terns from Scandinavia and eastern Canada fly to and from waters off Australia, New Zealand, and the Pacific (**Figure 3**). The shortest, round-trip flight to the Pacific exceeds 50 000 km. These birds can live up to 25 years, indicating that the lifetime migration distance could exceed 1 million km.

Murres, murrelets, auks, auklets, puffins, and guillemots (Alcidae) The 22 species of Alcids, confined to the northern hemisphere, have dispersive post-breeding movements. Compared with other seabirds, their dispersal distances are short (see Morphological Adaptations and Flight Behavior). The primary reasons are: (1) their very high wing loading and, thus, inefficient flight; (2) they are highly adapted pursuit divers that can exploit a range of subsurface habitats; and (3) they occur in waters of the Arctic and boundary currents where prey are abundant. In summary, long distance flights by Alcids are impractical, and are not required. This life history trait is like that of penguins, another group highly adapted for pursuit diving, but is in marked contrast to the movements of other seabirds with poorer diving abilities. Alcids with the longest distance dispersal are the little auk (*Alle alle*), tufted puffin (*Fratercula cirrhata*), horned puffin (*F. corniculata*), Atlantic puffin (*F. arctica*), and parakeet auklet (*Cyclorrhynchus psittacula*). Some individuals representing these species disperse up to 1000 km or more into the pelagic waters of the North Atlantic and North Pacific.

See also

Alcidae. Laridae, Sternidae and Rynchopidae. Pelecaniformes. Phalaropes. Procellariiformes. Seabird Conservation. Seabird Foraging Ecology. Seabird Overview. Seabird Population Dynamics. Seabird Reproductive Ecology. Seabird Responses to Climate Change. Seabirds and Fisheries Interactions. Seabirds as Indicators of Ocean Pollution. Sphenisciformes.

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SEABIRD OVERVIEW

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Seabirds or marine birds are species that make their living from the ocean. Of the approximately 9700 species of birds in the world, about 300–350 are considered seabirds. The definition as to what constitutes a seabird differs among authors, but generally includes the penguins (Sphenisciformes), petrels and albatrosses (Procellariiformes), pelicans, boobies and cormorants (Pelicaniformes), and the gulls, terns and auks (Lariformes) (**Table 1**). Sometimes included are loons (Gaviiformes), grebes (Podicipediformes), and those ducks that forage at sea throughout the year or during the winter (Anseriformes). Bird species that are restricted to obtaining their prey by wading along the margins of the sea, such as herons or sandpipers, are not included.

The distribution of types of seabirds shows striking differences between the northern and southern hemispheres, particularly at high latitudes. Best known are the restrictions of the auks (Alcidae) to

Table 1 Distribution and species richness of families of seabirds

Common name of family	*Family*	*Total number of species*	*Number of species nesting south of 30°S*	*Number of species nesting between 30°S and 30°N*	*Number of species nesting north of 30°N*	*Period of sea use*	*Flight type (flapping, flap-gliding or soaring)*	*Foraging region (primarily neritic or oceanic)*
Penguins	Spheniscidae	18	16	2	0	Year-round	Wing-propelled swimming	Mostly neritic
Loons or divers	Gaviidae	5	0	0	5	Migration and winter	Flapping	Neritic
Grebes	Podicipedidae	21	12	13	8	Migration and winter	Flapping	Neritic
Albatrosses	Diomedeidae	17	14	3	3	Year-round	Soaring	Oceanic
Petrels and shearwaters	Procellariidae	66	44	20	15	Year-round	Flap-gliding	Mostly oceanic
Storm petrels	Hydrobatidae	20	9	11	10	Year-round	Flap-gliding	Mostly oceanic
Diving petrels	Pelecanoididae	4	4	1	0	Year-round	Flapping	Mostly neritic
Frigate birds	Fregatidae	5	2	5	2	Year-round	Soaring	Mostly oceanic
Tropic birds	Phaethontidae	3	2	3	3	Year-round	Flapping, with some soaring	Oceanic
Gannets and boobies	Sulidae	9	6	7	5	Year-round	Flapping, with some gliding	Both neritic and oceanic
Pelicans	Pelecanidae	8	4	7	5	Most species fresh water	Flapping, and some gliding	Neritic
Cormorants	Phalacrocoracidae	28	20	17	10	Most species year-round	Flapping	Neritic
Sea ducks	Anatidae (part)	19	5	0	11	Migration and winter	Flapping	Neritic
Phalaropes	Scolopacidae	3	0	0	3	Migration and winter	Flapping	Neritic
Skuas, gulls, terns, noddies and skimmers	Laridae	100	36	49	59	Most species year-round	Flapping	Mostly neritic; some tropical terns and noddies oceanic
Auks	Alcidae	23	0	2	22	Year-round	Flapping	Neritic

