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Ecology of the Southern Ocean Region

GEORGE A. LLANO*

The author, a noted expert in Antarctic ecology, surveys the fauna of the area and discusses its potential commercial and scientific uses. He describes the Antarctic food chain in order to emphasize the delicate natural balance that has evolved over the millenia.

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I. INTRODUCTION

Our appreciation of the structure and function of the Antarctic marine ecosystem has been considerably enhanced by information and observations from investigations initiated after the International Geophysical Year of 1957-58. The data derived from physical and biological research are a new source for significant details important to the ecologist and biogeographer. Satellite photography exposes the global phenomena of the atmospheric turbulence, ice masses and oceanic expanse South Polar Region as a dynamic system interacting with the great land mass of Antarctica. The atmosphere is the major driving force for the surface currents of the Southern Ocean; its circulation as zonal currents, gyres, and upwellings, as fronts and bottom waters is a salient feature of the marine envi-

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1. The International Geophysical Year of 1957-58 [hereinafter I.G.Y.] was a worldwide effort coordinated by a special international committee to observe the sun, weather, aurora, magnetic fields, ionosphere and cosmic rays. Research in Antarctica was stressed, and, in order to relax potential international conflicts, the scientific nature of expeditions to the region was emphasized.
ronment influencing the ecology and responsible for the remarkable productivity of the Southern Ocean.

II. THE PHYSICAL BASIS

The relatively high atmospheric pressure over Antarctica is a prominent global feature and a dominant factor in the circulation of the Southern Ocean. The two major surface water movements are the East Wind Drift (Antarctic Coastal Current) and the West Wind Drift (Antarctic Circumpolar Current). The deeper water currents follow this same pattern although they are influenced and modified by submarine topography, coastal physiography and the earth's rotation.

The West Wind Drift is a paramount feature of the Southern Ocean and a unique feature of the ocean world. This complex and variable current system encircles Antarctica at approximately latitude 50° S. At about latitude 45° S., the northward drift of these surface waters meets warmer waters from the temperate latitudes so that within a few kilometers there are sharp changes in temperature and salinity and the development of a pronounced frontal system. At this point, the Antarctic surface waters sink beneath the less dense subantarctic surface waters. This occurrence forms the Antarctic Convergence or Polar Front Zone, which circumscription represents a major biotic boundary for phytoplankton, zooplankton, fishes and birds. Edmond observes that north of the Convergence organisms that secrete carbonate shells—cocolithophorids, foraminifera, and pteropods—are abundant; south it it, opaline organisms, especially diatoms, are the dominant species. Antarctica is therefore ringed with a series of sediment types: glacial debris close to the continent carried out in icebergs and dumped as they melt; then diatomite; and finally, beyond the frontal boundary, calcareous material . . . .

The cold Antarctic bottom water contributes to the productivity of the Southern Ocean. Its origin is related to the presence of the South Polar Ice Cap, the largest and oldest ice mass on earth, which acts as a great heat sink and is the source of the atmospheric interaction between the land and the surrounding ocean. One aspect is the strong continental winds which move snow seaward, cooling the surface waters in restricted areas and initiating the formation of sea ice. These winds increase the salinity and density of the ocean waters by freezing out fresh water. Similarly, the development of pack ice and the flow of glacier ice into the sea has a profound effect on

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the Antarctic marine ecosystem. The southward flow of the circum-polar deep water, which rises toward the surface, creates a zone of upwelling, pumping vast quantities of nutrients that contribute to the luxuriant growth of the phytoplankton and other marine life close to the coasts of Antarctica. The atmospheric circulation has particular relevance to Antarctic living resources, as atmospheric cyclones contribute to the formation of gyres in the ocean. These gyres are identified with concentrations of krill. The largest gyre, the Weddell Drift, extends from the Antarctic Peninsula to about longitude 30° E.

