BIRDS AS MARINE ORGANISMS: A REVIEW

DAVID G. AINLEY Point Reyes Bird Observatory Stinson Beach, CA 94970

ABSTRACT

Only 9 of 156 avian families are specialized as seabirds. These birds are involved in marine energy cycles during all aspects of their lives except for the 10% of time they spend in some nesting activities. As marine organisms their occurrence and distribution are directly affected by properties of their oceanic habitat, such as water temperature, salinity, and turbidity. In their trophic relationships, almost all are secondary or tertiary carnivores. As a group within specific ecosystems, estimates of their feeding rates range between 20 and 35% of annual prey production. Their usual prey are abundant, schooling organisms such as euphausiids and squid (invertebrates) and clupeids, engraulids, and exocœtids (fish). Their high rates of feeding and metabolism, and the large amounts of nutrients they return to the marine environment, indicate that seabirds are probably important components in pelagic ecosystems. As such they have been strongly affected by human fisheries; for example, decline in the size of Peruvian anchovy and South African sardine populations have led to tremendous reductions in associated bird numbers. Evidence indicates that seabirds could provide an understanding of fish stock dynamics prior to overexploitation by man.

RESUMEN

De 156 familias avícolas solamente 9 incluyen aves marinas. Estas aves están involucradas en los ciclos de la vida marina durante todos los aspectos de su vida excepto en el 10% del tiempo que pasan en los nidos. La distribución de estos organismos marinos está directamente afectado por las características del hábitat oceánico, tales como la temperatura del agua, salinidad, y turbulencia. En sus relaciones tróficas casi todas son carnívoras secundarias o terciarias. Como un grupo dentro de ecosistemas específicos, el cálculo de su porcentaje de alimentación fluctúa entre el 20 y 35% de la producción anual de presas. Sus presas comunes son bancos abundantes de organismos, tales como eufáusidos y calamares (invertebrados), y clupéidos, engráulidos y exocétidos (peces). Sus índices elevados de alimentación y metabolismo, y las grandes cantidades de nutrientes que retornan al ambiente marino, indican que las aves marinas son probablemente componentes importantes de los ecosistemas pelágicos. Así, han sido muy afectadas por el incremento de las pesquerías; por ejemplo, la reducción en el tamaño de las poblaciones de anchoveta peruana y de sardina surafricana ha contribuido a tremendas reducciones en el número de las aves

asociadas con esos peces. Se indica que el estudio de las aves marinas podría contribuir a comprender mejor la dinámica de las poblaciones de peces anterior a la sobreexplotación por el hombre.

BIRDS AS MARINE ORGANISMS: A REVIEW

As pointed out by Sanger(1972) and Ainley and Sanger (1979), otherwise comprehensive reviews of biological oceanography have said little or nothing about seabirds in spite of the fact that they are the most visible part of the marine biota. The reasons for this oversight are no doubt complex, but there are perhaps two major ones. First, because seabirds have not been commercially harvested to any significant degree, fisheries research, which supplies most of our knowledge about marine ecosystems, has ignored them. Second, because ornithologists have mostly studied seabird breeding behavior and biology, they, too, have discovered little about avian roles in marine ecosystems. The purpose of this paper, then, is to establish seabirds as bona fide marine organisms, review some of what we know about their marine biology, and encourage the idea that a more complete understanding of marine ecosystems will be attained by including studies of marine birds. In that my own research has been directed toward these goals, I will take this opportunity to summarize that work.

WHAT ARE SEABIRDS?