(Adapted with permission from Harrison 1983.)

the northern hemisphere, and the penguins (Spheniscidae), diving petrels (Pelecanoididae), and most species of albatrosses (Diomedeidae) to the southern oceans. There are also many more species of shearwaters and petrels (Procellariidae) that nest in the southern hemisphere than in the north.

The cost of flight varies greatly among seabird species. Some groups, such as diving petrels and auks, have heavy wing loading and require flapping flight that is relatively expensive. Others have low wing-loading and are able to make use of wind energy and soar extensively, flapping only occasionally. These species, including albatrosses and many of the petrels, can travel relatively long distances with minimal energy expenditure. Between these extremes are birds that alternate flapping flight with soaring or gliding. These species-specific differences in cost of flight probably had profound effects on the types of birds that were able to survive in different climate domains of the oceans. Seabirds in the southern hemisphere tend to be efficient fliers that cover large areas in search of food by using the wind to enhance their soaring flight. These birds may range up to 5000 km from their colonies in search of prey. In contrast, in the northern hemisphere, most species of seabirds depend on relatively expensive flapping flight, and forage within 100 km or less of their colonies. Costs of flight have also clearly had a strong effect on the types of foraging techniques and chick-provisioning routines used by different groups of seabirds.

During the breeding season, most seabirds nest in dense colonies on predator-free islands or on inaccessible cliffs. A few nest at low densities or as scattered individuals. All seabirds provision their young at the nest, and feed them at intervals from once every few hours to up to 15 days, depending upon the species. Because of their need to periodically return to their nests with food, seabirds are good examples of central place foragers.

The life history patterns of seabirds include long life spans, delayed reproduction, and small numbers of young produced in any one year. Interannual survival for adult birds, where estimated, is generally thought to be in the order of 90–95% or better. In contrast, survival through the first winter after fledging may be below 50%. The age of first reproduction varies between species as a function of expected life span. Most seabirds do not commence breeding until they are at least 3 or 4 years old, and some of the albatrosses delay the year of first breeding until they are 15 years of age. Clutch size is small. Most oceanic foragers lay only one egg per year. Some species of neritic foragers lay clutches of two or three eggs, with cormorants laying clutches of six or more eggs. Clutch sizes for species nesting in productive upwelling zones may be larger than is typical for their taxonomic relatives in less productive areas.

For most species of seabirds, reproductive rates are low and, except for those species adapted to upwelling regions, there is little opportunity to increase reproductive output in years of high prey abundance. In some ocean regions, years with successful reproduction are the exception. In those cases, it is likely that a few good years and a small percentage of particularly able parents may account for the majority of the young produced. Reproductive success improves with experience, and for many species mate retention from one year to the next is high, with diminished reproductive success associated with the changing of mates. Thus, high survival rates for adult birds are critical to maintain stable populations.

Seabirds obtain their prey by a wide variety of methods including pursuing fish and plankton at depths as great as 300 m or more, seizing prey on the wing from the surface of the ocean, and stealing prey from others (**Figure 1**). Prey most commonly taken by seabirds includes small fish and squid, and large zooplankton such as euphausiids and amphipods. A few seabird species specialize on copepods. The use of gelatinous zooplankton is known for albatrosses, petrels, and auks. Gelatinous