III. THE BIOLOGICAL BASIS

A. Food Chain

The most striking feature of the Southern Ocean is its high fertility. According to El-Sayed, the productivity of the Antarctic coastal waters is four hundred percent greater than the average primary productivity of the world's oceans. Even more impressive is the contrast between the depauperate and sparse vegetation of Antarctica, and the abundance of phytoplankton in the coastal waters and the submarine forests of brown and red algae of the benthic zone.

Organic production, however, varies widely in response to variations in the supply of phosphates, nitrates, silicates and other nutrients and is characterized by one major peak during the austral summer. Upwelling areas along the continental shelf and the frontal zones between major water masses are areas of highest productivity. The organic debris from the biological activity in the photic zone settles to the bottom where, through bacterial action, it is metabolized into nutrients. The continuous upward flow of the nutrient enriched abyssal water thus regenerates the surface photosynthetic process. Edmond notes that the "limiting factor to growth at these high latitudes is not nutrients but light." The reference is to the physical properties of sea water, which restrict submarine illumination, as well as to the six months of austral winter darkness and the effect of sea ice, which approximately halves the areal extent of open ocean south of the Antarctic Convergence.

6. Edmond, supra note 2, at 37.
The dominant phytoplankton are the diatoms. These microscopic, free-floating algae are characterized by a great diversity of species and high endemism. Other phytoplankton, dinoflagellates and silicoflagellates, are found almost exclusively in Antarctica. The large brown and red macroalgae of the subtidal and deepwater coastal areas are best developed around the subantarctic islands, but their distribution along the Antarctic coasts is not clearly known. These plant formations are important habitats for vertebrate and invertebrate marine fauna as well as a potential economic resource for agar and other algal products used in industry.

Phytoplankton are the fundamental unit in the simple Antarctic food chain and constitute the basis for all life in the Southern Ocean. Zooplankton, a wide assortment of free-floating organisms which vary in size, are equally important in the food chain and, like phytoplankton, are circumpolar in distribution. The dominant forms, copepods and euphausiids, constitute a principal food source for whales.

Of the euphausiids or krill, *Euphausia superba* has an eccentric distribution south of the Antarctic Convergence. It is endemic to the Southern Ocean but is found in massive swarms suitable for fishery operations. The highest concentrations have been recorded in the southern part of the Scotia Sea within the sweep of the Scotia Island Arc. Baleen whales have always been the primary consumers of krill. Krill are, however, also a major food for seals, birds, fish, squid and other invertebrates. These carnivores represent the final link in the Antarctic food chain.

B. Benthic Environment

The bottom fauna of the continental and island shelves is remarkable for its variety and abundance of species which are characterized as slow growers. The continental shelf is between 60 and 240 kilometers (37 to 149 miles) wide and drops precipitously into the abyss. This is narrow compared to the shelves of other continents. The intertidal zone, down to about fifteen meters (forty-nine feet), is heavily disturbed by ice scour and anchor ice, limiting the kinds and numbers of benthic organisms. Below this depth, ice-rafted rocks provide a prime substrate for sessile-filter-feeders. Over five hundred species of invertebrates have been found on the rocky bottoms where *Porifera, Tunicata* and *Hydrozoa* predominate. Some of the sponges grow to an extraordinary size.

The benthic marine environment of the Antarctic Peninsula and Scotia Island Arc differs from that found elsewhere on the continent. This is demonstrated by the difference in the composition of the fauna in these two regions. An important factor in the distribu-
tion pattern of Southern Ocean benthic fauna is the West Wind Drift which has influenced colonization, particularly among the subantarctic islands.

The biomass of the Antarctic benthic organisms is quite high, especially in shallow waters. However, while the benthic fauna of the “high Antarctic” is rich in variety and abundance of organisms, it includes no invertebrates of potential commercial interest. In fact, the food chain relationship of the Antarctic benthic fauna is not well known. While at one time it was thought to represent a dead end in the food chain, recent work by American biologists indicates that the “high standing crop” of the Antarctic benthic regions is recycled in the general web of life. The benthic environment of the subantarctic islands is characterized by the presence of heavy stands of the macroalga *Macrocyctis*, which appears extensively at the Kerguelen, South Georgia, Heard, Macquarie, Crozet and Marion Islands. The high biomass of *Macrocyctis* makes it a potentially important source of alginates. The other fishery resources include *Lithodes* crabs at Prince Edward and Crozet Islands.

