sea-bird communities. For example, one study in the Antarctic found no habitat expansion of the pack-ice assemblage into adjacent open waters seasonally vacated by another community (**Figure 3**), a shift that might be expected if competition affected community structure and habitat selection. In that study, sufficient epipelagic prey were available in the ice-free waters to be exploited successfully by sea birds (**Figure 5**).

Competition with Fisheries

Many of the forage species sought by sea birds are the same sought by industrial fisheries. The result is conflict, particularly in eastern boundary currents, where clupeid fishes are dominant and are of ideal size and shape to be consumed by sea birds. The tracking of bird populations with fish stocks has been especially well documented in the Benguela and Peru currents, where not only have fish stocks been heavily exploited but so have guano deposits accumulated by the sea birds. The bird populations have responded closely to geographic, temporal and numerical variation in the fish stocks. Well documented, also, have been fish stocks and avian predator populations in the North Sea. There, commercial depletion of predatory fish benefited seabird populations by reducing competition for forage fish; when fisheries turned to the forage fish themselves, seabird populations declined. In some areas, it has been proposed to use statistical models of predator populations as an indicator of fish-stock status independent of fishery data, for instance, the Convention for the Conservation of Antarctic Living Marine Resources. Much information is needed to calibrate seabird responses to prey populations before seabirds can be used reliably to estimate prey stocks.

See also

Benguela Current. Canary and Portugal Currents. Seabird Migration. Seabird Responses to Climate Change. Seabirds and Fisheries Interactions. Sea Ice: Variations in Extent and Thickness.

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SEABIRD MIGRATION

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doi:10.1006/rwos.2001.0238

Introduction

Bird migration is one of the most fascinating phenomena in our living environment, and accordingly has been studied since ancient times, particularly among nonmarine species. Studies of migration and navigation of nonmarine species have become quite sophisticated, examining in detail subjects including orientation and navigation, and physiological and morphological adaptations. In contrast, studies of migration among marine birds have been fewer and more simplistic. Indeed, until recently, much of the information on migration of seabirds had come from the recovery of individuals ringed (i.e., metal rings are attached to the legs, each stamped with a unique set of numbers) at their breeding sites. Although ringing has revealed considerable information about the migrations of species that stay close to coasts (thus, facilitating recoveries), it has provided little insight into the movements of species that stay far at sea during the nonbreeding period. In addition, studies at sea have been few, owing to the immense size of the world's oceans and the inherent logistical difficulties. Fortunately, however, an upsurge in pelagic investigations has occurred in the past 20 years, owing to the advent of ground-position satellite (GPS) telemeters that can be attached to larger avian species (e.g., albatrosses), and ship-board studies of the flight direction and flight behavior of birds on the high seas.

Background

Migration among seabirds ultimately is a response to the seasonally changing altitude of the sun's position, causing changes in environmental conditions to which the birds must adapt to survive and reproduce. Individual seabirds have the ability to go to a precise wintering location and then return to a precise breeding location. The duration between trips to and from wintering and breeding sites can be annual (as in adults), or last several years in the case of subadults of some species (notably the Procellariiformes, see below). In the latter case, fledgelings go to sea and do not return to land until reaching sexual maturity at ages of up to 10 years or more, such as in the wandering and royal albatrosses (*Diomedea exulans* and *D. epomophora*). On reaching breeding age, many seabirds return to the same colony from which they originated, in fact, they often nest on or adjacent to the exact location where they were hatched. After first breeding, a large proportion also return each year to the same nest site to breed. Furthermore, individual adults have the ability to return with pinpoint precision to the same wintering location each year following breeding. These locations are usually those where these individuals foraged during their subadult years.

Seabirds can home in on their breeding sites during all types of weather, during darkness (e.g., some species return to nesting burrows under dense vegetation only during the night, even during dense fog), and can navigate distances at sea approaching a global scale. The latter was demonstrated in two experiments in which the Manx shearwater (*Puffinus puffinus*) and 18 Laysan albatrosses (*Phoebastria immutibilis*) were taken from their breeding sites (where they were attending eggs or young) and air-freighted to locations thousands of kilometers away. Many were released at locations where they surely had not been before, and in environments for which they are not adapted. The shearwater returned to its nest site in Wales in 12.5 days, covering the 5200 km (shortest) distance from its release site at Boston, Massachusetts, at a rate of 415 km/day. Fourteen of the 18 albatrosses returned to their nest sites on Sand Island, Hawaii, with median trip duration and distance flown of 12 days, and 275 km/day (straight-line), respectively. One bird, released in Washington, took 10.1 days to cover the 5200 km distance back to Sand Island, although it probably flew a longer, tacking course because of the headwinds that it would have encountered if it flew directly to the island.

Sensory Mechanisms Used for Orientation and Navigation

As noted above, studies among terrestrial species have provided many insights into the sensory mechanisms by which birds navigate over long distances. Given the ability of seabirds to navigate long distances across the open ocean, they most likely use one or a combination of the sensory mechanisms indicated for terrestrial species. These mechanisms include endogenous (genetically transmitted) vector navigation, olfactory and time-compensated sun orientation; star, magnetic, UV, and polarized light orientation.

Endogenous vector navigation, in which birds are genetically programmed to follow the correct course and to start their migrations at the correct time, is thought to explain how young birds that have never migrated before, and that frequently do not accompany experienced individuals (as in the case for many seabirds), find their wintering areas. In this regard, spatial and temporal orientation appear to be coded to both celestial rotation and the geomagnetic field, this information being contained within a heritable, endogenous program.

