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Seals and whales of the Southern Ocean

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There are fewer species of marine mammals in the Antarctic than in the Arctic, probably because of the wide deep ocean with no geographical barriers to promote speciation. The stocks are substantially larger in the Antarctic and the body sizes of individual species are larger, probably owing to a more abundant food supply.

Seasonal changes in the environment in the Southern Ocean are marked and food available to baleen whales is very much greater in summer. Ecological interactions of the consumers, principally in relation to krill *Euphausia superba*, are discussed and attention drawn to some of the ways in which ecological separation is achieved, both within and between species.

Estimates of abundances, biomasses and food requirements are given for the seals and large whales.

The original numbers of whales in the Antarctic were far greater than in other oceans, but the stocks have been severely reduced by whaling. This may have increased the availability of krill to other consumers by as much as 150 million tonnes annually. Increased growth rates, earlier maturity and higher pregnancy rates have been demonstrated for baleen whale species, and earlier maturity for the crabeater seal. While it has not been possible to demonstrate increases in the populations of any of these species, the stocks of fur seals and penguins have been monitored and show significant population increases. A key question is whether the original balance of this ecosystem can be regained with appropriate management.

Introduction

The ecology of Antarctic seals has been the subject of a number of reviews (Carrick 1964; Laws 1964, 1977; Øritsland 1970, 1977; Ray 1970; Gilbert & Erickson 1977) which demonstrate the growing interest they attract. Mackintosh (1965, 1972*b*) has recently given a good general account of the biology of whales, while a recent conference was devoted to assessing their status (Schevill 1974); the Scientific Committee of the International Whaling Commission publishes its findings annually and these arouse great interest and controversy, because of the extreme current interest in whales and whaling. An International Convention for the Conservation of Antarctic Seals was recently signed by 12 nations (Anon 1972). What is the significance of the Antarctic marine mammals, both as a unique assemblage of particularly well adapted species and as a valuable resource to be conserved and properly managed?

The Antarctic marine mammals

An attempt at a rough estimate of the world stocks of pinnipeds suggests a total of about 30 million individuals (Scheffer 1958; Gilbert & Erickson 1977; this paper). Crude biomass estimates, obtained by applying published mean body masses when available, or interpolating on the basis of body length when not, suggest a world standing stock of about 4.4 million tonnes. The eared seals (Otariidae) and walruses (Odobenidae) comprise about 3.5 million individuals

(12%), the remaining 88% being true seals (Phocidae); standing stock biomasses are respectively 300000 tonnes (7%) and 4.063 million tonnes (93%).

Some 56% of total stocks and 79% of their biomass is in the Antarctic populations (Monachinae). To some extent this reflects the intensive hunting on other stocks in the last 200 years, but also the fact that the vast majority of Antarctic seals (99%) are phocids and of species that attain much larger sizes than those in northern seas. Typical northern phocids, of the genera *Phoca*, *Pusa*, *Histriophoca* and *Pagophilus*, weigh on average about 50–60 kg; the Antarctic species weigh on average about 220 kg (table 1) – that is about four times their northern counterparts. Only 5 genera of phocids, comprising 5 species and no subspecies, inhabit the 36 million square kilometres of the continuous deep ocean south of the Antarctic Convergence. Their populations are confined to the Antarctic, with the exception of the southern elephant seal *Mirounga leonina* which also occurs in lesser abundance on subantarctic islands, the Falkland Islands and South American coasts. The fur seal *Arctocephalus gazella* is occasionally reported north of the Antarctic Convergence. The true Antarctic seals, virtually confined to the pack and fast ice zone are the crabeater *Lobodon carcinophagus*, leopard *Hydrurga leptonyx*, Ross *Ommatophoca rossi*, and Weddell seals *Leptonychotes weddelli*. The biological characteristics of *Mirounga leonina* are described by Laws (1960); of *Arctocephalus gazella* by Bonner (1968); and of the pack-ice seals by Bertram (1940), Laws (1964, 1977), Øritsland (1970), Gilbert & Erickson (1977), Stirling (1971), Erickson & Hofmann (1974), and Kaufman, Siniff & Reichle (1975). In the northern hemisphere there are 9 genera of phocids, comprising 12 species and a number of subspecies associated with different regions; the Arctic Ocean is only 14 million square kilometres in area. None of the Antarctic species are bottom feeders like the northern bearded seal (*Erignathus barbatus*) and the walruses, *Odobenus* spp., probably because the Antarctic continental shelf uncovered by ice shelves is very limited in area compared with the Arctic continental shelves and is much deeper (500 m) than in the north (200 m).

It is now generally accepted that the pinniped families originated about 30 million years ago in the northern hemisphere and probably transgressed the tropics along the west coast of South America during a cold period, to radiate into the continuous Southern Ocean – the otariids and elephant seals usually remaining in lower latitudes, while the phocids occur south to the shores of the Antarctic continent. The only good evidence for the antiquity and ancestry of the monachine seals in the Southern Hemisphere is provided by fossils of the genus *Prionodelphis* from Argentina and South Africa. This was present in the late Pliocene of the South Atlantic (perhaps 4–5 million years ago); it is less advanced than the Antarctic seals, related to them but not ancestral (Hendey & Repenning 1972).

