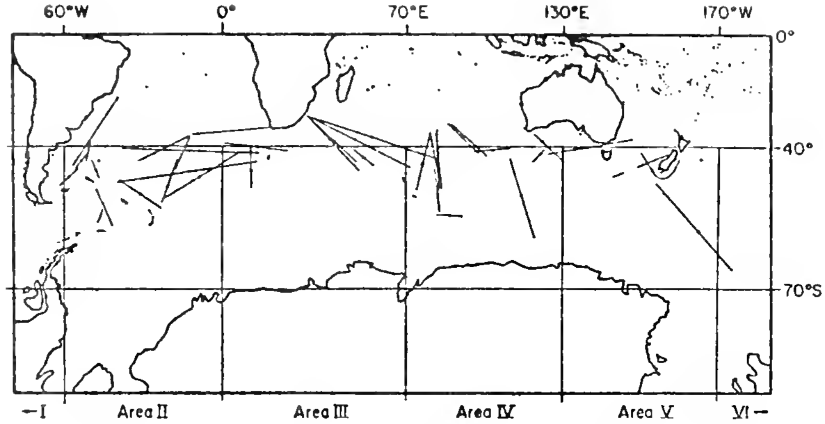
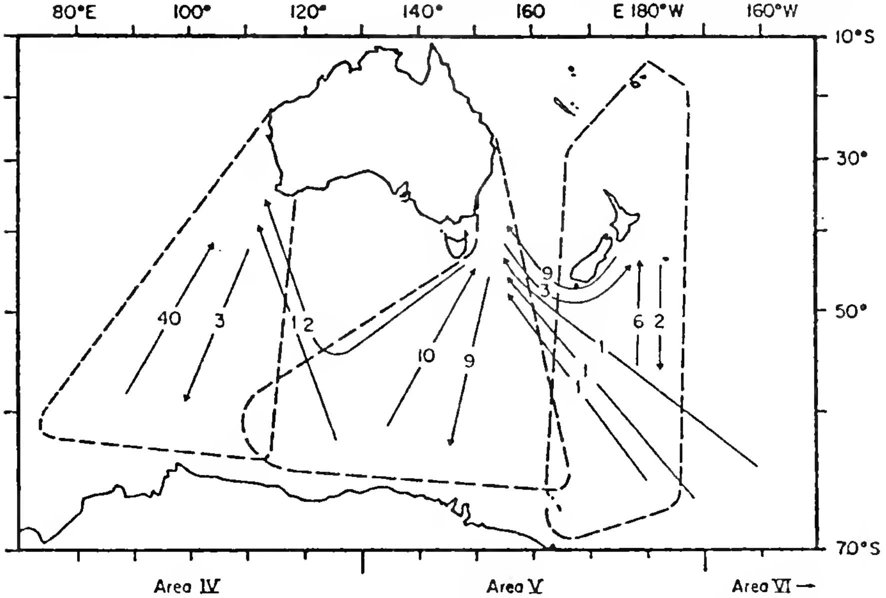


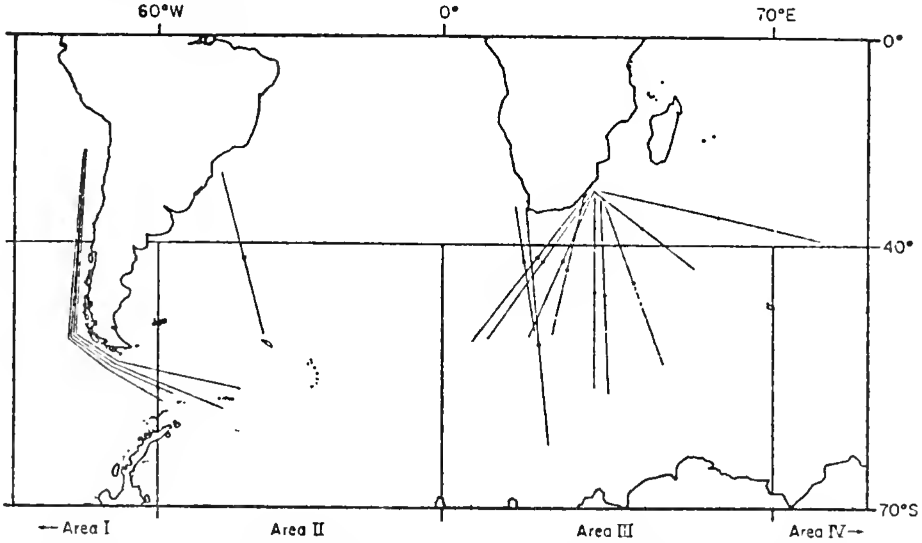
Figure 12. Movement patterns of sei, humpback, and fin whales on the basis of placement and recovery of whale marks (From Gambel, 1976e).



Main movements of marked sei whales in the southern hemisphere (data from Brown, 1968a, 1973; Ivashin, 1973).



Movements of marked humpback whales in the region around Australia and New Zealand, shown by numbers of whales moving between areas indicated (after Dawbin, 1966).



Movements of marked fin whales between the breeding and feeding grounds in the southern hemisphere (data from Brown, 1962-1973).

movements seem well established, whale marking suggests that east-west movements of baleen whales between the six statistical whaling areas are limited (Brown, 1962c). Hence, when areas I and V were set aside after World War II as whaling sanctuaries, agreement was possible because these areas of low whale abundance were unlikely to harbor stocks from outside the sanctuaries.

Gambell (1975c) noted that Antarctic populations of sei whales appear to follow the general large baleen whale pattern of breeding in equatorial or subtropical waters and then moving south in the summer to feed. As noted previously, they do not move as far south as other species such as fin, blue, and minke whales (Gambell, 1968). However, since sei whale harvest was not economically attractive until the last decade, there is less information on their movements than on those of other whales. Whale mark recoveries to date are not adequate to clarify important movements and statistically identify fine differences in sei whale stocks (Brown, 1968b, 1968c).

c. Stock Identification

An ecosystem perspective requires consideration of factors beyond just numbers of individuals to allow proper management of the system. Separate stocks within species must be identified and managed in relation to the ecosystem as a whole. This approach is supported by both domestic legislation (Marine Mammal Protection Act of 1972) and international law (Convention for the Conservation of Antarctic Seals).

1) Humpback Whale

Humpback whales are generally thought to have six separate stocks or populations in the Antarctic (Mackintosh, 1965; Winn, 1976) and are perhaps the best example in this ecosystem of a species with relatively well-identified stocks. Each breeding stock migrates south during the summer to feed at which time there is some stock intermingling. Chapman (1974b) notes that intermingling does not necessarily mean that the whales are together physically, rather that different stocks have the potential to enter the same statistical area in one season. Some humpback whale stocks were depressed much farther than others (Chittleborough, 1965; Mackintosh, 1970). Therefore, recovery of different humpback populations may progress at different rates and may be variably sensitive to further ecosystem manipulation (differential exploitation of stocks within other species, such as blue whales has also occurred). Consideration must be given to the ecosystem roles of individual humpback populations as well as other Antarctic species in formulating a conservation regime which allows further resource exploitation.

2) Blue Whale

On the basis of blue whale catch statistics and marking studies, the statistical whaling areas were established. Whale marks are generally recovered in the same statistical areas in which they are placed. Recoveries from areas other than where the tags were administered suggests some minimal movement between areas. For example, one blue whale tag administered in area II was recovered in area IV (Chapman, 1974b).

3) Pigmy Blue Whale

Fujino's (1962) research with population genetics suggested that there may be separate pigmy blue whale stocks feeding in Antarctic waters during the summer. Ichihara (1974) also presents limited information supporting the idea of separate stocks of pigmy blue whales.

4) Fin Whale

Identifying separate breeding stocks of fin whales is difficult because they are commonly more dispersed than humpback whales. However, general movement patterns and stock segregation similar to humpback whales may indeed be occurring (Chapman, 1974b). There is evidence that fin whales form relatively small subpopulations in certain northern areas (Fujino, 1964; Jonsgard, 1966). Perhaps similar patterns are present in Antarctic fin whales. Gambell (1975a) stated that segregated breeding stocks of southern hemisphere fin whale populations are often thought to exist, and that the six IWC statistical areas seem to approximate these stocks. However, using data from Ivashin (1969), Gambell (1975a) divided southern fin whales into eight stocks which apparently mix to some extent in the feeding grounds. Whale marking (Brown, 1962c, 1962e, 1972), body lengths of individuals in separate areas (Laws, 1960), iodine values of fin whale oil (Lund, 1950a, 1950b, 1951), and serological studies (Fujino, 1964) also suggest separate fin whale stocks.

5) Sei Whale

Sei whale stocks are poorly known because marking efforts were virtually non-existent prior to the 1960's when major exploitation of this species began. Knowledge of movements and breeding groups is scant. Even though sei whales do not range as far south as other whales, they do move south of the Antarctic Convergence in certain areas.

6) Minke Whale

Data on the entire southern minke whale population do not appear to support or contradict the existence of separate stocks.

d. Standing Stock

Standing stock estimates for Antarctic whales are not easily made. Information used for this purpose includes sighting records, catch per unit effort, reproductive parameters, mortality rates and mark-resight data on movements (Mackintosh, 1970). Gambell (1976e) discusses methods of estimating standing stocks of whales including sighting, marking, recruitment curve methods, mortality and catchability, least squares method, and the DeLury Method.

Various standing stock estimates for Southern Ocean baleen and sperm whales appear in Tables 5 and 6. Present and initial stock estimates of minke whales are close because minke whales were largely unexploited before 1971. According to Mackintosh (1972), less than 100 minke whales were taken annually until 1971,when 3,000 were taken.

Because of limited commercial interest in minke whales, information on this species is limited in comparison to other Southern Ocean baleen whales. Without more data, it is not possible to develop estimates with a high degree of confidence. Moreover, it is unclear how large the historic stocks of minke whales were prior to intensive harvest of the great whales in the Southern Ocean. Since population estimates have only been made in the last decade, estimates of pre-exploitation abundance are not good. It may be that the current minke whale populations exceed pre-exploitation levels. This possibility is discussed in a later section.

As shown in Figure 5, most species abundance estimates are within a reasonable interval of each other. An exception is Laws' (1977a) estimate for initial sei whale stocks which he puts at 75,000 individuals, roughly half other estimates. This is explained by Laws' conclusion that 75,000 individuals actually fed south of the Convergence while other estimates may have included Southern Hemisphere individuals which did not spend major time feeding south of the Convergence. In general, when abundance estimates are made for whales in the Southern Hemisphere, there are at least three levels for which estimates of whale abundance in the Southern Hemisphere are made: 1) the entire Southern Hemisphere, 2) south of 40° S, and 3) south of the Antarctic Convergence. Although most of the figures in Table 5 were chosen as those referring to abundances south of the Convergence, some may have incorporated larger areas. Gambell (1975c) pointed out

Table 5. Estimates of exploitable standing stocks of Antarctic whales.

Species	Stock size (thousands) initial	Stock size (thousands) present	Authority
Blue	100		Zenkovich, 1970
	210	6	Gulland, 1972
	150	6	Mackintosh, 1972a
		6	Masaki, 1973
	150	5-10	Chapman, 1974b
	200	10	Laws, 1977a
Pigmy Blue	10	8	Ichihara and Doi, 1964
		6	Mackintosh, 1972a
Fin	320-400		Jonsgard and Ruud, 1964
	200		Zenkovich, 1970
	350-425	80-85	Mackintosh, 1972a
	395-425	82-94	Ohsumi, 1973
	350-400	70-80	Chapman, 1974b
	450		Gulland, 1974
		83-84	Gambell, 1975a
	400	80.5	Gambell, 1976b
	400	84	Laws, 1977a
Sei	150		Doi and Ohsumi, 1969
	150	80	Mackintosh, 1972
	150	70-80	Chapman, 1974b
	150	50-55	Gambell, 1975c
	75(#S. of Conv.)	40.5	Laws, 1977a
Humpback	50	almost exterminated	Zenkovich, 1970
	100	3-4	Mackintosh, 1972a
	90-100	1.7-2.8	Chapman, 1974b
		3	Ohsumi and Masaki, 1974
	100	3	Laws, 1977a
Right		4-5	Ohsumi and Masaki, 1972
Minke	150-200	150-200	Mackintosh, 1972a
		204	Chapman, 1973
	299	291	Ohsumi and Masaki, 1974
		150	Gambell, 1975b
	200	200	Laws, 1977a
Sperm		85	Ohsumi, et al., 1971
	85	43	Laws, 1977a

Table 6. Crude estimates of large whale populations, biomass, and food consumption in the Antarctic (From Laws, 1977a).

Species	Stock (thousands)	Mean Weight (metric tons)	Mean Antarctic Biomass (10^3 metric tons)	Food Consumption (10^3 metric tons)		
				krill	squid	fish
		Initial Stocks				
baleen whales						
fin	400	50	20000	81480	840	1680
blue	200	88	17600	71702	740	1478
sei	75*	18.5	1887	5651	58	116
humpback	100	27	2700	11000	113	227
minke	200	7	1400	19827+	204	409
total	975	--	43087	189660	1955	3910
sperm whales	85*	30	2550	--	10200	500
		Present Stocks				
baleen whales						
fin	84	48	4032	16426	169	339
blue	10	83	830	3381	35	70
sei	40.5#	17.5	709	2888	30	60
humpback	3	26.5	79	322	3	7
minke	200	7	1400	19827+	204	409
total	337.5	--	7050	42844	441	885
sperm whale	43*	27	1161	--	4632	244

Half total sei whale stock assumed to feed south of the Antarctic Convergence

* One third total "exploitable male" sperm whales assumed to feed in the Antarctic

\+ Minke whale assumed to feed year round in Antarctic waters at 4% body mass/day that although sei whale populations remained fairly constant in the early seventies, population models used to describe this population's characteristics may not adequately represent its actual population dynamics. Population adjustments may have resulted from declines in other baleen whales and changed interactions with those species. The changes, which may include expanded sei whale feeding grounds and an increase in overall abundance, will be discussed later.

e. Feeding Habits

The quantities and type of food consumed by baleen whales in the Antarctic has received much attention (Mackintosh and Weller, 1929; Hardy and Gunther, 1935; Peter, 1955; Marr, 1956; Nemoto, 1959, 1962; Banister and Baker, 1967; Laws, 1977a, 1977b). Tables 6 and 7 present information on relative biomass and variety of food items consumed by whales in the Southern Ocean. Krill seems to be the main food for blue, fin, humpback, and minke whales (Mackintosh, 1965). About 80% of the blue, fin, and humpback whale diet is krill. It is all consumed during the whales' 3 to 5 month austral summer feeding period (Mackintosh 1970). Sei whales are somewhat less dependent on krill and it may account for less than half their diet (Mackintosh, 1970). But, since the serious decline of other whales, sei whales have been moving farther south into heavy krill zones where other whale species formerly fed and now may be eating more krill (Nemoto, 1962). Minke whales, with a current estimated total biomass of only 1.4 million tons, consume more krill than any other baleen whale in the Antarctic (Laws, 1977a). One reason for this high level is that minke whales presumably remain south of the Convergence all year long while other baleen whales are south of the Convergence only during their intensive feeding period.

Food habits of different Antarctic baleen whales reflect several factors, including food distribution, morphological characteristics of the whales' feeding apparatus, individual species' feeding behavior, and the presence of other whales and competitors. Comparing blue, fin, and sei whales, one notes a trend of feeding areas with sei whales in the more northerly areas, fin whales a little further south, and blue whales the farthest south (Gulland, 1974). Food items taken by the different species varies also. Blue whales eat Euphausiids primarily, fin whales euphausiids and copepods, and sei whales mainly copepods (Nemoto, 1970). The three species each have a characteristically different feeding apparatus representing different

Table 7. Stomach contents of baleen whales caught by Japanese pelagic catch from 1961 to 1965 in the Antarctic *(After Nemoto, 1970).

Food Species	Whale Species				
	Blue**	Fin	Sei	Humpback	Minke
Euphausiids	517	16158	5936	7	88
Euphausiids and others	4	18	4	--	--
Copepods	2	--	2472	--	--
Amphipods	6	9	1514	--	--
Munida decapods	--	--	75	--	--
Fish	--	76	31	--	--
Squids	--	--	5	--	--
Empty	674	18878	16145	2	10
No. of whales examined	1203	35139	26182	9	98

* Sei whales include 1966 season

** Mainly subspecies _Balaenoptera musculus brevicanda_ distributed in the lower Antarctic feeding strategies identified by Nemoto (1970): swallowers, skimmers, and combination swallowers/skimmers. Swallowers are adapted to feed on dense patches of plankton -- often Euphausiids. Skimmers can use sparser plankton patches commonly composed of amphipods, copepods, or decopods. In the Antarctic, blue, fin, minke, and humpback whales would be categorized as swallowers that feed primarily on krill. Antarctic right whales, on the other hand, would qualify as skimmers using amphipods and copepods as primary food sources. Sei whales, combination swallowers/skimmers, use a wide variety of food depending on availability. These three feeding strategies may be one mechanism to allow baleen whales to co-exist in Antarctic waters by partitioning food resources. Other mechanisms which allow greater partitioning of food resources include spatial and temporal segregation of whale stocks (Laws, 1977a).

Mitchell's (1975) paper on trophic relationships and competition for food among whales noted the likelihood of food competition between whale species. He suggested that trophic relationships among sympatric species might shift as the relative abundance of prey species varies through time. The implied food preference of different whale stocks provides evidence for competitive exclusion between groups of whales. Switching feeding habits to less preferred food items reduces overt competition. The significance of competition among whales and other krill consumers in relation to the decline of the great whales will be discussed later.

2. Toothed Whales

Nishiwaki (1977) recently reviewed toothed whale distribution in the Southern Ocean. He stated that most toothed whales, except for sperm and killer whales, do not go farther south than 60° S. Commerson's dolphin, known in southern portions of South America, occasionally strays south. The hourglass dolphin, dusky dolphin, and Peale's dolphin occasionally range as far south as the northern edge of the pack ice. However, Peale's dolphin is rarely found away from its usual range of the southern tip of South America, and the dusky dolphin does not usually go further than 58° S. The other small odontocete whales occur only rarely south of the Convergence (Brown et al., 1974).

a. Sperm Whale

The best known Antarctic toothed whale is the sperm whale because of data acquired during commercial exploitation. Sperm whales are thought to have widely dispersed feeding stocks in lower latitudes (Mackintosh, 1972a). Although Best (1975) found little direct evidence to support separate stocks of southern sperm whales, he reviews stock identification research including blood typing (Cushing et al., 1963), morphometry (Clarke and Poliza, 1972; and Machin, 1974) and whale mark recoveries. Gulland (1974) noted the well known phenomenon that only male sperm whales are found in polar areas, and suggested that this unexplained sexual segregation may be a social factor since he found no clearly identified food type differences in tropical and polar waters. Commercial sperm whaling yielded the highest catches from whaling statistical areas II, III, and IV -- similar to baleen whaling. Again, it is not known if this high level is due to increased effort or other factors.

b. Killer Whale

Killer whales are relatively small but highly predatory whales found all around Antarctica which may hunt in packs in excess of 25. They reputedly attack whales, seals, and birds, but, according to Erickson and Hofman (1974), their main food items are fish and squid. Although Siniff and Bengtson (1977) attribute the predominance of crabeater seal scars to leopard seals rather than killer whales, the authors hypothesize that killer whales probably take crabeater seals successfully, and hence leave no scars.

C. Antarctic Seals

Seals play important ecological roles in the Antarctic marine ecosystem. Those found south of the Convergence include the four true Antarctic seals of the subfamily Lobodontinae: crabeater, Weddell, leopard, and Ross as well as the southern elephant seal and southern fur seals. Recent reviews on Southern Ocean seals include those by Erickson and Hofman (1974), Laws (1977a, 1977b), Gilbert and Erickson (1977), and Øritsland (1977). Information on the distribution, movements, stock identification, standing stock, and food habits of these seals follows.

1. True Antarctic Seals

Accounts of the ecology and biology of the four true Antarctic seals are found in papers on 1) crabeater seals (Wilson, 1907; Lindsey, 1938; Bertram, 1940; Laws, 1958, 1964, 1977a, 1977b; Øritsland, 1970b; Erickson and Hofman, 1974; Siniff et al., 1977a, 1978); 2) Weddell seals (Bertram, 1940; Stirling, 1969c, 1971a, 1971b; Siniff et al., 1971, 1974, 1977b; Erickson and Hofman, 1974; Kaufman et al., 1974; DeMaster, 1978); 3) leopard seals (Wilson, 1907; Brown, 1957; Hamilton, 1939; Marlow, 1967b; Penney and Lowry, 1967; Erickson and Hofman, 1974; Hofman et al., 1977); and 4) Ross seals (Erickson et al., 1973).

a. Distribution

These seals have a circumpolar distribution (Figures 13, 14, 15, 16). Crabeater, leopard, and Ross seals use pack ice principally whereas Weddell seals are usually found in fast ice areas adjacent to the continent, ice shelves, and offshore islands.

1) Crabeater Seals

Crabeater seals appear to prefer being relatively close to the ice edge in cake and brash ice of 7 to 8 octas concentration (Gilbert and Erickson, 1977). Siniff et al. (1970) and Erickson et al. (1971) showed the relationship between crabeater seal distribution and the ice type selected. These authors found that seals selected unconsolidated pack ice covering between 30% and 70% of the water surface.

Concentrations of subadult crabeater seals observed by Siniff et al. (1977b) may have broad biological significance since similar crabeater concentrations have been previously observed, but perhaps not understood in the context of what they actually represented. Laws and Taylor (1957) reported a major die-off of crabeater seals and assumed that it was caused by a viral infection. Solyanik (1964) also reported a concentration of up to 3,000 crabeater seals. Lindsey (1938) described concentrations of crabeater seals in fast ice in the Bay of Whales in 1934. If concentrations of crabeater seal subadults are more prevalent than previously thought, it may be that young individuals from large areas of pack ice concentrate in the areas and feed as a group near continental areas or offshore islands. Localized concentration areas may, therefore, be critical to crabeater seal stock stability over a wide area, and disruption or harassment of seals in concentration areas may be particularly harmful.

2) Leopard Seals

Leopard seals are normally found in areas dominated by cake and brash ice between 60° S. and 80° S. although occasionally individuals have strayed to the southern tips of Africa, South America, Austrialia, and New Zealand. Normally solitary in pack ice, they sometimes concentrate on subantarctic islands (Kemp and Nelson, 1931; Marr, 1935, Hamilton, 1939; Bechervaise, 1962). Gilbert and Erickson (1977) showed a close correlation between leopard and crabeater seal densities and suggested that in addition to the physical characteristics of the ice flows, predation on crabeaters contributed to this high correlation.

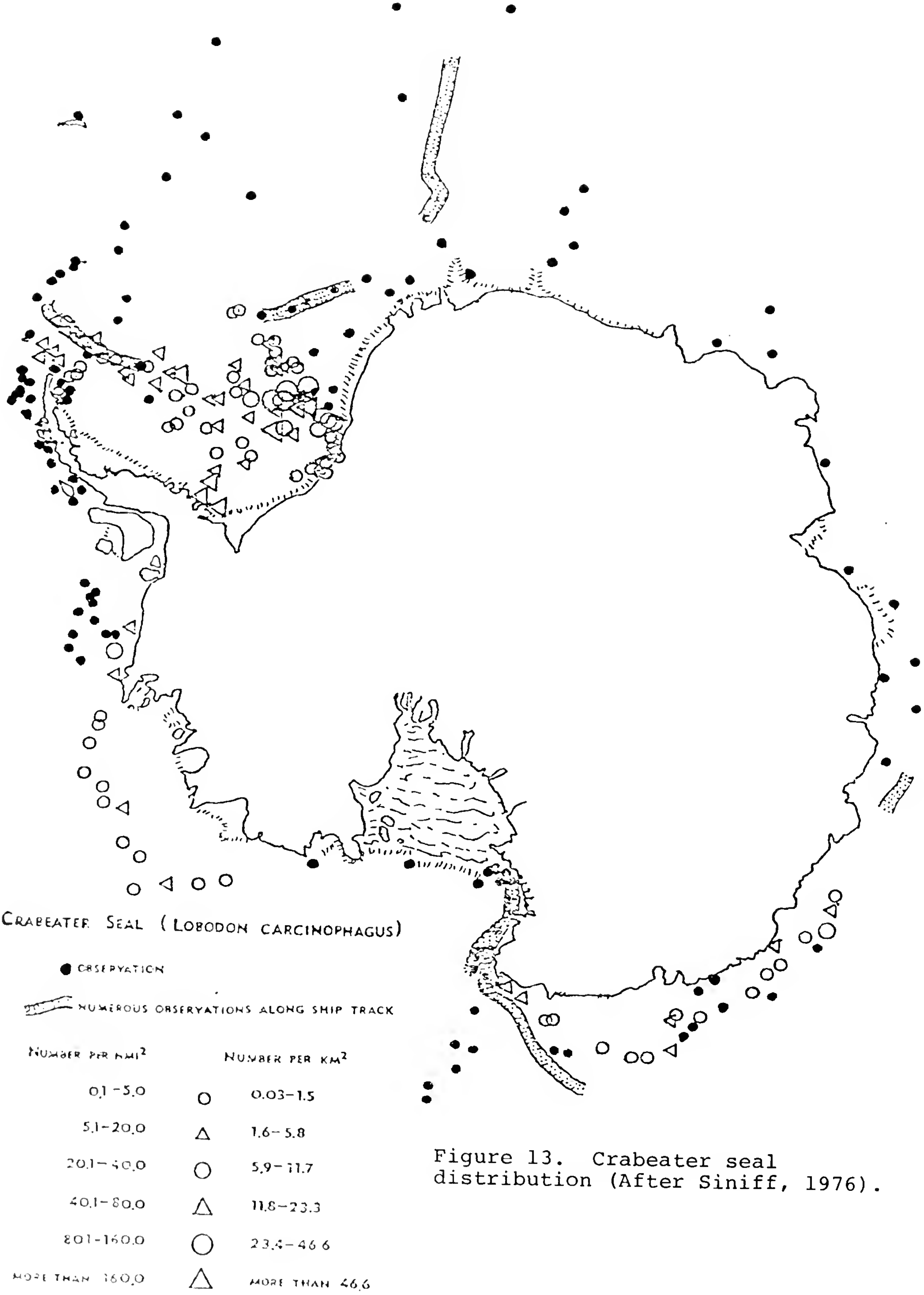


Figure 13. Crabeater seal distribution (After Siniff, 1976).