C. **Ichthyiofauna**

The Antarctic ichthyiofauna consists of about one hundred species, twelve of which have commercial value. Information on the abundance, distribution, spawning habits and ecological relationships is generally vague or incomplete. Since 1970, however, commercial fishing activities have revealed large concentrations of sexually mature fish on the Kerguelen and South Georgia Island shelves. It may be that the absence of favorable spawning areas along the narrow shelves is a limiting factor in the development of large fish stocks.

The Antarctic Convergence is less of a barrier to the deepwater fauna than to the shallow water species. The major group, the *Nototheniiformes*, is predominantly demersal. These are sluggish, attenuated, large-headed fish which are diverse both in habit and structure. About eighty percent of these are found only in the Southern Ocean where they constitute over sixty percent of the Antarctic individual species and over ninety percent of the total fish population found in Antarctic waters.

According to DeWitt, the physical and climatic isolation of the South Polar Region is responsible for this high endemism. He points out that temperatures in Antarctic waters are more uniform and have been so for a long geologic period.

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[T]here is ample evidence that the Antarctic continent has been isolated and bathed by a cool ocean for a considerable period of time, perhaps 40 million years or more. It is therefore not strange that the Antarctic fish fauna is characterized by the absence of northern types, the dominance of peculiar groups, very high percentages of endemic genera and species, and one endemic family

Overall, Antarctic fish resources are comparatively small and largely concentrated along island shelves. It has been observed, however, that even though Antarctic fish may not contribute significantly to the general dynamics of the Antarctic marine ecosystem, their role in the food web of Antarctic marine mammals is clearly evident. South Georgia and Kerguelen have been identified as major fishing grounds, and, in both areas Soviet fishing fleets have taken large catches since the late 1960's. The Soviet catch in Kerguelen waters in the 1971-72 season was estimated at 120,000 metric tons. In South Georgia, the catch was estimated at 400,000 metric tons. In both areas, the principal fish taken were Nototheniiformes.

Recently, catches have declined dramatically in South Georgia to a few thousand tons, indicating a great reduction in stock density which Everson calculates to represent an eighty percent drop in population. Everson adds that the paucity of information on fish biomass and production reflects the recent development of commercial fin-fish operations in Antarctic waters.

D. Avifauna

For more than half the year, and over most of its area, continental Antarctica is virtually lifeless. The exception is the emperor penguin which breeds on sea ice along the edge of the continent during the austral winter. As the days grow longer, an assortment of small and large sea birds, principally penguins, albatrosses and petrels, converge on Antarctica from all points, and the silent continent awakens to the sounds of life. About fifty species of birds,

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8. Id. at 5.
13. Id.
representing eight families, breed in the Antarctic region. What it lacks in species, the Antarctic avifauna makes up in numbers. The avifauna constitutes an important part of the Antarctic ecosystem; the total biomass is estimated at about 577,000 metric tons or about 180 million birds.

Antarctica is synonymatic with penguins; these flightless sea birds constitute sixty-five percent of the bird stocks and ninety percent of the biomass for the whole Antarctic region. Like most other elements of the Antarctic biota, birds are largely circumpolar in distribution, breeding mainly along the Antarctic coastal zone and subantarctic islands. They range over the pack ice zone to the Antarctic Convergence and the Subtropical Convergence.