Yet, migrants encounter many uncertainties due to unpredictable weather which can disrupt vector navigation. Through a series of experimental studies examining hypotheses addressing this problem, it has become the general consensus that birds have a compass sense as well as a very extensive grid/mosaic map sense. Birds can integrate combinations of time-compensated sun inclination (particularly at sunset), star, magnetic, UV, and polarized light cues, although the possibility that these capabilities vary among species remain open. Nevertheless, the evidence indicates that for short-term orientation, magnetic cues take precedence over celestial, that visual cues at sunset over-ride both the latter, and that polarized sky light is used during dusk orientation. The basis for the map aspect employed for navigation is not well studied and consists of two hypotheses: perceptions of a magnetic grid and/or an olfactory mosaic/gradient.

Physiological and Behavioral Adaptations

Many species of terrestrial birds have major shifts in their physiology just preceding the migration period, including dramatic increases in food intake and body fat, hypertrophy of breast muscles, increased hematocrit levels, and increases in body protein. Although few physiological studies of seabirds exist, most indicate a lack of, or smaller, physiological changes then occurs in land birds. During the post-breeding phase of migration, seabirds are generally lighter, with lower fat reserves, than when returning to their colonies at the beginning of the next breeding season. For example, adult sooty shearwaters (*P. griseus*) weigh 20–25% less during the post-breeding migration than when returning during the prenuptial period. Similar differences in the pre- and post-breeding body mass also occur in several Charadriformes (e.g., gulls, terns, auks).

Several factors could be responsible for the lack of more obvious physiological adaptations for migration among seabirds. First, most of the terrestrial species in which major physiological changes occur have small body masses (<75 g) and, thus, lower flight efficiency than larger species such as most seabirds. Second, and probably most importantly, many of the terrestrial species perform long-distance nonstop flights, often at high elevations, over obstacles where they cannot feed (e.g., large bodies of water, or deserts). In contrast, such migrations are rare among seabirds, because seabirds nearly always migrate at low elevations over the ocean, facilitating frequent feeding along the migration route. Hence, seabirds are seldom far from a habitat offering feeding opportunities, even during transequatorial migrations by species that feed mostly in temperate or boreal latitudes.

The post-breeding migration of seabirds is generally more leisurely than the pre-breeding migration. One reason is that seabirds, especially those moving longer distances, feed more during the post-breeding than the pre-breeding movement. This behavior is probably related to the poorer body condition of seabirds just after breeding. Two examples include the sooty shearwater and the Arctic tern. Both perform transequatorial migrations, although the shearwater is a southern hemisphere breeder, with its post-breeding migration during the boreal spring, whereas the tern is a northern hemisphere breeder that leaves its breeding grounds in the boreal autumn. Thus, the post-breeding movements by the two species are 6 months out of phase, indicating that seasonal differences in ocean productivity in equatorial waters (highest in the boreal autumn) are unrelated to the low feeding rate during the pre-breeding migration. Faster prenuptial migration probably occurs because ample fat reserves have been obtained on the winter grounds (i.e., feeding is not required). In addition, higher wing loading (from higher fat reserves) facilitates faster flight. Thus, the seasonal differences in fat reserves among species of seabirds are not likely adaptations for migration *per se*, but instead, are important in the life histories of many because early arrival on the breeding grounds facilitates the acquisition of a higher quality nesting territory favorable for successful breeding and because the amount of time available for foraging after arrival at the colony is greatly reduced.

Morphological Adaptations

The distance that seabirds migrate is strongly related to morphology. The most important morphological feature is the shape of the wings, measured as the aspect ratio, a dimensionless value calculated as the wing span^2 divided by total wing area. Hence, birds with high aspect ratios have narrower wings. They also have less profile drag (i.e., less friction with the air), lower air turbulence, and generally migrate longer distances compared with birds with lower aspect ratios. For instance, in the Laridae many species of terns, and smaller gulls and skuas with long narrow wings are transequatorial migrants, whereas larger gulls and skuas with lower aspect ratios usually move much shorter distances or are even sedentary.

Wing loading (wing area divided by body mass) is also related to migration patterns in seabirds, although this relationship differs with flight styles used by different seabird taxa, and is also confounded with aspect ratio. Higher wing loading requires swifter flight for the birds to remain airborne. Within taxa of seabirds that typically use gliding or flap-gliding flight (e.g., albatrosses, shearwaters, and petrels) those with higher wing loading tend to have longer migrations. The gliding species with higher wing loading also tend to have higher aspect ratios (**Figure 1**), which increases their flight efficiency. Swift, energy-efficient flight equates to longer distances travelled; however, the gliding species are heavily dependent on wind energy for flight because of their flight mode and high wing loading. As a result, those with higher wing loadings are confined to higher latitudes where the wind is usually stronger, although some species with moderate to high wing loading do make transequatorial crossings.

In contrast to gliders, seabirds that use flapping flight, such as Larids, have an inverse relationship between wing loading and migration distance (**Figure 1**). This is undoubtedly related to the lower flight efficiency of flapping species with higher wing loading compared with those with lower wing loading, all other factors being equal. Another factor is the inverse relationship between wing loading and aspect ratio when comparing gliding versus flapping species (with the exception of Alcids – see below). That is, aspect ratio decreases (and drag increases) with increases in wing loading among most seabird taxa that typically use flapping flight.