In contrast to the seals the whales are highly mobile, ranging over much of the world's oceans, many species occurring in both north and south hemispheres from the tropics to the polar seas. Knowledge of the large whales is reviewed by Mackintosh (1965, 1972*b*) and of the smaller Cetacea by Mitchell (1975); the Antarctic small Cetacea were recently reviewed by Brownell (1974). Their ancestry is about twice as long as that of the pinnipeds. The large baleen whales (Mysticeti) of the Southern Ocean comprise 3 genera, 6 species and 1 subspecies, namely the blue whale *Balaenoptera musculus*, its subspecies the pigmy blue *B.m. brevicaudata*, fin *B. physalus*, sei *B. borealis*, minke *B. acutorostrata*, humpback *Megaptera novaeangliae* and southern right whale *Eubalaena glacialis*, which rarely enters polar waters. There is one large toothed whale (Odontoceti) the sperm whale *Physeter catodon*, although only adult males enter Antarctic waters; and nine small toothed whales including the killer whale *Orcinus orca*, an important predator on seals, southern white-sided dolphin *Lagenorhynchus cruciger* and the beaked whales (Ziphiidae) *Berardius arnuxi* and *Hyperoodon planifrons*. Knowledge of the smaller odontocetes is still very slight (Brownell 1974) and they will receive no attention in this account.

Mackintosh (1965) considered that originally, before exploitation took effect, the southern stocks of baleen whales were probably about four times as abundant as the baleen whales in the north but have been greatly reduced by whaling. Because of their larger size (see below) their biomass was probably about five times as great. As with the seals, and probably for the same reason, there is less diversity in the Cetacea of the Southern Ocean and some types that are represented in the Arctic are lacking in the Antarctic – for example the gray whale *Eschrichtius robustus*, the narwhal *Monodon monoceros*, and beluga *Delphinapterus leucas*.

Some physiological considerations

It is well known that, in contrast to the Antarctic seals, the large balaenopterids and the sperm whale are migratory. Mackintosh (1965) has discussed the evidence and described the patterns. Brodie (1975) suggested that the propulsive energy required for the rorquals in migrating is no greater than the energy requirements of remaining in polar waters, because their heat loss is reduced in warmer waters. The advantage of migrating to the polar waters is associated with the greater food concentration in these seas where, as we shall see, the standing crop of zooplankton is higher (Foxton 1956; Mackintosh 1965). Lockyer (1972*b*) and Brodie (1975) have discussed the energy requirements of cetaceans in much greater detail than is possible in this brief review but some general points are worth emphasis.

In addition to its insulative function the blubber of marine mammals supplies energy during periods of fasting. A larger body size results in a larger blubber envelope and energy reserve. Female rorquals and pack-ice seals attain larger body sizes than the males, probably due to a lack of male dominance – in contrast to sperm whales, elephant seals and fur seals – and to accommodate the food reserve needed for suckling the young during migrations through less productive waters, or during the complete or partial fast in the breeding season (Norris 1966; Øritsland, 1977). Brodie (1975) suggested that selection in baleen whales favours a body size optimal for invading the productive polar seas for brief periods of intensive feeding, so as to build up reserves for maintenance during the period in warmer, less productive seas where energy conservation is easier. On this view the ‘larger body size reflects the selective pressure during the fasting period in warm water, rather than during the feeding period in colder water’. The larger body size of the males of polygynous seals, including *Mirounga leonina* and *Arctocephalus gazella*, is related to offshore marine feeding and the need for prolonged fasting on land by the males. Large mammals can go without food for longer than smaller ones because of their low metabolism in relation to mass (Bartholomew 1970; Stirling 1975).

Blue and fin whales are appreciably larger in the Southern Ocean than the same species in northern seas (Mackintosh 1965); on average the Antarctic fin whale is 8% longer and 30% heavier than the North Pacific fin whale (Brodie 1975), but paradoxically the duration of the period of intensive feeding is half as much again in the North Pacific, averaging 182 as against 120 days. This is related to the very dense swarms of food organisms (predominantly krill *Euphausia superba*) in the Antarctic and the higher diversity of prey in northern seas (Mackintosh 1965; Laws 1977). The smaller rorquals, for example the minke whale, appear not to be significantly different in size in the two hemispheres (Jonsgard 1951; Kasuya & Ichihara 1965;

Mackintosh 1965) ,and the year-round presence of minke whales in cold waters is probably indicative of the availability of suitable prey – a view supported by the smaller blubber mass, relative to body mass, namely 15% compared with 27% in blue whales (Brodie 1975; Laws 1977).

ECOLOGICAL INTERACTIONS

In figure 1 are shown some seasonal changes in the Southern Ocean related to feeding activities of seals and whales. Mackintosh (1973) demonstrated that the maximum extent of the pack-ice in spring was about 21.5×10^6 km^2 and that it contracted in the course of the summer to about 4×10^6 km^2; conversely the area of ice-free ocean south of the Antarctic Convergence increased from 14×10^6 km^2 at the end of winter to 32×10^6 km^2 in February–March. He also showed that the zone of krill, in quantities sufficient for baleen whales to feed on, was 19.24×10^6 km^2 in October–December, decreasing to 15.43×10^6 km^2 in January–March. In order to show the relation of this to the pack-ice edge, 2×10^6 km^2 has been added to these areas in figure 1 to allow for the shelf area, where *Euphausia crystallorophias* replaces *Euphausia superba*, and a generalized curve has been drawn to show the seasonal progression. Mackintosh himself did not claim more for his figures than that they were provisional estimates, and the present purpose is to show proportional changes rather than absolute values. Additionally, there are of course variations from year to year.