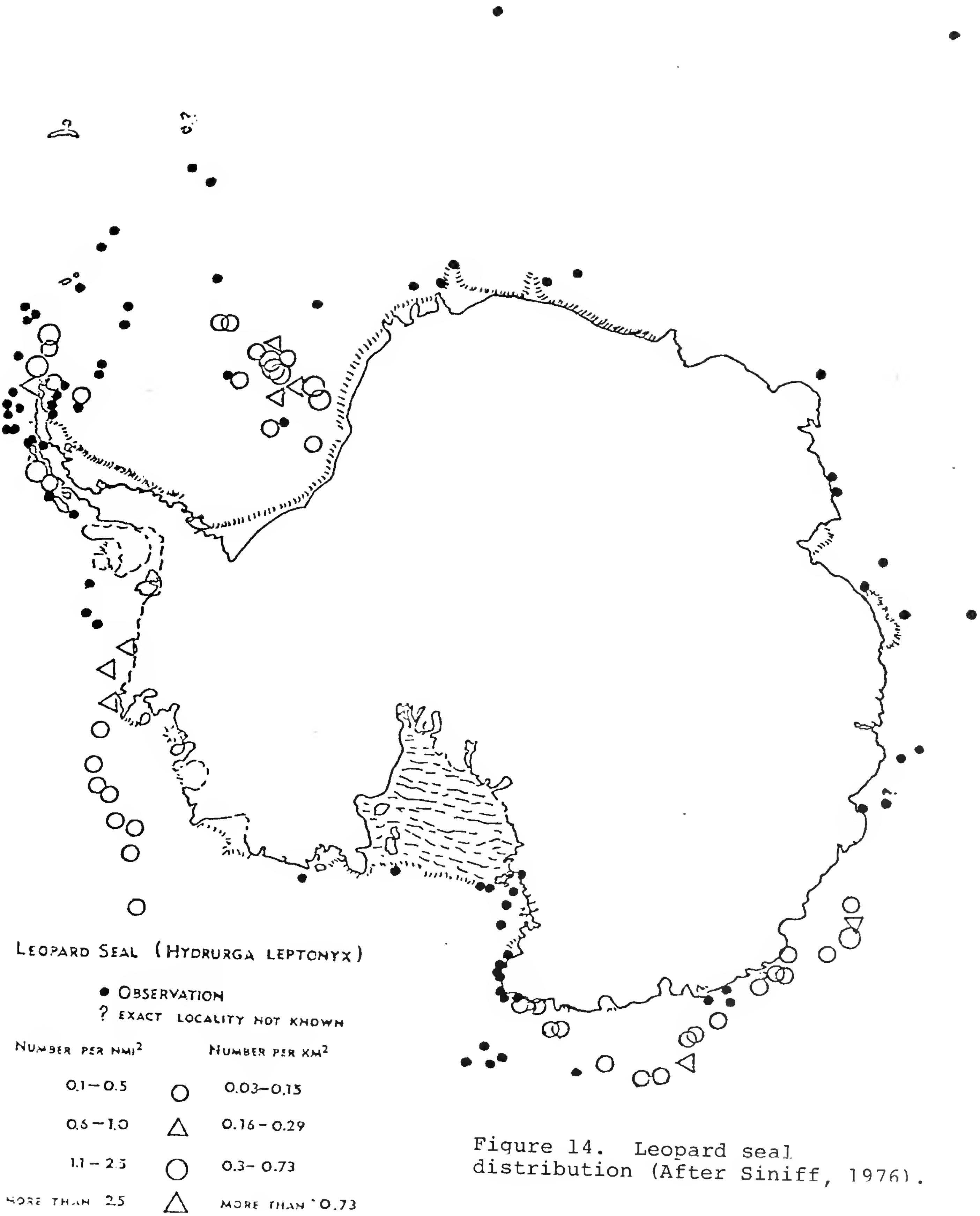
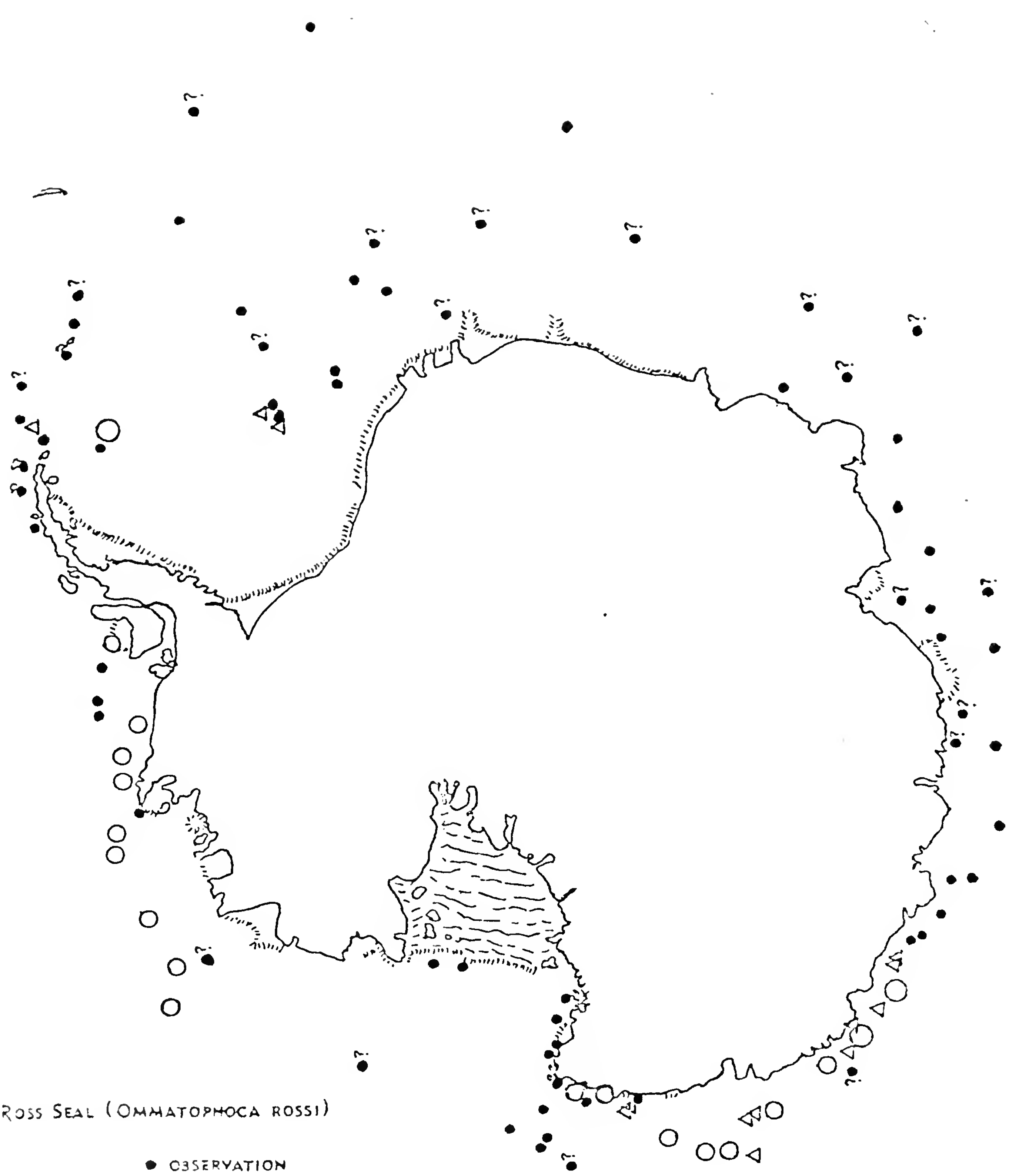


Figure 14. Leopard seal distribution (After Siniff, 1976).



ROSS SEAL (OMMATOPHOCA ROSSI)

● OBSERVATION

? EXACT LOCALITY NOT KNOWN

NUMBER PER NM²		NUMBER PER KM²
0.01-0.09	○	0.003-0.025
0.1-0.5	△	0.03-0.15
0.6-1.0	◯	0.16-0.29
MORE THAN 1.0	△	MORE THAN 0.29

Figure 15. Ross seal distribution (After Siniff, 1976).

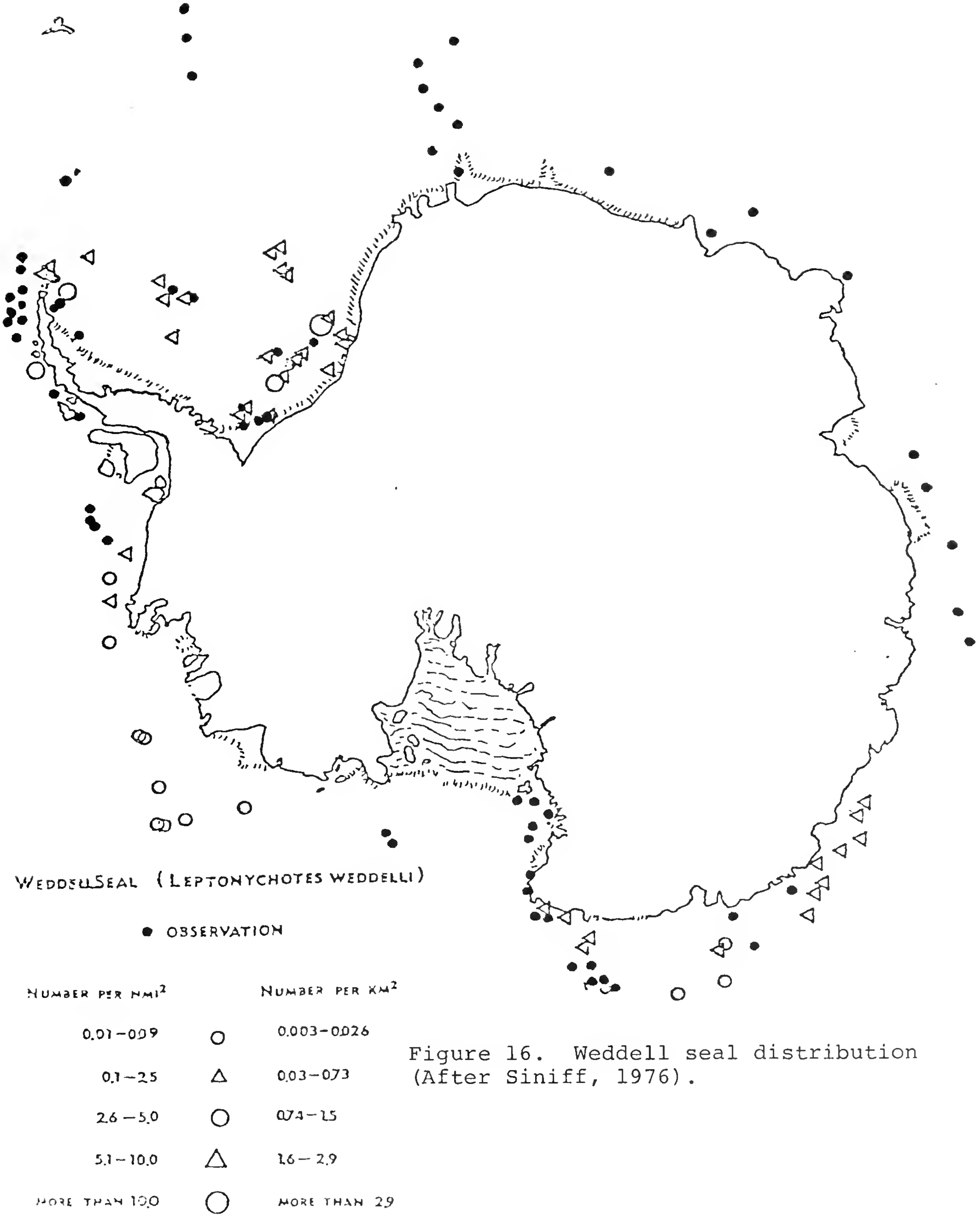


Figure 16. Weddell seal distribution (After Siniff, 1976).

3) Ross Seals

Ross seals are also distributed circumpolarly, (rarely north of 55^{o} S.) and prefer consolidated pack ice dominated by large floes. Some censuses suggest that Ross seals tend to be distributed in local, high density patches throughout the pack ice zone (King, 1964; Erickson et al., 1969; 1972; Erickson, 1971) although Gilbert and Erickson (1977) did not support this idea.

4) Weddell Seals

The preferred habitat of Weddell seals is fast ice. Although primarily a circumpolar coastal inhabitant, Weddell seals are occasionally found in pack ice and on the subantarctic islands.

Weddell seals use predictable pupping and breeding areas, usually tide cracks as shown by Stirling (1969b, 1969c), Siniff et al. (1976), and DeMaster (1978). In pack ice, Weddell seals did not exhibit observable pack ice type preferences (Gilbert and Erickson, 1977).

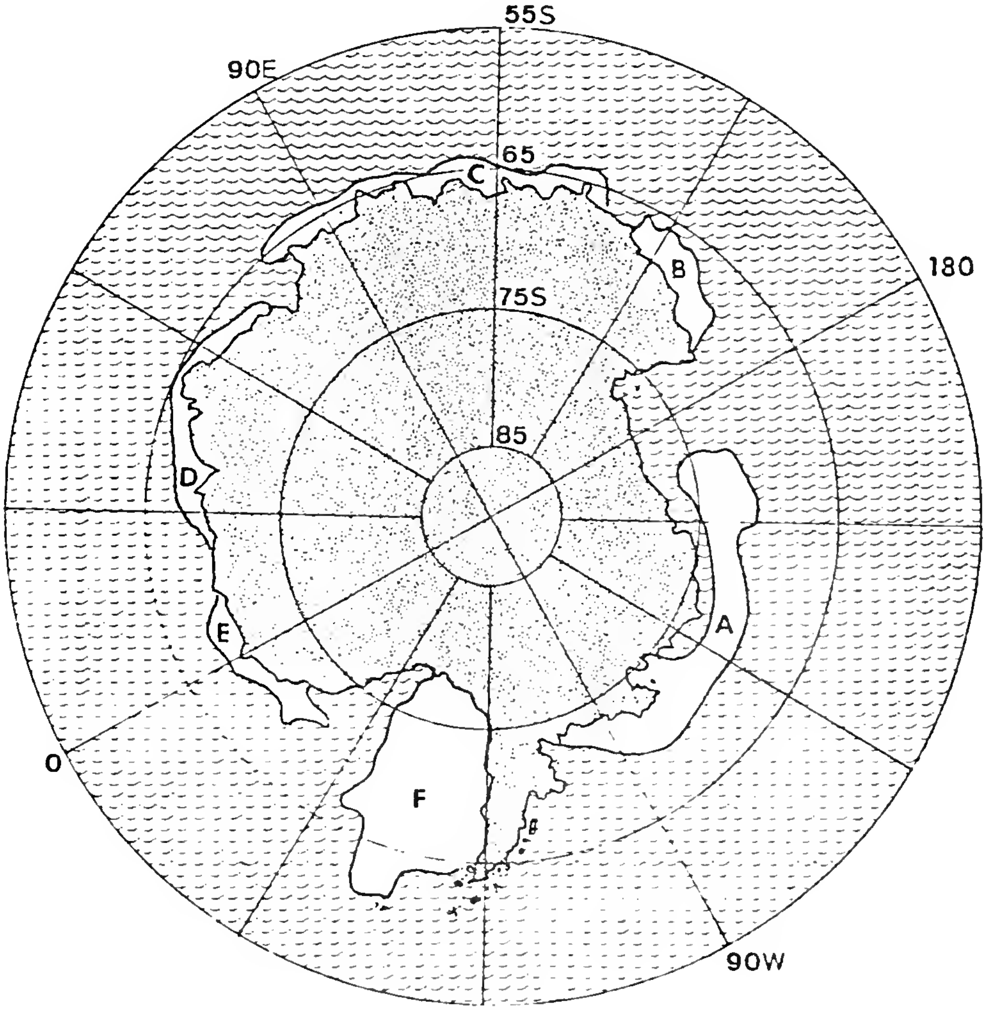
b. Movements and Annual Cycle

Movements of the four true Antarctic seals are not well known. Although it has not been specifically demonstrated, it seems likely that individuals in pack ice move with the pack ice during its general north-south seasonal fluctuation. Figure 17 illustrates six presumed residual pack ice areas which may serve as refugia during the Antarctic summer.

1) Crabeater Seals

Bertram (1940), Turbott (1952, Bonner and Laws (1964), and Solyanik (1964) have, among others, provided evidence of a southward movement of subadult crabeater seals during the summer. The seals then move northward as water freezes and suitable pack ice near the advancing edge only becomes available to the north. Crabeater seals pup during September and October in the pack ice (Øritsland, 1970b; Siniff and Reichle, 1976; Siniff et al., 1977b; Siniff et al., 1978). Following weaning, pups apparently congregate in pack ice areas and in fast ice bays while adults breed on the pack ice (Siniff et al., 1977b). Other authors have suggested that weaned pups congregate at areas of very dense pack ice near land (Lindsey, 1937; Bertram, 1940; Hofman, 1975). Presumably, most young individuals remain in these groups until they become reproductively active. Age of first reproduction appears to be between 2.5 and 6 years of age (Laws, 1958; Øritsland, 1970a; Siniff et al., unpublished data), and life span over 20 years (Laws, 1958; Øritsland, 1970b).

Figure 17. Six residual pack ice regions presumed to constitute population centers for pelagic Antarctic seals in the austral summer. The regions were: A, Admundsen and Bellingshausen Seas; B, Oates Coast; C, Wilkes Land; D, Queen Maud Land; E, Halley Bay; and F, Weddell Sea (From Gilbert and Erickson, 1977).



2) Leopard Seals

The movements and activity patterns of leopard seals have been only partially documented. Work on local movements and predatory impact has been conducted in the vicinity of several penguin colonies (Penney and Lowry, 1967; Muller-Schwarze and Muller-Schwarze, 1971; Dawson, 1974). General activity patterns of leopard seals have been reported by workers at penguin colonies and in the pack ice (Bechervaise, 1962; Øritsland, 1970b; Erickson et al., 1971; Muller-Schwarze and Muller-Schwarze, 1975). But long-range movements of leopard seals have received little attention. Despite unsupported assumptions of extensive movements associated with pack ice drift, there are indications that individuals may remain primarily in one area. In 1973, Hofman and Reichle (unpublished data) tagged leopard seals near Palmer Station on the Antarctic Peninsula and resighted the tags three years later in the same area. Hofman et al. (1977), following seasonal variations in leopard seal abundance near Palmer Station, found increased numbers from early December to mid-January suggesting that, although stocks may remain in one general area, seasonal movements within the area may occur.

Information on leopard seal behavior during pupping and breeding is scarce. Pupping occurs in the pack ice during November and December and observations have been made of adult females and pups (McWhinnie and Parmelee, pers. comm.; Siniff et al., unpublished data) in the pack ice zone. In the only documented leopard seal birth, a male was stillborn from a caged female on Heard Island in mid-November (Brown, 1952). Erickson and Hofman (1974) felt that parturition probably occurs in October through December. Although Harrison et al. (1968) suggested a nine to ten month gestation period with no delayed implantation, Sinha and Erickson (1972) suggested that delayed implantation does take place as with other Antarctic phocids.

3) Ross Seals

Ross seal movements are virtually unknown, although it is likely that populations may move according to seasonal pack ice fluctuations. Pupping is thought to occur some time from November to December in the pack ice zone. Erickson and Hofman (1974) report that a translation of Solyanik's (1964) Ross seal paper may indicate that a female and a pup were captured on December 6, 1950 in pack ice near the South Sandwich Islands.

4) Weddell Seals

Annual movements of Weddell seals are poorly known. Smith (1965) felt that 85% of the McMurdo Sound population migrated northward into pack ice regions during the winter. However, Stirling (1969c), Lindsey (1937), and Bertram (1940) stated that evidence indicates that most McMurdo Sound Weddell seals remain and winter under the ice. In the spring, pupping occurs on the fast ice in traditional haul-out areas (Stirling, 1969c).

c. Stock Identification

There may not be well segregated stocks within pack ice seal species (Seal et al., 1971b) as a result of potential mixing effect of the pack ice on the population genetics of crabeater, leopard, and Ross seals. Tagging studies on Weddell seals in McMurdo Sound have indicated that individuals either remain in an area year-round or return annually to the same haul-out areas (Stirling, 1969b, 1969c; DeMaster, 1978). This site fidelity may lead to the development of subgroups of Weddell seals at certain locations. Studies of gene frequencies in Weddell seals sampled at widely separated localities substantiate this idea (Shaughnessy, 1969; Seal et al., 1971a).

d. Standing Stock

Various estimates of abundance for the four true Antarctic seals are given in Table 8. Recent census efforts of Antarctic seals (Erickson et al., 1971; Gilbert, 1974; Hofman, 1975; Gilbert and Erickson, 1977) have improved earlier estimates of the abundances of Antarctic seals (Scheffer, 1958; Ecklund, 1964). Estimates vary because of the logistic difficulties in censusing and because daily activity patterns and haul-out timing may strongly affect them. For example, Siniff et al. (1970) and Erickson et al. (1971) pointed out that the crabeater seals' definite 24 hour activity pattern affects haul-out timing and accuracy of aerial estimates of abundance. Siniff et al. (1971) found the same true for Weddell seals which haul out mostly between 1100 and 1600 hours. Differences in activity patterns and haul-out rates must be considered when interpreting aerial survey or other census results.

e. Food Habits

Delineating the impact of seals upon the ecosystem requires far more than listing prey species. Factors such as amounts of specific prey eaten, feeding rates, and seasonal or age-specific shifts in food preference are all

Table 8. Estimates of seal standing stock in the Southern Ocean*

Species	Numbers (Thousands)	Reference
Crabeater	2-5000	Scheffer, 1958
	5-8000	Eklund, 1964
	50,000	Erickson et al., 1971b
	30,000	Erickson and Hofman, 1974
	14,858	Gilbert and Erickson, 1977
Leopard	200-300	Scheffer, 1958
	220	Gilbert and Erickson, 1977
Weddell	200-500	Scheffer, 1958
	730 (in pack ice alone)	Gilbert and Erickson, 1977
Ross	20-50	Scheffer, 1958
	100+	Hofman et al., 1973
	220	Gilbert and Erickson, 1977
Elephant	600±100	Laws, 1960, 1973
	600	Laws, 1977b
Antarctic fur	157-207	Bonner, 1976
	600	Laws (pers. comm.)

* Difference in estimates generally reflect improved census techniques.

essential to describing seals' predatory pressure on the ecosystem (Figure 18). Øritsland (1977) reviewed the food consumption of various species of pack ice seals. In general, he found that crabeater seals consume mainly krill with some supplemental fish; leopard seals take fish, krill, penguins, caphalopods; Ross seals consume mainly cephalopods and fish; and Weddell seals, when they are present in the pack ice, eat primarily fish and cephalopods. Tables 9, 10, and 11 show Øritsland's estimates of food types and amounts for each species. Coupled with biomass estimates, total annual consumption for each species can be estimated. In contrast to baleen whales (except minke whales) which spend only several months a year feeding in the Southern Ocean, these seals always remain south of the Convergence. Since seals can be assumed to be eating year-round except for minor seasonal fasting (Øritsland, 1977), the resultant prey consumption is rather large.

1) Crabeater Seals

The crabeater seal diet consists primarily of krill (94% as reported by Øritsland, 1977), 3% fish, 2% cephalopods, and 1% miscellaneous invertebrates. A specialized dental pattern, present in few other mammals (less specialized dentition is also seen in leopard seals), forms a seive when the jaws are closed and allows crabeater seals to feed heavily on krill.

2) Leopard Seals

Remains of krill, squid, fish, penguins, and seals have been found in leopard seal stomachs. Although penguins are often considered a major leopard seal food source, this conclusion is probably biased because of the extensive observations made near penguin rookeries (Brown, 1957; Penney and Lowry, 1967; Muller-Schwarze, 1971; Muller-Schwarze and Muller-Schwarze, 1971; Dawson, 1974). Hamilton (1939) and Laws (1964) showed that leopard seals also utilize fish and squid while Hofman et al. (1977) observed leopard seals feeding on krill even though large numbers of adelie penguins were nearby. Llano (pers. comm.) observed the feces of 19 leopard seals on ice floes in January, 1974. Eighteen had been feeding on krill and one on penguins in an area frequently traversed by penguins. There are also reports of leopard seals eating other seal species (Wilson, 1907; Bertram, 1940; Laws, 1964; Gilbert and Erickson, 1977) including fur seals (Rankin, 1951), Weddell and crabeater seals (Mawson, 1915; Hamilton, 1939; Mackintosh, 1967; Erickson and Hofman, 1974). Siniff and Bengtson (1977) hypothesized that the scars commonly seen on crabeater seals

Figure 18. Pie diagrams indicating food consumption in Antarctic marine mammals (After Laws, 1977a).

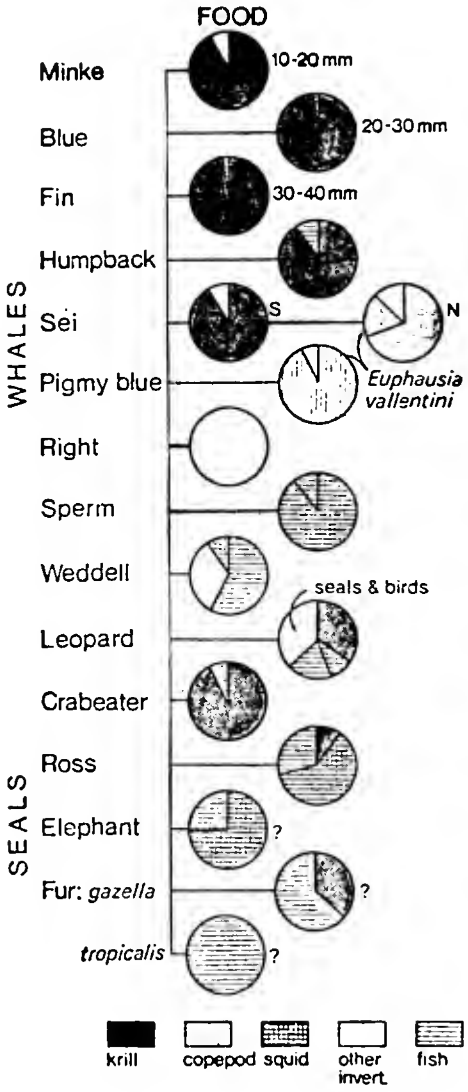


Table 9. Stomach contents and food items of seals recorded in the Southwestern Atlantic sector of the Southern Ocean pack ice in September-October 1964 (After Øritsland, 1977).

		Stomach Contents			Food Item Frequencies (%)							
						Cephalopods		Fish				
Sex	Total No.	No.	Mean volume (liters)	Maximum volume (liters)	Krill	Large	Small	Large	Small	Pen-guins	Seal	Gravel
					Crabeater Seal							
♂	88	24	2.1	5.0	90	2+		2	2			4
♀	131	41	2.5	8.0	96*	1	1	1				
♂ + ♀	219	65	2.4	8.0	94	2	1	2	1			2
					Leopard Seal							
♂	33	13	4.3	12.0	72‡	8	6		8	4		3
♀	51	25	4.7	16.0	51‡		5	4§	9	22	4#	4
♂ + ♀	84	38	4.6	16.0	58	3	6	3	9	16	3	4
					Ross Seal							
♂ + ♀	15	7	1.9	6.0		7	79	7	7			
					Elephant Seal							
♂	4	1		0.5			50		50			
					Fur Seal							
♂	1	0										

* *Euphausia superba* (two samples)
\+ *Gonatus antarcticus*
‡ *Euphausia superba* (one sample)
§ *Paralepis atlantica trionosa*
\# *Lobodon carcinophagus*

Table 10. The food consumption of Antarctic seals.
[Estimated from a feeding rate of 7 percent of the average recorded body weight and an assumed average of 335 days of feeding per year.] (After Ørtisland, 1977).

Species	Individual consumption		Stock size (millions)*	Average food item frequencies (percentages in parentheses) and annual food consumption of stocks (millions of metric tons)						
	Kilograms per day	Metric tons per year		Krill	Cephalopods	Other invertebrates	Fish	Birds	Seals and carrion	Total
Weddell	18	5.9	0.73	(1) 0.04	(11) 0.47	(35) 1.50	(53) 2.27			4.28
Crabeater	16	5.2	14.86	(94) 72.54	(2) 1.54	(1) 0.77	(3) 2.32			77.17
Leopard	20	6.6	0.22	(37) 0.54	(8) 0.11	(3) 0.04	(13) 0.19	(26) 0.38	(13) 0.19	1.45
Ross	12	4.1	0.22	(9) 0.08	(64) 0.57	(5) 0.05	(22) 0.19			0.89
All			16.03	(87) 73.20	(3) 2.69	(3) 2.36	(6) 4.97	(1) 0.38	0.19	83.79

* Stock estimates are from Gilbert and Erickson (1977)

Table 11. Stomach contents and food items of Weddell and crabeater seals as recorded by earlier investigators. [Average food item frequencies have been calculated from their incidence in recorded stomach contents (see text). Parentheses indicate incomplete data which have not been included in the totals. Information which could not be quantified is indicated by (+) = occurring and (++) = frequent.] (After Øritsland, 1977).

	Stomach contents		Food item frequencies (percent)								
No.	No.	Maximum volume (liter/kg)	Krill	Other crusta-ceans	Cepha-lopods	Lamelli-branchs	Holo-thurians	Fish	Gravel	Miscel-laneous	References
					Weddell Seals						
(6)	6			8	8			83			Hanson, 1902
6	5			5	32	12	7	38		7	Wilton et al., 1908
1	1	23			50			50			Bruce, 1913
25			(+)		(+)		(+)	(++)			Sapin-Jaloustre, 1952
44	36			39	8			49	4		Dearborn, 1965
290				(40)	(10)			(50)	0		Smith, 1966
(372)	48		(+)	31	11	1	1	52	3	1	Total
					Crabeater Seals						
12	1		100								Hanson, 1902
27	27		100					(+)			Wilson, 1907
2	1		100								Wilton, et al., 1908
2	2	2	100								Rustad, 1930
	1		(++)		50				50		Perkins, 1945
7	(4)			(38)					(62)		Sapin-Jaloustre, 1953
(13)	3		22	22				33	22		Solyanik, 1965
(63)	35		91	2	1			3	3		Total

Table 11. Continued.