In the early nineteenth century, the larger penguins of the subantarctic islands were rendered for oil by elephant seal hunters. Penguins and their eggs provided a source of fresh food for early Antarctic expeditions. Penguins are highly gregarious and form colonies of thousands of breeding pairs. The penguins’ annual deposit of guano discolors the ground a characteristic ashy to yellow and thereby creates an untapped source of phosphates. Antarctic marine birds have no commercial use and, for the most part, enjoy a protected status.

The importance of sea birds in the Antarctic ecosystem lies largely in their role as consumers. They consume an estimated thirty-nine million tons of food per year, of which the penguins consume eighty-six percent of the total. As consumers, birds are about equally important as the baleen whales and about half as important as the seals. Factors limiting the abundance of the avifauna include a lack of suitable nesting areas (as more than ninety percent of the land area is covered with ice and snow) and lack of zooplankton forage during the winter period.

E. Whales

Whales are still the primary economic resource of the Antarctic region and pelagic whaling in the Southern Ocean currently comprises a significant proportion of the total world catch. The region has been a global whaling ground for over 150 years, and the rise and decline of the Antarctic whaling industry has been the result of successive overexploitation of baleen whales. Blue (Balaenoptera musculus), humpback (Megaptera novaeanglia) and some stocks of fin (Balaenoptera physalus) whales, all species in the thirty-three to eighty-four ton range, have been depleted to well below their

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14. See BIOMASS, supra note 9.
optimum levels. The pressure of pelagic whaling has fallen currently upon the Minke whale which averages seven tons; these had previously been considered too small to be worth hunting.

According to Gulland, 825,300 baleen whales were taken between 1931 and 1968. It has been estimated that the stocks of baleen whales feeding in Antarctica have been reduced ninety percent in the past forty years. A survey of the catch localities showed that the whaling grounds south of the Atlantic were ten times more productive than other Antarctic areas. High catches have coincided with high krill concentrations and were most abundant along the edge of the pack ice. An exception has been a separate krill population around South Georgia.

Zenkovich has made some interesting observations on the food and feeding behavior of whales. He notes that whales, in cold areas, feed not less than four times per day. Age and condition provide more variables; large, old whales as well as pregnant whales feed more intensively than other whales. Blue, humpback and Minke feed primarily on euphausiids. Daily consumption for a blue whale is about four tons of crustaceans or 480 tons per 120 day season. The consumption of a humpback, however, totals about 240 tons per season. Fin whales feed on euphausiids and copepods; consumption of euphausiids alone is estimated at about 360 tons. Sei whales feed on euphausiids, copepods and amphipods. These whales are assumed to feed at least five times a day, consuming an estimated 150 tons of krill during the summer feeding period. Whales feeding along the edge of the pack ice consume large quantities of phytoplankton, which Zenkovich deems of great importance in the whale diet. All whales, however, take some fish and squid. The annual consumption of krill by whales has been estimated at 150 million metric tons.

Thus, the simple Antarctic, three-link food chain of phytoplankon/zooplankton/carnivores suggests a production of 100 million tons of carnivores, including baleen whales, seals, sea birds, fish and other predators such as squid.

It has been suggested that the reduction of whales must have resulted in an increase of krill and that this surplus may be harvested by man without upsetting the dynamics of the prevailing

ecosystem. Thus, it is possible to harvest both whales and krill. The krill surplus concept is unacceptable to those who maintain that other groups—such as seals, fish and birds—have utilized the surplus and through increases in their populations have established a new equilibrium in the marine ecosystem. Everson has cited new data indicating that the relative increase in food availability has favored early growth, lowered the age at which physical maturity has been attained and increased the pregnancy rate of some whales. 19

F. Seals

The Antarctic seals, like the whales, represent a substantial potential source of food. In terms of numbers and biomass, Antarctic seal stocks surpass their northern counterparts and other large mammal groups. Of the six Antarctic seal species, four closely related genera are characterized as true Antarctic seals. In order of abundance these are: the crabeater (*Lobodon carcinophagus*), the ubiquitous, ice-dwelling seal; the Weddell (*Leptonychotes weddelli*), primarily inhabiting the inshore fast ice; the leopard (*Hydrurga leptonyx*), of wide distribution and a predator of other seals and birds, and the Ross (*Ommatophoca rossi*), a reclusive and little-known species of the deep pack ice. Two other species of the subantarctic which occur in the Antarctic region are the elephant seal (*Mirounga leonina*) and the southern fur seal (*Arctocephalus sp.*).