In this way a curve showing the seasonal changes in the amount of the krill zone covered by pack-ice has been derived and is also included in the figure. This shows that most of the krill is covered by ice during the winter and spring, and the area uncovered increases from, say, 1×10^6 km^2 to 12.5×10^6 km^2 in February, but then decreases again as the pack-ice cover increases. The decline in the size of the krill zone during the summer reflects the progressive grazing down by immigrant baleen whales, so that it contracts southwards as suggested by Mackintosh (1973).

Foxton (1956) demonstrated that the standing crop of zooplankton in the Antarctic is at least four times that in the tropics – even though he excluded large krill (more than 20 mm long). The mean monthly volume in the top 100 m shows a marked seasonal variation, reaching a peak in March (figure 1, where Foxton's curves have been combined and smoothed). Mackintosh (1973) gives an indication of the seasonal variations in the relative quantities of krill per net haul, for 410 stations with positive samples from the top 5 m of the water column. The relative quantities obtained were 54 g in October–December, 518 g in January–March and 42 g in April. Even if stations with negative hauls are included the average January–March haul is 243 g compared with 52 g in October–December. He suggested that this five- or tenfold increase is probably brought about by recruitment of larvae to the stock from deep hatchings, and increased summer growth of the two or three year classes of krill about the turn of the year. This finding is also incorporated in figure 1; note the logarithmic scale. Coupled with the increase in the area of the krill zone uncovered by pack-ice, it suggests that the relative amount of krill available to marine mammals outside the pack-ice belt increases at least 60-fold, possibly over a 100-fold in the summer months. Thus, even if temperature associated metabolic problems did not exist for the baleen whales, they would probably be under nutritional stress in Antarctic waters in winter if present at summer densities.

Fish and squid relative abundances cannot yet be shown because too little is known about these groups. Knowledge was briefly summarized by Laws (1977) who drew attention to the seasonal migrations of certain fish species into Antarctic waters in summer where they feed on krill.

The third part of figure 1 is designed to give a diagrammatic representation of the relative inter-specific or inter-group feeding activities during the year. It is concerned with four representative groups of marine mammals in Antarctic seas, the balaenopterid whales and the crabeater seal as the predominant krill eaters, and therefore as potential competitors; and the sperm whale and elephant seal as representative squid eaters outside the pack-ice belt and therefore also potential competitors. The data on which the curves are based are provided first by Mackintosh & Brown (1956) who gave estimates, based on sightings, of seasonal fluctuations in the populations of large baleen whales, predominantly blue, fin and humpback, in the ice-free Antarctic waters in the period 1933–9; secondly, for sperm whales by Harrison Mathews (1938)

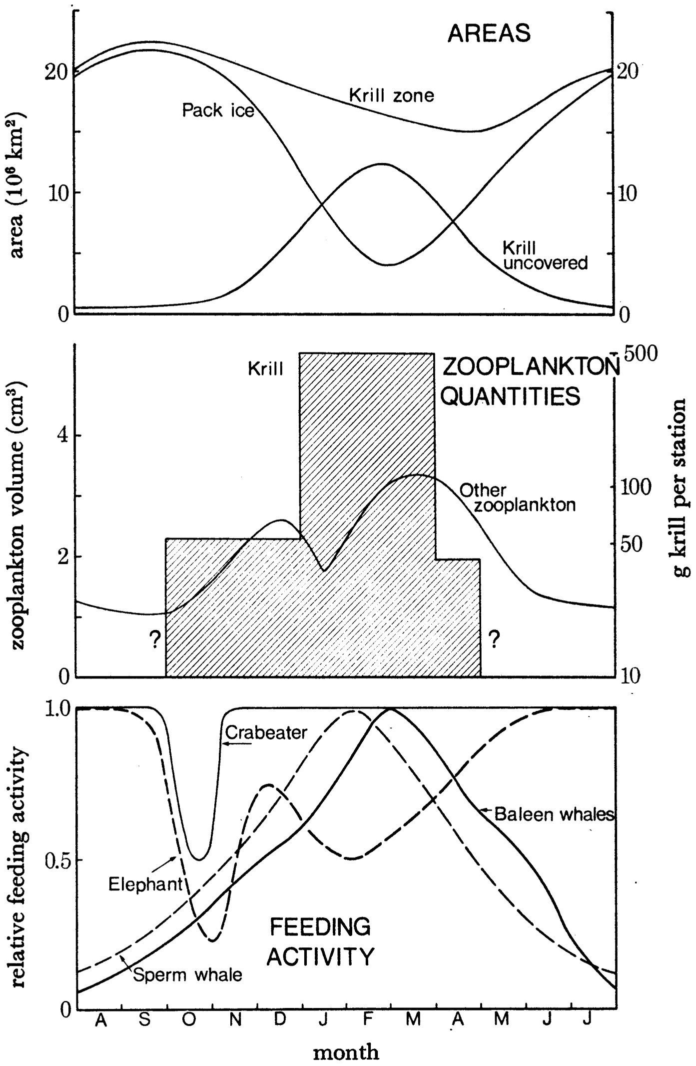

Figure 1. Seasonal changes in areas of pack ice, the krill zone and zone of krill uncovered by pack ice. Zooplankton quantities are shown for comparison but krill amounts are not available for winter months. The bottom curves show relative feeding activity on a seasonal basis for the main groups of consumers. Sources of data are given in the text.

and Gambell (1972) based on monthly catches in Antarctic and South African waters; thirdly, Laws (1956) gave quantitative data on the fasting haul out of elephant seals for breeding and moult; and fourthly, that for the crabeater seal is based on the assumption that adults of both sexes fast for 2–3 weeks in the breeding season in October, but do not fast during the moult in January–February (Øritsland, 1977). A representative of the smaller toothed whales is omitted because so little is known about their habits.