No.	No.	Maximum volume (liter/kg)	Krill	Other crusta-ceans	Cepha-lopods	Lamelli-branchs	Ascid-ians	Fish	Pen-guins	Other birds	Seal	Car-rion	Algae	Gravel	References
							Leopard Seal								
1	1				100										Borchgrevink,1901
2	2		100												Hanson, 1902
1*	1					50		50							Wilton et al., 1908
1	1											100			Mawson,1915
3	3								67		33			(+)	R.N.R. Brown, 1915
	1							100							Shackleton,1919
	2							(+)	(+)	50	50	(+)			Matthews,1929
1	(1)	5	(+)					(++)							Rustad,1930
36+	32	13	3	6	13		3	13	25	3	13	16	6		Hamilton,1939
1	1	64							100						Murphy,1948
8	7							43	29	14	14				Paulian,1953
20	8				62			13			13	13			Gwynn,1953
31	22							23	59	5	9	5			K.G. Brown,1957
3	3								100						Prevost,1964
39‡	37		90					3	7						Hofman et al., 1977
147	121		30	2	8	1	1	13	26	3	8	7	1	(+)	Total
							Ross Seal								
4	3				50								50		Hanson,1902
6	0														Wilson,1907
2	2		16		42			42							Wilton et al., 1908
1	1			100											Shackleton,1919
1	1				100										King,1965
8	7		19		40			33					7		Solyanik,1965
22	14		12	7	44			23					14		Total

* Not cited by Bruce (1913) and hence not by Hamilton (1939)

\+ Includes data from other investigators

‡ Includes 35 fecal samples and 4 stomachs

result from leopard seal attacks upon them when young. Hofman et al. (1977) postulated an age-related shift in prey in leopard seals; young seals were shown to rely more heavily upon krill than mature seals which utilized a variety of vertebrate prey. Thus, leopard seals clearly use a wide variety of prey species.

3) Ross Seals

Ross seal food habits are unclear. Although scattered individuals in dense pack ice are thought to feed primarily on cephalopods, fish and krill have been found in their stomachs (Barrett-Hamilton, 1901; Wilson, 1907; Brown, 1913; Solyanik, 1964). King (1965b) suggested that Ross seals may feed on larger cephalopods than other seals which feed on cephalopods.

4) Weddell Seals

According to Dearborn (1965), fish were present in 97% of the Weddell seal stomachs analyzed at McMurdo Sound. Weddell seals sometimes catch fish of considerable size, such as *Dissostichus mawsonii* (Calhaem and Christoffel, 1969). Lindsey (1937) and Bertram (1940) suggested a dietary transition between newly weaned pups and adults. The primary food of newly weaned pups being crustaceans (isopods, amphipods, and Euphausiids such as *Euphausia superba*. Although Dearborn (1965) found these invertebrate species in adult stomachs, these small crustaceans may be easier prey for pups (Bertram, 1940).

2. Other Antarctic Seals

a. Southern Fur Seals

1) Distribution

The taxonomic status of southern fur seals was reviewed by Repenning et al. (1971). There are three species of *Arctocephalus* which may occur south of the Antarctic Convergence. Of these, *A. gazella* is the most common -- present near subantarctic islands and pelagically just south of the Convergence. The other two species, *A. tropicalis* and *A. forsteri* occasionally penetrate south into Antarctic waters. Bonner (1968) presents distributional maps of the three species.

The Antarctic fur seals (*A. gazella*) frequent the islands and surrounding oceans south of 60° S. off the Antarctic Peninsula. During the pupping/mating season, major breeding populations are located on South Georgia, Sandwich and Bouvetoya Islands, and smaller ones on the South Shetland, South Orkney, Kerguelen, and Heard Islands (Bonner, 1976).

2) Movements

Movement patterns for southern fur seals are relatively unknown (Bonner, 1976). They remain on island beaches during the pupping/mating season (September to April) and then return to open ocean, remaining there until the next reproductive season. It is not known if post-reproductive season movements are a directional migration or simple dispersal. Both subspecies are polygamous with 5 to 15 females per harem. Non-breeding males sometimes occupy the periphery of the breeding colony or do not even return to breeding areas. Males are most commonly sighted at sea, but recently established colonies give evidence that females disperse through open water to new localities. In general, fur seal abundance has increased in the last fifty years and their range has extended (Bonner, 1976). Laws (1977a) suggested that the recent fur seal increases may be in response to increased krill abundance resulting from reduced whale stocks.

3) Standing Stock

Arctocephalus gazella: With pre-exploitation estimates of 1 to 2 million seals, the 1973 population estimate was 200,000 (Bonner, 1976), the majority being on South Georgia. The 1930 South Georgia population of 100 seals had, by 1957, increased to 15,000. The present population estimate is 350,000 (Payne, 1977), and current annual pup production is about 90,000.

Twenty-three years after sighting the first fur seal on South Ornkney Island since fur seal over-exploitation, the total 1971 population (primarily males) was over 2,000 seals (Laws, 1973).

A substantial population increase has been observed in the South Shetland Islands. Aguayo and Torres (1966) recorded 200 fur seals on Livingston Island and 300 seals on Elephant, Cornwallis, and Clarence Islands. Erickson et al. (1970) reported about 200 seals at Cape Shireff (of which 27 were pups). On South Shetland Island, 400 fur seals were reported by O'Gorman in 1960 and two years later 800 to 900 were counted by Holdgate (1963). At Bouvet, Holdate et al. (1968) recorded 500 seals and estimated annual pup production at 150 to 180 pups for the 1964 season. On Kerguelen Island, Paulian (1952) recorded the first fur seals' return in the 20th century, and by 1969, Budd and Downes sighted 143 there. The 1963 fur seal population on Heard Island of 500 seals reached 1,000 by 1969 (Budd, 1970).

4) Food Habits

The staple food of southern fur seals is krill, *Euphasia superba*, with fish (Nototheniidae) of importance to juvenile and non-breeding adult diets (Bonner, 1968). Squid are also eaten. Russian harvest of *Notothenia rossii* (240,000 tons/season) off the coast of Kerguelen and South Georgia did not have an apparent effect on the nearby fur seal populations (Bonner, 1976).

b. Southern elephant Seals (*Mirounga leonina*)

This species has been the focus of several Antarctic and subantarctic investigations (Laws, 1953a, 1953b, 1964, 1956a, 1956b, 1960). The elephant seal review in Erickson and Hofman (1974) is also relied on in the following paragraphs.

1) Distribution

Prior to heavy exploitation in the 1800's, elephant seals were found throughout the subantarctic islands and northerly continental areas. Intense sealing either reduced numbers to minor remnant populations or wiped them out altogether. Herds on South Georgia (presently the largest), Macquarie Island, Kerguelen, Heard Island, Marion Island, the South Orkney Islands, and the South Shetland Islands are known to have existed in the past, and in some cases persist. The elephant seals' range appears to be expanding as it slowly recovers.

2) Standing Stock

Still below initial population levels, the present southern elephant seal population level is about 600,000 (Table 8). These estimates (Bonner and Laws, 1964; Laws, 1977a) are probably fairly accurate approximations of abundance at breeding when seals congregate in traditional areas and can easily be counted. Of course, non-breeding individuals and unknown rookeries must be accounted for in the estimates.

3) Reproduction and Annual Cycle

Mature bulls first return to the rookeries and establish territories sometime in August (depending upon rookery location). Mature cows join them in about three weeks to form harems of up to 30 cows per bull. Within a week, the cows give birth to a single pup and then become sexually receptive two to three weeks later. Following copulation on land, the harems break up and the bulls return to the ocean for a short interval before reforming groups on land to molt.

Most female elephant seals become mature at one to three years. Males, apparently mature at four years, remain reproductively inactive until six (Laws, 1956a).

4) Food Habits

Although much is known about certain features of elephant seal natural history, its feeding habits are not well known. When on land, where most studies have been done, they invariably fast (Laws, 1977a), making determination of foods taken impossible. It does seem, however, that the majority of their food consists of fish and cephalopods (Table 9). Young seals may feed on amphipods for a short time after weaning (Laws, 1956a).

D. Antarctic Birds

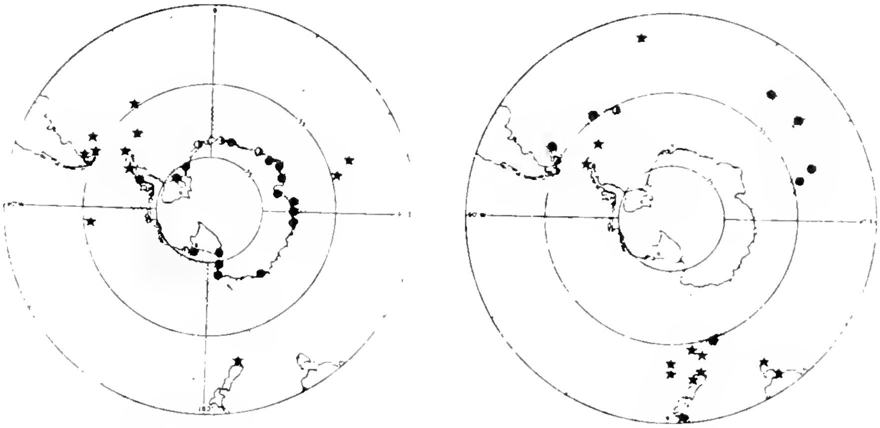
Birds play a critical role in the Antarctic marine environment. This section relates standing stock and biomass estimates to feeding in order to assess the ecological significance of Antarctic avian populations. Thirty-eight seabird species with breeding and/or feeding ranges extending south of the Convergence are considered (some move into Antarctic waters after breeding on islands like Marion and Prince Edward, the Crozets, Kerguelen, and Macquarie). Antarctic and subantarctic faunal zones have been delineated (review in Watson et al., 1971) along a track which roughly follows the northern limits of the pack ice. Related species are grouped and discussed in terms of their overall position within the Antarctic region.

1. Penguins

a. Distribution

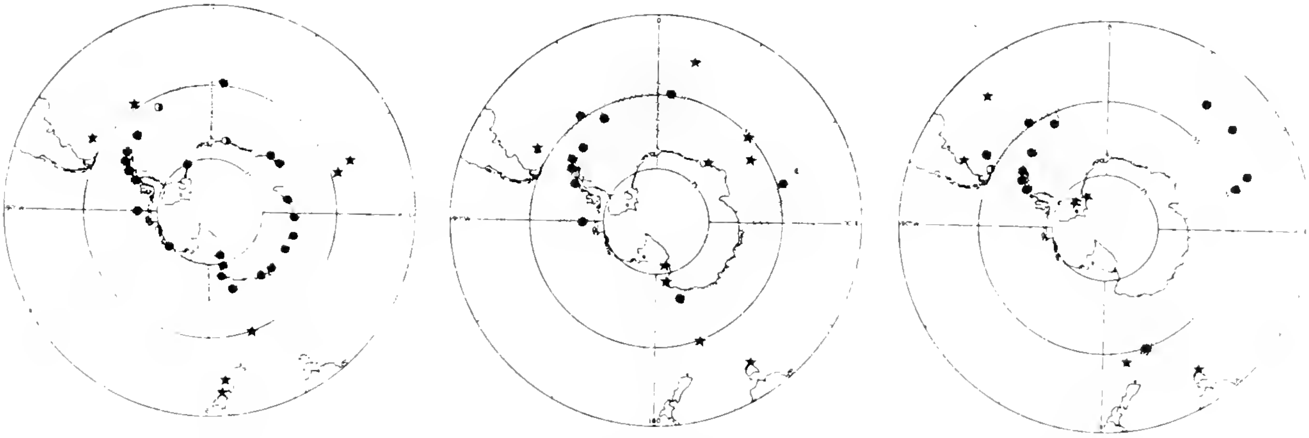
The circumpolar distributions of the seven penguin species breeding in the Antarctic are shown in Figure 19. Of the two large *Aptenodytes* species, emperor penguins breed on continental fast ice (Voous, 1965) and king penguins breed on islands north of the pack ice zone (Conroy and White, 1973). The three *Pygoscelis* species show a graded series of ranges from north to south. Adelie penguins occur

Figure 19. Distribution maps of the seven Antarctic penguin species known to breed south of the Antarctic Convergence (From Watson, 1975).



Emperor penguin

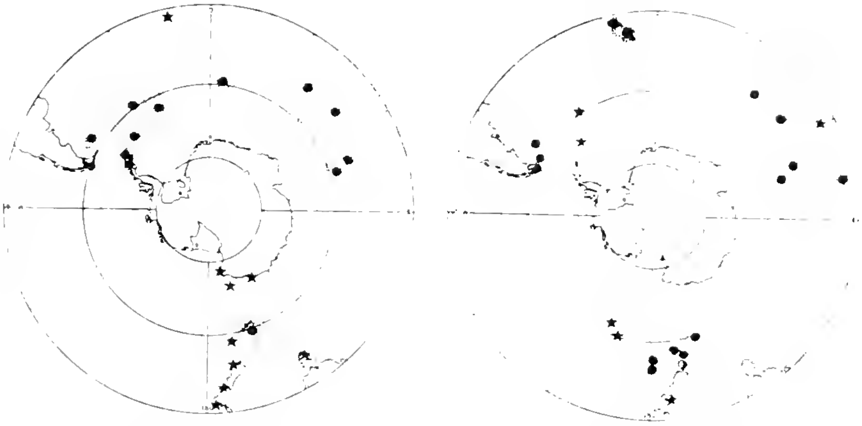
King penguin



Adélie penguin

Chinstrap penguin

Gentoo penguin



Macaroni penguin

Rockhopper penguin

farthest south, chinstrap penguins are somewhat intermediate, and gentoo penguins are generally closer to the Convergence (Sladen, 1964; Watson et al., 1971). There are, however, large areas in which species overlap. While both macaroni and rockhopper penguins breed together on a few islands near the Convergence, macaroni penguins extend their range to the South Shetland Islands while rockhopper penguins do not.

Carrick and Ingham (1967) related distribution patterns of these species to nesting and feeding area availability, and found some evidence suggesting that feeding areas are especially critical. Emperor penguins have a theoretically unlimited supply of fast ice to breed on, yet colonies remain in traditional areas (presumably) near adequate fishing grounds (Carrick and Ingham, 1967). The relationship of food resources and penguin distribution is also illustrated by the pattern of chinstrap marked range expansion within the past 20 years. This pattern may have resulted from reduced competition for food following zonal depletion of whale stocks (Sladen, 1964; Conroy, 1975).

b. Movements and Stock Identification

With the possible exception of gentoo penguins, there are no data to reject the idea that most of these species, either as immatures or seasonally as adults, move considerable distances on a regular basis. Both adelie and chinstrap penguins generally associate with the pack ice in winter, and chinstrap penguins are found in pelagic habitats considerable distances from known breeding areas (Routh, 1949; Szijj, 1967; Fraser, pers. comm.). In contrast, a well marked size dimorphism existing between northern and southern populations of gentoo penguins suggests limited movement and gene flow between these two areas (Watson et al., 1971). A similar dimorphism exists among other island-breeding species such as rockhopper penguins -- thorough present information is inadequate to confirm if these populations may be considered demes.

c. Standing Stock

Data on either the biomass or standing stock of penguins are not easily acquired (Falla, 1964; Laws, 1977b). This difficulty is reflected in the ranges of estimates (Table 12). It is agreed that penguins are the most important avian Antarctic group and account for 88% to 91% of total avian biomass (Croxall, unpub. MS.; Prevost, 1978). If these estimates are reasonably accurate, a biomass between 418 and 461 thousand metric tons of feeding penguins must certainly have an important impact on zooplankton levels.

Table 12. Available Spheniscidae standing stock and biomass estimates

Species	Standing Stock (Individuals)	Source	Biomass (Metric tons)
Emperor	570,000	Prevost (1976)	14,500
	500,000	Croxall (Unpl. MS)	15,000
	240,000	In Pryor (1968)	-
	350,000	In Pryor (1968)	-
King	5,500,000	Prevost (1976)	66,000
	5,000,000	Croxall (Unpl. MS)	75,000
Adelie	27,000,000	Prevost (1976)	122,000
	50,000,000	Croxall (Unpl. MS)	250,000
	50,000,000	Ainley in Prevost (1976)	225,000
Gentoo	900,000	Prevost (1976)	5,000
	5,000,000	Croxall (Unpl. MS)	30,000
Chinstrap	6,800,000	Prevost (1976)	27,200
	2,500,000	Croxall (Unpl. MS)	11,250
Rock-hopper & Macaroni	22,000,000	Prevost (1976)	183,000
	10,000,000	Croxall (Unpl. MS)	80,000
Totals	62,770,000	Prevost (1976)	417,700
(other)	73,000,000	Croxall (Unpl. MS)	461,250

d. Food Habits

Estimates of the amounts and types of food consumed by penguins are given in Table 13. This list is not exhaustive and fails to take into account localized feeding patterns. In rockhopper penguins, for example, Ealey (1954a) found that at Heard Island, amphipods (Euthemisto) were a major food item, whereas at South Georgia, Carrick and Ingham (1967) found the diet dominated by krill (E. superba).

Sympatric species feeding on the same food items may avoid overt competition for food by eating prey of different sizes, and this must be considered, too. Chinstrap and adelie penguins, for example, take krill of significantly different sizes in their overlapping ranges at Signey Island (White and Conroy, 1973). Finally, much of the data on penguin food habits is limited to that obtained during the breeding season. Virtually nothing is known regarding seasonal diet variation, especially in winter.

2. Other Seabirds

a. Distribution

Seabird distribution in the Southern Ocean (Figure 20) has been extensively reviewed (Voous, 1965; Carrick and Ingham, 1967, 1970; Murphy, 1964; Falla, 1964). Generally, most species occupy a circumpolar zone which changes seasonally (Mackintosh, 1960). The pattern of seasonal oscillations is largely set by the retreat and advance of the pack ice. Relative species densities primarily of the albatrosses, fulmars, prions, petrels, and shearwaters, are not uniform. In summer, major bird concentrations are in the south Atlantic, the southern Indian Ocean, and along the eastern coast of Antarctica, with notably fewer birds in the south Pacific and western coast of Antarctica (Voous, 1965). This pattern approximates large Euphausiid distribution in January, February, and March (Marr, 1956).

b. Movements

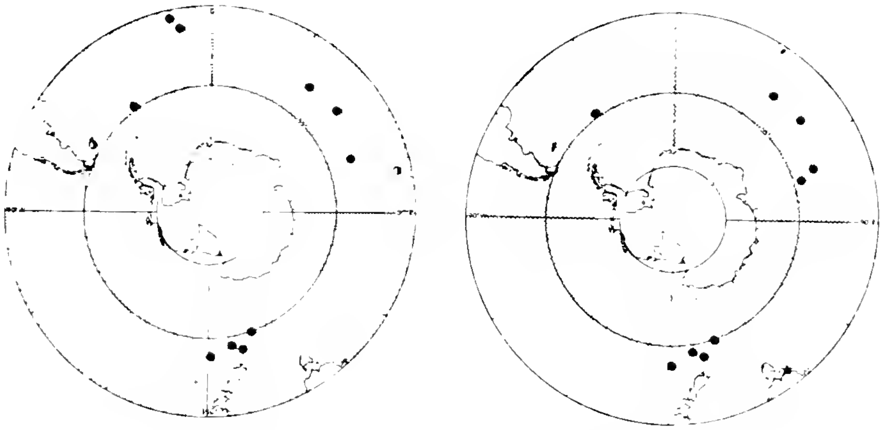
These species are known to undertake a significant migration analogous to those of whales (Falla, 1964; Ashmole, 1971; Carrick and Ingham, 1970; Voous, 1965). Apparently attracted by vast food supplies in summer, large-scale movements of sooty shearwaters, several gadfly petrels, prions, blue petrels and several albatrosses move near the continent, but go north to breed, often to islands near the Convergence (Watson et al., 1971). Oordt and Kruyt (1953) have observed that migrant age structure includes both young of the year and adults. Thus, summer feeding localities

Table 13. Prey types and food consumption estimates in Spheniscidae

	Prey Item			Source	Total food consumption (thousands of metric tons (Croxall, unpublished MS)
	Krill	Fish	Squid		
Emperor		X	X	Falla (1937) Prevost and Sapin-Jaloustre (1965)	304-371
King		*	X	Croxall (Unpl.MS)	2074-2266
Adelie	X	*		Emison (1968) White & Conroy (1975)	7800-9167
Chinstrap	X			White & Conroy (1975)	894-1066
Gentoo		X		Ealey (1954) Conroy & Twelves (1972)	398-435
Macaroni	X			Falla (1937)	2668-3051 (Macaroni and rockhopper)
Rockhopper	X			Carrick & Ingham (1967)	
Total					14138-16356

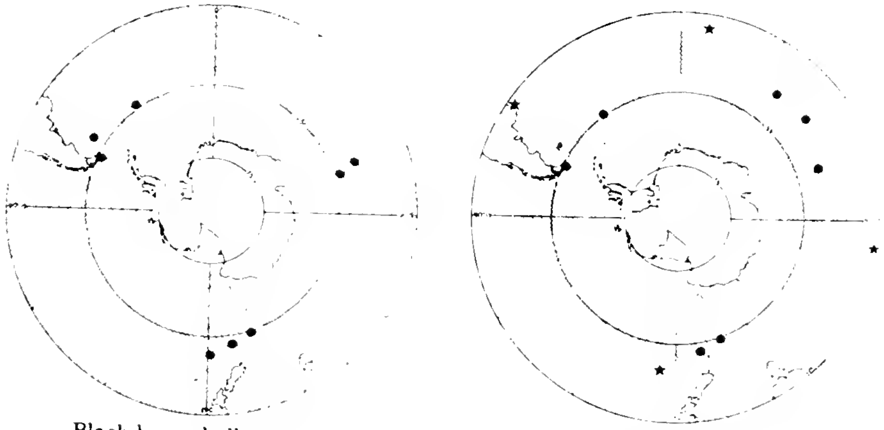
X = primary food source
* = secondary food source

Figure 20. Distribution maps of the other Antarctic seabirds known to utilize areas south of the Antarctic Convergence (From Watson, 1975).



Wandering albatross

Light-mantled sooty



Black-browed albatross

Gray-headed albatross

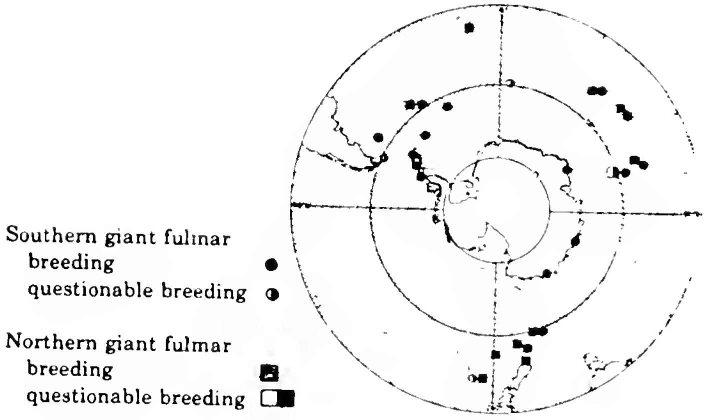
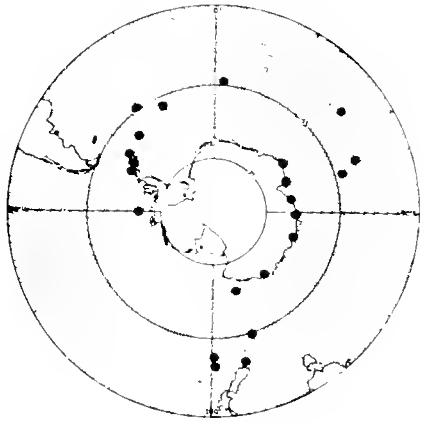
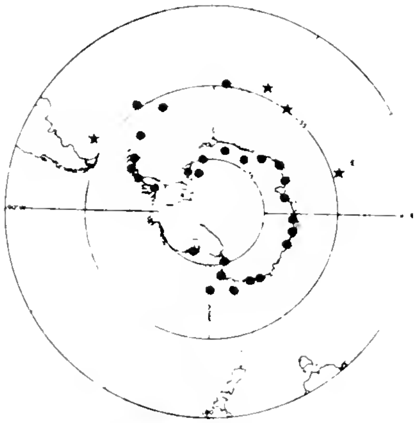


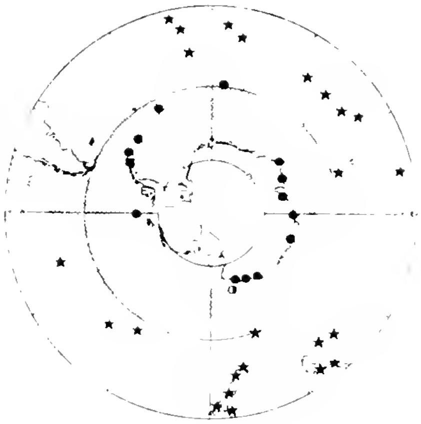
Figure 20. (Continued)



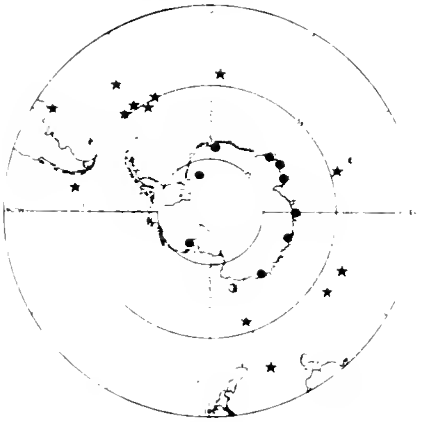
Cape pigeon



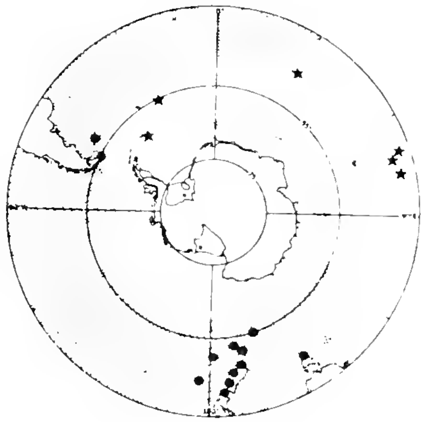
Snow petrel



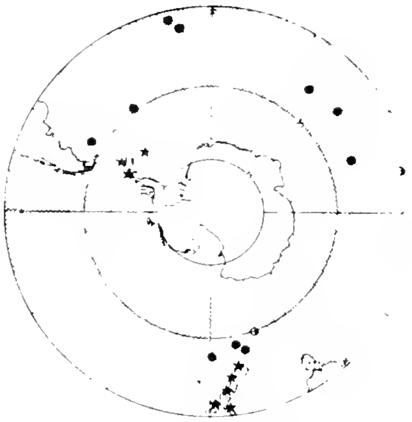
Southern fulmar



Antarctic petrel

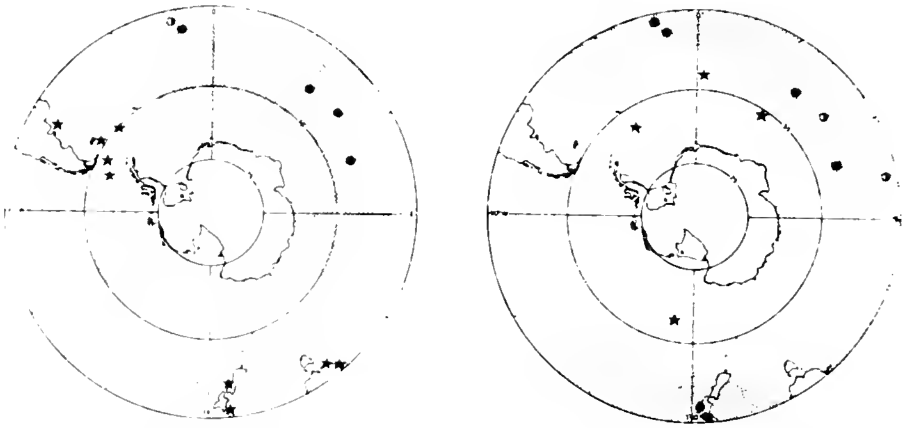


Sooty shearwater



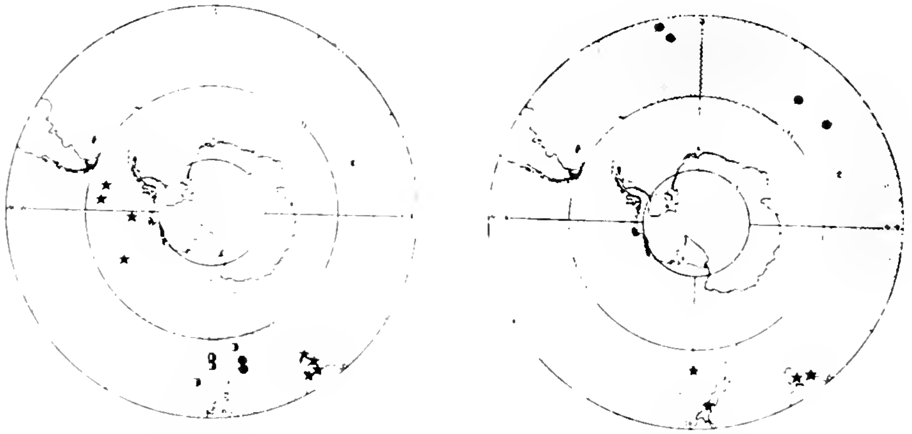
White-chinned petrel

Figure 20. (Continued)