As noted above, Alcids (auks, auklets, murres, murrelets, and guillemots) are an exception to the wing loading versus aspect ratio relationship for species using flapping flight. Aspect ratios of Alcids increase with wing loading (**Figure 1**), i.e., a relationship similar to that of Procellariiformes (primarily gliders). However, unlike the Procellariiformes and Larids, there does not appear to be a relationship between wing loading, or aspect ratio, and migration tendency among Alcids. This may be because Alcid wings are highly adapted for underwater propulsion (i.e., similar to penguins) resulting in small wing sizes and the highest wing loading among avian species. Thus, their foraging ranges

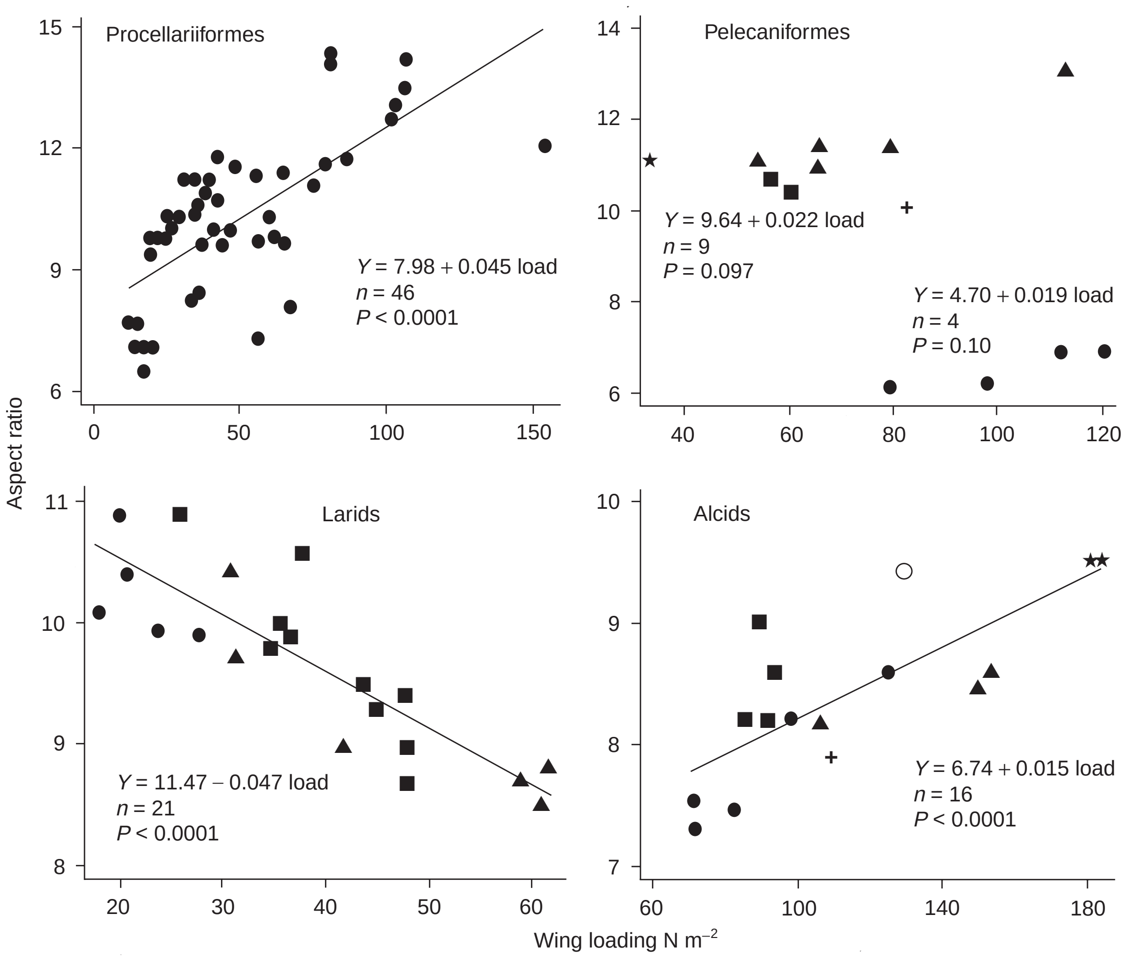

Figure 1 Relationship between wing loading and aspect ratio of four groups of seabirds, as indicated by data presented in 1997 by Spear and Ainley. Each point denotes the average for a given species. Lines indicate the best regression fit. Values of *n* are number of species, and *P* values indicate the level of significance by which slopes deviated from zero. Among the Pelecaniformes, the cormorants (●) were considered to be distinct from six species representing pelicans (+), tropic birds (■), boobies (▲), and frigate birds (★). Larids included terns (●), skuas (▲), and gulls (■). Alcids included auklets (●) murrelets (■), puffins (▲), pigeon guillemot (+), razorbill (○), and murres (★).

and nonbreeding movements are short. Indeed, many Alcid species are flightless during part of the dispersal period due to primary molt, indicating that a significant part of the dispersal is traversed by swimming.

Types of Migration

Several types of 'migration' are recognized. These include 'true migration' in which all members of a population move from a breeding area to a wintering area disjunct from the former; and 'partial migration', in which some members of a population migrate and others do not. Yet another type of movement, 'dispersal', is found in populations in which individuals move various distances after the breeding season, such that they occur at all distances within a given radius of the breeding site. Although a large proportion of the terrestrial avifauna exhibits true annual migration, this is rare among seabirds, probably because the marine environment is more stable in that it does not have the extreme seasonal warming and cooling of land masses. In addition, seabirds usually expand their at-sea ranges without having to cross as many barriers as are encountered during movements by terrestrial species. Even so, seabirds have the notoriety of having the longest distance migrants among the animal kingdom. The following is a review of the movement patterns of seabirds.