This figure is a diagrammatic representation drawn up from data of variable accuracy and should be considered as no more than a tentative first attempt to bring the information together with a view to illuminating the question of competition and ecological separation between the various groups of marine mammals inhabiting the Antarctic seas. It demonstrates some major features of the system. For example the balaenopterid and male sperm whale abundances in the Antarctic are very low in the winter months, when their distributions are more northerly, and at peak numbers in January–March when they are able to penetrate further south. In contrast the crabeater seal, and indeed all the ice-inhabiting seals are resident in Antarctic seas year round, as also are probably the smaller toothed whales and possibly a large part of the minke whale population (Laws 1977).

Despite the temporal overlap, ecological separation between the pack-ice seals and baleen and sperm whales is fairly complete because their distributions are complementary; the seals require fast ice as a platform for basking, moulting and breeding, and the whales generally avoid it. We do not know the pelagic feeding régime of the fur seal outside the breeding season, when the bulls fast completely for long periods and the cows make frequent short trips to sea to feed on krill. But this requirement of the lactating females is perhaps partly complementary to baleen whale food requirements, because fur seal births occur in November–December, well before the whale abundance peaks (Bonner 1968; Payne 1977). Although sperm whales and both sexes of elephant seals are potential competitors for squid in the Antarctic, figure 1 suggests that at the time of maximal potential competition, when the sperm whales are at peak abundance, a large part of the elephant seal population is hauled out on land, and fasting.

What of the intra- and inter-specific interactions in the ice-free ocean and in the pack-ice zone? The migrations of the baleen whales (Mackintosh 1965) are staggered so that the largest species tend to arrive earliest in Antarctic waters – the blue first, fin and humpback next, followed by sei. The waves of migration also reflect the extent to which different species penetrate the colder waters and this is also correlated with their body size, the minke being a notable exception for reasons already mentioned. As a result, although the Antarctic distributions of species overlap, each occupies a characteristic latitudinal zone (Ohsumi, Masaki & Kawamura 1970; Laws 1977) shown diagrammatically in figure 2. There are also longitudinal variations in abundance, within and between species. Within each species the migrations of different classes, by sex, age and reproductive status, are staggered in relation to energy needs. Larger and older individuals tend to reach higher latitudes than smaller and younger ones; pregnant females arrive early and leave later and females with calves postpone their entry into the cold polar waters (Laws 1961). Laws (1960*a*) presented evidence for longitudinal segregation of fin whales by size which suggested intraspecific competition (Laws 1977). The migrations are described in greater detail by Mackintosh (1965) and he concluded that the average annual feeding period south of the Antarctic Convergence was 120 days (Mackintosh 1972*a*).

The morphology of the baleen whales is functionally adapted to the size of their food organisms, notably in terms of the size, spacing and degree of fineness of the filtration. There are different types of feeding behaviour characteristic of species, broadly swallowing, skimming or a combination of the two (Nemoto 1959).

As a result there is a considerable degree of ecological separation on the feeding grounds although it is by no means complete. An attempt has been made in figure 2 to summarize the major distributional and prey selection factors contributing to this. Of the two seals characteristic of the ice-free waters, the elephant seal probably feeds on squid and fish pelagically and fish in inshore waters (see below) whereas the fur seal feeds on krill near the breeding grounds and its pelagic food is unknown. Different age classes haul out and fast in the breeding season and during the moult, at different times and for differing periods (Laws 1956; Bonner 1968).

Within the pack-ice zone logistic problems make investigation difficult. Of the Cetacea, only the blue whale, minke whale, killer whale and beaked whales significantly penetrate this belt.