Avian taxonomists currently recognize about 156 existing families of birds, and only 9 of these are rather specialized as seabirds: the Speniscidæ (penquins), Diomedeidæ (albatrosses), Procellariidæ (petrels), Hydrobatidæ (storm-petrels), Pelecanoididæ (diving petrels), Phæthontidæ (tropicbirds), Sulidæ (Boobies), Fregatidæ (frigatebirds), Alcidæ (auks), and a few species (terns) of Laridæ (gulls and terns). Members of these families share the following characteristics: they derive all their food from the sea, they void virtually all their feces into the sea, and when individuals die they do so at sea. They are full-time participants of marine energy cycles. Because of these characteristics, and in spite of the fact that most birds can travel above the sea's surface instead of being confined to the water (as are fish or marine mammals) or that they have to spend some time on land to raise young, these birds should be recognized as true marine organisms. The time that they do spend away from the sea is in fact minimal. Using the Adélie Penguin

(*Pygoscelis adeliae*) as an example, and the data in Ainley (1978) and Ainley and DeMaster (in press), it can be calculated that a typical seabird spends about 85% of its time annually at sea during its breeding years; over its entire lifetime, it spends 90% of its time at sea. This assumes 6 years of breeding and a life span of 10 years. All of the time on land is devoted to breeding activities, mainly the incubation of eggs, and during these activities, seabirds rely entirely on fat reserves built up at sea. Some species that live much longer than Adélie Penguins and that breed every other year, for instance some albatrosses, probably spend even less time on land over the duration of their lives.

Oftentimes avian species that undertake even a small part of their life cycle at sea are also considered to be "seabirds." Included are species from 15 other families, principally the Gaviidæ (loons), Podicipedidæ (grebes), Pelecanidæ (pelicans), Phalacrocoracidæ (cormorants), Anatidæ (ducks and geese), Scolopacidæ (shorebirds), Stercorariidæ (skuas), Rynchopidæ (skimmers), and the majority of the Laridæ. It is from these groups that the general but rather misleading conception of a seabird is derived, the one shared by most people. The "sea gull" is the typical example. Such birds, like man, are based on land and from there undertake trips to sea or to terrestrial and freshwater habitats for food. They are involved only part time in marine energy cycles; and because they spend a third or more of their time on land, they remove energy from marine ecosystems that is not returned.

THE MARINE DISTRIBUTION OF SEABIRDS

Much has been written about the distribution of seabirds at sea, but the factors that affect occurrence are not well understood. Murphy (1936) was among the earliest writers to point out that around South America (since proved to be true elsewhere) some species were confined to the "blue" oceanic waters offshore whereas others occurred in more turbid coastal waters. From there, through the work of many authors (for example Wynne-Edwards 1935; Jehl 1973) the idea has arisen that seabirds occur in concentric zones spaced outward from continents and islands. This view explains the occurrence of some species, especially the coastal ones, most of which are only part-time marine organisms, but it is biased towards the land orientation of man and the sea gull type of seabird. It is further biased to the breeding season (10% of a seabird's life) when birds must return repeatedly to their nests.

We are beginning to understand that the distribution of seabirds is affected by some of the same oceanographic factors that affect the distributions of what are thought of as typical marine organisms, such as fish. One such factor is water temperature. For instance, when the California Current weakens, as it periodically does (Sette and Isaacs

1960), California waters become warmer and species of warmwater birds move farther north than they normally occur in the eastern North Pacific (Ainley and Lewis 1974; Ainley 1976). Since the California Current moves parallel to the coast and displaces warmer waters westward, warmwater bird species also move closer to shore in such circumstances. This concept that birds live where their preferred water occurs is complicated by their abilities to fly over, but still technically occur in, unsuitable waters. For instance, Leach's Storm-Petrels (Oceanodroma leucorhoa) prefer warm oceanic waters, but because the only suitable West Coast breeding sites in the Pacific are coastal islands they must cross cold waters of the California Current as they fly between feeding and breeding areas (Ainley et al. 1975; Wiens and Scott 1975; Ainley 1976).

It is rather amazing, in light of the present land-oriented zonal conception of seabird distribution, that on two cruises from North America to the New Zealand sector of Antarctica, during which seabirds and sea temperatures were monitored continuously, with a temperature range of 28° to 0°C, 1-2°C changes brought about a consistent turnover of 30-70% (\bar{x} about 45%) of bird species (Ainley and co-workers, work in progress). Some species were very precisely related to certain temperature ranges, i.e. stenothermal, whereas others occurred over larger ranges, i.e. eurythermal. This same pattern is evident in other groups of marine organisms.