Sphenisciformes

Penguins (Spheniscidae) The pelagic ranges of the penguins are confined to the southern hemisphere. Relatively little is known of the post-breeding movements of these 17 flightless species. The four species of the genus *Spheniscus* have the lowest latitude distributions among penguins and probably move the shortest distances. Two, the Galapagos and Humboldt penguins (*S. mendiculus* and *S. humboldti*), are relatively sedentary along the coasts of the Galapagos Islands, and Peru to northern Chile, respectively. These species rarely are found more than 10 km from shore. The two other *Spheniscus* species usually stay within 50 km of the coasts of Africa (African penguin, *S. demerus*) and southern South America (Magellanic penguin, *S. magallenicus*), although there have been sightings of the latter to 250 km offshore. Satellite telemetry has shown that the Magellanic penguins breeding on Punta Tombo, Argentina, disperse for up to 4000 km northeastward to wintering areas off Brazil, although other population members winter along the coast of Argentina, closer to the colony. Three of the four telemetered Magellanic penguins which moved to coastal Brazil traveled 20 km/day.

Dispersal by some of the species breeding in higher, temperature to subpolar, latitudes (king, *Aptenodytes patagonicus*; rockhopper, *Eudyptes chrysocome*; Snares Island, *E. robustus*; Fiordland crested, *E. pachyrhynchus*; erect-crested, *E. sclateri*; royal, *E. schlegeli*; macaroni, *E. chytsolophus*; Gentoo, *Pygoscelis papua*; yellow-eyed, *Megadyptes antipodes*; and little penguins, *Eudyptula minor*) is probably more extensive than is true for *Spheniscus*, as they are often seen hundreds of kilometers from shore. Finally, two of the three penguin species that breed only on the Antarctic continent (Adelie and chinstrap penguins, *Pygoscelis adeliae* and *P. antarctica*) migrate north to areas near or inside of the ice pack (Adelies; e.g., polynyas, leads) or open water (chinstraps) after waters near the continent become covered with solid ice. Movements of the third species, the Emperor penguin (*Aptenodytes forsteri*), are not well know; however, there are sighting records for this species from the coasts of Argentina and New Zealand.

Procellariiformes

Albatrosses (Diomedeidae) The albatrosses are under extensive taxonomic reclassification, and number between 14 and 24 species. Post-breeding movements of albatrosses are mostly longitudinal; no species undertakes transequatorial movements. These birds range long distances from their colonies during the nonbreeding period as well as during foraging trips undertaken while they are breeding. For example, six wandering albatrosses equipped with satellite transmitters flew 3660–15 200 km during single foraging trips after being relieved by their mates from incubation duties at the nest. Even breeding waved albatrosses (*Phoebastria irrorata*), with the smallest pelagic range among the group, have a round-trip commute of no less than 2000 km between the breeding colony on the Galapagos Islands and the nearest edge of their foraging area along the coast of Ecuador and Peru.

Most albatross species range farthest from their colonies during the nonbreeding period. In fact, many species are partially migratory (as opposed to being dispersers). As explained above, these species are considered as partially migratory because individuals are found in both the wintering and breeding areas during winter, but do not winter (or winter in small numbers) between the two locations. For example, Buller's (*Thalassarche bulleri*), Chatham (*T. eremita*), Salvin's (*T. salvini*), and shy (*T. cauta*) albatrosses breed on islands near New Zealand (the first three) and Australia (shy).

Although some birds stay near the colonies throughout the year, large proportions of the Buller's, Chatham, and Salvin's albatrosses migrate at least 8500 km eastward across the South Pacific to the coast of South America, and many shy albatrosses migrate westward across the Indian Ocean to the coast of South Africa.

Three other species, the wandering, black-browed (*T. melanophris*), and gray-headed (*T. crysostoma*) albatrosses, have breeding colonies located circumpolarly across southern latitudes near 50°S. The South Georgia populations may be partially migratory, although the distinction from dispersive is not clear. South Georgian wandering albatross fly north to waters off Argentina, and then eastward to important wintering areas off South Africa. Some continue to Australian waters and may even circumnavigate the Southern Ocean. One of several of these birds equipped with a satellite transmitter averaged 690 km/day. A large proportion (*c.* 85%) of South Georgian black-browed albatrosses also winter off South Africa, and many South Georgian gray-headed albatrosses are thought to fly westward to waters off the Pacific coast of Chile, and then to New Zealand.

The waved albatross is unique among the albatross group. Besides having the smallest pelagic range, it breeds near the Equator, i.e., at a latitude $> 25°$ lower than any of the other species. Furthermore, the foraging area used while breeding is the same, or nearly the same, as that used post-breeding. Thus, the classification of this species as a 'disperser', or even as 'partially migratory', is appropriate only in that it leaves the colony post-breeding (and does not occupy the 900 km stretch between the Galapagos and the mainland), although the size of the foraging area changes little.

The post-breeding movements of yellow-nosed (*T. chlororhynchos*), sooty (*Phoebetria fusca*), light-mantled sooty (*P. palpebrata*), royal, black-footed (*Phoebastria nigripes*), short-tailed (*P. albatrus*), and Laysan albatrosses are less clear, although each apparently disperses post-breeding to seas adjacent to their colonies.