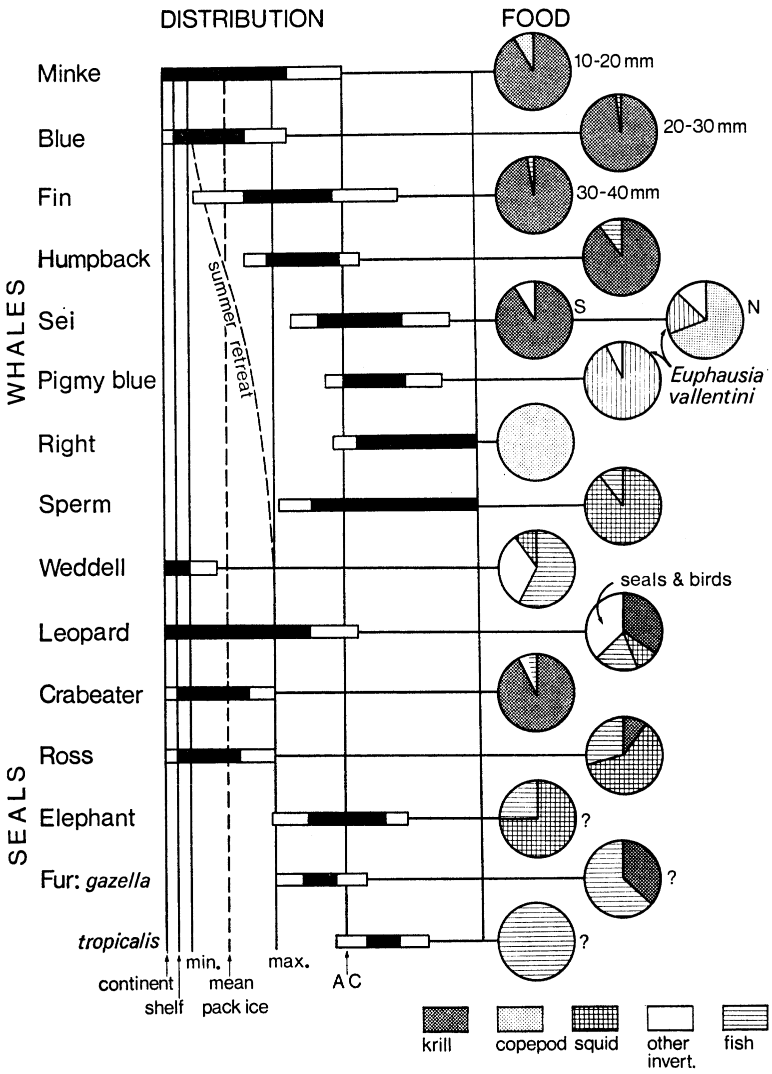

FIGURE 2. Comparison of the zones occupied by whale and seal species from the Antarctic Continent northwards. The relative area of the shelf; the minimum, mean and maximum pack-ice area; and the area south of the Antarctic Convergence (AC) are indicated. Each species, except the fur seals, has a circumpolar distribution and the ranges indicated are the approximate average latitudinal ranges in the Southern Ocean, the black part indicating higher densities. Pie diagrams indicate the food composition and major uncertainties are shown (?).

The minke feeds on smaller food organisms than blue, including copepods and both take *Euphausia crystallorophias* over the continental shelf. The elephant and fur seals are rarely found in pack-ice, and the other four species are characteristically distributed according to the type of ice. The leopard and crabeater have similar distributions in the pack-ice zone, occurring in greatest abundance in cake ice with 30–70 % cover; but the leopard seal distribution also extends to subantarctic islands and even lower latitudes. The Ross seal is characteristic of denser, heavier pack-ice and the Weddell has a much more southerly distribution nearer continental shores, but also has breeding populations around Antarctic and subantarctic islands (Brown *et al.* 1974). Their feeding habits are described below and the ecological separation summarized in figure 2.

The Weddell seal has adapted to fill a specific niche – the inshore fast ice zone – where it winters under the ice, keeping open breathing holes with its teeth. This enables it to exploit inshore benthic or demersal prey and incidentally confers protection from killer whale and leopard seal predation. A penalty incurred may be higher adult mortality caused by tooth wear (Bertram 1940; Stirling 1969). At the other extreme the crabeater seal is subject to heavy predation on the young, by killer whales and leopard seals, but lives longer. These differences are reflected in survival curves for the two species (Stirling 1971; Laws 1977). The stable fast ice breeding platform of the Weddell seal has made possible gregarious colonies and the development of a male hierarchical system, the dominant males defending three-dimensional underwater territories (Kaufman *et al.* 1975). The sexual dimorphism still favours the female, however, and the polygynous Weddell breeding behaviour is intermediate between the highly polygynous (and strongly dimorphic) land breeding elephant and fur seals and the monogamous crabeater seal and other species breeding on shifting pack-ice (Stirling 1975).

Abundance, biomass and food requirements

Seals

The abundances of land breeding seal species can be estimated from counts of pups, converted to population size by means of raising factors that can be established from the age structure of the population. Laws (1960*b*) attempted to assess the elephant seal stocks in this way and concluded that they totalled about 600 000; this is still the best estimate. Payne (this meeting) as a result of his intensive studies has given a figure of 300 000 for the fur seal, which is more reliable than the estimated population size of any other Antarctic seal. For dispersed pelagic species the problems are much greater, especially in the Antarctic where the area of their distribution is so vast, but they do haul out on the pack and fast ice and so are easier to count than the completely aquatic whales. Erickson, Siniff, Cline & Hofman (1971) and Gilbert & Erickson (1977) estimated numbers and densities of the pack-ice seals by means of strip censuses using helicopters, ice breakers and aerial photography. Adjustments were made for daily activity patterns but stratification of sampling effort based on ice type was not possible. The pack-ice area was determined from satellite imagery and total numbers estimated by extrapolation and converted to population sizes of the individual species by the application of proportional species abundances obtained from the strip sample counts. These gave an overall composition by species of 92.7 % crabeater, 4.55 % Weddell, 1.37 % Ross and 1.37 % leopard seals. Full details of their methodology are given by Gilbert & Erickson (1977). The estimated populations by species were: crabeater 14.858 million, Weddell 730 000, Ross 220 000 and leopard seal 220 000.

The mean mass of 3 leopard seals sampled was 271.7 kg, for 224 Weddell seals it was 245.8 kg, for 205 crabeater seals 192.6 kg, and for 10 Ross seals 173.1 kg (Øritsland 1977; Laws unpublished). Laws (1960) gave biomass data which indicate a mean individual mass of 500 kg for elephant seals and he estimated a mean mass for fur seals of 50 kg (Laws 1977).

Øritsland (1977) discussed daily food intake and tentatively concluded that it averages 7% of body mass for 335 days a year for the four pack-ice seals; this allows for 30 days fasting during the breeding season and gives an annual consumption of 23.45 × mean body mass. A similar ratio seems reasonable for the fur seal, but the elephant seal is much larger and so probably has a somewhat lower daily requirement, but it fasts during the breeding season and also during the moult; the adult male fasts for about 3 months and the female for 2 months (Laws 1956). An intake of 6% of body mass per day for 9 months for bulls, 10 months in the case of cows and rather longer for immatures appears reasonable. It indicates an average annual food intake of about 20 × mean body mass.