Brown et al. (1975) recently tried to correlate seabird occurrence in Chilean fjords with not just temperature but also salinity profiles. Pocklington (1979) attempted the same for seabirds in the Indian Ocean. They found several good correlations. It is rather easy to understand how seabirds might sense temperature changes, but it is not easy to visualize how they might sense changes in salinity, even though they do drink seawater. It is just that, as far as we know, they do not fly about continuously sampling salinity as they would be able to "monitor" temperature. Brown et al. and Pocklington tried to explain the correlation as an indirect one involving the temperature/ salinity profiles of the preferred prey of different bird species. The opportunistic and unspecialized feeding habits of most seabirds, as reviewed below, would also argue against this for all but exceptional species.

Other physical oceanographic factors can also affect seabird occurrence. For instance, some species that employ certain methods of food capture live only where conditions favor those methods. The prime example is given by birds that plunge for food (Ashmole 1971), principally the boobies and tropicbirds. Spotting prey as deep as 10 m or more below the surface while flying 15 m or more above it, and thereafter using only momentum from a "fall" to reach the prey, requires water of high clarity. For this reason deep plungers occur only in tropical/subtropical waters where low phytoplankton standing stocks (compared to those in cooler waters) result in very clear water (Ainley 1977). Supporting this is the fact that deepplunging species occur most consistently off California during the later summer and fall when the annual marine cycle is in its oceanic period (Ainley 1976). At that time water temperatures reach the subtropical range and phytoplankton standing stocks are lowest for the year (Bolin and Abbott 1963).

TROPHIC RELATIONSHIPS

Marine biologists, in their discussions of food webs, rarely make specific mention of marine birds, but the latter are part of what they refer to as "primary," "secondary," and "tertiary carnivores" or, in other words, the "third trophic level" (see Steele 1974), or "other carnivores" (Cushing 1975), or "nekton" (Sverdrup et al. 1942). In their review of trophic relations among marine birds of five oceanographic domains in the North Pacific. Ainley and Sanger (1979) found that 77% of seabird species were predators at the secondary and tertiary carnivore levels. Most of the remainder (21%) were scavengers, which still put them in the third trophic level. Only 2%, in that they feed principally on other species of seabirds, were in the fourth trophic level. Seabirds thus by and large occupy the same position in marine food webs as do the larger fish, mammals, and man.

The crux of the matter is how important are marine birds as predators relative to other occupants of the third trophic level in marine food webs. Quite a bit is known about the species of prev eaten by seabirds (e.g. review by Ainley and Sanger 1979), but little is known about their food consumption rates to compare with other upper trophic level predators. Some estimates though have been attempted. Wiens and Scott (1975), by computer simulation, estimated that Common Murres (Uria aalge) consumed 11% of pelagic fishes produced annually in Oregon's neritic zone. They also estimated that four seabird species off Oregon alone consumed annually about four times the tonnage of anchovies (Engraulis mordax) caught commercially each year in the northern permit area (Point Conception to Oregon) during the years 1966 to 1971. They also figured that 22% of the annual pelagic fish production off Oregon was eaten by seabirds. Furness (1978), using a different computer simulation, estimated that within 45 km of breeding colonies in the Shetland Islands, seabirds consumed between 20 and 35% of annual food-fish production. It has been calculated that off Peru during the height of the commercial anchovy (Engraulis ringens) harvest in the late 1960's, birds consumed 2.5×10^6 metric tons of the fish or as much as a quarter of what was harvested commercially (Idyll 1973). That commercial harvest, of course, was by far the largest in the world. Laws (1977) estimated that in the Antarctic pelagic ecosystems birds and seals equal each other in biomass, an amount for each that is about half that of whales. Prévost (1976) figured that all three groups consumed about equal amounts of euphausiids, about 30-40 $\times 10^6$ tons each. Both authors agreed, however, that more information was needed. More data are also needed elsewhere, but with seabird food consumption estimates of such high magnitudes, it is surprising that fishery and marine biologists, and ornithologists, have not paid more attention to the seemingly significant impact that marine birds may have in pelagic ecosystems.