Fulmars, Shearwaters, Petrels, Prions, and Diving Petrels (Procellariidae) The migration tendencies of this family of 78 species is not well known, although those that have been studied are either partially migratory or dispersers. The pelagic range of 38 species (49%) is confined to the southern hemisphere, including the 18 species of fulmarine petrels and prions, three of the four species of diving petrels, seven (33%) of the shearwaters, and 10 (29%) of the gadfly petrels (**Table 1**). Another 19 (25%) of the 78 species perform extensive transequatorial migrations. These include nine species (43%) of the shearwaters and 10 species (29%) of gadfly petrels. Twenty (26%) others are primarily tropical, including one species of diving petrel, five species (24%) of shearwaters, and 14 (40%) gadfly petrels. Many of the 'tropical' species disperse across the Equator, but like species having nontransequatorial movements, movements of these species usually have a greater longitudinal than latitudinal component, and are usually of shorter distances than those of transequatorial migrants.

The detailed migration/dispersal routes of most Procellariids are poorly known. Two exceptions are the sooty shearwater and Juan Fernandez petrels, which are very abundant and appear to be partial migrants. Two populations of sooty shearwaters exist, one breeding in New Zealand and the other in Chile. Many individuals from each population migrate to and from the North Pacific each year, and none winter in the equatorial Pacific. Observations of flight directions in the equatorial Pacific indicate that many complete a figure of eight route (*c.* 40 500 km). The route apparently involves easterly flight from New Zealand to the Peru Current in winter, northwesterly flight to the western North Pacific in spring, eastward movement to the eastern North Pacific during summer, and southwest flight to New Zealand during autumn (**Figure 2**). Most are probably nonbreeders, possibly from both the New Zealand and Chilean populations. Many, probably breeders from both populations, likely use shorter routes to and from the North Pacific (*c.* 28 000–29 000 km). Other (nonmigratory) individuals from both populations apparently stay in the southern hemisphere. Migration routes are coordinated with wind regimes in the Pacific, such that the usual flight direction utilizes quartering tail winds (**Figure 2**).

Juan Fernandez petrels breed in the Juan Fernandez archipelago off Chile. Many migrate into the North Pacific where they winter mostly between 5°N and 20°N. Another large component of the population stays in the South Pacific, mostly between 12°S and 35°S. Collections of specimens indicate that the great majority found in the North Pacific are subadults, whereas those in the South Pacific are predominantly adults.

It is likely that many other Procellariids also perform partial migration (e.g., Cook's, white-winged, black-winged, and mottled petrels), or even complete migrations (e.g., Cook's petrel, Hutton's shearwater, Magenta and Bonin petrels.

Storm Petrels (Oceanitidae) The 19 species of storm petrels include eight with nontransequatorial

Table 1 Migration tendencies (transequatorial, nontransequatorial, and tropical) of the 78 species of Procellariids and 19 species of Oceanitids[a]

PROCELLARIIDAE

FULMARINE PETRELS Nontransequatorial (12)

Northern giant petrel *Macronectes halli*
Southern giant petrel *M. giganteus*
Northern fulmar *Fulmarus glacialis*
Southern fulmar *F. glacialoides*
Antarctic petrel *Thalassoica antarctica*
Cape petrel *Daption capnse*
Snow petrel *Pagodroma nivea*
White-chinned petrel *Procellaria aequinoctialis*
Parkinson's petrel *P. parkinsoni*
Westland petrel *P. westlandica*
Grey petrel *P. cinerea*

GADFLY PETRELS

Nontransequatorial (10)

Great-winged petrel *Pterodroma macoptera*
Atlantic petrel *P. incerta*
Kerguelen petrel *P. brevirostris*
Magenta petrel *P. magentae*
Soft-plumaged petrel *P. mollis*
Barau's petrel *P. baraui*
White-headed petrel *P. lessoni*
Bonin petrel *P. hypoleuca*
Chatham petrel *P. axillaris*
Defilippe's petrel *P. defilippiana*

Transequatorial (10)

Mottled petrel *P. inexpectata*
Murphy's petrel *P. ultima*
Solander's petrel *P. solandri*
Kermadec petrel *P. neglecta*
Juan Fernandez petrel *P. externa*
White-necked petrel *P. cervicalis*
Cook's petrel *P. cooki*
Black-winged petrel *P. nigripennis*
Pycroft's petrel *P. pycrofti*
Stejneger's petrel *P. longirostris*

Tropical (14)

Phoenix petrel *P. alba*
Trinidad petrel *P. arminjoniana*
Herald petrel *P. heraldica*
Hendersons's petrel *P. atrata*
Tahiti petrel *P. rostrata*
Mascarene petrel *P. aterrima*
Bermuda petrel *P. cahow*
Black-capped petrel *P. hasitata*
Hawiian petrel *P. sandwichensis*
Galapagos petrel *P. phaeopygia*
White-winged petrel *P. leucoptera*
Collared petrel *P. brevipes*
Bulwer's petrel *Bulweria bulwerii*
Jouanin's petrel *B. fallax*

Unknown (1)

Macgillivray's petrel *P. macgillivrayi*

PRIONS Nontransequatorial (7)

Blue petrel *Halobaena caerulea*
Broad-billed prion *Pachyptila vittata*
Antarctic prion *P. desolata*
Salvin's prion *P. salvini*
Fairy prion *P. turtur*
Fulmar prion *P. crassirostris*
Slender-billed prion *P. belcheri*

DIVING PETRELS

Nontransequatorial (3)

Georgian diving petrel *Pelecanoides georgicus*
Common diving petrel *P. urinatrix*
Magellan diving petrel *P. magellani*