Table 1. Crude estimates of antarctic seal populations, biomass and food consumption

				annual food consumption (10^3 t)			
species	stock (thousands)	mean weight kg	population biomass 10^3 t	total	krill	squid	fish
elephant	600	500	300	6000	—	4500†	1500†
leopard	220	272	60	1403	519	112	182
Weddell	730	246	180	4211	—	463	2232
crabeater	14858	193	2868	67245	63210	1345	2017
Ross	220	173	38	892	80	571	196
fur	200	50	15	351	117	117	117
total	16828	—	3456	80102	63926	7108	6244

† See text for basis of estimate.

Øritsland (1977) has recently reviewed the qualitative food consumption of seals in the Antarctic pack-ice zone. He concluded that on average Weddell seals take 53% fish, 11% cephalopods, and 36% other invertebrates; crabeater seals take 94% krill, 3% fish and 2% squid; leopard seals take 37% krill, 13% fish, 8% squid, 3% other invertebrates and 39% birds, seals and carrion; and Ross seals take 22% fish, 64% squid, 9% krill and 5% other invertebrates. The elephant seal diet is not known because when they are hauled out on land they invariably fast (Laws 1956) and they have not yet been sampled pelagically. Laws found fresh food in only 6 out of 139 stomachs he examined and concluded that they probably fed on fish in inshore waters and squid elsewhere. In the absence of better information it is assumed for present purposes that they consume approximately 75% squid and 25% fish; the completely pelagic Ross seal takes 22% of fish. The fur seal at South Georgia feeds almost exclusively on krill, but fish (commonly) and squid (rarely) are also found in stomachs sampled there (Bonner 1968). Until it is possible to sample them at sea, the proportions consumed cannot be accurately determined, but it is assumed here that they consume 34% krill, 33% squid and 33% fish year round.

From the estimates given of population sizes, body masses and food consumption, table 1 is derived. The present estimates are subject to quite large possible errors from various sources, which Øritsland (1977) has briefly discussed in relation to the pack-ice seals, but which are unlikely to be cumulative. One point which needs emphasis is that the population estimates of the pack-ice seals are likely to be low because unknown proportions are in the water even at the times of the maximal daily haul out.

Whales

Knowledge of the population sizes of the baleen whales is still developing, but the figures given in table 2 represent a current consensus of whale biologists (Mackintosh 1965, 1973; Laws 1977; Chapman 1974; International Whaling Commission 1973, 1974). The best estimates for sperm whale stocks are given by the International Whaling Commission (1973); it has been assumed that about one third of the exploitable males, currently estimated to number 128000, feed in Antarctic waters during the summer. Half the total sei whale stock is thought to feed south of the Antarctic Convergence during the summer.

Table 2 shows that the stocks of baleen whales have been reduced by whaling to about a third of their former numbers and blue, fin, sei and humpback combined to about 18% of their former numbers. The humpback and blue whales are hardest hit, having been reduced to about 3 and 5% of the estimated initial stocks. The exploitable male sperm whale stocks are considered to have been reduced to about half their former abundance. Consequently the Antarctic baleen whales now consume an estimated 147 million tonnes less krill than they did before Antarctic whaling began. They and the sperm whale also consume an estimated 8 million tonnes less squid and over 3 million tonnes less fish than formerly.

Because the large whales are migratory, with the partial exception of the minke whale, they transfer material in their bodies out of the Antarctic (Laws 1977). On arrival in Antarctic waters they are thin and it has been estimated that as a result of the intensive feeding activity they add at least 50% to their mass (Lockyer 1972*b*). This reserve is used up during the remaining 8 months of the year when they undergo an almost complete fast. Consequently there is a loss of energy and nutrients to the Antarctic system. It is here assumed that the male sperm whales feeding in the Antarctic increase in weight by only 20%, because they do feed significantly north of the Antarctic Convergence, but presumably at a lesser rate; there are no data to support this estimate, but wide variations would have little effect on the overall conclusions.

In addition any mortality that occurs outside Antarctic waters will result in a loss of material and energy originating largely from Antarctic primary and secondary production. In these crude estimates it has been assumed that mortality is spread evenly over the year so that two-thirds of natural mortality would occur north of the Antarctic Convergence. Estimated natural mortality rates for baleen whales were given by Laws (1977). The values used here for sperm whales are 6% annually for the initial stock, reducing to 4% annually as a result of exploitation; these approximate to the instantaneous rates given by Best (1974).

Table 2 indicates that biomass transfer due to metabolic losses is some 13 times greater than that expected from deaths in baleen whales and 5–7 times greater in sperm whales. Total estimated losses from the Antarctic system by both of these pathways were nearly 18 million tonnes from the initial baleen whale stocks and 612000 tonnes from the sperm whale stocks. From the present stocks they are estimated at 2.4 million and 263000 tonnes respectively.