High rates of food consumption and very high metabolic rates in turn mean that seabirds, through production of excrement, may also play a significant role in the recycling of nutrients and energy in pelagic ecosystems. This, as pointed out by Wiens and Scott (1975), may be especially true in areas where upwelling is not strong but where some species of seabirds are abundant. There is, in fact, compared to knowledge on food consumption, even less known about the role seabirds play in nutrient recycling. Sanger (1972) estimated that seabirds in the Central Subarctic Domain (see Dodimead et al. 1963) consumed 278×10^3 tons of food and voided up to $74 \times$ 10³ tons of feces per year. Wiens and Scott (1975) estimated that off Oregon four seabird species, with numbers fluctuating seasonally from about 1.2×10^5 to 4.4×10^6 birds, consumed about 62,500 metric tons of fish, or 7.56 \times 10¹⁰ kcal of food, and returned 2.32 \times 10¹⁰ kcal to the system each year in their feces. They were not able to equate kcal of guano to nutrients. On an artificial platform in South Africa, less than 240,000 seabirds produced, at a minimum, an average (1941-1965) 777 metric tons of guano per year, the composition of which included 16% nitrates, 9% phosphates, and 4% potash (Rand 1963; Berry 1975).

In the types of prey they feed on, most seabirds do not appear to specialize. In the review by Ainley and Sanger (1979), it was evident that certain prey over and over again predominated in the diets of different marine birds of the eastern North Pacific. These prey included species of Euphausia, Loligo, Clupea, Engraulis, and Sebastes. As specific examples, 43% of prey eaten by four Oregon seabirds (Wiens and Scott 1975) and 80 to 95% of prev eaten by three Peruvian "guano birds" was Engraulis (Idyll 1973); 23% of prey eaten by seven seabirds in the central tropical Pacific was exocoetids (Ashmole and Ashmole 1967); somewhat more than 50% and often more than 75% of prey eaten by six species nesting at the Farallon Islands was Sebastes (Ainley unpublished); 26 to 85% of prey eaten by nine species in the Farne Islands was Ammodytes (Pearson 1968); 19 to 85% of prey eaten by three South African "guano birds" was Sardinops (Crawford and Shelton 1978); and 50 to 90% of prey eaten by most Antarctic penquins and petrels was Euphausia (Emison 1968; Mougin 1975). There is thus great overlap in what they eat, and it seems that whatever prey species is most readily available predominates in seabird diets. "Readily available" prey, it would seem, are those species that tend to occur in dense concentrations and within 70 m of the surface. The latter seems to be a typical maximum feeding depth for diving seabirds (Kooyman 1974). Offsetting the lack of specialization, seabird species differ in their feeding by the size of their prey, which relates to predator bill size (Ashmole and Ashmole 1967; Bedard 1969), and by the habitat and method of food capture (Ashmole 1971; Ainley 1977, unpublished).

SEABIRDS AND FISHERIES

The prey that seabirds prefer, largely because of availability, are often sought in pelagic fisheries for the same reason, or they are also the prey of pelagic predatory fish that in turn are fished for by man. Since the time that man first established pelagic fisheries, he often looked for feeding flocks of birds to tell where the sought-after fish were located. Direct or indirect "competition" for fish between birds and man is thus theoretically possible, and the fact that both birds and man are capable of tremendous fish harvest makes an interrelationship likely. Whether or not the fish harvest by birds can affect or has affected that by man, or vice versa, must be considered on a case-by-case basis.

There is little doubt that the crash of Peruvian anchovy populations resulted in the crash of seabird populations from 30 to 1 million individuals. As summarized by Idyll (1973), overfishing in conjunction with natural environmental stress was probably responsible for the reduction in fish. It is also fairly evident that in the several years before the ultimate crash, intense fishing pressure resulted in depressed bird populations, or at least prevented recovery of bird numbers from an earlier natural reduction.