Tropical (1)

Peruvian diving petrel *P. garnoti*

SHEARWATERS (21 species)

Nontransequatorial (7)

Little shearwater *Puffinus assimilis*
Black-vented shearwater *P. opisthomelas*
Fluttering shearwater *P. gavia*
Hutton's shearwater *P. huttoni*
Heinroth's shearwater *P. heinrothi*
Balearic shearwater *P. mauretanicus*
Levantine shearwater *P. yelkouan*

Tropical (5)

Wedge-tailed shearwater *P. pacificus*
Christmas shearwater *P. nativitatis*
Newell's shearwater *P. newelli*
Townsend's shearwater *P. auricularis*
Audubon's shearwater *P. lherminieri*

Transequatorial (9)

Streaked shearwater *Calonectris leucomelas*
Cory's shearwater *C. diomedea*
Pink-footed shearwater *Puffinus creatopus*
Flesh-footed shearwater *P. carneipes*
Great shearwater *P. gravis*
Buller's shearwater *P. bulleri*
Sooty shearwater *P. griseus*
Short-tailed shearwater *P. tenuirostris*
Manx shearwater *P. puffinus*

Table 1 *Continued*

Nontransequatorial / Transequatorial and Tropical	
OCEANITIDAE	
STORM PETRELS	
Nontransequatorial (8)	**Transequatorial (5)**
Gray-backed storm petrel *Garrodia nereis*	Wilson's storm petrel *Oceanites oceanicus*
White-faced storm petrel *Pelagodroma marina*	British storm petrel *Hydrobates pelagicus*
Black-bellied storm petrel *Fregetta tropica*	Leach's storm petrel *Oceanodroma leucorhoa*
White-bellied storm petrel *F. grallaria*	Black storm petrel *O. melania*
Tristram's storm petrel *O. tristrami*	Matsudaira's storm petrel *O. matsudairae*
Swinhoe's storm petrel *O. monorhis*	
Ashy storm petrel *O. homochroa*	**Tropical (6)**
Least storm petrel *O. microsoma*	Elliot's storm petrel *Oceanites gracilis*
	White-throated storm petrol *Nesofregetta fuliginosa*
	Wedge-rumped storm petrel *Oceanodroma tethys*
	Harcourt's storm petrel *O. castro*
	Markham's storm petrel *O. markhami*
	Hornby's storm petrel *O. hornbyi*

[a]Tropical species are those in which most individuals stay between the tropic of Cancer/Capricorn.

movements, five transequatorial, and six that stay primarily in tropical latitudes. Storm petrels are mostly dispersive. Leach's and Wilson's storm petrels disperse the farthest and also are the most abundant, with circumpolar distributions. The former breeds mostly between 25°N and 50°N, and winters as far south as waters near New Zealand (about 35°S). Similarly, the Wilson's storm petrel breeds from about 45°S to 60°S, and winters north to about 40°N.

Two species of storm petrels that may be migratory, or partially migratory, include the white-faced and white-bellied storm petrels. Many white-faced storm petrels (race *maoriana)* that breed adjacent to New Zealand apparently migrate east to waters off Chile and Peru. In warm-water (El Niño) years, some birds continue westward from the Peru Current, out along the Equator, in association with waters of the South Equatorial Current. The *grallaria* race of white-bellied storm petrel is represented by a very small population breeding on islands north of New Zealand and Australia. This population is particularly interesting in that new information from the equatorial Pacific indicates that many or all of these birds migrate about 2500 km to a relatively small (1 million km^2) section of waters between 135°W and 145°W and between 5°S and about 12°S, adjacent to the Marquesas.

Pelecaniformes

Pelicans (Pelecanidae, 4 marine species), boobies and gannets (Sulidae, 9 species), cormorants (Phalacrocoracidae; 29 marine species), frigate birds (Fregatidae; 5 species), and tropic birds (Phaethontidae, 3 species) Distributions of the marine species of pelicans and cormorants are coastal, whereas those of boobies, frigate birds, and tropic birds are pelagic. Movements of most Pelecaniformes are dispersive, and none of the nontropical species performs transequatorial migrations. Many species, including all boobies, frigate birds, and tropic birds, are tropical; most of the cormorants, pelicans, and gannets prefer temperate to polar latitudes. Movements of the tropical species are primarily nondirectional (i.e., direction can include combinations of north, south, east, and west orientation), whereas those of temperate to polar species usually have a stronger latitudinal component.

Charadriiformes

Phalaropes (Scolopacidae) Two of the three phalarope species breed in the northern hemisphere, either in the continental interiors (red-necked phalarope, *Phalaropus lobatus*) or Arctic slopes (red phalarope, *P. fulicarius*), and perform extensive migrations to marine habitat. Movements of a large proportion of both populations, particularly those of the red phalarope, are transequatorial, with many individuals wintering along the west coasts of South America and Africa. A major concentration also winters in the Panama Bight.