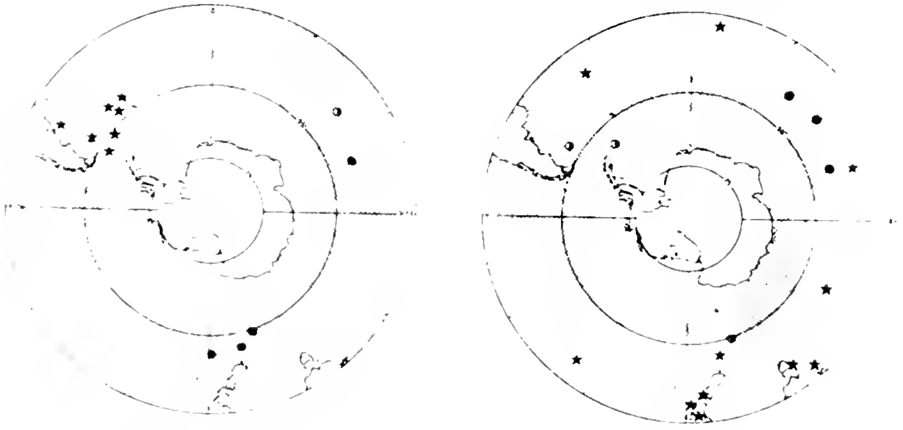
Kerguelen petrel

Great-winged petrel



Mottled petrel

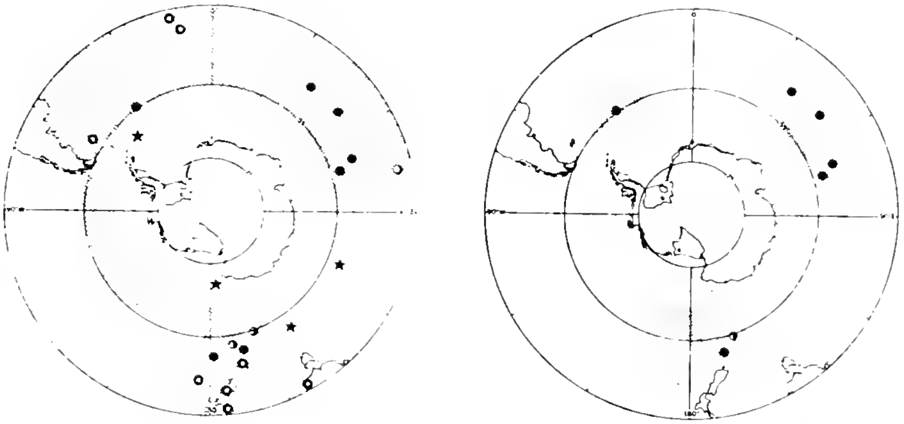
Soft-plumaged petrel



White-headed petrel

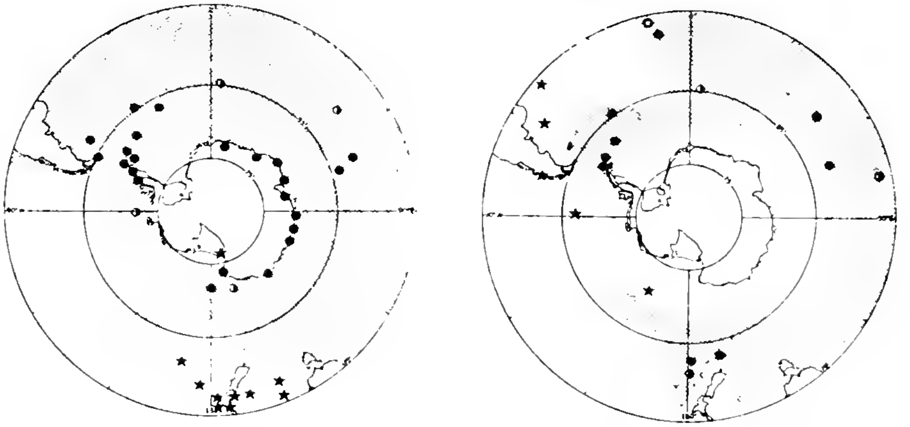
Blue petrel

Figure 20. (Continued)



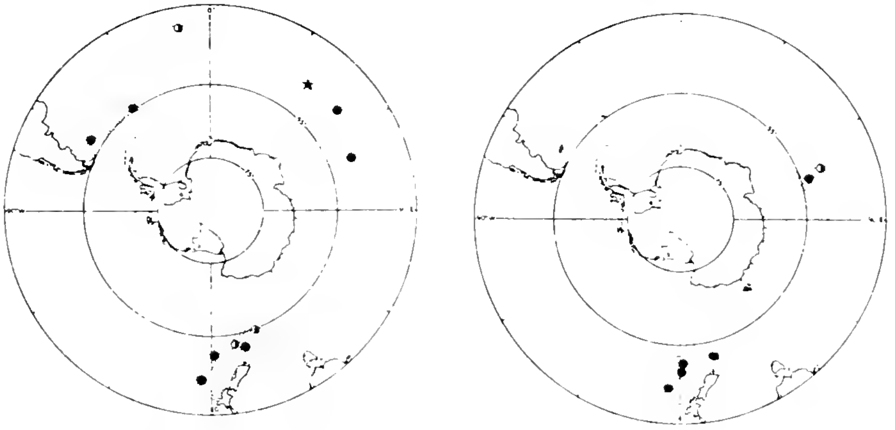
Kerguelen diving petrel

South Georgia diving petrel



Wilson's storm petrel

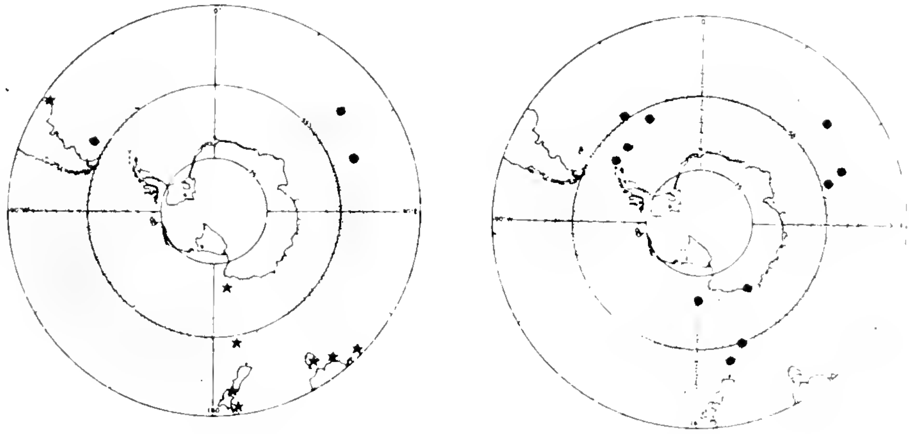
Black-bellied storm petrel ●



Gray-backed storm petrel

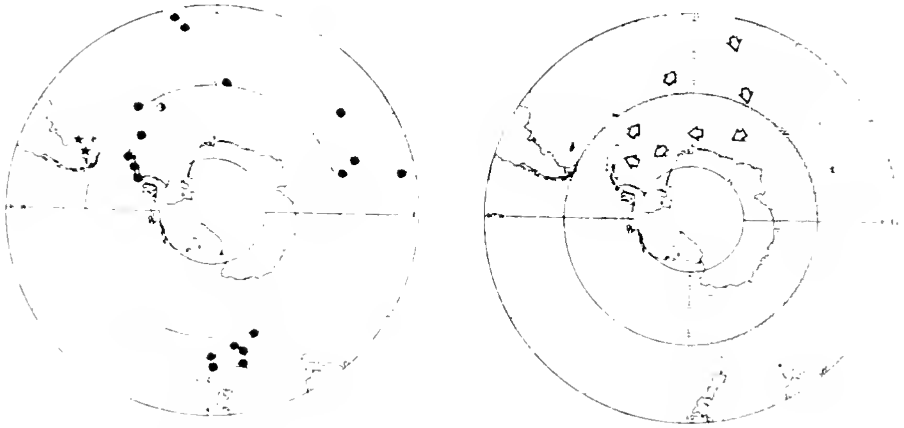
Fulmar prion

Figure 20. (Continued)



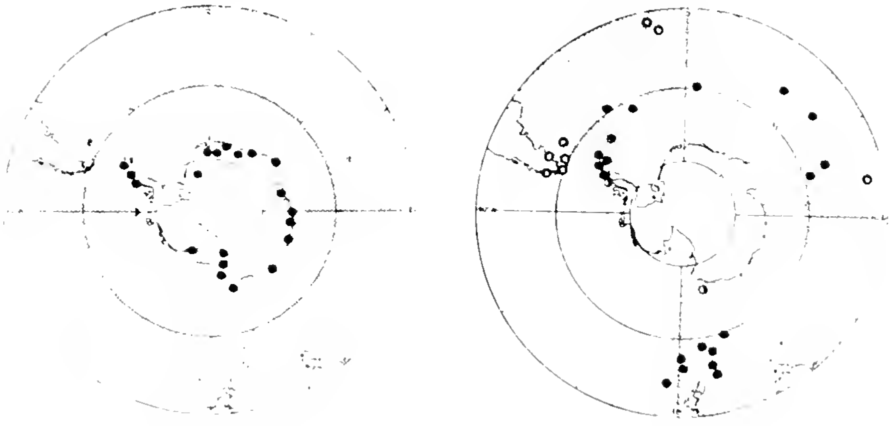
Narrow-billed prion

Antarctic prion



Antarctic tern

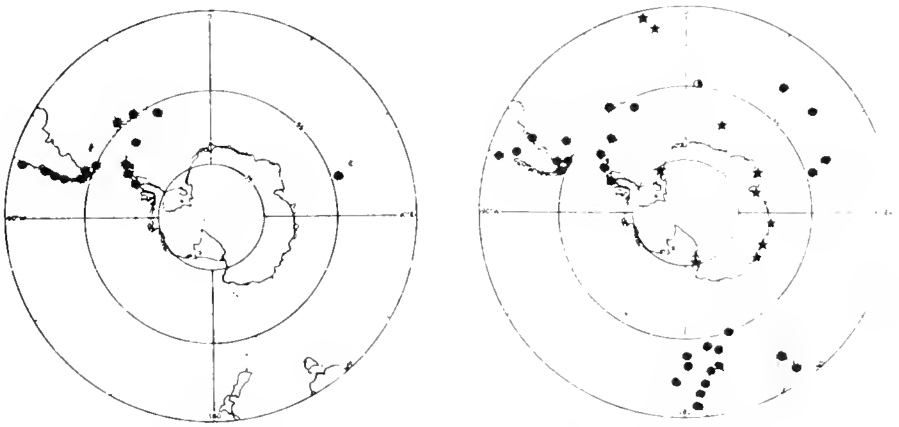
Arctic tern



South polar skua

Brown skua

Figure 20. (Continued)



Blue-eyed shag

Southern black-backed gull

may be vital to the food requirements of many species of seabirds, including some which breed outside the Antarctic region.

Information on seabird distribution and movements in winter is virtually non-existent although extensive movements away from the continent have been reported in East Antarctica (Oordt and Kruyt, 1953) and analogous movements recently noted along the Antarctic Peninsula (Fraser, pers. comm.). Laws (1977b) estimated the winter avian biomass to be only about 80% of that in summer. However, since penguins may comprise 90% of this biomass (and most evidence indicates that penguins remain in the Antarctic over winter), his estimates are most likely incorrect.

c. Standing Stock and Productivity

As with penguins, estimating biomass and standing stocks of other seabirds is difficult. The burrowing, nocturnal habits of some species and the remote, inaccessible breeding sites of others make research difficult. Hence, the comparative summary of standing stock and biomass estimates in Table 14 may include underestimates.

Ecological data on these species are, except for the Diomedeidae and Stercorariidae, rather incomplete. Generally, however, reproductive rates of most species seem low as is the proportion of young reaching breeding age (Carrick and Ingham, 1967). For species on which data are available, the percentage reaching breeding age is often well below 50%, while adult survival is often more than 90% (Pryor, 1967; Ashmole, 1971; Hudson, 1966; Tickell, 1968b, 1970; Tickell and Pinder, 1975; Beck, 1969, 1970).

d. Food Habits

Table 15 summarizes the feeding habits of Antarctic sea birds. Though some species such as the blue and snow petrels, Antarctic terns and Wilson's petrels are known to depend heavily on krill, all seabirds may feed on krill at times (Voous, 1965). In some species, krill are key prey items during particular times of the year. Dominican gulls, for example, utilize krill extensively prior to egg-laying, while at other times molluscs are more important food items (Fraser, pers. comm.). Other marine crustaceans (amphipods and isopods) are also important to some diving petrels and southern fulmars, though again seasonality and feeding location are important factors. Ozawa et al. (1968) reported that several species of seabirds concentrate to feed on patches of krill (Table 16), and suggested that, for many species, aggregations almost twice the average density would

Table 14. Avian standing stock, biomass, and food consumption summary.

	Penguins	% of Total	Other Seabirds	% of Total	Total	Source
Standing Stock (Individuals)	62,770,000	49	66,434,500	51	129,000,000	1
	73,000,000	31	165,200,000	69	238,200,000	2
Biomass (Metric tons)	417,700	88	56,705	12	474,405	1
	461,250	91	45,385	09	506,635	2
Food Consumption (Metric tons)	26,184,500	83	5,489,500	17	31,674,000	1
	14,138,000 to 16,356,000	92 86	1,277,130 to 2,753,600	08 14	15,415,130 to 19,109,600	2

1 Prevost (1976)

2 Croxall (unpublished ms)

Table 15. Standing stock, biomass, food preferences and food consumption of other seabirds

Species	Standing Stock # of Individuals	Source	Biomass Metric Tons	Prey Item Krill	Prey Item Fish	Prey Item Squid	Prey Item Other	Source	Total food consumed thousands of metric tons, Croxall (Unpl. MS)
Wandering	70,000**	1	600						
Albatross	50,000	2	430			X		Tickell (1968)	5.6-14.1
Black-browed	12,000,000	1	42,000					Tickell (1964)	206.8-261.8
Albatross	1,750,000	2	6,475		X	X			
Grey-headed	385,000	1	1,400						
Albatross	100,000	2	370		X	X		Tickell (1964)	11.0-15.0
Light-mantled Sooty	130,000	1	350					Murphy (1936)	8.0-13.3
Albatross	100,000	2	290			X			
Giant	65,000	1	280					Johnstone (1977)	5.9-18.0
Petrel	100,000	2	500	*	*		*scavenger		
Southern	68,000	1	53					Falla (1937)	94.4-223.2
Fulmar	5,000,000	2	4,000	X		X			

Table 15. Continued.

Species	Standing Stock # of Individuals	Source	Biomass Metric tons	Prey Item Krill	Prey Item Fish	Prey Item Squid	Prey Item Other	Source	Total food consumed thousands of metric tons Croxall (Unpl. MS)
Cape	432,000	1	194					Beck (1969)	67.9-145.5
Pigeon	5,000,000	2	2,250	X		X	amphipods		
Snow	1,600,000	1	480					Maher (1962)	25.2-74.8
Petrel	3,500,000	2	950	X	X				
Antarctic	2,600,000	1	1,820					Voous (1965)	169.9-404.6
Petrel	10,000,000	2	7,000	*	*	X			
Prion spp.	32,000,000	1	4,800					Ealey (1954)	
	50,000,000	2	7,500	X	X	X		Harper (1972)	260.6-628.6
Blue	-	1	-					Voous	
Petrel	1,000,000	2	200	X	*	*		(1965)	4.7-15.7
Pterodroma spp.	800,000	1	320					Warham (1956)	17.4-53.0
Gadfly Petrels	2,000,000	2	800		X	X		Falla (1937)	

Table 15. Continued.

Species	Standing Stock # of Individuals	Source	Biomass Metric tons	Prey Item					Total food consumed thousands of metric tons Croxall (Unpl. MS)
				Krill	Fish	Squid	Other	Source	
White-chinned	+	1	+					Murphy (1936)	116.4-306.9
Petrel	5,000,000	2	6,000	*	*	X			
Sooty	+	1	+						77.8-204.7
Shearwater	5,000,000	2	3,500	-	-	-	-		
Storm	2,400,000	1	80					Fraser (pers. comm.)	141.8-361.9
Petrels	75,000,000	2	3,000	X			amphipods		
Diving	11,000,000	1	1,300					Ealey (1954)	5.3-10.6
Petrels	1,000,000	2	1,250				amphipods		
Blue-eyed	146,000	1	307					Fraser (pers. comm.)	13.7-12.8
Shags	100,000	2	300		X				
Skuas	155,000	1	240					Fraser (pers. comm.)	18.9-16.2
	200,000	2	360	X	X				
Dominican	72,000	1	72				amphipods	Fraser (pers. comm.)	15.43-11.9
Gull	200,000	2	200	*	*		molluscs		

Table 15. Continued.

Species	Standing Stock # of Individuals	Source	Biomass Metric tons	Prey Item Krill	Fish	Squid	Other	Source	Total food consumed thousands of metric tons Croxall (Unpl. MS)
Terns	61,000	1	8.6					Fraser (Pers. comm.)	10.4-1.0
	100,000	2	10.0	X	X				
Totals	66,434,500	1	56,705						5,489,500
	165,200,000	2	45,385						1,277,130-2,753,600

1 Prevost (1976)

2 Croxall (unpublished ms)

** Tickell (1968) estimates 58,760 birds

+ Prevost combined estimate of white-chinned petrel and sooty shearwater standing stock is 2,450,000; biomass 2,400

X Primary food source

* Secondary food source

Table 16. Birds observed present in the vicinity of krill patches (After Ozawa et al., 1968)

Scientific name	English common name
Diomedea melanophyris *	black-browed albatross
Macronectes giganteus *	giant petrel
Daption capensis *	cape pigeon
Fulmarus glacialoides *	silver-grey fulmar
Halobaena caerulec	blue petrel
Pachyptila sp. *	whale birds or prion
Thalassoica antarctica *	Antarctic petrel
Procellaria aequinoctialis	white-chinned petrel
Pterodroma lessoni	white-headed petrel
P. inexpectata	Peale's or mottled petrel
Pagodroma nivea *	snow petrel
Oceanites oceanicus *	Wilson's storm-petrel
Catharacta sp.	skua
Sterna vittata	Antarctic tern
S. paradisea	Arctic tern
Aptenodytes forsteri *	emperor penguin
Pygoscelis adeliae *	adelie penguin

* Species congregated on the krill patches during the observation

gather to feed on krill swarms. Pelagic fish and squids are taken by most petrels and albatrosses, and there is evidence that competition is avoided by prey size selection (Voous, 1965).

E. Antarctic Fish

The dominant Antarctic ichthyofauna group is the Nototheniiformes comprised of five families that make up nearly three quarters of all coastal fish species (Andriashev, 1965, 1970; Everson, 1977). Most are sluggish bottom dwellers, though in the genera Pleuragramma and Dissostichus, some pelagic types occur (Marchall, 1964). Other Antarctic fish groups include the Zoracidae (eel pouts), Liparidae (sea snails), Macrouridae (rat-tailed fishes), and Gadidae (cod-like fishes).

1. Distribution

Information on many species' distribution is incomplete. Many species seem restricted to continental shelves, and over 80% are found at depths between 200 and 500 meters (Andriashev, 1965). Nybelin (in Andriashev, 1965) categorized Antarctic fish into seven zoogeographical zones which aid in delineating relative species abundance geographically. The zones include: Circumpolar Antarctic, 20 species; East Antarctic, 30 species; West Antarctic, 8 species; West Antarctic/South Georgia, 4 species limited to those respective areas; South Georgia, 10 species; Kerguelen, 11 species; and Antarctic-notal, 7 species which penetrate Antarctic waters from Patagonia and New Zealand. It is beyond the scope of this work to describe individual species distributions, and what follows is a brief and general review.

Antarctic fish distributions are best known for those species offering research and/or fisheries potential due either to accessibility or abundance. The following is drawn from information in Everson (1977), Andriashev (1965), and Marshall (1964).

The skates (Rajidae) are an important family including three species which may have economic importance: Raja georgica, R. murraijii and R. eatonii. Their distribution is primarily limited to the South Georgia, South Orkney, Kerguelen and South Sandwich Island shelves (Table 17).

Antarctic "cods" (Nototheniidae) dominate the fish fauna both in terms of numbers of species and number of

Table 17. Distribution of Antarctic fish (From Everson, 1977).

Species	Habitat and Mode of Life	Depth Range	Reference
Raja georgiana	Demersal, South Georgia Shelf also from a submerged elevation between South Orkney and S. Sandwich Island (-1.44 to -1.47° C)	180-830	1,2,3
R. murrayii	Demersal, Kerguelen	20-60	1
R. eatonii	Demersal, Kerguelen	30	1
Micromesistius australis	In the Antarctic. Reports indicate that this species is *generally* pelagic in the vicinity of the continental shelf. Has been caught in bottom trawls although larger catches have been made with pelagic trawls.	200-650 10-70	2,4,5,6
Merluccius hubbsii	Reported on only one occasion Pelagic, assumed migrated to Scotia Sea from Patagonia		7
Notothenia gibberifrons	Demersal in shelf area of Scotia Arc	5-350	1
N. coriiceps	Demersal, Shelf area Kerguelen, Crozet	0-200	1
N. neglecta	Dermersal in Shelf area of Scotia Arc & around continent	0-200	1
N. rossii rossii &	Juveniles demersal in shallow water	0-30	8,9
N. rossii marmorata	Adults demersal/pelagic in shelf area	0-400	
N. magellanica	Originally considered coastal species living on kelp, now known to be pelagic krill feeder	0-80	1
Dissostichus mawsoni	Mainly pelagic in open ocean	20-220	10
D. eleginoides	Mainly pelagic	70-800	10
Pleuragramma antarcticum	Open ocean pelagic although often associated with Continental Shelf		11,1,14
Champsocephalus gunnari	Pelagic/demersal in Shelf area	0-450	12,1
Channichthys rhinoceratus	Demersal	0-140	13,1
Pseudochaenichthys georgianus	Demersal/pelagic in Shelf area	0-270	12
Chaenocephalus sp.	Demersal	5-350	12,1
Chionodraco sp.	Demersal	0-800	1

1. DeWitt (1971)
2. Permitin (1969)
3. Bigelow and Schroeder (1965)
4. Merrett (1963)
5. Basalaev and Petukhov (1969)
6. Shuntov (1971)
7. Mikheyev (1967)
8. Olsen (1954)
9. Hureau (1970)
10. Yukhov (1970, 1971(a), 1972)
11. DeWitt and Hopkins (1977)
12. Olsen (1955)
13. Hureau (1966)
14. Lyubimova *et al*. (1973)

potentially economically important species -- Notothenia gibberifrons, N. coriiceps, N. neglecta, N. rossi marmorata, Dissostichus mawsoni, D. eleginoides, and Pleuragramma antarcticum. Members of the genus Notothenia are found in the Scotia Arc from South Georgia to the South Shetland Islands and around the continent to Bouvet, Marion, Kerguelen, and Heard Islands. Nearly all Notothenia are bottom dwellers along the eastern coast continental shelf. Another genus, Trematomus, is also found near the eastern coast. Except for two species at South Georgia, Trematomus does not inhabit other inland waters. The genus Dissostichus includes two pelagic species (only one of which breeds in Antarctica), weighing from 20 to 40 kg, and distributed on an almost circumpolar pattern. A final important genus, Pleuragramma includes a single truly pelagic circumpolar species.

Members of the Chanichthyidal family include the white-blooded or ice fishes of which seventeen species and ten genera are known to inhabit the whole Antarctic region. Of the eleven species found coastally, two are circumpolar and the others are limited to eastern Antarctica. Pelagic and/or demersal modes of life characterize the family. Species with potential commercial importance are Champsocephalus gunnari, Channichthys rhinoceratus, Pseudochaenichthys georgianus, Chaenocephalus sp., and Chronodraco sp.

2. Movements

Two basic movement patterns appear to characterize Antarctic fish: spawning and seasonal feeding migrations. Spawning migrations have been observed in a few species, and negative evidence suggests that the phenomenon may be more common than thought (Everson, 1977). Observing that only sexually mature fish are seasonally caught in localized areas, Keysner et al. (1974) described a May N. rossi migration from feeding grounds north of Kerguelen to spawning areas south of Kerguelen. This migration is thought to be consistent with the prevailing current. Similarly, catch rates of Champsocephalus gunnari at South Georgia clearly indicate the species moves inshore to spawn since Olsen (1955) caught sexually mature adults only in these areas at certain times of the year. This pattern has recently been confirmed through research by the British Antarctic Survey (Everson, 1977), and a similar migration has been described for C. rhinoceratus (Everson, 1977).

Seasonal feeding migrations have been reported for species endemic to the Antarctic, as well as for some which breed north of the Convergence but feed in Antarctic waters. Among endemic species (namely Notothenia rossi, N. corriceps.

N. rossi marmorata, Champsocephalus gunnari, and Pseudochaenichthys georgianus) schools feed on krill patches offshore in summer, and disperse from April to December (Marchall, 1964; Andriashev, 1965; Keysner et al., 1974; Laws, 1977b). Dissostichus mawsoni also migrates north to the Convergence to feed on krill (Yukhov, 1970).

Considerable evidence suggests that species spawning in subantarctic coastal waters or on the continental shelf of Patagonia also make extensive summer fattening migrations into Antarctic waters. Among these, the Patagonian hake and southern blue whiting are already commercially exploited north of the Convergence (Everson, 1977). Two other species, Notothenia magellanica and Dissostichus elenginoides, also enter Antarctic waters annually. (Permitin, 1969; Lyubimova et al., 1973).

3. Stock Identification

Evidence for multiple management stocks is unavailable for most Southern Ocean fish. Table 18 gives information about subpopulations of two species.

4. Standing Stock

Antarctic fish biomass and productivity data are quite limited. Everson's (1970a) intensive study of Notothenia neglecta at Signey Island showed that mean biomass was 194 kg/hectare and that annual production was 66 kg/hectare. Estimates of the biomass of the Patagonian hake stock, which migrates into the Southern Ocean, is from 3 to 6 million metric tons (Everson, 1977).

Present information suggests that much of the reported catch adjacent to Antarctic waters consists of Antarctic Nototheniiformes. Reported catches have led to estimates of an initial standing stock of about 500,000 metric tons for the South Georgia Shelf area (which may have been reduced by as much as 80% by intensive fisheries). Similar data indicate an initial standing stock of 220,000 metric tons with an estimated maximum sustainable yield (MSY) of 80,000 metric tons/year north of Kerguelen. However, trawling serveys suggest initial standing stocks of 120,000 metric tons with a MSY of 20,000 metric tons/year. This disparity underlines the need for further research and reporting of complete catch information (Everson, 1977).

5. Production

There is little published on seasonal reproductive cycles of Antarctic fish. Spawning periods vary between

Table 18. Antarctic fish species for which there is convincing evidence for more than one discrete management stock (After Everson, 1977).

Species	Stock Localties	Reference
Micromesistius australis	(a) Scotia Sea, probably Southern limit of Patagonian population.	
	(b) Campbell Plateau	
	(a) and (b) Related subspecies on morphological grounds	Inada and Nakamura (1975)
	(a) and (b) Not considered of sub-specific status but considered isolated	Shpak (1975)
	This species has also been reported from S. W. Indian Ocean	FAO
Notothenia rossii	(a) Kerguelen, Crozet group considered of subspecific status *N. rossii rossii*, Richardson	Nybelin (1947)
	(b) Scotia Arc, considered of subspecific status *N. rossii marmorata*, Fischer	Nybelin (1947)

and within species and continental shelf areas are likely to be important (Everson, 1977). Fecundity increases and egg size decreases along a gradient from south to north among related genera such as Trematomus and Notothenia (Andriashev, 1965; Permitin and Schlyanova, 1971), as well as in the families Chaenichthiyidae, Mucsenolepidae, and Bathydraconidae (Permitin, 1973).