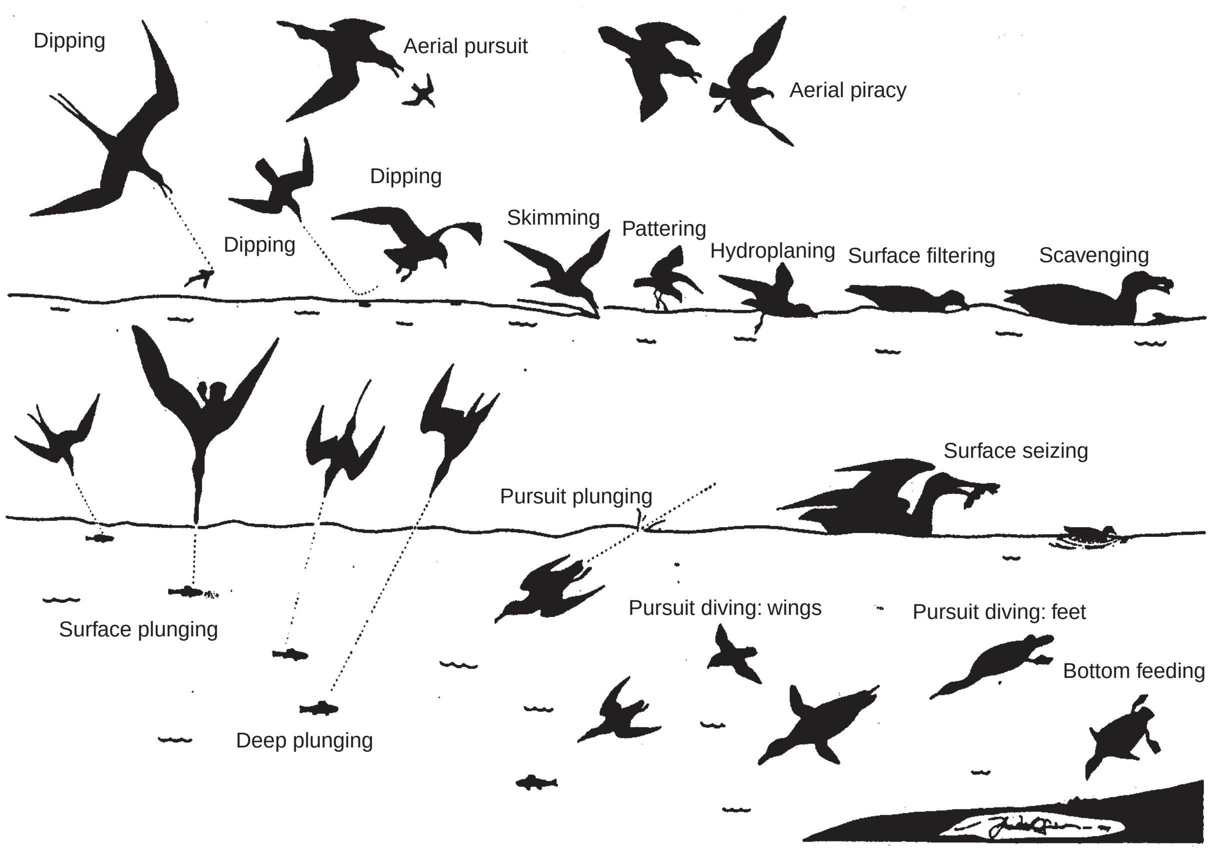

Figure 1 Seabird feeding methods. The types of birds silhouetted in the drawing from left to right: *top*, skua pursuing a phalarope; skua pursuing a gull; *second row*, frigate bird, noddy, gull, skimmer, storm petrel, prion, Cape petrel, giant petrel; *third row*, tern, pelican, tropic bird, gannet, albatross, phalarope; *underwater*, shearwater, murre, diving petrel, penguin, cormorant, a sea duck. (Reproduced with permission from Ashmole, 1971.)

zooplankton may be more commonly consumed by other species than is appreciated, as remains of gelatinous species are difficult to detect in stomachs or preserved food samples.

Foraging methods used by seabirds vary with the density of prey and may also vary with water clarity. Plunge diving for prey and surface seizing of prey are particularly common in clear tropical waters. In more turbid and prey-rich polar and subpolar waters, many seabirds pursue their prey beneath the sea. In the Southern Ocean, where continental shelf regions are deep and limited in area, most seabirds other than penguins are efficient fliers that can cover vast areas in search of patchy prey. In the northern hemisphere, most species of seabirds forage over broad, shallow continental shelves where interactions between currents and bathymetry result in predictable concentrations of prey. These prime foraging locations are often close to shore, where tidal currents create convergence fronts and other physical features that force aggregations of zooplankton upon which small fish forage. Frontal systems associated with shelf edges are important in both hemispheres.