The story of the Peruvian anchovy remains the outstanding, relatively unequivocal example of a human fishery out-competing birds for fish. Few other examples are as conclusive. Another example though is given by Crawford and Shelton (1978), who equated seabird numbers, guano production, fish availablity, and fishery catches of pelagic species (mainly Sardinops) off South Africa from 1940 to the present. Beginning about 1965 the fishery began a sharp decline from which it has not recovered, and with it the bird populations declined as well. The authors concluded that the fishery was ultimately responsible for the decline in bird numbers. In a less conclusive example, Ainley and Lewis (1974) hypothesized that the disappearance of Pacific sardines (Sardinops coerulea) prevented recovery in several California populations of seabirds previously reduced by unrelated factors. In this case, one major question involved the extent to which overfishing played a role in the disappearance of these fish (Cushing 1975). Other instances of fishing impact on seabird prey, and ultimately on the seabirds themselves, are in the realm of discussions over the potential for such interaction. For example, Furness (1978) and Bailey and Hislop (1978) recently presented arguments, pro and con, over whether fisheries in the northeastern Atlantic could have depressing effects on seabird populations. The only clear conclusion from this particular instance was that more information was needed, particularly on seabirds.

There is also controversy over whether fishery harvest of predatory fish, by reducing species that naturally compete with seabirds for food, would result in increased availability of prey for birds and other predators. Few unequivocal examples are available. Furness (1978) and Bailey and Hislop (1978) presented arguments on the potential for this situation in the North Atlantic, and they concluded that such an interrelationship is theoretically possible. On the other hand, several authors (e.g. Sladen 1964; Conroy 1975; Laws 1977) have proposed that increases in southern fur seals (Arctocephalus gazella) and Adélie and Chinstrap Penguins (P. adelie and P. antarctica) in the Scotia Sea area are the result of overfishing on baleen whales, which formerly "competed" with seals and birds for Antarctic krill (Euphausia superba). The reduction in whales, in fact, has led some fisheries experts (e.g. Gulland 1970) to propose that a large "surplus" krill stock now exists and should be harvested.

There are also potential interrelationships between fisheries and seabirds that are even more indirect. A dramatic decline of Thick-Billed Murres (Uria lomvia) in West Greenland waters has been attributed in large part to heavy mortality due to drowning in drift nets set for salmon (Salmo salar; Evans and Waterston 1978). Ripley (1976) indicated the potential for such an interaction in the North Pacific as well. An increase in Northern Fulmar populations (Fulmarus glacialis) in the North Atlantic during this century has been attribued to an increase in fish offal resulting from fisheries, largely on demersal species (Fisher 1952, 1966). Others (e.g. Brown 1970; Bailey and Hislop 1978) argue against such an explanation for the increase. As in other controversies, it is clear that information on seabird trophic and energetic relationships in marine ecosystems is inadequate.

SUMMARY AND CONCLUDING REMARKS

Established in this review are the facts that seabirds are marine organisms and that they can be important predators on marine vertebrate and invertebrate prey species. Potentially, they may play another important role in pelagic ecosystems, that role being in the recycling of

AINLEY: BIRDS AS MARINE ORGANISMS: A REVIEW CalCOFI Rep., Vol. XXI, 1980

nutrients. In light of these real and potential impacts, the fact that marine ecologists generally overlook seabirds is surprising. Because birds are so visible, they should be of use in helping us to understand marine ecosystem interactions. Indeed, and rather surprisingly, a marine biologist, Green (1971), on the basis of a computer simulation, recently suggested that the study of seabirds may provide a sensitive and relatively inexpensive means to monitor ecosystem state in the Antarctic. Using much more complete data, and an interaction less extensive than an entire ecosystem, Crawford and Shelton (1978), fisheries research biologists, proposed that seabirds "have value in providing an understanding of fish stocks prior to exploitation and as indicators of the current state of the resources."