The development of ova may take up to two years in (Notothenia neglecta) (Everson, 1970); gestation periods several months (3 to 4 in Chaenocephalus aceratus, Everson, 1968); and larvae may not undergo metamorphosis into adults for extended periods (Everson, 1968, 1970). Many species' young often show extensive pelagic adaptations, a feature believed to facilitate at-sea phytoplankton exploitation and one which is lost during adult benthic stages (Marshall, 1964; Andriashev, 1965). Growth is slow, mortality is high, and sexual maturity is not reached for several years (Everson, 1977; 1970; Dearborn, 1965; Wohlschlag, 1962).

Estimates of Southern Ocean fish production have been made based on estimates of annual consumption by predators (Table 19). This table includes many Antarctic fish species, not just those of commercial potential. Therefore, production figures may be lower although to an unknown extent. Production of sexually mature fish is probably about 5 million tons (Everson, 1977).

6. Food Habits

The dietary importance of krill to many resident and seasonal Antarctic fishes was originally felt to be rather insignificant (Marshall, 1964). Recent findings (Table 20), however, suggest that fish consume more krill than previously thought (Nasu, 1968). While in their summer feeding grounds in the Scotia Sea, a variety of species feed on krill (Permitin, 1969, 1970; Olsen, 1955).

In the South Georgia area, Permitin and Tarverdujeva (1972) observed that krill were principal foods in 6 species, secondary food in 3 species, and tertiary food in 1 species. One-thousand stomachs of adult southern blue whiting were all full of krill (Permitin, 1970). In the Scotia Sea, krill were found in 31 species of 12 families and inhabiting bottom, bathypelagic, pelagic, and epipelagic habitats (Permitin, 1970). Off Queen Maud Land, Kawamura (1978) observed that many sampled fish subsisted largely on krill. Knox (1970) stated that "recent Russian work indicates that the stocks of fishes are very much higher than formerly estimated. Thus, the amount (of krill) consumed by...(fish and cephalopods)...could be at least of the same order as that formerly consumed by the whales."

Table 19. Consumption of Antarctic fish by whales, seals, and birds (after Everson, 1977 using data from Laws, 1977a, and Croxall, unpublished MS).

Group	Fish Consumption in Antarctic (thousands metric ton/yr)	
	Initial Stocks	Present Stocks
Whales	4410	1129
Seals	?	7685
Birds	?	6750
Total	?	15564

Table 20. Diet of Antarctic fish. Percent frequency of occurrence (After Everson, 1977).

Algae		X	*						18	34										
Polychaeta	10	29	*						6	3				X						
Castropoda			*						1	8										
Bivalvia		3	*						X	19										
Cephalopoda	2	2	*									**	*							
Amphipoda	6	10	**			*			40	19				X				*		
Isopoda	3	9	**			*			51	40										
Decapoda	18	3	*			*			6	24			7				10			
Other Crustacea		1	*			*				4				1		X				
Echinodermata	1	6																		
Other Benthos		1	*																	
Cinderia/ Ctenophone	1	8	*	82	3		*	*						X						
Parathemisto		1.5		1.5	3		*	*						24	X					
Euphausia	10	11	*	4	80		**	*	6		**		1	38	**	48	11		**	**
Mysidecea	24	5	*	1	8		*						7	30		2	48			
Salps		X			1		*	*												
Fish	16	1.5	*		3	*			38	16		*	84	3		40	15	**		
	SG	SG	SO	SG	SG	SG	SG	K	K	K	O	O	SG	SG	SG	SG	SG	SG	O	SO
	Raja georgianus (1)	Notothenia gibberifrons (1)	Notothenia neglecta (2)	N. rossii marmorata (3)	(3)	juv (4)	Adult (4)	N. rossii rossii (5)	Juvenile (6)	N. magellanica (6)	(7)	Dissostichus mawsoni (8)	Dissostichus eleginoides (1)	Champsocephalus (1)	(4)	Pseudochaenichthys (1)	Chaenocephalus (1)	(9)	Pleurogramma (10)	Micromesistius

References from Table 20.

(1) Permitin and Tarverdiyeva (1972)

(2) Everson (1977)

(3) Tarverdiyeva (1972)

(4) Olsen (1954)

(5) Keysner et al. (1974)

(6) Hureau (1970)

(7) DeWitt (1971)

(8) Yukhov (1971a)

(9) Olsen (1955)

(10) DeWitt and Hopkins (in press)

(11) Permitin (1969)

South Georgia	SG
South Orkney Islands	SO
Kerguelen	K
Oceanic	O
Present but not quantifiable	x
Present	*
Dominant Item	**

F. Antarctic Cephalopods

Cephalopods include squid, cuttlefish, and octopuses, and are one of the least known groups in the Antarctic marine ecosystem. This lack of knowledge is directly related to the sampling problems (Roper, 1978) resulting from their abaility to avoid nets. They have a highly developed nervous system and motor responses which facilitate strong swimming (El-Sayed, 1977). Whale and seal stomachs examined by Clarke (1977) in the Southern Ocean showed less species diversity of squid in contrast to what conventional sampling gear was capturing. Since these predators usually took Onychoteuthids while the samplers took Pathyteuthids and Brachioteuthids, Clarke concluded that present techniques could give highly biased estimates of which cephalopod families are most abundant.

1. Distribution

This group's distribution is generally circumpolar, though certain species appear to occur in restricted localities (Table 21). Everson (1977) has stated that the Convergence, essentially a surface phenomenon, is unlikely to greatly influence distribution because of the group's diurnal migrations. Filippova (1972) observed that 55% of the known Antarctic squid species are endemic, but few genera are restricted below the Convergence.

Cephalopods include benthopelagic, bathypelagic, and epipelagic types (Young, 1977). Within the benthic cephalopods, the genus *Octopus* is rare in the Antarctic where it is replaced ecologically by the genus *Pareledone* (Hureau, 1976). Octopods appear more frequently near subantarctic islands (Roper, 1978); Antarctic waters support primarily pelagic squids. In western Antarctica, stocks of *Martiola hyadesi* are found while *Notodarus sloani* is abundant in the region between Australia and New Zealand (Hureau, 1976). Also abundant are *Bathyteuthis abyssicola* and *Goliteuthis glacialis*, both of which are widespread below about 50° S. *Brachioteuthis sp.* is extremely common in the Scotia Sea (Filippova, 1972). The minor squid research that has been done has dealt largely with the Magellanic stocks of *Martiola hyaderi* and the Australian-New Zealand stock of *Nototodarus sloani*, two commercially exploited species (Hureau, 1976). How and where population densities of squid are specifically distributed throughout the Southern Ocean is not known.

2. Movements

Voss (1973) indicated that squids are short-lived sexually mature in one year and probably spawn only once.

Table 21. Cephalopod species which may be present in the Southern Ocean in fishable concentrations (After Everson, 1977).

	Distribution	Vert. Range (m)	Diet of Sperm Whales	Current Fishery	Source
ONYCHOTEUTHIDAE					
Onychoteuthis banksii	Subantarctic	0-150	X	X	1,7
Moroteuthis ingens	Antarctic	0-400	X		1,7
Moroteuthis robsoni	South Atlantic	0-500	X		1
THYSANOTEUTHIDAE					
Thysanoteuthis rhombus	South Atlantic				1
OMMASTREPHIDAE					
Nototodarus sloani sloani	New Zealand	0-500		X	1,8
Nototodarus gouldi	Southern Australia	0-500		X	1,3,4
Todarodes sagittatus	S. Atlantic, S. Ind. S. Africa	0-800	X	X	1,5
Todarodes filippovae	Subantarctic				
Illex argentinus	Patagonian Shelf	0-500		X	2
Martialia hyadesi	S. Pac. Convergence			X	2
Symplectoteuthis Oualaniensis	S. India, S. Pacific S. Africa	0-1000		X	1
Dosidicus gigas	S. Pac. Chile	0-1000	X	X	1,2,6
Ommastrephes pteropus	S. Atl. S. Africa	0-1000			1
Ommastrephes bartrami	S. Pacific Chile	0-1000			1
HISTIOTEUTHIDAE					
Histioteuthis bonelli	Subantarctic	100-800	X		1
ARCHITEUTHIDAE					
Architeuthis sp.	Atl. Pac. Ind.		X		1,7
GONATIDAE					
Gonatus fabricii	Antarctic		X		1
(antarcticus)	Subantarctic		X		1
LOLIGINIDAE					
Loligo sp.	Subantarctic Patagonian Shelf S. Atl.	0-200		X	2
OCTOPODINAE					
Pareledone sp.	Antarctic Subantarctic				

References:
1. Clarke (1966)
2. Voss (1973)
3. Anon. (1964)
4. Allen (1945)
5. Nesis (1964)
6. Nesis (1970)
7. Listed by Castellanos (1964) as being of economic importance although no data available to suggest that commercial concentrations exist (Voss, 1973)
8. Saito (1976)

Among some Southern Ocean species such as Todarodes pacificus, Illex illecebrosus, I. argentinus, and Dosidicous gigas, the inshore breeding migration (Voss, 1973) presents the only available evidence on movement patterns. In Newfoundland, Squires (1957) indicated that Illex illecebrosus migrates seasonally over the Grand Banks, eventually heading inshore to breed in a movement pattern led by the males. The extent of this movement in related Antarctic species is not known.

The occurrence of squid beaks in the stomachs of surface feeding birds, suggests these cephalopods are present in surface water layers periodically. Because squid are also captured by trawls in deeper layers, they must undertake rather extensive vertical migrations. Clarke (1977) stated this movement occurs primarily at night and may result in nutrient redistribution.

3. Standing Stock

Information on abundance of cephalopods is extremely sparse. As previously stated, no effective sampling techniques have been developed to allow reliable standing stock estimation. Presently, no cephalopod fisheries exist in the Southern Ocean. However, in adjacent New Zealand waters, a fishery was established in 1972 (Nasu, 1978), and a sizeable fishery could also develop adjacent to Argentina. Development of Southern Ocean fisheries and supplemental research programs are necessary to provide catch data for stock assessment (Everson, 1977).

4. Food Habits

Little is known about squid food habits. Marr (1962) and Dell (1965) noted that squid are major krill predators, and Filippova (1972) observed that many squid species exhibit specialized adaptations for krill feeding. Among these he listed Kondakovia longimana, whose distribution never extends beyond the range of krill.

The impact of squid predation on krill populations cannot be estimated without reliable data on squid biomass. Acknowledging this lack of direct production and biomass data, Everson (1977) presents an annual estimate combining information from Laws (1977a) and Croxall (unpublished MS) for annual squid consumption by birds, whales, and seals. The total eaten by these groups excluding sperm whales (which according to Clarke (1966) eat squid that do not prey on krill) may be 13 million metric tons (Table 22). Assuming a krill to squid conversion rate of approximately

Table 22. The most numerically important cephalopod families in samples obtained by three different methods (After Everson, 1977, incorporating data from Clarke).

Family	Stomach Contents of		
	Sperm Whale	Weddell Seal	Nets
Onychoteuthidae	54%	32%	---
Cranchidae	23%	---	25%
Histioteuthidae	11%	---	---
Octopoda	---	35%	---
Bathyteuthidae	---	---	42%
Brachioteuthidae	---	---	13%

10:1, squid potentially consume about 87 x 10^6 metric tons of krill a year (Everson, pers. comm.). This amount is about three times the current estimated consumption by birds and twice that of baleen whales. Therefore, squid are potentially one of the principal krill consumers in the Antarctic marine ecosystem.

VI. ECOSYSTEM ASPECTS OF THE ANTARCTIC MARINE SYSTEM

In addition to the contributions made by various species groups to the Antarctic marine ecosystem, there are several other factors which must be considered in managing the ecosystem as a whole. The following section discusses three such aspects: primary productivity, nutrient cycling, and energy flow.

A. Primary Productivity

Primary productivity is essential to all ecosystems, including that of the Southern Ocean. Although other factors affecting primary productivity doubtless exist, nutrient levels, geographical areas, currents, seasonality, light, and temperature have been examined south of the Convergence.

Hardy and Gunther (1935) concluded that the "simpler" nutrients (nitrates, phosphates, and silicates) are found in great enough concentrations that they do not limit primary production. Other investigators (El-Sayed, 1968; Knox, 1970; Everson, 1977) also felt these nutrients were probably not rate-limiting. However, not all scientists agree. Holm-Hansen et al., (1977) state that in cold Antarctic waters, nitrate, phosphate, and silicate concentrations are high. On crossing the Convengence from north to south, these researchers noted that nitrate and phosphate levels increased but that silicic acid levels did not. They thus concluded that silicic acid may limit phytoplankton growth. Although nitrates, phosphates, and silicates are important to primary production, other trace elements must be present before maximum primary production can be realized. Volkovinsky (1966) found a correlation between primary production and levels of manganese and molybdenum. El-Sayed (1968) maintained that cobalt, zinc, copper, and vanadium may also be important.

Geographical factors also enter into primary production determinations. By measuring carbon 14 uptake and chlorophyll-a levels, scientists have calculated productivity values for many Southern Ocean regions. Ichimura and Fukushima (1963) reported "very low" productivity values for the Indian Ocean sector. El-Sayed (1970) recorded low carbon 14 uptake values and low chlorophyll-a values for the northern Drake Passage, east and south Weddell Sea, Bellingshausen Sea, and much of the Pacific sector. He reported high chlorophyll-a levels and rapid carbon 14 uptake in the southern Drake

Passage, Gerlache Straits, Bransfield Straits, and northern and southwestern Weddell Sea. He also estimated the Atlantic sector to be five times as rich as the Pacific sector. Despite general agreement on geographical production variation, conclusions should be drawn with caution. First, techniques vary among investigators and are not standardized. A more serious problem is the lack of systematic time-spatial studies of productivity. Up to now, most studies have sampled phytoplankton in limited areas at intermittent time periods thus making it difficult to separate geographical from seasonal or yearly variations. Ideally, representative Southern Ocean areas should be studied simultaneously.

Currents may also influence productivity. El-Sayed (1968) attributed the low productivity of the Convergence and other areas to surface water instability. Sverdrup (1955) stated that vertical mixing maintains high productivity levels while Fogg (1977) reported that "areas of high primary productivity are those in which comparative stability of the water column occurs." Hart (1942) concludes that the continental shelf, by causing upwelling, is responsible for high productivity values. Russell-Hunter (1970) agreed that the rich trophic conditions of the Antarctic are due to ascending nutrient-rich water. Even from this brief review, it is evident that the relationship between currents and productivity is not fully understood. Some consider currents and upwelling important for supplying nutrients while others believe stable water conditions to be conducive to high productivity.

Seasonality has a major impact on primary productivity in the Antarctic. Early studies by Hart (1934, 1942) showed productivity to be limited to summer months. Moiseev (1971) found that phytoplankton grows for 7-8 months at 55^o S. to 56^o S.; for 6 months at 60^o S. to 65^o S.; and for less than 3 months south of 65^o S. El-Sayed (1970) found a seasonal variation in the concentration of chlorophyll-a and carbon 14 uptake with highest levels occurring in the summer and lower levels during the winter. Foxton (1964), in examining different euphotic zone levels at different times of the year, found high productivity in upper levels during the summer and lower productivity in lower levels. The opposite occurred in winter. Further winter studies would help to clarify ambiguities in this area.

Closely related to seasonality is the amount of solar radiation available for photosynthesis. El-Sayed and Mandelli

(1965) believed that light and temperature were the most important factors affecting primary production in the Weddell Sea. Knox (1970) and El-Sayed (1970) felt that not enough is known about light in Antarctic waters to reach definite conclusions. Moiseev (1971) attributed low production to low light levels. Holm-Hansen et al. (1977) maintained that summer solar energy is higher in Antarctica than in the tropics and solar radiation intensity is so great that photo-inhibition occurs in surface phytoplankton. With respect to winter month activity, Fogg (1977) speculated that in winter algae may reassimilate extracellular organic products formerly liberated when light intensities were higher.

Temperature may also affect productivity. Moiseev (1971) believes that low temperatures could explain, at least partially, depressed growth rates as one travelled south from the Convergence. Knox (1970), on the other hand, discounted temperature because the greatest annual surface temperature range was less than 4-5° C. Holm-Hansen et al. (1977) agreed that Antarctic algae are psychrophilic. However, after comparing observed data and expected calculations for algal growth rates, they decided that Antarctic phytoplankton may not be physiologically adapted for high growth rates at low temperature, and that temperature may limit primary productivity.

In summary, no single factor necessarily limits Antarctic primary production. Growth may be controlled by combinations of the factors discussed or by completely different phenomena.

B. Energy Flow and Nutrient Cycling

Energy flow in the Antarctic marine ecosystem is poorly understood (El-sayed, 1971). A crude way to view energy flow is by examining trophic relationships within the ecosystem (Figures 21 and 22). Figure 22 quantitatively delineates interactions between the various trophic levels.

In contrast to those of other oceans, the Southern Ocean's food chain involving phytoplankton-krill-vertebrates can be short and relatively simple (Knox, 1970). Nevertheless, there are serious gaps in our knowledge of energy flow (e.g., consumption rates). For example, squid and fish are potentially the ecosystem's greatest krill consumers, thereby potentially accounting for a major portion of energy in the system. Yet poor data on these key groups clouds the reliability of energy flow estimates.

Figure 21. Important food chain links in the Southern Ocean (From Everson, 1977).

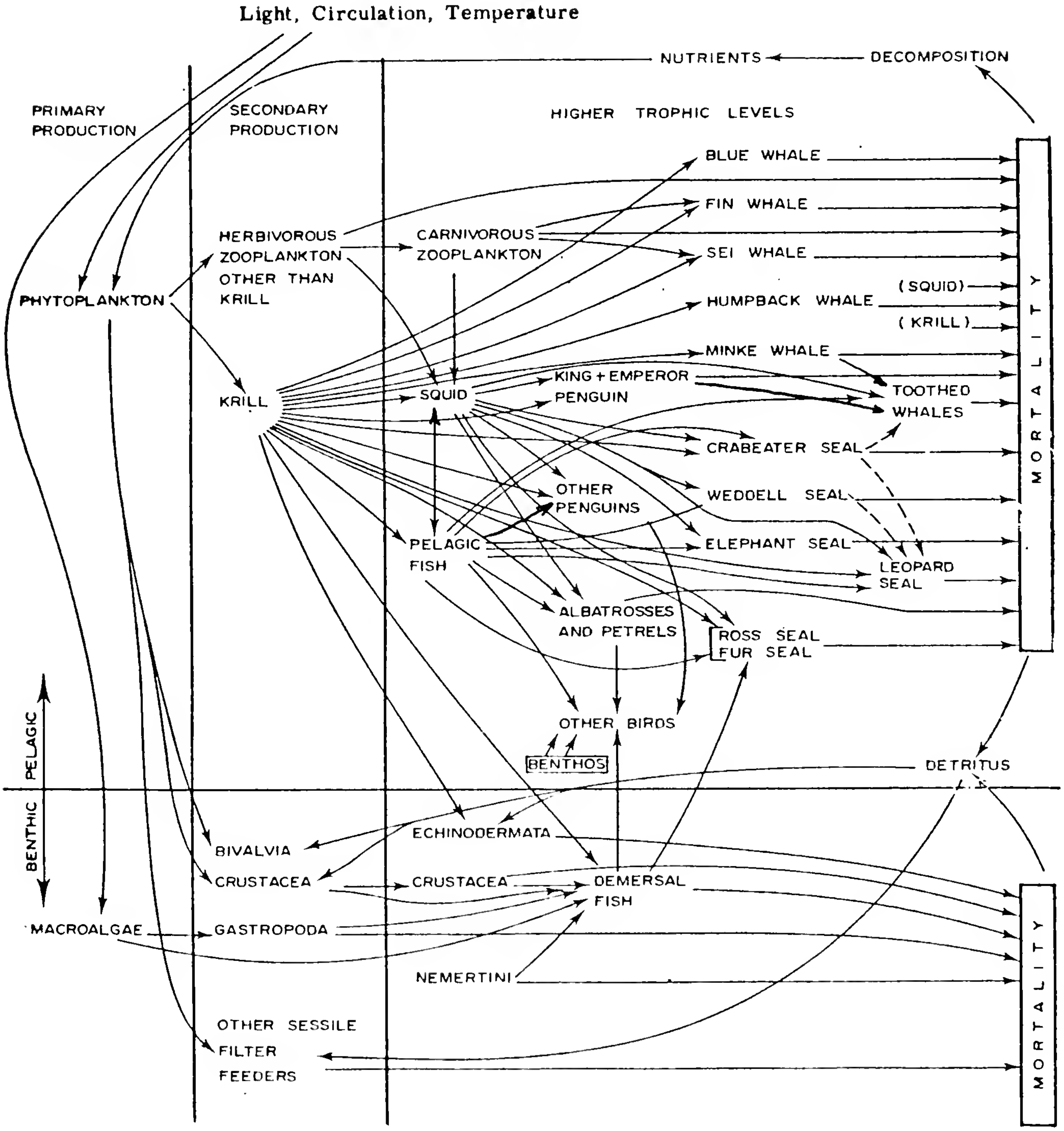
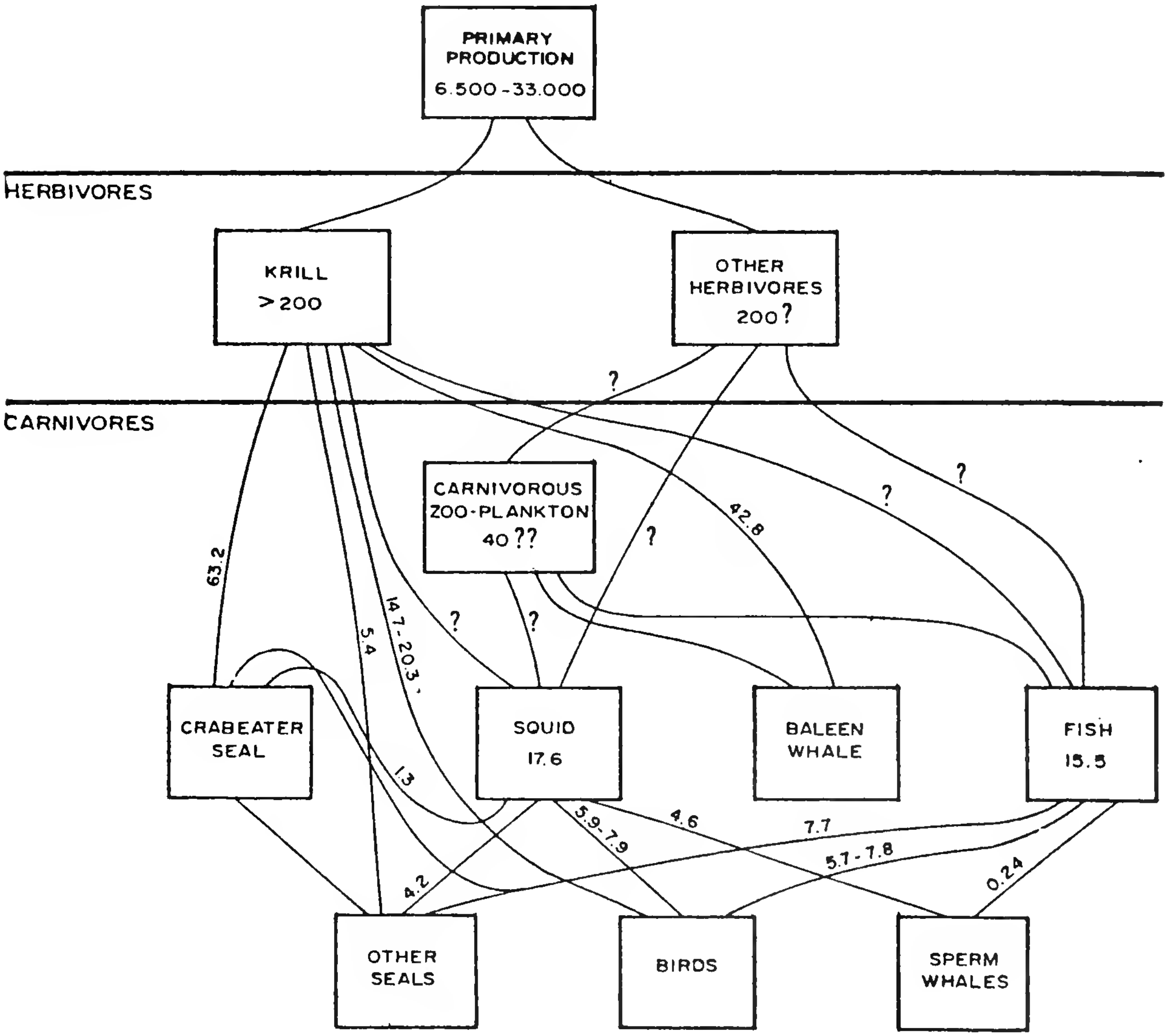


Figure 22. Main quantitative interactions between groups of animals in the Southern Ocean. Figures in boxes denote annual production at each stage and those alongside lines, annual consumption, in millions of tons (From Everson, 1977).



Another important ecosystem feature (not considered in these diagramatical representations) concerns the amount of energy leaving the system. Energy in the form of biomass is removed by the northward migration of whales and fish (e.g., great whales and Patagonian hake). Increased commercial exploitation of living resources will also remove energy from the ecosystem. In natural systems, net energy losses may be relatively insignificant either because metabolic products return energy to the system or long migrations out of the system are limited.

On the other hand, large-scale, commercial harvesting of krill, fish, and squid would permanently remove these system components thereby altering energy available to the ecosystem. One cannot accurately predict the repercussions of such activities.

The role of organisms in nutrient cycling must also be considered (Herbert and Bell, 1974). Nutrients enter the ecosystem in a variety of ways, probably one of the most important being the nutrient rich Warm Deep Layer which moves south and upwells near the coast. Phytoplankton assimilate these nutrients and are then consumed by krill and other zooplankton. In their diurnal migrations, krill distribute nutrients through the upper water column and therefore may be important in recycling these substances (Mauchline and Fisher, 1969). The nutrients released in their feces are in turn taken up by copepods, bacteria, and other organisms -- the net effect being the recruitment and maintenance of richer nutrient concentrations in upper water levels. Moreover, both Marr (1962) and Clowes (1938) felt that krill gut activity was important in creating silicate concentrations in Antarctic waters. Clarke (1977) suggested that, similar to krill, diurnal squid migrations may redistribute nutrients. The consequences of a krill and/or squid harvest on nutrient recycling within the Antarctic marine ecosystem is unknown.

VII. EFFECTS OF ECOSYSTEM MANIPULATION ON LIVING RESOURCES

Ecosystems are dynamic entities of complex relationships in which all subtle but influential factors are rarely understood. Biotic components of ecosystems evolve and adapt to survival in each other's presence. Ecological interactions such as competition, predation, and limitation by the physical environment affect each group's distribution and population dynamics.

Relatively little is known about all of the Antarctic marine ecosystem's relationships. As in any ecosystem, trophic relationships are important in determining interactions between the system's biological components. South of the Convergence, Antarctic krill is the dominant prey species at the base of the food web, affecting species groups such as whales, seals, birds, fish, and squid. Although biomass estimates of krill-consumer populations are somewhat uncertain, there is no doubt that vast amounts of krill are fundamental to the functioning of the Southern Ocean ecosystem.

A. Ecosystem Changes Following the Decline of Whale Stocks

The intensity of competition for krill between consumers is uncertain. Parameters affecting krill and krill-consumer populations may include subtle spatial and temporal interactions. If one assumes that before the exploitation of baleen whales there was significant competition between krill-eating species, it follows that reduced whale populations would allow greater use of krill resources by competitors. This may have led to increased populations of seals, seabirds, fish, squid and baleen whale populations which had not been heavily exploited.

Authors do not agree on population level shifts between krill consumers due to changing levels of available krill. Mackintosh (1970) felt that available information to assess population changes in seals, birds and unexploited baleen whale groups were insufficient to conclude that there had been significant population shifts resulting from trophic interactions. He did, however, acknowledge the possibility that fish and squid populations could have benefited from the krill no longer eaten by whales. Nemoto (1964) felt that the decrease of whales would almost certainly cause major shifts in marine food chains. The following discussion reviews information supporting the idea that various species groups have manifested population responses following the marked decline in baleen whale populations due to harvest.