Some responses to the decrease in whale stocks

Although the combined seal populations (table 1) are 16 times more abundant than even the initial stocks of whales (table 2), the combined standing stock biomass of Antarctic seals is relatively small compared with that of the large whales – a mere 3.5 million tonnes compared

TABLE 2. CRUDE ESTIMATES OF LARGE WHALE POPULATIONS, BIOMASS AND FOOD CONSUMPTION IN THE ANTARCTIC AND OF THEIR BIOMASS LOSS OUTSIDE THE ANTARCTIC

				food consumption in Antarctic (10^3 t)			biomass loss outside Antarctic (10^3 t)			
species	stock (thousands)	mean weight t	mean antarctic biomass 10^3 t	krill	squid	fish	metabolic	mortality	total	% of mean Antarctic biomass
					initial stocks					
baleen whales										
fin	400	50	20000	81480	840	1680	8000	530	8530	
blue	200	88	17600	71702	740	1478	7040	580	7620	
sei	75‡	18.5	1387	5651	58	116	555	67	622	
humpback	100	27	2700	11000	113	227	1080	124	1204	
minke	200	7	1400	19827§	204	409	—	—	—	
total	**975**	—	**43087**	189660	1955	3910	16675	1301	**17976**	41.7
sperm whale	**85‡**	30	**2550**	—	10200	500	510	102	**612**	24.0
					present stocks					
baleen whales										
fin	84	48	4032	16426	169	339	1612	109	1721	
blue	10	83	830	3381	35	70	332	27	359	
sei	40.5†	17.5	709	2888	30	60	284	33	317	
humpback	3	26.5	79	322	3	7	32	4	37	
minke	200	7	1400	19827§	204	409	—	—	—	
total	**337.5**	—	**7050**	42844	441	885	2260	173	**2434**	34.5
sperm whale	**43‡**	27	**1161**	—	4632	244	232	31	**263**	23.0

† 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.

with the 45.6 million tonnes of the initial stocks of large whales and the 8.2 million tonnes of the present stocks. But the seals are present in Antarctic waters year round, except perhaps for fur seals and part of the elephant seal population. Having smaller body sizes their metabolic rate and relative food consumption is higher – about 7% of body mass daily (Øritsland 1977). Consequently the seals are estimated to consume annually about 80 million tonnes of krill, squid and fish – more than the total world fisheries catches by man (United Nations FAO 1975).

Their present consumption of krill is a third of the amount formerly thought to have been consumed by the initial stocks of baleen whales and 1½ times the estimated present consumption of krill by the baleen whales. Thus, the seals now appear to have overtaken the baleen whales as major consumers of krill.

The seals also consume an estimated 7.1 million tonnes of squid, over half the estimated consumption by the initial stocks of the large whales and rather more than the estimated present consumption of squid in the Antarctic by large whales. They consume an estimated 6.2 million tonnes of fish, 1½ times the amount consumed by the initial stocks of whales and almost 6 times greater than the consumption by the present whale stocks. With the possible exception of minor transfers by metabolism and death of fur seals and possibly elephant seals, all this energy remains in the Antarctic, because the pack-ice seals are non-migratory.

The estimates presented in table 2 indicate that the total stocks of large whales have been reduced by 680000 animals since exploitation began. Food consumption by them is estimated to have declined by 147 million tonnes of krill, 7.1 million tonnes of squid and 3.3 million tonnes of fish. Although these are rough estimates it is clear that a large amount of food formerly consumed by the whales should have become available to the remaining stocks of whales and to other consumers. What effects has this potentially greater resource had on the consumers?

Sladen (1964) was the first to suggest that increases in the chinstrap *Pygoscelis antarctica* and Adelie *P. adeliae* penguins were a result of the decline in the baleen whale stocks, and others (listed by Laws 1977) confirmed the population increases of these species and of the king penguin *Aptenodytes patagonica* and gentoo penguin *P. papua*. Laws (1977) discussed these increases and those of the fur seal *Arctocephalus gazella* at South Georgia, now well documented by Payne (1977). It is also a krill feeder and has increased more rapidly than would be expected by comparison with other species recovering from over-exploitation. It has expanded from a few hundred at most in the 1930s to at least 300000 today – a figure indicated by the estimate of 90000 pups given by Payne.

Data on population sizes and trends of abundance in other marine mammals are less reliable but other evidence pointing to changed behaviour, increased growth and reproductive rates strongly suggests that a more abundant food supply is having effect. There is good evidence that the sei whale has altered the timing of its migrations in recent years (Gambell 1968). In the 1930s their peak abundance in the Antarctic was in March, but since the late 1950s it has been in January. Also sei whales now penetrate much further south than formerly. This may reflect reduced competition from blue, fin and humpback whales, but could possibly be due to a long-term change in the environment, as yet undocumented.

Mackintosh (1942) and Laws (1961) showed that the pregnancy rates of mature Southern Hemisphere blue and fin whales increased up to 1939, fell during the war years to 1946, when there was very little whaling, and rose again as the catches increased in the post-war years. It was suggested that this was a response to the decline in the whale stocks (and their feeding densities) and the resulting increase in food availability. Gambell (1973) reviewed the evidence, making use of more recent data and his figures for blue, fin and sei whales are presented in figure 3. The increases in pre-war and post-war periods are from 25 % of mature females pregnant to 50–60 % pregnant. His findings for sei whales were even more significant because the increase in pregnancy rate preceded large-scale exploitation of this species which began in the 1960s. It strengthens the conclusion that an indirect effect of whaling is involved, presumably through the expected greater availability of food, rather than directly.