Marine birds are assumed to play only an insignificant role in oceanic carbon cycling. However, where their consumption has been examined, they have been found to take significant amounts of prey. In the southeastern Bering Sea, seabirds have been estimated to consume between $0.12\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ and $0.29\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ depending on the region of the shelf and the year. Since the seabirds are foraging between the second and third trophic levels, this consumption accounts for between 12 and $29\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ of the $200–400\,\mathrm{g\,C\,m^{-2}\,a^{-1}}$ of primary production over the shelf. Where estimates have been made of the proportion of secondary production consumed, seabirds have been found to take between 5 and 30% of local secondary production (**Table 2**). In the North Sea, seabird consumption of sand eels is in the order of 197 000 tonnes. Over half of this consumption is concentrated near the Shetland Islands. However, seabird consumption of sand eels in the North Sea as a whole is small compared with the overall production of sand eels or the take by the industrial fishery which focuses on offshore banks. Recent calculations of the fraction of total exploitable stocks in the eastern Bering Sea that are consumed by seabirds suggest that about 3% of walleye pollock and 1% of herring are taken by birds. Recent shifts in the diets of shearwaters in the eastern Bering Sea could mean that the estimate for pollock is low by a factor of two or more. In the North Pacific, depending on the region of concern, estimates of prey consumption by marine birds vary between $0.01\,\mathrm{t\,km^{-2}}$ and $1.72\,\mathrm{t\,km^{-2}}$ for the summer months of June, July and August.

The effects of fisheries on seabirds are almost always greater than the effect of birds on fisheries. Seabirds have been used by fishers as indicators of the presence of large predatory fish. Commercial fishing activity frequently provides offal and discards to seabirds, and a number of seabird populations have benefited from this supplemental source of food. Indeed, juvenile albatrosses in the North Pacific may be experiencing increased winter survival rates thanks to the availability of discards and offal from commercial fisheries. However, seabirds attracted to fishing vessels do not distinguish between discarded fish and baited hooks. Between 1990 and 1994, $>30\,000$ Laysan albatrosses and

Table 2 Community energetics models of fish consumption by seabirds (modified from Hunt *et al.,* 1996[a])

Location	*Estimated % pelagic fish production consumed*	*Major consumers*	*Major prey species*
Oregon Coast	22	Shearwaters, storm petrels, cormorants, murre	Northern anchovy, juvenile hake
Foula, Shetland Islands	29	Fulmar, murre, shag, puffin	Sand eels
North Sea	5–8	Fulmar, gulls, terns, murre, puffin	Sand eels
North Sea	5–10	Fulmar, gannet, shag, gulls, kittiwake, terns, razorbill, murre, puffin	Sand eels
Saldanha Bay, South Africa	29	Penguin, gannet, cormorant	Pilchard
Benguela Region	6	Gannet, cormorant	Pilchard
Vancouver Island, British Columbia[b]	11, 17, and 21	Shearwater, murre	Juvenile herring

[a]Hunt GL, Barrett RT, Joiris C and Montevecchi W (1996) Seabird/fish interactions: an introduction. *ICES Coop. Res. Rep.* 216: 2–5.

[b]Logerwell EA and Hargraves NB (1997) *Seabird Impacts on Forage Fish: Population and Behavioral Interactions*. Proceedings of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program AK-SG-97-01.

20 000 black-footed albatrosses were killed on long-lines off Hawaii. In the southern hemisphere, up to 20 000 shy albatrosses and 10 000 wandering albatrosses are entangled annually in the blue-fin tuna long-line fishery. Approximately 10% of the world population of wandering albatrosses is killed annually. A loss of this magnitude cannot be sustained in a species that has a life history strategy that depends on extraordinarily high annual rates of adult survival. Not surprisingly, populations of 6 of 17 species of albatross are now declining rapidly.

Seabirds have proven to be useful indicators of changes in marine ecosystems. Because of their position at the top of marine food chains, they tend to accumulate a number of pollutants. For example, DDE, which concentrates in lipids, can result in eggshell thinning in some species. Eggshell thinning in various pelican and cormorant populations was one of the first indicators that DDE was present in certain coastal waters. Likewise, recent work has shown seabirds bio-accumulate mercury and other heavy metals. Seabirds also provide information about the status of populations of prey on which they depend. Changes in prey abundance are reflected by changes in annual rates of production of young, or in extreme cases, changes in seabird population size. Climate-driven changes in prey abundance, at scales from years to hundreds of years, are reflected by changes in seabird distribution, abundance, and reproductive output. Although it has been a goal of a number of studies, the ability to estimate the standing stocks of prey populations based on indices derived from seabirds has yet to be accomplished. Calibration of the responses of the seabirds to shifts in prey abundance has been difficult to achieve.