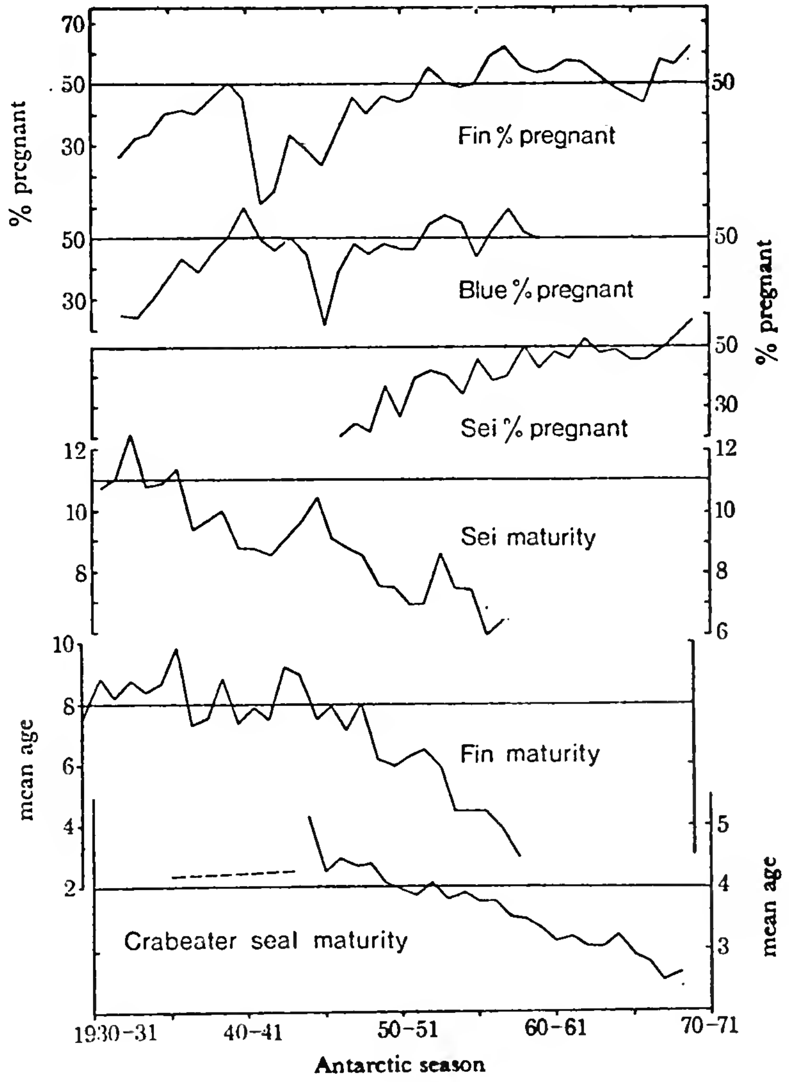
1. Baleen Whales

Gambell (1973), Laws (1961, 1962, 1977a), Lockyer (1972), and Mackintosh (1942) noted that shifts in the growth rates, pregnancy rates, and age at sexual maturity in fin and blue whale populations had a high correlation with whaling activities in the Southern Ocean. They interpreted these changes to imply that whale stocks were food-limited and perhaps close to maximum population levels before exploitation. Under those conditions, growth may have been slowed and sexual maturity delayed. Following whale stock decreases, more krill would presumably have been available to surviving whales, allowing growth and attainment of sexual maturity to proceed faster (Figure 23). Hence, age at first reproduction may be a historical index of the relative food availability to some whale stocks. The authors speculated that unexploited populations of krill consumers (e.g., fin whale stocks prior to 1900) would likely increase until food-limited. These arguments cast doubt on the premise that krill abundance is so great that its predators could not be limited by its availability. Instead, it seems reasonable that the aggregate effects of krill competition could critically limit a variety of krill predators.

Mitchell (1974) discussed trophic relationships and competition for food between baleen whales. Using distributions and food preferences of North Atlantic whale populations, he suggested that distribution and feeding patterns resulted from food competition pressures. For example, fin whales may restrict their feeding range, thereby avoiding direct competition with blue, humpback, and minke whales by using other foods. He felt that analagous situations also occur in the Southern Ocean where sei whales benefited when decreased blue and fin whale populations reduced competition for krill. As evidence, he quoted Townsend (1935) who proposed that following the reduction of southern right whales in southern waters, sei whales extended their range to utilize food resources previously unavailable to them due to the presence of right whales. Mitchell also felt that other whales in the Antarctic marine ecosystem may have exhibited marked changes in their abundance and distribution following whale harvest, and proposed the sei whales and minke whales as the two species one could expect to show the greatest density-dependent responses. Since sei whales were not heavily exploited prior to the 1960's, they may have increased and extended their range into former blue and fin whale feeding grounds.

Minke whales, not harvested in earnest until 1971 and originally sympatric with blue and fin whales in Antarctic feeding grounds, might have exhibited even larger increases

Figure 23. Collective evidence for changes in pregnancy rates and age at sexual maturity in female fin, blue, and sei whales and advancing age at sexual maturity in crabeater seals (After Laws, 1977a, incorporating data from Lockyer, 1972, 1974; Gambel, 1973; Laws, 1977b).



in abundance. Moreover, minke whales rapidly reach sexual maturity, have a relatively short calving interval (one or two years), and feed in the Antarctic year-round. Thus, minke whales may have been in an optimal position to benefit from increased krill availability. Unfortunately, scant information on almost all aspects of minke whale biology and ecology precludes assessing the magnitude of any population changes which have occurred. Estimates of "initial" minke whale population levels are made with reference to the early 1970's. Recent evidence presented to the International Whaling Commission indicates that the age of sexual maturity in minke whales has, over the past several decades, decreased from 14 to 7 years (R. M. Laws, pers. comm.). If their populations had increased following harvest of their krill competitors, population increases might have begun decades ago. Therefore, comments that minke whales have shown no measurable increase in their abundance (Mackintosh, 1970) do not take into account earlier ecosystem adjustments between krill consumers. Minke whale population changes may well have taken place before the first standing stock estimate of the species was ever made.

2. Seals

Seals which use krill may have responded to the baleen whale decline also. Of the four true Antarctic seals, leopard and crabeater seals depend most heavily on krill. Since crabeater seals are the most abundant and depend almost completely on krill, they may have shown the most marked response. Despite reports that seal populations have not increased following heavy whaling (Mackintosh, 1970), Laws (1977a) presented evidence that seal populations may indeed be increasing. He stated that the age at first reproduction of crabeater seals has been decreasing for the last several decades similarly to fin and humpback whales (Figure 23). Laws attributed the decrease in age of first reproduction to a decrease in the competition for food resources, primarily krill. He also cited evidence from the area west of the Antarctic Peninsula which was a whaling sanctuary prior to 1955. When this area was opened to whaling in 1955, stocks were rapidly depleted. Crabeater seal reproductive material from that area showed that age at first reproduction decreased from 4 years of age in 1955 to 2 1/2 years of age in 1970. Laws interpreted these data to suggest that the population had increased during the last two decades as a result of diminished competition with whale stocks for food.

Southern fur seals may have increased due to whaling (Laws, 1973, 1977a). Throughout the Southern fur seals' Antarctic range, slow population comebacks have occurred since commercial sealing stopped. However, in areas of particularly intensive whaling around South Georgia, the recolonization of beaches and general population increase has been faster than in areas of less intensive whaling. Laws (1973) pointed out that unlike many other fur seals, Arctocephalus gazella feeds on krill and that its most rapid population increases have occurred in the Scotia Arc region where it is sympatric with the feeding grounds of Antarctic whales. These data suggest that some seal populations were food-limited through competition with other krill consumers, and that when one competitor was largely removed, seal populations increased because of reduced competition.

3. Penguins and Other Seabirds

Although Prevost (1976) inferred that penguin populations have not increased since the decline of whale stocks, other authors disagree (Rankin, 1951; Sladen, 1964; Stonehouse, 1967a). An extensive literature review (Conroy and White, 1973 and Conroy, 1975) indicated increases in king, emperor, macaroni, adelie, chinstrap, and gentoo penguin populations in the Scotia Arc region. This area of high krill concentration also represents the area of greatest overlap in the feeding distributions of baleen whales and penguins (Laws, 1977a). Conroy (1975) notes that of the three pygoscelid species present there, chinstrap and adelie penguins, both of which rely more heavily on krill than gentoo penguins, increased more than gentoo penguins. Caughley (1960) and Taylor (1962) did not observe penguin population increases in the Ross sea, an area lacking intensive whaling. Their data and information from Mackintosh (1973) provides an interesting contrast to areas of major whaling where penguin populations increased.

With the possible exception of Pryor (1968), there are few data suggesting seabird populations increased as reported in penguins. Pryor indicated that populations of southern fulmars, Antarctic, snow, and Wilson's petrels as well as cape pigeons may have increased at Hazwell Island in past years, although in terms of total avian biomass in the Southern Ocean, other seabirds may not be dominant krill consumers. Still, it seems reasonable to assume that seabirds for which krill is an important food (Mackintosh, 1964; Tickle, 1965; Holdgate, 1967; Beck, 1970; Knox, 1970) may have increased as baleen whale stocks decreased.

4. Fish and Squid

Fish and squid have had perhaps the largest potential for population increases resulting from the loss of whale biomass. However, they are also two of the groups about which we know virtually nothing and which are unlikely to be noticed changing in population size (Mackintosh, 1970). Both fish and squid may have potentially large stock sizes and an important effect on cropping krill to lower levels. Unfortunately, reliable data on the total biomass, distribution, and metabolic rates of fish and squid are not available to demonstrate conclusively the significance of these groups' krill predation. If feeding and metabolic rates of squid and fish were better known, it might be shown that these smaller species, many of which presumably feed on krill year-round, may consume tremendous volumes of krill per unit biomass annually.

5. Discussion

Under pristine (unharvested) conditions, the Antarctic marine ecosystem was subject to continual shifts in biological interactions and physical parameters such as currents, nutrient upwelling, and climatic change. In response to these minor oscillations within the system, the biological constituents fluctuated constantly. The system is inherently dynamic; relationships and abundances of populations are by no means static. Manipulation of major portions of the ecosystem through commercial harvest of whales and seals conceivably caused greater fluctuations within the ecosystem than normally occurred. Moreover, just as the ecosystem would respond to minor fluctuations in the past, so would it respond to major changes in the trophic balance. It is difficult to doubt that following the severe reduction of whales, the various other elements of the Antarctic marine food web readjusted to more fully utilize krill resources formerly consumed by the whales. For these reasons, arguments proposing a krill "surplus" are unconvincing and fail to acknowledge likely ecosystem responses.

B. Potential Ecosystem Changes Resulting from Future Krill Harvest

Just as the Antarctic marine system reacted to commercial harvesting of whales and seals in the past, so may we expect future commercial harvests to cause ecological reverberations throughout the ecosystem.

1. Competition, Predation, and Ecosystem Stability

Acknowledging that ecosystems and their biotic communities are dynamic, one is faced with the difficult question of how the system will respond to various perturbations. The large gaps in our specific understanding of interactions within Antarctic communities tremendously complicates predicting likely outcomes of human interference. Even so, ecological generalities may lend insight into future possibilities for the Antarctic marine ecosystem. Three topics which relate to current discussions of the Southern Ocean are competition, predation, and ecosystem stability. Review of the voluminous ecological literature pertaining to these areas is clearly beyond the scope of this paper. Therefore, selected examples will be used to illustrate the sorts of relationships present in similar systems.

In his paper on the nature of a particular Antarctic marine community, Dayton (1972) reviewed some ecological principles regarding competition, predation, and community resilience. He cited research on competition and predation in marine and intertidal invertebrates (Connell, 1961a, 1961b, 1970; Glynn, 1965; Paine, 1966; Dayton, 1971). These studies demonstrated the striking effects which the competitory and predatory pressures contributed by all members of the community have on each other in shaping the community. Barnacles, snails, mussels, and sea-stars compete for resources and form complex predator-prey relationships. Modifying the environment or manipulating the population levels of any of these components had a strong effect on the whole community.

Similar to Paine's (1969) reference to a "keystone predator" (one which has dominant influence in structuring the community), Dayton (1972) defined "foundation species" as those species at low levels in the food web which contribute in a major way to community structure. In communities which have been manipulated, one can identify foundation species which are critical to the preservation of the community structure itself. Altering the birth or death rates of such species can have serious consequences in altering the organization and relationships within the community. Species through which a significant portion of the energy and nutrients of a system flow represent a fundamental unit of the system (e.g., krill). If they are removed or disturbed, the effects on the ecosystem can be much more dramatic than disturbing species which do not occur in such critical roles (e.g., whales).

Of immediate concern is whether or not krill fisheries will impact krill stocks to the point where they, as a foundation species, might be involved in a shift in community structure. Would a shift in trophic relationships from a phytoplankton-krill-marine mammal food chain to a phytoplankton-copepod-fish food chain be facilitated by manipulating krill?

Such questions must be given serious consideration as plans for conservation and fisheries are developed.

Several studies have shown that dramatic shifts and fluctuations in community structure occur in response to various combinations of ecological pressures (Dayton, 1975; Dayton et al., 1970, 1974; Schaefer, 1970; Paine and Vaas, 1969; Estes and Palmisano, 1974; Simenstad et al., 1978). These studies demonstrate that ecosystems and communities are subject to impacts at a variety of levels, and depending on the relative stability of the system, marked changes may occur in the total community. Botkin and Sobel (1977) discuss the concept of ecosystem stability, making the point that we usually think of them as being relatively stable if left alone from human interference. On the other hand, there is much evidence that ecosystems in fact vary quite a bit within normal boundaries due to a variety of environmental factors. These authors cite Lack's (1954) examples of animal populations which fluctuated widely. We have little information about long-term population abundance levels for many wild animal populations, so it is difficult to estimate the actual extent of these fluctuations -- particularly for marine mammals. These authors state that if the ecosystems fluctuate naturally, then the carrying capacity and optimum sustainable populations (OSP) within these systems will also vary. Such variations demand that management of living resources be tuned to all sides of the ecosystem.

Any krill harvest will impact the ecosystem to some degree. When weighing the relative consequences of various levels of harvest, one must ask what magnitude of krill exploitation will cause significant shifts in the trophodynamics of the ecosystem? Our present understanding of natural ecosystem relationships is insufficient to allow prediction of system sensitivity to manipulation of its food web foundation. Major krill exploitation may disrupt all higher levels of the food web, extending beyond individual faunal stocks back to the krill themselves. In light of the uncertainties associated with our knowledge of ecological mechanisms operating in the Antarctic, one is forced to speculate on possible impacts, acknowledging that ecosystem interactions are subtle and highly complex. Relationships may exist of which we are totally unaware. One can say with certainty, however, that krill is a fundamental unit within the ecosystem upon which a large number of species depend. In calculating the consequences of our actions, we must bear this critical fact in mind.

2. Potential Levels of Impact

With the specific case of krill exploitation, one can identify at least three levels in the ecosystem where harvest impacts might be felt. Impacts may affect target species, dependent and related species, and relationships throughout the ecosystem.

Perhaps the most obvious direct impact on krill through harvest would result from over-fishing to the point where harvests might exceed the stock recruitment required to maintain a viable population. Hazards of over-harvest must be considered in relation to the possibility of krill subpopulations requiring individual management plans. Because of the suggestions presented earlier about the existence of such separate stocks, care should be taken to identify and conserve discrete stocks.

Development of a commercial krill fishery might also affect krill predators. The removal of major food competitors (great baleen whales) allowed greater utilization of krill by other whales and consumers such as seals, birds, fish, and squid. It is not unreasonable to assume that a krill harvest would have an opposite effect on these dependent groups. Rather than increasing the availability of krill, harvest would decrease the food available and increase the degree of competition among krill predators.

Species which feed directly on krill would not be the only groups impacted through reduction in krill stocks -- some krill predators are in turn eaten by other carnivores such as toothed whales, seals, birds, and other fish. For example, fluctuations in krill abundance may affect some squid populations which are important food items for Weddell seals and elephant seals. Impacts at this level are difficult to predict because the particular species affected will depend on the results of competition between krill predators. Therefore, when considering indirect impacts of krill harvest, it is important to consider the variety of trophic pathways through which impacts on target species can be conveyed to other levels of the food web. Krill harvest must be carefully regulated in order that other members of the marine ecosystem are not adversely affected, either directly by reduced food supply, or indirectly by competition with other predators for the reduced krill stock.

A third impact of a krill harvest might be the upsetting of basic interrelationships in the ecosystem itself. For example, the increased ship traffic associated with a fishery might affect important spawning regions for fish and krill damaging stocks through polluting the ocean. Likewise, shore support stations could harm local terrestrial and marine environments through harassment, habitat destruction, and dumping of polluting effluents. Seabird nesting areas and seal rookeries could easily be affected by harvest-related activities as well as by harassment by tourists.

3. Summary

There is evidence that whaling caused shifts in the Southern Ocean trophodynamic structure by removing a major biological component, baleen whales, from the upper levels of the food web. An intensive krill harvest could again cause major, and even more dramatic, shifts in the trophodynamics of the Antarctic marine ecosystem by exploiting a resource at the foundation of the entire food web. Because the implications of exploiting a resource on which so many other species are directly or indirectly dependent are largely unknown, it is clear that extreme caution must be exercised.

VIII. CURRENT INFORMATION AND FUTURE MANAGEMENT DECISIONS

A. Reliability of Data and Estimates

In light of the information so far presented, one inevitably faces the problem of assessing the validity and reliability of available data. Discrepancies in various biomass, productivity, and consumption estimates for Antarctic stocks prompts one to ask which estimates are most realistic. Gulland (1976a) noted that there is not necessarily a single best estimation method and that combinations of methods can provide information on facets of a central theme. For example, he stated that all that one could be sure of regarding whale abundance is that: 1) visual observation confirms whales' presence in the wild, 2) catch per unit effort information confirms that fewer whales exist today than before harvesting, and 3) that whale populations may be increasing, based on comparing reproductive parameters and other population characteristics. His point is that different techniques will work more or less favorably for different problems of estimation.

Other factors affecting the relative accuracy of different biomass or productivity estimates are the sampling techniques and assumptions used when extrapolating sample data to entire populations. The estimates of Southern Ocean primary productivity previously discussed varied because often different areas had been sampled at different times of the year. These data were then used to describe the primary productivity of large ocean sectors. These extrapolations were made on the assumption that local measurements also applied to larger areas. Whenever sampling techniques are used to estimate biomass or productivity, the final estimate is only as sound as the weakest assumption used in the sampling data.

When considering estimates of various features of the Antarctic marine ecosystem, one aspect quickly becomes evident: many of these calculations are made with minimal data. Complex models will be of little use if based on insufficient data. Theoretical treatments of various ecosystem impacts or results of living resource exploitation are important; however, without real information to test hypotheses and to suggest new ones, understanding of the Antarctic marine ecosystem will not improve. In light of the gaps in our knowledge concerning virtually all aspects of the Antarctic marine ecosystem, more data must be collected in an organized and cooperative manner with specific goals in mind. In the meantime, discussions should be undertaken to determine the best techniques to estimate various parameters using the minimal data currently available.

B. Risks Associated With Making Management Decisions Upon Current Information

Due to an incomplete understanding of the Antarctic marine ecosystem, attempts to integrate quantitative trophic relationships, subtle ecosystem interactions, and enlightened management decisions are associated with a certain degree of risk. It is essential that more adequate information be gathered to ensure that irreversible reactions to man's manipulations do not result. For example, further research may demonstrate that certain geographical areas are sometimes critical (e.g., breeding). Without that knowledge, overharvest in such an area could have a relatively high impact on target and dependent species.

Dependent species may be subject to trophodynamic shifts if other living resources are harvested. An obvious example is the impact of krill harvests on various krill predators. Krill consumers would undoubtedly experience some degree of impact as a result of commercial krill exploitation -- the critical question is what the changes would be. To what extent would harvesting krill adversely affect recovery of the seriously depleted baleen whales? The increased competition for krill could slow or stop the comeback. Krill harvesting might also upset certain fundamental ecosystem patterns which are critical to maintaining the ecosystem. In short, uninformed exploitation of Southern Ocean marine life may adversely affect target species, dependent species, and the ecological viability of the system as a whole.

IX. CONCLUSION

A strong conservation regime coupled with sound scientific research programs is imperative for the Antarctic marine ecosystem. The need for harvest regulations is clearly evident. These must be in force in time to guide the development of a fishery which ensures optimal management policies based upon scientific information and principles of conservation.

A. Different Approaches to Management of Living Resources

Traditionally, renewable resource management has been conducted with reference to effects on harvested species alone. Broader conservation principles and enlightened management practices, however, require an ecosystem approach which takes into account the other biotic components as well as their physical environment.

Single species and ecosystem approaches each have sets of contrasting assumptions. The single species strategy assumes that examination of only those features directly associated with the target species will provide adequate information on that stock's reaction to human manipulation. The ecosystem approach, on the other hand, not only looks at parameters directly effecting the target species, but also those important in maintaining ecological relationships. Furthermore, the biotic and physical environments in which a target species exists are ultimately critical to the population dynamics and ecology of the target species itself. Species cannot exist within systems without affecting each other. Therefore, manipulation of major system constituents will, to a greater or lesser extent, affect other component populations of the ecosystem.

B. The Need for an Ecosystem Approach in Managing Antarctic Krill

Preceding sections outlined the major faunal groups in the Southern Ocean that are directly or indirectly related to each other through their dependence on krill. In order to ensure a comprehensive management plan for the Southern Ocean, regulations must be formulated within an ecosystem context. Both krill and their consumers have functional roles in the ecosystem as a whole. Primary productivity, energy flow, and nutrient cycling within the ecosystem were acknowledged earlier as dynamic features of the system. Attempting to manage or manipulate solely one component of this system ignores the fact that all parts of an ecosystem will inevitably respond to changes in any component part, depending on the degree of manipulation.

The position of the manipulated component in the food web has an important bearing on the reactions in the ecosystem. For example, maximum sustainable yield (MSY) approaches to whale management in the Southern Ocean attempted to manage individual whale stocks without regard to their position and role in the ecosystem as a whole. Harvesting most of the Southern Ocean whale biomass removed a large block of krill consumers in upper trophic levels. Possible reactions to this harvest have been discussed above. Reactions to manipulating other trophic levels in the Antarctic marine ecosystem (e.g., primary consumers instead of terminal consumers) may well be expected to have different results than those experienced with the whale harvest. Significant ecosystem disruptions may occur if fundamental producers are heavily exploited.

The effects of such a disruption could be quite widespread. In the case of krill, removing large amounts of krill may increase the competition between krill consumers, the extent of which must be determined to predict ultimate krill harvesting impacts. In extreme over-fishing, the integrity of stocks of marine mammals, birds, fish, and cephalopods as well as other invertebrates might be seriously threatened.

The type of integrated, comprehensive conservation plan which makes provision for rational, controlled harvesting cannot be realized through a single species maximum sustainable yield approach. If the Antarctic marine ecosystem is to be maintained as a viable, dynamic system, an ecosystem approach to the management and conservation of all Southern Ocean marine life must be implemented.

X. ACKNOWLEDGEMENTS

The many people who aided the preparation of this report are thanked for their help. D. G. Ainley, D. G. Chapman, P. K. Dayton, C. J. Denys, S. Z. El-Sayed, I. Everson, R. J. Hofman, L. L. Jones, G. L. Kooyman, R. M. Laws, M. A. McWhinnie, G. C. Ray, D. B. Siniff, I. Stirling, and J. R. Twiss, Jr., provided helpful comments. J. Crist, W. Fraser, D. Schneider, and J. A. Thomas helped with writing and editing various portions of the manuscript. R. Daly, J. K. Drevenak, L. Ferm, D. Gable, K. Michels, J. Pauly, C. Ribic, R. Rice, L. D. Roberts, M. Taylor, and J. Wendt also helped with a variety of stages of preparations. All of these people are thanked for their efforts in finishing this report in the short time available.

LITERATURE CITED

Aguayo, L., and D. Torres. 1968. A first census of pinnipedia in the South Shetland Islands. Pp. 166-168 in Currie, R.I. (ed.), Symposium on Antarctic Oceanography; Santiago, Chile, 1966. Scott Polar Research Institute/SCAR: Cambridge. 268 pp.

Allen, J. 1945. Planktonic Cephalopod Larvae from the eastern Australian coast. Rec. Aust. Mus., 21:317-350.

Andriashev, A.P. 1965. A general review of the Antarctic fish fauna. Pp. 491-550 in Van Mieghem, J., and P. Van Oye (eds.), Biogeography and Ecology in Antarctica. Dr. W. Junk Publishers: The Hague. 762 pp.

Andriashev, A.P. 1970. Cryopelagic fishes of the Arctic and Antarctic and their significance in polar ecosystems. Pp. 297-304 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Anon. 1964. Squid as sea-food. Fisheries Newsletter, Australia, 23:23.

Anon. 1975. Chilean vessel catches krill. Fish. News Int., 14:64.

Anon. 1976a. German trawlers and major krill research voyage. Fish. News Int., 15:23.

Anon. 1976b. Japanese krill fishing. Nippon Suisan Kaizai; 17 June 76.

Anon. 1977a. Out to the high seas as limits cut fishing areas. Fish. News Int., 16:35-41.

Anon. 1977b. Ship en route to Antarctic for studies. Free China Weekly, 17(48).

Ashmole, P.N. 1971. Sea bird ecology and the marine environment. Pp. 223-286 in King, J.R., and D.S. Farner (eds.), Avian Biology, Vol. 1. Academic Press: New York. 586 pp.

Baker, A. 1954. The circumpolar continuity of Antarctic plankton species. Discovery Rep., 27:201-218.

Bannister, J., and A. Baker. 1967. Observations of food and feeding of baleen whales at Durban. Norsk Hvalfangsttid., 56:78-82.

Bargmann, H.E. 1937. The reproductive system of _Euphausia superba_. Discovery Rep., 14:325-350.

Bargmann, H. 1954. The development and life history of adolescent and adult krill (_Euphausia superba_). Discovery Rep., 23:103-176.

Barkley, E. 1940. Nahrung und filter-apparat des wlkrebschens _Euphausia superba_ Dana. A. Fisch., 1:65-156.

Barrett-Hamilton, G.E.H. 1901. Seals. Exped. Antarctique Belg. Result. Voyage "Belgica" 1897-1899. Rapp. Sci. Zool.:1-19.

Basalev, V.N., and A.G. Petukhov. 1969. Experimental fishing in the Scotia Sea from the research factory ship Akademik Knipovich. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr., 66:307-310. (Nat. Lending Library Transl., RTS 5596).

Bechervaise, J. 1963. The four bays. Victorian Nat., 79:4-9.

Beck, J. 1969. Food, moult and age of first breeding in the cape pigeon, _Daption capensis_(Linneaus) Brit. Antarct. Surv. Bull., 21:33-44.

Beck, J. 1970. Breeding seasons and moult in some smaller Antarctic petrels. Pp. 542-550 _in_ Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Beklemishev, K.W. 1960. Southern atmospheric cyclones and the whale feeding grounds in the Antarctic. Nature, Lond., 187:530-531.

Beklemishev, K.W. 1961. The influence of atmospheric cyclones on the feeding field of whales in Antarctica. Trans. Inst. Okeanol., 51:121-141.

Bertram, G.C.L. 1940. The biology of the Weddell and crabeater seals: with a study of the comparative behavior of the Pinnipedia. British Graham Land Exped. 1934-1937. Sci. Reps., 1:1-139.

Best, P.B. 1975. Review of world sperm whale stocks. FAO Advisory committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/8.

Bigelow, H.B., and W.C. Schroeder. 1965. Notes on a small collection of rajids from the subantarctic region. Limnol. Oceanogr., 10 Suppl.:34-49.

Bonner, W.N. 1968. The fur seal of South Georgia. Sci. Rep. Brit. Antarct. Surv., 56:1-81.

Bonner, W.N. 1976. The status of the antarctic fur seal *Arctocephalus gazella*. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/50.

Bonner, W.N., and R.M. Laws. 1964. Seals and sealing. Pp. 163-190 *in* Priestley, R., R.J. Adie, and G. de Q. Robin (eds.), Antarctic Research. Butterworths: London. 360 pp.

Borchgrevink. C.E. 1901. First on the Antarctic continent, being an account of the British Antarctic Expedition, 1898-1900. George Newnes, Ltd.: London.

Botkin, D.B., and M.J. Sobel. 1977. Optimum sustainable marine mammal populations. Report to the U.S. Marine Mammal Commission, Contract #MM7AL003. 126 pp.

Brinton, E. 1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull., 74:733-762.

Brown, K.G. 1952. Observations on the newly born leopard seal. Nature, Lond., 170:982-83.

Brown, K.G. 1957. The leopard seal at Heard Island, 1951-1954. Austr. Natl. Antarct. Res. Exped. Interim Rept. 16. 34 pp.

Brown, R.N. 1913. The seals of the Weddell Sea: notes on their habits and distribution. Scottish Nat. Antarct. Exped., Vol. 4.