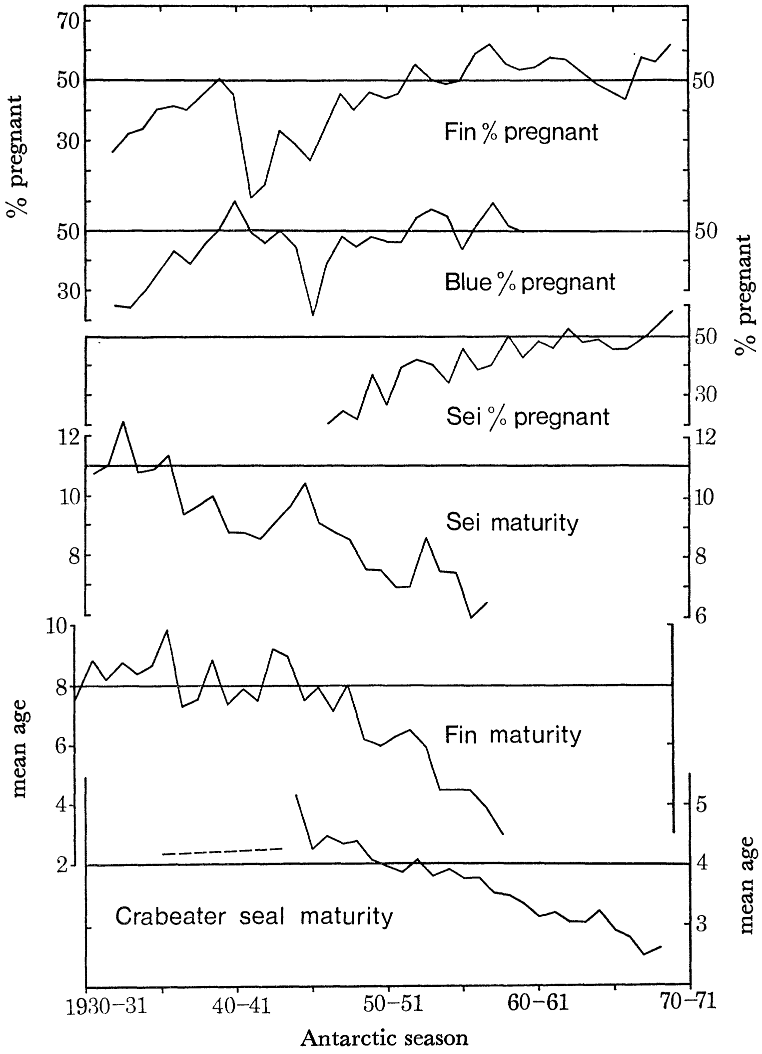

Figure 3. Collective evidence for changes in pregnancy rates and age at sexual maturity in female fin, blue and sei whales and advancing age at sexual maturity in crabeater seals. (After Gambell 1973; Laws 1977; Lockyer 1972, 1974.)

Laws (1962) also presented evidence indicating that the mean age at sexual maturity of female fin whales decreased from 1945 to 1956, and from comparison of the body length and ovarian criteria of sexual maturity, he inferred that the earlier maturity was brought about by an increase in the rate of growth, which in turn resulted from increased food intake. Confirmation of this inference came from studies on the ear plug of fin and sei whales. Lockyer (1972*a*) found that in fin whale ear plugs the immature/mature transition zone can be identified because immature annual layers are irregular and unevenly spaced and are generally succeeded by more even and closely packed layers laid down in mature whales. The age at which sexual maturity was attained can be determined for each year class represented in the samples by mature animals. She found that the age at maturity was constant at about 10 years in both sexes between 1910 and 1930 and then decreased to 5–6 years in the most recently mature year classes (figure 3). This age was confirmed by direct examination of reproductive status and age in current samples. There was no detectable change in mean body length at maturity, confirming Laws' (1962) deduction that an acceleration in body growth rate induced precocious puberty. Subsequently Lockyer (1974) extended the findings to the sei whale which showed similar advancement of the age at sexual maturity as estimated from the ear plug transition zone (figure 3). Again the start of this trend towards earlier puberty preceded the start of large-scale exploitation of this species, and so also supports the idea of an indirect relationship to whaling.

Laws (1977) obtained similar evidence of an advancement of the age at sexual maturity in crabeater seals in the area to the west of the Antarctic Peninsula. The cementum layers on the roots of the teeth which are laid down in the immature years are usually broader and more irregular than those laid down in adult teeth. Measurements demonstrate a transition zone as in the whale ear plug. The mean age at puberty appears to have been about 4 years until the whaling zone known as the 'Sanctuary' was reopened to whaling. Subsequently it decreased to about 2.5 years (figure 3), an interpretation in agreement with direct examination of reproductive condition and age in recent years. Because crabeater seals are not hunted in significant numbers (a few hundreds annually, Laws 1972) compared with the population of 15 million, the evidence suggests that this crabeater seal stock has been increasing over recent decades. Similar responses to the decline in the whale stocks would be expected in other Antarctic areas.

The evidence is still largely indirect but it seems reasonable to conclude that a consequence of the dramatically reduced density of baleen whales would be a greater standing stock of krill, but that the remaining baleen whales are eating more, and growing and breeding faster. At the same time other groups have begun to consume more, with effects on their growth and reproductive rates (and possibly on survival rates?), and their population sizes. Whaling has already greatly altered the trophodynamics of the Antarctic marine ecosystem and a key question that remains to be answered is whether the putative original balance in the Southern Ocean can be regained with appropriate management.

A new factor to be considered is the developing effect of man as a consumer of Antarctic krill and fish. In recent years several nations have mounted exploratory fishing operations in the Southern Ocean and it seems likely that full-scale commercial exploitation may be about to begin. The effects of this new competitor for their food resource could be as far reaching for whales, seals and seabirds as the whaling industry has been. The urgent problems of conservation and management are taken up by Roberts (1977).

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