The most serious threats to the conservation of seabirds are those that result in the deaths of adult birds, particularly those individuals that have been successful breeders. Seabird populations can usually recover from a single instance of mortality, but chronic elevated rates of mortality are devastating. Seabirds are extremely vulnerable to predation in their colonies. Thus, the presence of foxes, cats, rats, and other introduced predators on islands where seabirds nest is of great concern. Past introductions of predators have resulted in the extirpation of nesting birds, and the removal of predators has resulted in their return. Also of great concern is the annual drowning of high numbers of seabirds in gill nets and on long-lines. The situation with respect to albatrosses and other large procellariiform birds is of particular concern, as these birds require long adult life spans to insure the production of sufficient young to maintain stable populations. Oil spills can have devastating local effects, but if the resulting pollution is not long-lasting, populations are likely to recover. Chronic pollution by oil or other chemicals may have both lethal and sublethal effects, and can damage populations of seabirds over time. Competition for resources such as nesting space or food is occasionally of concern. Development of islands and beaches affects a few populations of seabirds. Likewise there are a few instances where fisheries may be competing with seabirds for particular size-classes or species of prey. However, since most fisheries target large predatory fish and discard offal and small fishes, many of which would otherwise not have been available to seabirds, it is unclear how widespread competitive interactions with fisheries may be.

See also

Alcidae. Laridae, Sternidae and Rynchopidae. Pelecaniformes. Phalaropes. Procellariiformes. Seabird Conservation. Seabird Migration. Seabird Reproductive Ecology. Seabird Responses to Climate Change. Seabirds and Fisheries Interactions. Seabirds as Indicators of Ocean Pollution. Sphenisciformes.

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SEABIRD POPULATION DYNAMICS

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The population biology of seabirds is characterized by delayed breeding, low reproductive rates, and long life spans. During the breeding season, the distribution of seabirds is clumped around breeding colonies, whereas when not breeding, birds are more dispersed. These population traits have important consequences for interactions between people and seabirds. The aggregation of large portions of the adult population of a species in colonies means that a single catastrophic event, such as an oil spill, can kill a large segment of the local breeding population. Although seabird populations can withstand the failure to produce young in one or even a few years without suffering severe population-level consequences, the loss of adults has an immediate and long-lasting impact on population dynamics. Even a small decrease in adult survival rates may cause population decline.

Seabirds breed in colonies on islands, cliffs, and other places where they are protected from attacks by terrestrial predators. Species that forage at large distances from their colonies usually choose locations for their colonies that are less vulnerable to incursions by predators than are the colonies of species that forage in the immediate vicinity of the colony. For the offshore species, the cost of increased travel to a more protected site may be minor compared with the benefit of freedom from unwanted visitors. In contrast, for species that need to forage close to their colonies, even a short increase in the distance traveled between colony and foraging site may mean that it is uneconomical to occupy a particular breeding site.

Colony size tends to vary with the distance that a species travels in search of food. Inshore-foraging seabirds may nest singly or in small groups, whereas species that forage far at sea may have colonies that are comprised of hundreds of thousands of pairs. Two hypotheses have been offered to explain this trend. One hypothesis focuses on the issue of food availability. If birds forage far from their colonies, there is a much greater area in which food may be encountered than if foraging is restricted to a small radius around the colony, and thus a larger size colony can be supported. This hypothesis assumes that seabird colony size is limited by food availability. For species that forage near their colonies, there is evidence that reproductive parameters sensitive to prey availability, such as chick growth rates and fledging success, vary negatively with colony size. Likewise, there is evidence that colony size and location may be sensitive to the size and location of neighboring colonies. Evidence that seabirds depress prey populations near their colonies is limited. The second hypothesis focuses on the role that colonies may play in the process of information acquisition by birds seeking prey. When birds forage far from their colony, there may be a need for large numbers of birds so that those flying out from the colony are able to observe successful returning foragers and thereby work their way to productive foraging areas using the stream of birds returning to the colony for guidance. The longer the distance from the colony, the greater the number of birds that are required to provide an unbroken stream of birds to guide the out-bound individuals. The evolution of a system of this sort is possible because each individual will benefit from information on food resources gained by being part of a large colony. Selection for large colony size will continue so long as the colony is not so large that food supplies are severely depressed.

Seabirds show considerable philopatry, with individuals often returning to the same colony, or even the same part of the colony from which they fledged. Once a nest site or territory is established, individuals and pairs may use the same site in subsequent years. Pairing tends to be for multiple