Brown, R.N.R. 1915. The seals of the Weddell Sea: notes on their habits and distribution. Rep. Sci Results Scot. Natl. Antarct. Exped., 1902-1904, 4 (Zool.), Part 13:181-198.

Brown, S.G. 1962a. A note on migration in fin whales. Norsk Hvalfangsttid., 51:13-16.

Brown, S.G. 1962b. The movements of fin and blue whales within the Antarctic zone. Discovery Rep., 33:1-54.

Brown, S.G. 1962c. Whale marks recovered in the Antarctic whaling season 1967/1968. Norsk Hvalfangsttid., 57:139-140.

Brown, S.G. 1968a. Feeding of sei whales at South Georgia. Norsk. Hvalfangsttid., 57:118-125.

Brown, S.G. 1968b. The results of sei whale marking in the Southern Ocean in 1967. Norsk Hvalfangsttid., 57:77-83.

Brown, S.G. 1968c. Whale marks recovered in the Antarctic whaling season 1967/1968. Norsk Hvalfangsttid., 57:139-140.

Brown, S.G. 1972. Whale marking--progress report, 1971. Rep. IWC, 22:37-40.

Brown, S.G. 1973. Functional anatomy of marine mammals. Deep Sea Res., 20:868-69.

Brown, S.G., R.L. Brownell, Jr., A.W. Erickson, R.J. Hofman, G.A. Llano, and N.A. Mackintosh. 1974. Antarctic mammals. American Geographical Society, Antarctic Map Folio Series, 18:1-19.

Bruce, W.S. 1913. Measurements and weights of Antarctic seals taken by the Scottish National Antarctic Expedition. Trans. Roy. Soc. Edinburgh, 49:567-577.

Budd, G.M. 1970. Rapid population increase in the Kerguelen fur seal, _Arctocephalus_ _tropicalis_ _gazella_, at Heard Island. Mammalia, 34:410-414.

Burukovskii, R.N. 1967. Certain problems of the biology of the Antarctic krill _Euphausia_ _superba_ Dana from the south-western region of the Scotia Sea. Pp. 37-54 _in_ Burukovski, R.N. (ed.), Soviet Fishery Research on the Antarctic Krill. U.S. Clearinghouse for Fed. Sci. and Tech. Info., TT367-32683.

Burukovskii, R.N., and B.A. Yaragov. 1967. Studying the Antarctic krill for the purpose of organizing krill fisheries. Pp. 5-17 _in_ Burukovskii, R.N. (ed.), Soviet Fishery Research on the Antarctic Krill. U.S. Clearinghouse for Fed. Sci. and Tech. Info., TT367-32683.

Calhaem, I., and D.A. Christoffel. 1969. Some observations of the feeding habits of a Weddell seal, and measurements of its prey, _Dissostichus_ _mawsoni_, at McMurdo Sound, Antarctica. N.Z. J. Mar. Freshwater Res., 3:181-190.

Carrick, R., and S.E. Ingham. 1967. Antarctic sea birds as subjects for ecological research. Proc. of the Symp. on Pacific Antarctic Sciences, Tokyo, 1966, JARE Sci. Rep., 1:151-184.

Carrick, R., and S.E. Ingham. 1970. Ecology and population dynamics of Antarctic sea birds. Pp. 505-525 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Caughley, G. 1960. The adelie penguins of the Ross and Beaufort Islands. Rec. Dominion Mus. Wellington, 3:263-282.

Chapman, D.G. 1973. Maximum sustainable yield of minke whales in the Antarctic. Contributed paper to the meeting of the Scientific Committee of the International Whaling Commission, London, June, 1973, MS.

Chapman, D.G. 1974a. Estimation of population parameters of Antarctic baleen whales. Pp. 336-351 in Schevill, W. (ed.), The Whale Problem. Harvard Univ. Press: Cambridge. 419 pp.

Chapman, D.G. 1974b. Status of Antarctic rorqual stocks. Pp. 218-238 in Schevill, W. (ed.), The Whale Problem. Harvard Univ. Press: Cambridge. 419 pp.

Chapman, D.G., K.R. Allen, and S.J. Holt. 1964. Reports of the Committee of Three Scientists on the special scientific investigation of the Antarctic whale stocks. Rep. IWC, 14:32-106.

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, Megaptera noraeangliae (Borowski). Aust. J. Mar. Freshwater Res., 16:33-128.

Clarke, M.R. 1966. A review of the systematics and ecology of oceanic squids. Adv. Mar. Biol., 4:91-300.

Clarke, M.R. 1977. Beaks, nets, and numbers. Symp. Zoo. Soc. Lond., 38:89-126.

Clarke, R. and O. Paliza. 1972. Sperm whales of the Southeast Pacific. Part III: Morphometry. Hvalrad, Skr., 53:1-106.

Clowes, A.J. 1938. Phosphate and silicate in the Southern Ocean. Discovery Rep., 19:1-120.

Connell, J.H. 1961a. Effect of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides. Ecol. Monogr., 31:61-104.

Connell, J.H. 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecol., 42:710-723.

Connell, J.H. 1970. A predator-prey system in the marine intertidal region. 1. Balanus glandula and several predatory species of Thais. Ecol. Monogr., 40:49-78.

Conroy, J.W.H. 1975. Recent increases in penguin populations in Antarctica and the subantarctic. Pp. 321-336 in Stonehouse, B. (ed.), The Biology of Penguins. Univ. Park Press: Baltimore. 555 pp.

Conroy, J.W.H., and E.L. Twelves. 1972. Diving depths of the gentoo penguin (Pygoscelis papua) and the blue-eyed shag (Phalacracorax atriceps) from the South Orkney Islands. Brit. Antarct. Surv. Bull., 30:106-108.

Conroy, J.W.H., and M.G. White. 1973. The breeding status of the king penguin (Aptenodytes patagonica). Brit. Antarct. Surv. Bull., 32:31-40.

Croxall, J. Food consumption of Antarctic birds. Unpublished MS. British Antarctic Survey: Cambridge.

Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. Pp. 145-70 in Norris, K.S. (ed.), Whales, Dolphins, and Porpoises. University of California Press: Los Angeles. 789 pp.

Dawbin, W.H. 1976. World stocks of humpback whales. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/140.

Dawson, E.W. 1974. Adelie penguins and leopard seals; illustrations of predation-history, legend and fact. Notornis, 21(1):36-39.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr., 41:351-389.

Dayton, P.K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pp. 81-96 in Parker, B.C. (ed.), Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press. 356 pp.

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr., 45:137-159.

Dayton, P.K., G.A. Robilliard, and R.T. Paine. 1970. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctic. Pp. 244-258 in Holdgate, M. W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Dayton, P.K., G.A. Robilliard, R.T. Paine, and L.B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol. Monogr., 44:105-128.

Deacon, G.E.R. 1976. The cyclonic circulation in the Weddell Sea. Deep Sea Res., 23:125-126.

Dearborn, J.H. 1965. Food of Weddell seals at McMurdo Sound, Antarctica. J. Mammal., 46:37-43.

Dell, R.K. 1965. Marine biology. Pp. 129-152 in Hatherton, T. (ed.), Antarctica. Metheun: London. 511 pp.

DeMaster, D.P. 1978. Estimation and analysis of factors that control a population of Weddell seals. Unpublished Ph.D. Thesis. University of Minnesota. 80 pp.

DeWitt, H.H. 1971. Coastal and deep water benthic fishes of the Antarctic. American Geographical Society, Antarctic Map Folio Series. 15:1-10.

DeWitt, H.H., and T.L. Hopkins. 1977. Aspects of the diet of the Antarctic silverfish *Pleuragramma antarcticum*. Pp. 557-567 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Doi, T., and S. Ohsumi. 1969. The present state of sei whale population in the Antarctic. Rep. IWC, 19:118-120.

Ealey, E.H.M. 1954a. Analysis of stomach contents of some Heard Island birds. Emu, 54:204-210.

Ealey, E.H.M. 1954b. Ecological notes on the birds of Heard Island. Emu, 54:91-112.

Eddie, G.C. 1977. The harvesting of krill. FAO Rep., GLO/SO/77/2. Southern Ocean Fisheries Survey Programme, Rome.

Eklund, C.R. 1964. Population studies of Antarctic seals and birds. Pp. 415-419 in Carrick, R., M.W. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

El-Sayed, S.Z. 1968. Prospects of primary productivity studies in Antarctic waters. Pp. 227-239 in Currie, R.I. (ed.), Symposium on Antarctic Oceanography; Santiago, Chile, 1966. Scott Polar Research Institute/ SCAR: Cambridge. 268 pp.

El-Sayed, S.Z. 1970. On the productivity of the Southern Ocean. Pp. 119-135 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

El-Sayed, S.Z. 1971. Biological aspects of the pack ice ecosystem. Pp. 35-54 in Deacon, C. (ed.), Symposium on Antarctic Ice and Water Masses. W. Heffer and Sons, Ltd.: Cambridge. 113 pp.

El-Sayed, S.Z., and E.F. Mandelli. 1965. Primary production in the southeastern Indian Ocean. Pp. 131-142 in Zeitzschel, B. (ed.), The Biology of the Indian Ocean, Ecological Studies: Analysis and Synthesis, Vol. 3. Springer-Verlag: Berlin.

Emison, W.B. 1968. Feeding preferences of the adelie penguin at Cape Crozier, Ross Island. Pp. 191-212 in Austin, O.L. (ed.), Antarctic Bird Studies. Antarctic Research Series, No. 12. American Geophysical Union: Washington, D.C. 262 pp.

Erickson, A.W. 1971. Seal population studies in the Ross Sea. Antarct. J. U.S., 6:98-99.

Erickson, A.W., and R.J. Hofman. 1974. Antarctic Seals. American Geographical Society, Antarctic Map Folio Series, 18:4-12.

Erickson, A.W., D.R. Cline, R.J. Hofman. 1969. Population study of seals in the Weddell Sea. Antarct. J. U.S., 4:99-100.

Erickson, A.W., J.R. Gilbert, and J. Otis. 1973. Census of pelagic seals off the Oates and George V coasts, Antarctica. Antarct. J. U.S., 8:191-194.

Erickson, A.W., J.R. Gilbert, G.A. Petrides, R.J. Oehlenschlager, A.A. Sinha, J. Otis. 1972. Populations of seals, whales, and birds in the Bellingshausen and Amundsen Seas. Antarct. J. U.S., 7:70-72.

Erickson, A.W., R.J. Hofman, R.J. Oehlenschlager, J. Otis, and D. Kuehn. 1971. Seal population studies in the Ross Sea. Antarct. J. U.S., 6:98-99.

Erickson, A.W., R.J. Hofman, W.L. Thomas and R.J. Oehlenschlager. 1970. Seal survey in the South Shetland and South Orkney Islands. Antarct. J. U.S., 5:130-131.

Erickson, A.W., D.B. Siniff, D.R. Cline, and R.J. Hofman. 1971. Distributional ecology of Antarctic seals. Pp. 55-76 in Deacon, G. (ed.), Symposium on Antarctic Ice and Water Masses (Tokyo, 1970). Scientific Committee on Antarctic Research: Cambridge.

Estes, J.A., and J.F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science, 185:1058-1060.

Everson, I. 1968. Larval stages of certain Antarctic fishes. Brit. Antarct. Surv. Bull., 16:65-70.

Everson, I. 1970. The population dynamics and energy budget of Notothenia neglecta Nybelin at Signy Island, South Orkney Islands. Brit. Antarct. Surv. Bull., 23:25-50.

Everson, I. 1976. Antarctic krill: a reappraisal of its distribution. Polar Rec., 8:15-23.

Everson, I. 1977. The Southern Ocean: the living resources of the Southern Ocean FAO Rep., GLO/SO/77/1. Southern Ocean Fisheries Survey Programme, Rome. 156 pp.

Falla, R.A. 1937. Birds. Banzare Rep., B,2:1-304.

Falla, R.A. 1964. Distribution patterns of birds in the Antarctic and high latitude subantarctic. Pp. 367-376 in Carrick, R., M.W. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Filippova, J.A. 1972. New data on the squids (Cephalopoda, Oegosida) from the Scotia Sea. (Antarctic). Malcologia; 11:391-406.

Fischer, W. 1976. Tagesperiodische Wanderungen des Antarktischen Krill. Inf. Fischwirtsch., 3:90-92.

Fogg, G.E. 1977. Aquatic primary production in the Antarctic. Phil. Trans. R. Soc. Lond., B 279:27-38.

Foster, T. 1976. The physical oceanography of the Southern Ocean: key to understanding its biology. In El-Sayed, S.Z. (ed.), Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) Vol. II. (in press).

Foxton, P. 1956. The distribution of standing crop of zooplankton in the Southern Ocean. Discovery Rep., 28:191-236.

Foxton, P. 1964. Seasonal variations in the plankton of Antarctic waters. Pp. 311-318 in Carrick, R., M.W. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Fraser, F.C. 1936. On the development and distribution of the young stages of krill (*Euphausia superba*). Discovery Rep., 14:1-192.

Fujino, K. 1962. Blood types of some species of Antarctic whales. Am. Nat., 96:205-210.

Fujino, K. 1964. Fin whale subpopulations in the Antarctic whaling areas II, III, and IV. Sci. Rep. Whale Res. Inst., Tokyo. No. 18:1-27.

Gambell, R. 1968. Seasonal cycles and reproduction in sei whales of the Southern Ocean. Discovery Rep., 35:31-134.

Gambell, R. 1973. Some effects of exploitation on reproduction in whales. J. Reprod. Fert. (suppl.), 19:533-553.

Gambell, R. 1975a. A review of population assessments of Antarctic fin whales. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/9.

Gambell, R. 1975b. A review of population assessments southern minke whales. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/11.

Gambell, R. 1975c. A review of population assessments of Antarctic sei whales. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/10.

Gambell, R. 1976a. A note on the changes observed in the pregnancy rate and age at sexual maturity of some baleen whales in the Antarctic. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/37.

Gambell, R. 1976b. A review of population assessments of Antarctic fin whales. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/9 Add. 1.

Gambell, R. 1976c. A review of population assessments of Antarctic sei whales: addendum. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/10 Add. 1.

Gambell, R. 1976d. A review of population assessments of southern minke whales: addendum. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/11 Add. 1.

Gambell, R. 1976e. Population biology and management of whales. Pp. 247-336 in Coaker, T.H. (ed.), Applied Biology. Academic Press: London. 358 pp.

Gilbert, J.R. 1974. The biology and distribution of seals in Antarctic pack ice. Unpublished Ph.D. thesis. Univ. of Idaho, Moscow. 125 pp.

Gilbert, J.R., and A.W. Erickson. 1977. Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. Pp. 703-740 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Glynn, P.W. 1965. Community composition, structure, and inter-relationships in the marine intertidal Endocladia muricata--Balanus glandula association in Monterey Bay, California. Beaufortia, 12:1-98.

Gordon, A.L., and R.D. Goldberg. 1970. Circumpolar characteristics of Antarctic waters. American Geographical Society, Antarctic Map Folio Series. 13:1-19.

Gulland, J.A. 1970. The development of the resources of the Antarctic seas. Pp. 217-223 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Gulland, J.A. 1972. Future of the blue whale. New Scient., 54:198.

Gulland, J.A. 1974. Distribution and abundance of whales in relation to basic productivity. Pp. 27-52 in Schevill, W.E. (ed.), The Whale Problem. Harvard Univ. Press: Cambridge. 419 pp.

Gulland, J.A. 1976a. A note on the abundance of Antarctic blue whales. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/76.

Gulland, J.A. 1976b. Antarctic baleen whales: history and prospects. Polar Rec., 18:5-13.

Gunther, E.R. 1949. The habits of fin whales. Discovery Rep., 25:113-142.

Gwynn, A.M. 1953. The status of the leopard seal at Heard Island and Macquarie Island, 1948-1950. Australian Natl. Antarctic Exped. Interim Rep., 3:1-33.

Hamilton, J.E. 1939. The leopard seal Hydrurga leptonyx (De Blainville). Discovery Rep., 18:240-264.

Hanson, N. 1902. Extracts from the private diary of the late Nicolai Hanson. Pp. 79-105 in Sharpe, B., and J. Bell (eds.), Report on the Collections of Natural History Made in the Antarctic Regions During the Voyage of the Southern Cross. British Museum (Natural History): London.

Hardy, A.C. 1965. The Krill-Ocean harvest of the future? New Scient., 27:41-46.

Hardy, A.C. and E.R. Gunther. 1935. The plankton of the South Georgia whaling grounds and adjacent water: 1926-1927. Discovery Rep., 11:1-146.

Harper, P.C. 1972. The field identification and distribution of the thin-billed prion (Pachyptila belcheri) and the Antarctic prion (Pachyptila desolata). Nortornis, 19:140-175.

Harrison, J.R., R.C. Hubbard, R.S. Petuson, C.E. Rice, R.J. Schusterman, 1968. The Behavior and Physiology of pinnipeds. Appleton-Century-Crofts: New York. 411 pp.

Hart, T.J. 1934. On the phytoplankton of the southwest Atlantic and Bellingshausen Sea. Discovery Rep., 8:1-268.

Hart, T.J. 1942. Phytoplankton periodicity in Antarctic surface waters. Discovery Rep., 21:261-356.

Herbert, R.A., and C.R. Bell. 1974. Nutrient cycling in the Antarctic marine environment. Brit. Antarct. Surv. Bull., 39:7-11.

Hofman, R.J. 1975. Distribution patterns and population structure of Antarctic seals. Unpublished Ph.D. thesis. Univ. of Minnesota. 155 pp.

Hofman, R., A.W. Erickson, D.B. Siniff. 1973. The Ross Seal, *Ommatophoca rossi*. Int. Union Conserv. Nature Natural Resources. Publ. New ser. suppl. pap., 39:129-139.

Hofman, R.J., R.A. Reichle, D.B. Siniff, and D. Muller-Schwarze. 1977. The leopard seal (*Hydrurga leptonyx*) at Palmer Station, Antarctica. Pp. 769-782 *in* Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Holdgate, M.W. 1963. Observations of birds and seals at Anvers Island, Palmer Archipelago, *in* 1955-57. Brit. Antarct. Surv. Bull., 2:45-51.

Holdgate, M.W. 1967. The Antarctic ecosystem. Phil. Trans. Roy. Soc., 252:363-383.

Holdgate, M.W., P.J. Tibrook, and R.W. Vaughan. 1968. The biology of Bourvetoya. Brit. Antarct. Surv. Bull., 15:1-7.

Holm-Hansen, O., S.Z. El-Sayed, G.A. Franceschini, and R.L. Cuhel. 1977. Primary production and the factors controlling phytoplankton growth in the Southern Ocean. Pp. 11-50 *in* Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1255 pp.

Hudson, R. 1966. Adult survival estimates for two Antarctic petrels. Brit. Antarct. Surv. Bull., 8:63-73.

Huffaker, C.B., and C.E. Kennett. 1959. A ten-year study of vegetation changes associated with biological control of klamath weed. J. Range Manage., 12:69-82.

Hureau, J.C. 1966. Biologie de Chaenichthys rhinoceratus Richardson, et problème du sang incolore des Chaenicthidae, poissons des mers australes. Bull. Soc. Zool. Fr., 91:735-751.

Hureau, J.C. 1970. Biologie comparée de quelques poissons antarctiques (Nototheniidae). Bull. Inst. Oceanogr. Monaco, 68:1-244.

Hureau, J.C. 1976. Population dynamics and ecology of fishes, squids, and other living resources. Pp. 53-68 in Study of the Living Resources of the Southern Ocean. Draft Proposal Prepared by SCAR/SCOR Group of Specialists on Living Resources of the Southern Ocean, 17-21 August 1976, Woods Hole, Massachusetts, U.S.A. Texas A & M University: College Station.

Hustedt, F. 1958. Diatomeen aus der-Antarktis und dem Sudatlanik, Dtsch. Antarkt. Exped. 1938-1939. Wiss Ergebn. II Lief, 2:103-191.

Ichihara, T. 1966. The pygmy blue whale, Balaenoptera musculus brevicauda, a new subspecies from the Antarctic. Pp. 79-111 in Norris, K.S. (ed.), Whales, Dolphins, and Porpoises. Univ. Calif. Press: Los Angeles. 789 pp.

Ichihara, T. 1975. Review of pygmy blue whale stock in the Antarctic. FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/28.

Ichihara, T., and T. Doi. 1964. Stock assessment of pigmy blue whales in the Antarctic. Norsk Hvalfangsttid., 53:145-167.

Ichimura, S., and H. Fukushima. 1963. On the chlorophyll content of the surface water of the Indian and Antarctic oceans. Bot. Mag. (Tokyo), 76:395-399.

Il'icher, Ye. G. 1967. The chemical composition of krill and its use for feed and food purposes. Pp. 55-60 in R.N. Burukovskiy (ed.), Soviet Fishery Research on the Antarctic Krill. U.S. Clearinghouse for Fed. Sci. and Tech. Info., TT67-32683.

Inada, T., and I. Nakamura. 1975. A comparative study of two populations of the gadoid fish Micromesistius australis from the New Zealand and Patagonian-Falkland regions. Bull. Far Seas Fish. Res. Lab., 13:1-26.

Ivanov, B.G. 1970. On the biology of the Antarctic Krill (Euphausia superba Dana). Mar. Biol., 7:340-351.

Ivashin, M.V. 1969. O lokal'nosti nekotorykh promyslovykh vidov kitov v iuzhnom polusharii. Rybn. Khoz., 45-11-13.

Ivashin, M.V. 1973. Marking of whales in the southern hemisphere (Soviet materials). Rep. IWC, 23:174-191.

Johnstone, G.W. 1977. Comparative feeding ecology of the giant petrels Macronectes giganteus (Gmelin) and M. halli (Mathews). Pp. 647-668 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Jonsgard, A. 1966. Biology of the North Atlantic fin whale Balaenoptera physalus (L); Taxonomy, distribution, migration and food. Hvalrad. Skr., 49:1-62.

Jonsgard, A., and J.T. Ruud. 1964. Studies on the southern stocks of blue and fin whales. Pp. 333-339 in Carrick, R., M.W. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Kaufman, G., D. Siniff and R. Reichle. 1974. Colony behavior of Weddell seals, Leptonychotes weddelli, at Hutton Cliffs, Antarctica. Pp. 228-246 in Ronald, K., and A.W. Mansfield (eds.) Biology of the Seal. Rapp. Proces-Verbaux Reunions, Vol. 169.

Kawamura, A. 1978. Food habit of Euphausia superba and the diatom community: a review In El-Sayed, S.Z. (ed.), Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) Vol. II. (in press).

Kemp, S., and L. Nelson. 1931. The South Sandwich Islands. Discovery Rep., 3:133-198.

Keysner, E.E. Tot, V.S., and Shilor, V.N. 1974. Characteristic of the behavior and biological cycles of the marbled Notothenia (Notothenia rossi) in relation to bottom topography, bottom materials and currents. J. Icthyol. 14:610-613.

Khvatskiy, N.V. 1972. On the dynamics of water and concentrations of Antarctic krill, (Euphausia superba Dana) in the southern Scotia Sea. Tr. Vses. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 57:118-124.

King, J.E. 1964. Seals of the world. British Museum (Natural History): London. 164 pp.

King, J.E. 1965a. Swallowing modifications in the Ross seal. J. Anat., 99:206-207.

King, J.E. 1965b. The Ross and other Antarctic seals. Austr. Nat. Hist., 16:29-32.

Knox, G.A. 1970. Antarctic marine ecosystems. Pp. 69-96 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Komaki, Y. 1967. On the surface swarming of Euphausiid crustaceans. Pacific Science, 21:433-448.

Kort, V.G. 1968. Frontal zones of the Southern Ocean. Pp. 3-7 in Currie, R.I. (ed.), Symposium on Antarctic Oceanography; Santiago, Chile, 1966. Scott Polar Research Institute/SCAR: Cambridge. 268 pp.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press: Oxford. 343 pp.

Laws, R.M. 1953a. The elephant seal industry at South Georgia. Polar Rec., 6:746-754.

Laws, R.M. 1953b. The elephant seal (Mirounga leonina Linn.), 1. Growth and age. Falkland Is. Dep. Surv., Sci. Rep., 8.

Laws, R.M. 1953c. A new method of age determination in mammals with special reference to the elephant seal (Mirounga leonina Linn.). Falkland Is. Dep. Surv., Sci. Rep., 2.

Laws, R.M. 1956a. The elephant seal (Mirounga leonina Linn.), 2. General, social, and reproductive behaviour. Falkland Is. Dep. Surv. Sci. Rep., 13.

Laws, R.M. 1956b. The elephant seal (Mirounga leonina Linn.), 3. The physiology of reproduction. Falkland Is. Dep. Surv., Sci. Rep., 15.

Laws, R.M. 1958. Growth rates and ages of crabeater seals, Lobodon carcinophagus Jacquinot and Pucheran. Proc. Zool. Soc. Lond., 130:275-288.

Laws, R.M. 1960. The southern elephant seal (Mirounga leonina Linn.) at South Georgia. Norsk Hvalfangsttid., 49:466-476, 520-542.

Laws, R.M. 1961. Reproduction, growth and age of Southern Hemisphere fin whales. Discovery Rep. 31:327-485.

Laws, R.M. 1962. Some effects of whaling on the southern stocks of baleen whales. Pp. 137-158 in Le Cren, E.D., and M.W. Holdgate (eds.), The Exploitation of Natural Animal Populations. Blackwell Scientific Publications: Oxford. 399 pp.

Laws, R.M. 1964. Comparative biology of Antarctic seals. Pp. 445-454 in Carrick, R., M. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Laws, R.M. 1973. Population increase of fur seals at South Georgia. Polar Rec., 16:856-858.

Laws, R.M. 1977a. Seals and whales in the Southern Ocean. Phil. Trans. Roy. Soc. Lond. B., 279:81-96.

Laws, R.M. 1977b. The significance of vertebrates in the Antarctic marine ecosystem. Pp. 411-438 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C., 1252 pp.

Laws, R.M., and R.J.F. Taylor. 1957. A mass dying of crabeater seals, Lobodon carcinophagus (Gray). Proc. Zool. Soc. Lond., 129:315-324.

Lindsey, A.A. 1937. The Weddell seal in the Bay of Whales, Antarctica, J. Mammal., 18, 127-144.

Lindsey, A.A. 1938. Notes on the crabeater seal. J. Mammal., 19:456-461.

Lockyer, C.H. 1972. The age of sexual maturity of the southern fin whale (Balaenoptera physalus) using annual layer counts in the ear plug. J. Cons. Perm. Int. Explor. Mer., 34:276-294.

Lockyer, C.H. 1974. Investigation of the ear plug of the southern sei whale (Balaenoptera borealis) as a valid means of determining age. J. Cons. Perm. Int. Explor. Mer., 36:71-81.

Lund, J. 1950a. Charting of whale stocks in the Antarctic in the season 1949/50 on the basis of iodine values. Norsk Hvalfangsttid., 39:298-305.

Lund, J. 1950b. Charting of whale stocks in the Antarctic on the basis of iodine values. Norsk Hvalfangsttid., 39:53-60.

Lund, J. 1951. Charting the whale stocks in the Antarctic in the season 1950/51 on the basis of iodine values. Norsk Hvalfangsttid., 40:124-146.

Lyubimova, T.G., A.G. Naumov, and L. L. Lagunov. 1973. Prospects of the utilization of krill and other unconventional resources of the world ocean. J. Fish. Res. Bd. Can., 30:2196-2201.

Machin, D. 1974. A multivariate study of external measurements of the sperm whale, Physeter catodon. J. Zool., Lond., 172:267-288.

Mackintosh, N.A. 1937. A seasonal circulation of the Antarctic macroplankton. Discovery Rep., 16:365-412.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. Discovery Rep., 22:197-200.

Mackintosh, N.A. 1960. The pattern of distribution of the Antarctic fauna. Phil. Trans. Roy. Soc. Lond. B., 152:624-631.

Mackintosh, N.A. 1964. A survey of Antarctic biology up to 1945. Pp. 3-38 in Carrick, R., M. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Mackintosh, N.A. 1965. The stocks of whales. Fishing News (Books), Ltd.: London. 232 pp.

Mackintosh, N.A. 1966. The swarming of krill and problems of estimating the standing stock. Norsk Hvalfangsttid., 11:213-216.

Mackintosh, N.A. 1967. Maintenance of living Euphausia superba and frequency of molts. Norsk Hvalfangsttid., 56:97-102.