The functional area of the crabeater and Ross seals is the Antarctic pack ice and fast ice zones. Like the ice zones, they have a circumpolar distribution. They differ in their preference for ice platforms and ice cover, in food habits, daily activities and distribution. Consequently, they co-exist in the Antarctic without interference. 20

Crabeater seals are almost exclusively krill consumers as are Ross and fur seals, along with the predatory leopard. Personal observation of nineteen leopard seals resting on ice floes off a penguin rookery in Arthur Harbor in 1975 indicated that only one had fed on penguins; all the others had consumed euphausiids. The total seal population numbers about seventeen million. The seals of the Southern Ocean clearly constitute a significant biomass with an important role in the Antarctic marine ecosystem.

Exploitation of Antarctic marine mammal resources began early in the nineteenth century with the harvesting of the southern fur seal. There was an initial harvest in the early 1800's, which

decimated many of the rookeries, followed by a second, but smaller, harvest about fifty years later that virtually exterminated the *Arctocephalus* species. The reappearance of fur seals in the 1930's, followed by their marked population growth during the 1940's and 1950's, and their reestablishment in former haunts, is as extraordinary as their initial persecution. Concurrent hunting of elephant seals for oil seriously depleted many rookeries, but was stopped for economic reasons. Harvesting was initiated in South Georgia with the establishment of shorebased hunting under license control. This has now been discontinued, and, as in the case of *Arctocephalus*, the southern elephant seal has reappeared throughout its range which extends from the Valdez Peninsula, Argentina, to as far south as the South Orkney Islands. While there is no commercial sealing today, controls have been established under the 1972 Convention for the Conservation of Antarctic Seals, 21 to prevent the recurrence of past practices in any future exploitation.

IV. THE ECOLOGICAL BASIS

Knox's description of the Antarctic Ocean as a ring of water moving easterly around Antarctica identifies one of the key elements of the Antarctic ecosystem. 22 The surging of the West Wind Drift through the narrow Drake Passage, combined with the strong circulation and nutrient rich upwelling, mark the surface waters of the Scotia Sea and the Weddell Drift as one of the most productive on earth. Hedgpeth categorized the region between the Antarctic Convergence and Antarctica as a well defined oceanic ecosystem.

He noted:

1. It is certainly a large system, indeed probably the largest marine ecosystem on the globe, and it is also a "major biotic province" (Hedgpeth, 1969(a)).

2. It is semi-closed, especially in the overlying water masses; the northward distribution of the deep benthos may constitute a sort of leakage of the system into deeper waters north of the convergence, but the most dynamic aspects of the system are the events within the overlying water masses south of the convergence.

3. It is an old system ... and, to judge by the diversity and abundance of the bottom fauna and the mid-water fish stocks, it has a much longer evolutionary history.

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5. ... [T]here is a sameness in the Antarctic ecosystem. The principal variation is that of the productivity; that is, productivity is greater in certain regions within the boundaries than in others, but most of the taxonomic components are circumpolar in distribution.

6. The quantitative and qualitative features of the basic processes of the Antarctic system are obviously different from those of the adjacent systems, as demonstrated by the distribution of the dominant herbivore and key species of the system, *Euphausia superba*.

7. Until recent years, it appeared that the Antarctic ecosystem could not be disturbed by the activities of man, and almost complete removal of the blue whale does not seem to have upset or changed the system. However, recent proposals to harvest krill on as large a scale as possible ... and to resume intensive killing of seals may in time alter the pelagic phase of the Antarctic ecosystem. ... [T]here will undoubtedly be some unanticipated effect on a system in which man has previously had no significant ecological role.