It was pointed out in this review that overharvest of a fish stock can depress seabird populations. It would be unusual if other predator populations were not affected. The recent history of the Peruvian anchovy made this clear, at least regarding birds, and the potential exists or has existed for similar interrelationships elsewhere. There are certain species of marine fish and invertebrates that, because of their abundance, availability, and suitability as food, are important prey for many predators. Of these predators, only man has the power to "manage" the resource. Especially in the cases of "universal prey" species, management from an ecosystem perspective, rather than that of the single stock sustainable yield approach, would seem to be the wisest course of action. In that way the impact of the fishery elsewhere in the food web may be lessened before it is too late to do so.

ACKNOWLEDGMENTS

I wish to thank Alec MacCall for the opprtunity to participate in this CalCOFI symposium, for which this paper was prepared, and Judy Bausor and David B. Clark for help in its preparation. This is contribution No. 188 of the Point Reyes Bird Observatory.

LITERATURE CITED

- Ainley, D.G. 1976. The occurence of seabirds in the coastal region of California. Western Birds 7:33-68.
- . 1977. Feeding methods of seabirds; a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. P. 669-686 In G.A. Llano (ed.), Adaptations within Antarctic ecosystems. Gulf Publ. Co., Houston.
- . 1978. Activity patterns and social behavior of nonbreeding Adélie Penguins. Condor 80:138-146.
- Ainley, D.G., and D.P. DeMaster. (in press) Survival and mortality in a population of Adélie Penguins. Ecology.
- Ainley, D.G., and T.J. Lewis. 1974. The history of Farallon Island marine bird populations 1854-1972. Condor 76:432-446.
- Ainley, D.G., S. Morrell, and T.J. Lewis. 1975. Patterns in the life histories of storm-petrels on the Farallon Islands. Living Bird 13: 295-312.

- Ainley, D.G., and G.A. Sanger. 1979. Trophic relationships of seabirds in the northeastern Pacific Ocean and Bering Sea. In J.C. Bartonek and D.N. Nettleship (eds.), Conservation of marine birds in northern North America. U.S. Dept. Inter., Wildl. Res. Rept. 11.
- Ashmole, N.P. 1971. Seabird ecology and the marine environment. P. 223-286 In D.S. Farner, J.R. King, and K.C. Parkes (eds.), Avian biology, Vol. I, Academic Press. N.Y.
- Ashmole, N.P., and M.J. Ashmole. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. Peabody Mus. Nat. Hist., Yale Univ. Bull. 24:1-131.
- Bailey, R.S., and J.R.G. Hislop. 1978. The effects of fisheries on seabirds in the northeast Atlantic (abstract). Ibis 120:104-105.
- Bédard, J. 1969. Adaptive radiation in Alcidæ. Ibis 111:189-198.
- Berry, H.H. 1975. History of the guano platform on bird rock, Walvis Bay, South West Africa. Bokmakierie 27:60-64.
- Bolin, R.L., and D.P. Abbott. 1963. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Oceanic Fish. Invest. Rep. 9:23-45.
- Brown, R.G.B. 1970. Fulmar distribution: a Canadian perspective. Ibis 112:44-51.
- Brown, R.G.B., F. Cooke, P.K. Kinnear, and E.L. Mills. 1975. Summer seabird distributions in Drake Passage, the Chilean fjords and off southern South America. Ibis 117:339-356.
- Conroy, J.W.H. 1975. Recent increases in penguin populations in the Antarctic and Subantarctic. P. 321-336 In B. Stonehouse (ed.), The biology of penguins, Macmillan, London.
- Crawford, R.J.M., and P.A. Shelton. 1978. Pelagic fish and seabird interrelationships off the coast of southwest and South Africa. Biol. Conser. 14:85-109.
- Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge.
- Dodimead, A.J., F. Favorite, and T. Hirano. 1963.Review of oceanography of the subarctic Pacific region. Int. N. Pacific Fish. Comm. Bull. 13:1-195.
- Emison, W.B. 1968. Food preferences of the Adélie Penguin at Cape Crozier, Ross Island. P. 191-212. In O.L. Austin, Jr. (ed.), Antarctic bird studies, Ant. Res. Ser., Vol. 12, Amer. Geophys. Union, Wash., D.C.
- Evans, P.G.H., and G. Waterston. 1978. The decline of the Brunnich's Guillemot in West Greenland (abstract). Ibis 120:131-132.
- Fisher, J. 1952. The fulmar. Collins, London.
- . 1966. The fulmar population of Britain and Ireland, 1959. Bird Study 13:5-76.
- Furness, R.W. 1978. Shetland seabird communities: the possible impact of new fishing techniques (abstract). Ibis 120:108-109.
- Green, K.A. 1971. Simulation of the pelagic ecosystem of the Ross Sea, Antarctica: a time varying compartmental model. PhD Dissertation, Texas A&M Univ., College Station.
- Gulland, J.A. 1970. Fish resources of the ocean. FAO, Rome.
- Idyll, C.P. 1973. The anchovy crisis. Sci. Amer. 228:22-29.
- Jehl, J.R. 1973. The distribution of marine birds in Chilean waters in winter. Auk 90:114-135.
- Kooyman, G.L. 1974. Behaviour and physiology of diving. P. 115-138 In B. Stonehouse (ed.), The biology of penguins, Macmillan, London.
- Laws, R.M. 1977. The significance of vertebrates in the Antarctic marine ecosystem. P. 411-438 *In* G.A. Llano (ed.), Adaptations within Antarctic ecosystems, Gulf Publ. Co., Houston.
- Mougin, J.L. 1975 Écologie comparée des Procellariidæ Antarctiques et Subantarctiques. Comité National Francais de Récherches Antarctique, No. 36:1-195.