Skuas (Stercoracidae) Like the two phalaropes, the three smaller skuas (pomarine, *Stercorarius pomarinus;* Arctic, *S. parasiticus*; and long-tailed, *S. longicaudus*) breed on the Arctic slope and winter in oceanic waters. A large proportion of these birds also perform extensive transequatorial migrations, with large numbers wintering off the west coasts of South America and South Africa. Individuals are also occasionally seen off Australia, New Zealand, and in the Indian Ocean. Another large percentage winters off Mexico, Central America, and northern

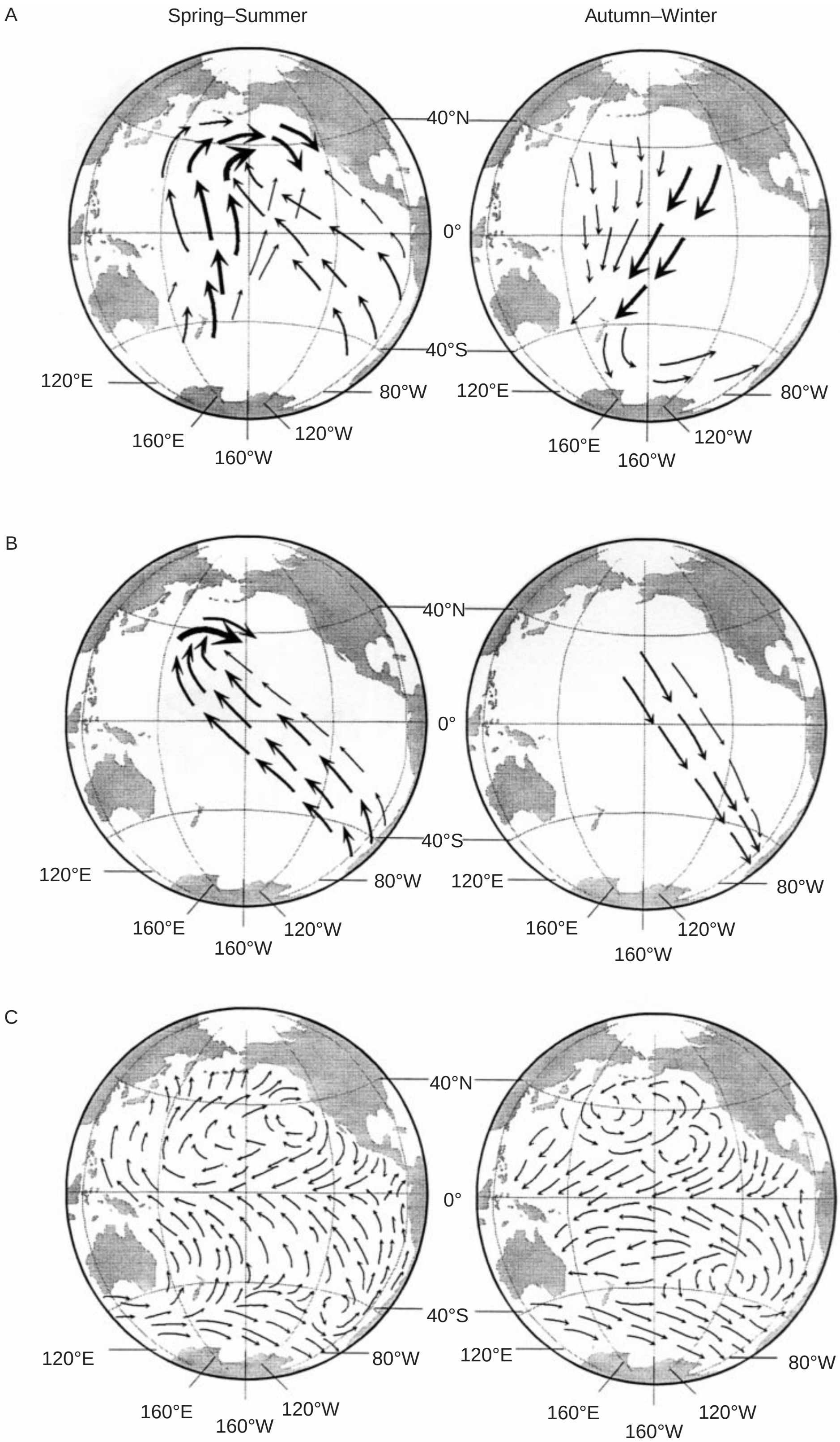

Figure 2 Suggested migration routes of sooty shearwaters from colonies near (A) New Zealand and Australia, and (B) Chile. Sizes of vectors reflect differences in the number of shearwaters, as suggested in 1974 by Shuntov from observations in the South and North Pacific, and in 1999 by Spear and Ainley, from observations in the equatorial Pacific. (C) Wind regimes of the Pacific Ocean during two seasonal periods as depicted in 1966 by Gentilli.

Table 2 Migration tendencies of the Larids (transequatorial, nontransequatorial, and tropical), including 48 species of gulls and 44 species of terns[a]

GULLS

Nontransequatorial (40)

Great black-backed gull *Larus marinus*
Western gull *L. occidentalis*
Yellow-footed gull *L. livens*
Herring gull *L. argentatus*
Kelp gull *L. dominicanus*
Glaucous-winged gull *L. glaucescens*
Glaucous gull *L. hyperboreus*
Slaty-backed gull *L. shistisagus*
Great black-headed gull *L. ichthyaetus*
Indian black-headed gull *L. brunnicephalus*
Chinese black-headed gull *L. saundersi*
Pacific gull *L. pacificus*
Band-tailed gull *L. belcheri*
Iceland gull *L. glaucoides*
Kumlien's gull *L. kumlieni*
Thayer's gull *L. thayeri*
California gull *L. californicus*
Black-tailed gull *L. crassirostris*
Sooty gull *L. hemprichii*
White-eyed gull *L. leucophthalmus*
Dolphin gull *L. scoresbii*
Common gull *L. canus*
Ring-billed gull *L. delewarensis*
Black-headed gull *L. ridibundus*
Laughing gull *L. atricilla*
Bonaparte's gull *L. philadelphia*
Relict gull *L. relictus*
Hartlaub's gull *L. hartlaubii*
Heermann's gull *L. heermanni*
Brown-hooded gull *L. maculipennis*
Silver gull *L. novaehollandiae*
Black-billed gull *L. bulleri*
Little gull *L. minutus*
Audouin's gull *L. audouinii*
Mediterranean gull *L. melanocephalus*
Slender-billed gull *L. genei*
Black-legged kittiwake *Rissa tridactyla*
Red-legged kittiwake *R. brevirostris*
Ross's gull *Rhodostethia rosea*
Ivory gull *Pagophila eburnean*