Man has, in fact, twice interfered with the Antarctic ecosystem. In the early nineteenth century uncontrolled sealing nearly exterminated the widely distributed and populous southern fur seal, which had numbered in the millions. The second interference was the exploitation of the southern elephant seal which, while hunted less intensely than other seals, was seriously depleted in some parts of its range. As Hedgpeth points out, until man appeared there was no top predator in the Antarctic ecosystem, and while many animals fed on euphausiids, none preyed on the blue whale. Man has concentrated his efforts on the top trophic feeders of krill—seals, whales and, currently, fishes—with no visible impact upon the ecological system. Commercial harvesting of krill, however, could potentially have adverse impacts on marine mammals, fishes, birds and other krill-foraging organisms.

A far more subtle, and perhaps more difficult, problem to assess is the possible irreversible damage on the nutrient dynamics of the Antarctic marine ecosystem by the removal of vast quantities of krill. Green estimates that the annual predation on krill amounts to some 330 x 10^4 tons. Crabeater seals account for over 100 x 10^4 tons of that amount, while squid consume nearly as much. Current stocks of baleen whales take about 43 x 10^4 tons, and Antarctic


24. Id.

marine birds consume about $14.4 \times 10^6$ tons annually. Except for the guano deposited on land by birds, the bulk of the waste generated by krill-foragers is presently released into the sea as organic and inorganic nutrients which are recycled. These nutrients are important in the transfer of organic matter or energy at the ecosystem level.

Moiseev states that the phosphorus balance in sea water is fairly critical and may control the intensity of bioproductive processes. He estimates that fishing removes 300,000 tons of phosphorus annually from the ocean. Estimates of sustainable krill yield range from $70 \times 10^6$ to $150 \times 10^6$ tons per year—more than twice the existing fisheries. Thus, man's harvesting would accelerate the depletion of key nutrient elements from the Antarctic food chain and might adversely affect the normal regeneration of phytoplankton and zooplankton.

While upwelling raises massive amounts of nutrients to the ocean surface, regeneration in the euphotic zone during the austral spring is still necessary to account for the high observed levels of primary productivity. As Hedgpeth notes:

> [W]e have a paradox in the Antarctic seas: a rich, apparently highly productive plankton-pelagic system supporting (at least in the past) great populations of whales and millions of penguins, fishes, and seals, and possibly abundant intermediate populations of fishes and cephalopods, depending on the near-surface productivity and an apparently rich and obviously diverse bottom community that may have a very slow turnover and correspondingly low productivity. This suggests a loss from the overlying waters that is not recycled in the same time scale to this stable, long-lived, and possibly predominate necrophagous bottom community. What influence this potential nutrient resource of the deep Antarctic waters may have upon the abyssal benthos of other oceans remains to be determined, but the implication of such influence to waste disposal practices and other pollution sources in the Antarctic should not be overlooked.

V. CONCLUSION

Antarctica is the only land mass wherein there is no extractive industrial activities. This is not, however, because of a lack of mineral or hydrocarbon deposits. While areas of potential exploitive

value have been identified, normal exploratory work has been held back by economic, geographic and climatic factors. It is merely a matter of time before economic pressures and new techniques foster the necessary technology. When these activities occur on the continent, the ecological stresses of mineral and offshore oil extraction coupled with associated maritime requirements and new settlements will combine to drastically affect the Antarctic marine ecosystem.

These events pose a serious challenge to ecologists. Ecology, however, has tremendous amplitude, as is proven by its application in political, economic and social arenas. It has become more pragmatic and, in the evolution of ecosystem analysis, has focused on the development of models to simulate reality. Regardless of the direction it progresses, ecology is basically biology, therefore the emphasis must be on field observations and experiments, with related taxonomical verification. Thus, for the scientist, free access to the entire Antarctic assumes paramount importance during this time of increased ecological awareness.