Mackintosh, N.A. 1968. The swarming of krill and problems of estimating the standing stock. Pp. 259-260 in Currie, R. I. (ed.), Symposium on Antarctic Oceanography; Santiago Chile, 1966. Scott Polar Research Institute/SCAR: Cambridge. 268 pp.

Mackintosh, N.A. 1970. Whales and krill in the twentieth century. Pp. 195-212 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Mackintosh, N.A. 1972a. Biology of the populations of large whales. Sci. Prog. Oxford, 60:449-464.

Mackintosh, N.A. 1972b. Life cycle of Antarctic krill in relation to ice and water conditions. Discovery Rep., 36:1-94.

Mackintosh, N.A. 1973. Distribution of post-larval krill in the Antarctic. Discovery Rep., 36:95-156.

Mackintosh, N.A. 1974. Sizes of krill eaten by whales in the Antarctic. Discovery Rep., 36:157-178.

Mackintosh, N.A. and J.F.G. Wheeler, 1929. Southern blue and fin whales. Discovery Rep., 1:257-540.

Maher, W.J. 1962. Breeding biology of the snow petrel near Cape Hallett, Antarctica. Condor, 64:488-499.

Makarov, R.R. 1972. Life cycle and distribution pattern of Euphausia superba Dana. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr., 77:85-92.

Makarov, R.R. 1974. Dominance of larval forms of Euphausiid (Crustacea: Eucaridae) ontagenesis. Mar. Biol., 27:93-99.

Makarov, R.R., and V.V. Shevtsov. 1972. Some problems in the distribution and biology of Antarctic krill. Israel Prog. for Sci. Transl., Jerusalem, TT72-50077.

Makarov, R.R., A.G. Naumov, and V.V. Shevtson. 1970. The biology and distribution of the Antarctic krill. Pp. 173-176 in Holdgate, M.W., (ed.), Antarctic Ecology, Vol. I. Academic Press: London. 604 pp.

Marlow, B.J. 1967a. Australian seals. Aust. Nat. Hist., 15:290-293.

Marlow, B.J. 1967b. Mating behavior in the leopard seal, Hydruga leptonyx, in captivity. Aust. J. Zool., 15:1-5.

Marr, J.W.S. 1935. The South Orkney Islands. Discovery Rep., 10:283-382.

Marr, J.W.S. 1956. Krill and the Antarctic surface currents, an advance note on the distribution of the whale food. Norsk Hvalfangsttid., 45:127-134.

Marr, J.W.S. 1962. The natural history and geography of the Antarctic krill (Euphausia superba). Discovery Rep., 32:33-464.

Marshall, N.B. 1964. Fish. Pp. 206-218 in Priestley, R., R.J. Adie, and G. de Q. Robin (eds.), Antarctic Research. Butterworths: London. 360 pp.

Marty, J.J. (ed.). 1969. Marine biological resources of the Antarctic (first expedition of the research vessel Akademician Knipovich). Tr. Vses. Nauchno-Issled. Inst. Morsk, Rybn. Khoz., Okeanogr., 66:1-340.

Matthews, L.H. 1929. The natural biology of the elephant seal, with notes on other seals found at South Georgia. Discovery Rep., 1:235-256.

Mauchline, J., and L.R. Fisher. 1969. The biology of Euphausiids. Pp. 1-454 in Russell, F.S., and M. Yonge (eds.), Advances in Marine Biology, Vol. 7. Academic Press: London. 454 pp.

Mawson, D. 1915. The home of the blizzard. Lippincott: Philadelphia. 305 pp.

Merrett, N.R. 1963. Pelagic Gadoid fish in the Antarctic. Norsk Hvalfangsttid., 52:245-247.

Mikheyev, B.I. 1967. On the biology and fisheries of certain fishes from the Patagonian Shelf (Falkland Region) and the Scotia Sea. Pp. 85-93 in Burukovskii, R.N. (ed.), Soviet Fishery Research on the Antarctic Krill. U.S. Clearinghouse for Fed. Sci. and Tech. Info., TT67-32683.

Mitchell, E. 1975. Trophic relationships and competition for food in northwest Atlantic whales. Pp. 123-133 in Burt, M.D.B. (ed.), Proceedings of the Canadian Society of Zoologists Annual Meeting, 1974.

Moiseev, P.A. 1970. Some aspects of the commercial use of the krill resources of the Antarctic seals. Pp. 213-216 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Moiseev, P.A. 1971. The living resources of the world ocean. Israel Program for Sci. Transl., Jerusalem, :87-125.

Muller-Schwarze, D. 1971. Behavior of Antarctic penguins and seals. Pp. 259-276 in Research in the Antarctic. American Association for the Advancement of Science: Washington, D.C.

Muller-Schwarze, D., and C. Muller-Schwarze. 1971. Antipredator and social behavior in adelie penguins. Antarct. J. U.S., 6:99-100.

Muller-Schwarze, D., and C. Muller-Schwarze. 1975. Relations between leopard seals and adelie penguins. Pp. 394-404 in Ronald, K., and A.W. Mansfield (eds.), Biology of the Seal. Rapp. Proces-Verbaux Reunions, Vol. 169.

Murphy, R.C. 1936. Oceanic birds of South America. American Museum of Natural History: New York. 1245 pp.

Murphy, R.C. 1948. Logbook for grace: whaling brig Daisy, 1912-1913. Robert Hale, Ltd.: London.

Murphy, R.C. 1964. Systematics and distribution of Antarctic petrels. Pp. 349-358 in Carrick, R., M.W. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Nakamura, S. 1975. Report on the trial fishing of Antarctic krill. Polar News, Jap. Pol. Res. Assoc., 10:21-27.

Nasu, K. 1978. A note on the stomach contents of some fishes taken in the exploratory trawl fishing on the krill, Euphausia superba Dana. In El-Sayed, S.Z. (ed.), Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) Vol. II (in press).

Nasu, K. 1978. Recent Japanese investigations on the marine living resources in the Antarctic Ocean--mainly on krill. In El-Sayed, S.Z. (ed.), Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) Vol. II (in press).

Nemoto, T. 1959. Food of baleen whales with reference to whale movements. Sci. Rep. Whale Res. Inst. Tokyo, 14:149-290.

Nemoto, T. 1962. Food of baleen whales collected in recent Japanese Antarctic whaling expeditions. Sci. Rep. Whale Res. Inst. Tokyo, 16:89-103.

Nemoto, T. 1968. Feeding of baleen whales and the value of krill as a marine resource in the Antarctic. Pp. 240-253 in Currie, R.I. (ed.), Symposium on Antarctic Oceanography; Santiago, Chile, 1966. Scott Polar Research Institute/SCAR: Cambridge. 268 pp.

Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. Pp. 241-252 in Steele, J.H. (ed.), Marine Food Chains. Univ. of California Press: Berkeley. 522 pp.

Nemoto, T., and K. Nasu. 1975. Present status of exploitation and biology of krill in the Antarctic. Pp. 353-360 in Oceanology International 75, March 1975, Brighton, England.

Nemoto, T., M. Araki, and E. Brinton. 1971. Clinal variation in the frequency of one-and two-spined forms of *Thysanoessa inermis* (Krøyer, 1849) (Euphausiacea) in the North Pacific. Crustaceana, 24:318-322.

Nesis, K.N. 1964. (Footnotes in translation of 'The Economic importance of the North Atlantic squid,' Clarke, M.R. (ed.), New Sci., 17:568-570). Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 40:86-89.

Nesis, K.N. 1970. The biology of the giant squid of Peru and Chile, *Dosidicus gigas*. Oceanology, 10: 108-118.

Nishiwaki, M. 1977. Distribution of toothed whales in the Antarctic Ocean. Pp. 783-791 in Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Nybelin, O. 1947. Antarctic fishes. Sci. Res. Norw. Antarct. Exped., 1927-1928, 26:1-76.

O'Gorman, F.A. 1961. Fur seals breeding in the Falkland Islands Dependencies. Nature, Lond., 192:914-916.

Ohsumi, S. 1973. Revised estimates of recruitment rate in the Antarctic fin whales. Rep. IWC, 23:192-199.

Ohsumi, S., and Y. Masaki. 1974. Status of whale stocks in the Antarctic, 1972/73. Rep. IWC, 24:102-113.

Ohsumi, S., Masaki, Y., and A. Kawamura, 1970. Stocks of the Antarctic minke whale. Sci. Rep. Whales Res. Inst. Tokyo. No. 22:75-125.

Ohsumi, S., Y. Shimadzu, and T. Doi. 1971. The seventh memorandum on the results of Japanesse stock assessment of whales in the North Pacific. Rep. IWC, 21:76-89.

Olsen, S. 1954. South Georgian cod. Norsk Hvalfangsttid., 43:373-382.

Olsen, S. 1955. A contribution to the systematics and biology of Chaenichthyid fishes from the South Georgia. Nytt. Mag. Zool., 3:79-93.

Oordt, G.J. van, and J.P. Kruyt, 1953. On the pelagic distribution of some Procellariiformes in the Atlantic and southern oceans. Ibis, 95:615-637.

Øritsland, T. 1970a. Biology and population dynamics of Antarctic seals. Pp. 361-366 _in_ Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Øritsland, T. 1970b. Sealing and seal research in the southwest Atlantic pack ice, Sept.-Oct., 1964. Pp. 367-376 _in_ Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Øritsland, T. 1977. Food consumption of seals in the Antarctic pack ice. Pp. 749-768 _in_ Llano, G.A. (ed.), Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution: Washington, D.C. 1252 pp.

Osochenko, E.I. 1967. An economic evaluation of using krill for making fish meal. Pp. 79-84 _in_ Burukovskii, R.N. (ed.), Soviet Fishery Research on the Antarctic Krill. U.S. Clearinghouse for Fed. Sci. and Tech. Info., TT67-32683.

Ozawa, K., T. Yamada, K. Masatoshi, and T. Shimizu. 1968. Observations of patches of _Euphausia superba_. J. Tokyo Univ. Fish., 9:101-109.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat., 100:65-75.

Paine, R.T. 1969. A note on trophic complexity and community stability. Am. Nat., 103:91-93.

Paine, R.T., and R.L. Vaas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnol. and Oceanogr., 14:710-719.

Paulian, P. 1952. Sur La presence aux iles Kerguelen D'Hydrurga leptonyx (Bl.) Et D'Arctocephalus gazella (Pet.) Et notes Biologiques sur Beux phocides. Mammalia, 16:223-227.

Paulian, P. 1953. Pinnipedes, cetaces, oiseaux des Iles Kerguelen et Amsterdam; Mission Kerguelen, 1951. Mem. Inst. Rech. Sci. Madagascar Ser. A; Biol. Anim., 8:111-234.

Pavlov, V. Ya. 1969. The feeding of krill and some features of its behavior. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr., 66:207-222.

Pavlov, V. Ya. 1971. On the qualitative composition of food for Euphausia superba Dana. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr., 86:42-54.

Pavlov, V. Ya. 1974. On the relationship between the feeding habits and the behavioral characteristics of Euphausia superba Dana. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr., 99:104-116.

Payne, M.R. 1977. Growth of a fur seal population. Phil. Trans. Roy. Soc. Lond. (B:Biol. Sci.), 279: 67-79.

Penney, R.L., and G. Lowry. 1967. Leopard seal predation on adelie penguins. Ecol., 48:878-882.

Perkins, J.E. 1945. Biology at Little America III, the west base of the United States Antarctic Service Expedition, 1939-1941. Proc. Am. Phil. Soc., 89:270-284.

Permitin, Yu. E. 1969. New data on the species composition and distribution of fishes in the Scotia Sea. J. Ichthyol., 9:167-81.

Permitin, Yu. E. 1970. The consumption of krill by Antarctic fishes. Pp. 177-182 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Permitin, Yu. E. 1973. Fecundity and reproductive biology of icefish (Channichtyidae), fish of the family Hurainolepidae and dragon fish (Pathydraconidae) of the Scotia Sea (Antarctica). J. Ichthyol., 13:204-215.

Permitin, Yu. E., and Z. S. Sil'yahova. 1971. New data on the reproductive biology and fecundity of fishes of the genus Notothenia Rich in the Scotia Sea (Antarctica). J. Ichthyol., 11:693-705.

Permitin, Yu. E. and M. I. Tarverdieva. 1972. Feeding of some species of Antarctic fishes in the South Georgia Island area. J. Ichthyol., 12:104-114.

Peters, H. 1955. Presence of krill Euphausia superba Dana and its significance of a food for southern finback whales. Arch. Fischer., 6:288-304.

Peterson, R.T. 1973. Render the penguins, butcher the seals; the Antarctic's bloody past may foretell its future. Audubon, 75:90-109.

Prevost, J. 1964. Observations complementaires sur les pinnipedes de l'Archipel de Pointe Geologie. Mammalia, 28:351-358.

Prevost, J. 1978. Population, biomass, and energy requirements of Antarctic birds. In El-Sayed, S.Z. (ed.), Biological Investigations of Antarctic Systems and Stocks (BIOMASS) Vol. II. (in press).

Prevost, J., and J. Sapin-Jaloustre. 1965. Ecologie des manchots Antarctiques. Pp. 551-648 in Van Mieghem, J., and P. Van Oye (eds.), Biogeography and Ecology in Antarctica. Dr. W. Junk Publishers: The Hague. 762 pp.

Pryor, M.E. 1968. The avifauna of Haswell Island, Antarctica. Pp. 57-82 in Austin, O.L., Jr. (ed.), Antarctic Bird Studies. Antarctic Research Series, Vol. 12. American Geophysical Union: Washington, D.C. 262 pp.

Rankin, N. 1951. Antarctic Isle. Collins: London. 383 pp.

Ray, G.C. 1970. Population ecology of Antarctic seals. Pp. 398-414 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Repenning, C.A., R.S. Peterson, and C.L. Hubbs. 1971. Contributions to the systematics of the southern fur seals, with particular reference to the Juan Fernandez and Guadelupe species. Pp. 1-34 in Burt, W.H. (ed.), Antarctic Pinnipedia. Antarctic Research Series, Vol. 18. American Geophysical Union: Washington, D.C. 226 pp.

Roper, C.F.E. 1978. Cephalopods of the Southern Ocean region: potential resources and bibliography. In El-Sayed, S.Z. (ed.), Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) Vol. II (in press).

Routh, M. 1949. Ornithological observations in the Antarctic seas. Ibis, 91:577-606.

Russell-Hunter, W.D. 1970. Aquatic productivity. Macmillan Co.: London. 306 pp.

Rustad, D. 1930. Euphausiacea with notes on their biogeography and development. Sci. Res. Norweg. Antarct. Exped., 5:1-83.

Ruud, J.T. 1932. On the biology of the southern Euphausiidae. Hvalrad. Skr., Oslo, 2:1-105.

Saito, R. 1976. The Japanese fishery for *Nototodarus sloani sloani* in New Zealand waters. FAO Fish. Rep., 170:53-60.

Sapin-Jaloustre, J. 1952. Les phoques de Terre Adelie. Mammalia, 16:179-212.

Sapin-Jaloustre, J. 1953. Les phoques de Terre Adelie. Mammalia, 17:1-20.

Sasaki, Y., K. Inoue, and K. Matsuike. 1968. Distribution of *Euphausia superba* in the Antarctic Ocean from viewpoints of fishing operation. Tokyo. Univ. Fish. J. (Spec. ed.), 9:129-134.

Schaefer, M.B. 1965. The potential harvest of the sea. Trans. Am. Fish. Soc., 94:123-128.

Schaefer, M.B. 1970. Men, birds and anchovies in the Peru Current--dynamic interactions. Trans. Am. Fish. Soc., 99:461-467.

Scheffer, V.B. 1958. Seals, sea lions, and walruses. Stanford Univ. Press: Stanford. 179 pp.

Seal, U.S., A.W. Erickson, D.B. Siniff, and D.R. Cline. 1971a. Blood chemistry and protein polymorphisms in three species of Antarctic seals (Lobodon carcinophagus, Leptonychotes weddelli, and Mirounga leonina). Pp. 181-192 in Burt, W.H. (ed.), Antarctic Pinnipedia. Antarctic Research Series, Vol. 18. American Geophysical Union: Washington, D.C. 226pp.

Seal, U.S., A.W. Erickson, D.B. Siniff, and R.J. Hofman. 1971b. Biochemical, population genetic, phylogenetic and cytological studies of Antarctic seal species. Pp. 77-95 in Deacon, G. (ed.), Symposium on Antarctic Ice and Water Masses, Tokyo, Japan, 1970. Scientific Committee on Antarctic Research: Cambridge.

Semenov, V.N. 1969. Aquarium observations on the behavior of krill. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr., 66:235-239.

Shackleton, E.H. 1919. South; the story of Shakleton's last expedition, 1914-1917. Heinemann: London.

Shaughnessy, P.D. 1969. Transferrin polymorphism and population structure of the Weddell seal. Just. J. Biol. Sci., 22:1581-1584.

Shaughnessy, P.D. 1975. Biochemical comparison of the harbour seals Phoca vitulina Richardii and P. v. largha. Pp. 70-73 in Ronald, K., and A.W. Mansfield (eds.), Biology of the Seal. Rapp. Proces-Verbaux Reunions, Vol. 169.

Shevtsov, V.V. and R.R. Makarov. 1969. On the biology of Antarctic krill. Tr. Vses. Nauchno-Isled. Inst. Morsk, Rybn. Khoz. Okeanogr., 66:177-206.

Shpak, V.M. 1975. Morphometric description of southern poutassou Micromesistius australis Norman from the area of the New Zealand plateau with notes on the diagnosis of the genus Micromesistius Gill. J. Ichthyol., 15:175-181.

Shuntov, V.P. 1971. Fishes of the upper bathyal zone of the New Zealand Plateau. J. Ichthyol., 11:336-345.

Simenstad, C.A., J.A. Estes, and K.W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. Science, 200:400-411.

Sinha, N.A., and A.W. Erickson, 1972. Ultrastructure of the corpus luteum of Antarctic seals during pregnancy. Z. Zellforch. Mikosic. Anat., 133:13-20.

Siniff, D.B. 1976. Preliminary assessment, Antarctic biological environment; marine mammals. In Elliot, D.H. (ed.), A Framework for Assessing Environmental impacts of possible Antarctic Mineral Development, Part II: Appendix. Inst. Polar Studies, Ohio State Univ., Columbus.

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 R.A. Reichle. 1976. Biota of the Antarctic pack ice: R/V Hero cruise 75-6. Antarct. J. U.S., 11:61.

Siniff, D.B., D.R. Cline, and A.W. Erickson. 1970. Population densities of seals in the Weddell Sea, Antarctica, 1968. Pp. 377-394 in Holdgate, M.W. (ed.), Antarctic Ecology, Vol. I. Academic Press: New York. 604 pp.

Siniff, D.B., J.R. Tester, and V.B. Kuechle. 1971. Some observations on the activity patterns of Weddell seals as recorded by telemetry. Pp. 173-180 in Burt, H.W. (ed.), Antarctic Pinnipedia. Antarctic Research Series, Vol. 18. American Geophysical Union: Washington, D.C. 226 pp.

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. Monogr., 47:319-335.

Siniff, D.B., R.A. Reichle, R.J. Hofman, and D. Kuehn. 1975. Movements of Weddell seals in McMurdo Sound, Antarctica, as monitored by telemetery. Pp. 387-393 in Ronald, K., and A.W. Mansfield (eds.), Biology of the Seal. Rapp. Proces-Verbaux Reunions, Vol. 169.

Siniff, D.B., R.A. Reichle, G. Kaufman, and D. Kuehn. 1971. Population dynamics and behavior of Weddell seals at McMurdo Station. Antarct. J. U.S., 6:97-98.

Siniff, D.B., I. Stirling, J.L. Bengtson, and R.A. Reichle. 1977. Biota of the Antarctic pack ice: R/V Hero Cruise 76-6. Antarct. J. U.S., 12:10-11.

Siniff, D.B., I. Stirling, J.L. Bengtson, and R.A. Reichle. 1978. Observations on the social structure and behavior of crabeater seals (*Lobodon carcinophagus*) in the austral spring. (in preparation).

Sladen, W.J.L. 1964. The distribution of the adelie and chinstrap penguins. Pp. 359-365 *in* Carrick, R., M.W. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Smith, M.S.R. 1965. Seasonal movements of the Weddell seal in McMurdo Sound, Antarctica. J. Wildl. Manage., 29:464-470.

Smith, M.S.R. 1966. Studies on the Weddell seal (*Leptonychotes weddelli* Lesson) in McMurdo Sound, Antarctica. Unpublished Ph.D. thesis. Univ. Canterbury, Christchurch, New Zealand.

Solyanik, G.A. 1964. Experiment in marking seals from small ships. Soviet Antarct. Exped. Info. Bull., 5:212.

Solyanik, G.A. 1965. Some information on Antarctic seals. Sov. Antarct. Exped. Info. Bull., 5:179-182.

Squires, H.J. 1957. Squid, *Illex illecebrosus* (LeSueur), in the Newfoundland fishing area. J. Fish, Res. Board., Can., 14:693-728.

Stasenko, V.D. 1967. Determining the rational krill fishing methods and the commercial effectiveness of the chosen fishing gear. Pp. 61-78 *in* Burukovskii, R.N. (ed.), Soviet Fishery Research on the Antarctic Krill. U.S. Clearinghouse for Fed. Sci. and Tech. Info., TT67-32683.

Stirling, I. 1969a. Birth of a Weddell seal pup. J. Mammal., 50:155-156.

Stirling, I. 1969b. Distribution and abundance of the Weddell seal in the western Ross Sea, Antarctica. N.Z. J. Mar. and Freshwater Res., 3:191-200.

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

Stirling, I. 1969d. The Weddell seal. Antarctic, 5:234-236.

Stirling, I. 1969e. Tooth wear as a mortality factor in the Weddell seal, Leptonychotes weddelli. J. Mammal., 50:559-565.

Stirling, I. 1971a. Population dynamics of the Weddell seal in McMurdo Sound, Antarctica, 1966-1968. Pp. 141-161 in Burt, W.H. (ed.), Antarctic Pinnipedia. Antarctic Research Series, Vol. 18. American Geophysical Union: Washington, D.C. 226 pp.

Stirling, I. 1971b. Population aspects of Weddell seal harvesting at McMurdo Sound, Antarctica. Polar Rec., 15:653-667.

Stirling, I. 1971c. Studies on the behavior of the South Australian fur seal, Arctocephalus forsteri Lesson. I. Annual cycle, postures and calls, and adult males during the breeding season. Aust. J. of Zool., 19:243-266.

Stirling, I. 1971d. Studies on the behavior of the South Australian fur seal, Arctocephalus forsteri Lesson. II. Adult females and pups. Aust. J. of Zool., 19:267-273.

Stirling, I. 1971e. Variation in the sea ratio of newborn Weddell seals during the pupping season. J. Mammal., 52:842-844.

Stonehouse, B. 1967a. Expanding population of Pygoscelis antarctica on South Georgia. Ibis, 109:277-278.

Stonehouse, B. 1967b. Occurrence and effects of open water in McMurdo Sound, Antarctica, during winter and early spring. Polar Rec., 13:775-778.

Stonehouse, B. 1972. Animals of the Antarctic: the ecology of the far south. Holt, Rinehart, and Winston: New York. 171 pp.

Sverdrup, H.U. 1955. The place of physical oceanography in oceanographic research. J. Mar. Res., 14:287-294.

Szijj, L.J. 1967. Notes on the winter distribution of birds in the western Antarctic and adjacent Pacific waters. Auk, 84:336-378.

Tarverdiyeva, M.I. 1972. Daily food consumption and feeding pattern of the South Georgian cod (Notothenia rossii marmorata) and the Patagonian toothfish (Dissostichus eleginoides Smiff) in the South Georgia area. J. Ichthyol., 12:684-692.

Taylor, R.H. 1962. The adelie penguin (*Pygoscelis adeliae*) at Cape Royds. Ibis, 104:176-204.

Taylor, R.J.F. 1957. An unusual record of three species of whale being found restricted to pools in the Antarctic sea ice. Zool. Soc. Lond. Proc., 129:325-331.

Tickell, W.L.N. 1964. Feeding preferences of the albatrosses *Diomedea melanophris* and *D. chrysostoma* at South Georgia. Pp. 383-387 *in* Carrick, R., M. Holdgate, and J. Prevost (eds.), Biologie Antarctique. Hermann: Paris. 651 pp.

Tickell, W.L.N. 1968a. Ice conditions in McMurdo Sound; effect on adelie penguins. Polar Rec., 14:235.

Tickell, W.L.N. 1968b. The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora*. Pp. 1-55 *in* Austin, O.L., Jr., (ed.), Antarctic Bird Studies. Antarctic Research Series, Vol. 12. American Geophysical Union: Washington, D.C. 262 pp.

Tickell, W.L.N. 1970. Biennial breeding in albatrosses. Pp. 551-557 *in* Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.

Tickell, W.L.N., and R. Pinder. 1975. Breeding biology of the black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. Ibis, 4:433-451.

Tomo, A.P., and E.R. Marschoff. 1977. The krill and its importance. Argentinian Institute for the Antarctic Publ. No. 12.

Townsend, C.H. 1935. The distribution of certain whales as shown by the log book records of American whale ships. Zoologica, 19:1-50.

Treshhnikov, A.F. 1971. Oceanological investigations in the Antarctic and Arctic during the Soviet regime. Oceanology, 11:684-689.

Turbott, E.G. 1952. Seals of the Southern Ocean. Pp. 195-215 *in* Simpson, F.A. (ed.), The Antarctic Today; a Mid-Century Survey by the New Zealand Antarctic Society. A.H. Reed and A.W. Reed: Wellington.

Voous, K.H. 1965. Antarctic birds. Pp. 649-689 in Van Mieghem, J., and P. Van Oye (eds.), Biogeography and Ecology in Antarctica. Dr. W. Junk Publishers: The Hague. 762 pp.

Voronina, N.M. 1966. The zooplankton of the Southern Ocean: some study results. Oceanology, 6:557-563.

Voronina, N.M. 1974. An attempt at a functional analysis of the distributional range of Euphausia superba. Marine Biol., 24:347-352.

Voss, G.L. 1973. Cephalopod resources of the world. FAO Fish. Circ., 149:75.

Warham, J. 1956. The breeding of the great-winged petrel Pterodroma macroptera. Ibis, 98:171-185.

Watson, G.E. 1975. Birds of the Antarctic and subantarctic. American Geophysical Union: Washington, D.C. 350 pp.

Watson, G.E., J.P. Angle, P.C. Harper, M.A. Bridge, R.P. Schlatter, W.L.N. Tickell, J.C. Boyd, and M.M. Boyd. 1971. Birds of the Antarctic and subantarctic. American Geographical Society, Antarctic Map Folio Series, 14:1-18.

White, M.G., and J.W.H. Conroy. 1975. Aspects of competition between Pygoscelid penguins at Signy Island, South Orkney Islands. Ibis, 118:371-373.

Winn, H.E. 1976. The humpback whale--populations, energetics, distribution, migratory routes, environmental requirements, models of the effects of man, and sanctuaries (a proposal submitted to FAO). FAO Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals. ACMRR/MM/SC/WG 1.2.

Wilson, E.A. 1907. Stenorhinchus leptonyx, the sea leopard. National Antarctic Expedition, 1901-1904. Nat. Hist. Zool., 2:26-30.

Wilton, D.W., J.H.H. Pirie, and R.N.R. Brown. 1908. Zoological log. Rep. Sci. Results Scot. Natl. Antarctic Exped., 4 (Zool.), Part 1:1-105.

Wohlschlag, D.E. 1962. Antarctic fish growth and metabolic differences related to sea. Ecol., 43:589-597.

Young, J.Z. 1977. Brain, behavior and evolution of cephalopods. Symp. Zool. Soc. Lond., 38:377-434.

Yukhov, V.L. 1970. New data on the distribution and biology of *Dissostichus mawsoni* (Norman) in Antarctic high latitudes. J. Ichthyol., 10:422-424.

Yukhov, V.L. 1971a. Otolith structure in the Antarctic and Patagonian blennies (*Dissostichus mawsoni* Norman and *D. eleginoides* Smitt, Family Nototheniidae) of the Southern Ocean. J. Ichthyol., 11:485-492.

Yukhov, V.L. 1971b. The range of *Dissostichus mawsoni* Norman and some features of its biology. J. Ichthyol., 11:14-25.

Yukhov, V.L. 1972. The range of fish of the genus *Dissostichus* in Antarctic waters of the Indian Ocean. J. Ichthyol., 12:346-347.

Zenkovich, B.A. 1970. Whales and plankton in Antarctic waters. Pp. 183-190 *in* Holdgate, M.W. (ed.), Antarctic Ecology, Vol. 1. Academic Press: New York. 604 pp.