AINLEY: BIRDS AS MARINE ORGANISMS: A REVIEW CalCOFI Rep., Vol. XXI, 1980

Murphy, R.C. 1936. Oceanic birds of South America. Macmillan, N.Y.

- Pearson, J.H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.
- Pocklington, R. 1979. An oceanographic interpretation of seabird distributions in the Indian Ocean. Mar. Biol. 51:9-21.
- Prévost, J. 1976. Population, biomass, and energy requirements of Antarctic birds; attempted synthesis. SCAR/SCOR Conf. Living Marine Resources of the Southern Oceans. Woods Hole (mimeo).
- Rand, R.W. 1963. The biology of guano-producing seabirds. 5. Composition of colonies on the South West African islands. Div. Sea Fish., Invest. Rep. No. 46. Pretoria.

Ripley, S.D. 1976. The view from the castle. Smithsonian 6(1):6.

Sanger, G.A. 1972. Preliminary standing stock and biomass estimates of seabirds in the subarctic Pacific region. P. 589-611 In A.Y. Takenouti et al. (eds.), Biological oceanography of the northern North Pacific Ocean, Idemitsu Shoten, Tokyo.

- Sette, O.E., and J.D. Isaacs, eds. 1960. The changing Pacific Ocean in 1957 and 1958. Calif. Coop. Ocean. Fish. Invest. Rep. 7:13-217.
- Sladen, W.J.L. 1964. The distribution of Adélie and Chinstrap Penguins. P. 359-365 In R. Carrick, M.W. Holdgate, and J. Prévost (eds.), Biologie antarctique, Hermann, Paris.
- Steele, J.H. 1974. The structure of marine ecosystems. Harvard Univ. Press, Cambridge.
- Sverdrup, H.E., M.W. Johnson, and R.H. Fleming. 1942. The oceans; their physics, chemistry, and general biology. Prentice-Hall, Englewood Cliffs, New Jersey.
- Wiens, J.A., and J.M. Scott. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77:439-452.
- Wynne-Edwards, V.C. 1935. On the habits and distribution of the birds on the North Atlantic. Boston Soc. Nat. Hist., Proc. 40:223-340.