Transequatorial (3)

Lesser black-backed gull *L. fuscus*
Franklin's gull *L. pipixcan*
Sabine's gull *L. sabini*

Tropical (5)

Lava gull *L. fuliginosis*
Gray gull *L. modestus*
Gray-headed gull *L. cirrocephalus*
Andean gull *L. serranus*
Swallow-tailed gull *L. furcatus*

TERNS

Nontransequatorial (14)

Caspian tern *Sterna caspia*
South American tern *S. hirundinacea*
Antarctic tern *S. vittata*
Kerguelen tern *S. virgata*
Forster's tern *S. forsteri*
Trudeau's tern *S. trudeaui*
Roseate tern *S. dougalii*
White-fronted tern *S. striata*
Aleutian tern *S. aleutica*
Fairy tern *S. nereis*
Black-fronted tern *S. albostriata*
Damara tern *S. balaenarum*
Little tern *S. albifrons*
Least tern *S. antillarum*

Transequatorial (8)

Sandwich tern *S. sandvicensis*
Common tern *S. hirundo*
Arctic tern *S. paradisaea*
Royal tern *S. maxima*
Elegant tern *S. elegans*
Black tern *Childonias niger*
Whiskered tern *C. hybridus*
White-winged tern *C. leucopterus*

Tropical (22)

Large-billed tern *S. simplex*
Gull-billed tern *S. nilotica*
Indian River tern *S. aurantia*
White-cheeked tern *S. repressa*
Black-napped tern *S. sumatrana*
Black-billed tern *S. meganogastra*
Gray-backed tern *S. lunata*
Bridled tern *S. anaethetus*
Sooty tern *S. furcata*
Amazon tern *S. superciliaris*
Peruvian tern *S. lorata*
Crested tern *S. bergii*
Lesser-crested tern *S. bengalensis*
Chinese crested tern *S. bernsteini*
Cayenne tern *S. eurygnatha*
Saunder's little tern *S. saundersi*
Blue-gray noddy *procelsterna cerulea*
Brown noddy *Anos stolidus*
Black noddy *A. minutus*
Lesser noddy *A. tenuirostris*
Inca tern *Larosterna inca*
White tern *Gygis alba*

[a]Tropical species are those in which most individuals stay between tropic of Cancer/Capricorn.

Africa. Finally, a minority, primarily adults, stay in temperate to subpolar latitudes of the northern hemisphere during winter.

The four larger skuas (great, *Catharacta skua*; brown, *C. lonnbergi;* South Polar, *C. maccormicki*; and Chilean, *C. chilensis*) generally perform only short, dispersive post-breeding movements. An exception is the South Polar skua, many of which disperse widely from their Antarctic breeding sites, even into the more northern latitudes (e.g., Alaska) of the northern hemisphere.

Gulls and Terns (Laridae) The 48 gull species (subfamily, Larinae) are mostly dispersive, although for some species the post-breeding dispersal of some birds can extend for thousands of kilometres. As noted above, the larger species, with higher wing loading, tend to move shorter distances post-breeding than do smaller species. The five migratory species include the Franklin's, Sabine's, Thayer's, lesser black-backed, and California gulls. Of these, the movements of three (6% of the 48 species) are transequatorial (**Table 2**). In fact, these three species are the only ones with regular transequatorial movements among the gulls that have nontropical breeding grounds. Of the remaining species, the range of 40 (83%) is confined to one hemisphere or the other, and that of five others (10%) is confined within tropical latitudes.

Of the five migrants, only the Sabine's and Thayer's gulls breed in Arctic latitudes. Interestingly, other species that also breed in the Arctic, including the Ivory, Ross's, glaucous, and Iceland gulls remain there, or disperse relatively short distances to subArctic latitudes, during winter. It is likely that different foraging habitats or prey requirements are responsible for these differences in movement patterns.

The post-breeding, dispersive movements of larger gull species have been studied in detail. These studies indicate that breeding adults leave the colony and fly quickly to specific locations, such as a particular bay or fishing port. The locations, 'vacation spots', are those with which they have become familiar during their subadult years (first 4 years of life), such that the birds know the foraging logistics and availability of a predictable food supply. This is important. After reaching the vacation location the adults must molt and replace the primary wing feathers (making them less mobile for about a month) and replenish body reserves in preparation for the next breeding season.

The 44 species of terms (subfamily, Sterninae) are mostly smaller than gulls and have higher aspect ratios (i.e., longer, narrower wings). Not surprisingly, this group is represented by a higher proportion of species that migrate, including eight species (18%) whose migrations are transequatorial, compared with 14 species (32%) whose movements are mostly confined to one hemisphere, and 21 species (50%) that remain primarily within tropical latitudes.

Arctic terns are unique because they have the longest migrations known among the world's animal species. These terns breed in the Arctic to 80°N, and winter in the Southern Ocean to 75°S. Based on band returns and observations at sea, some Arctic

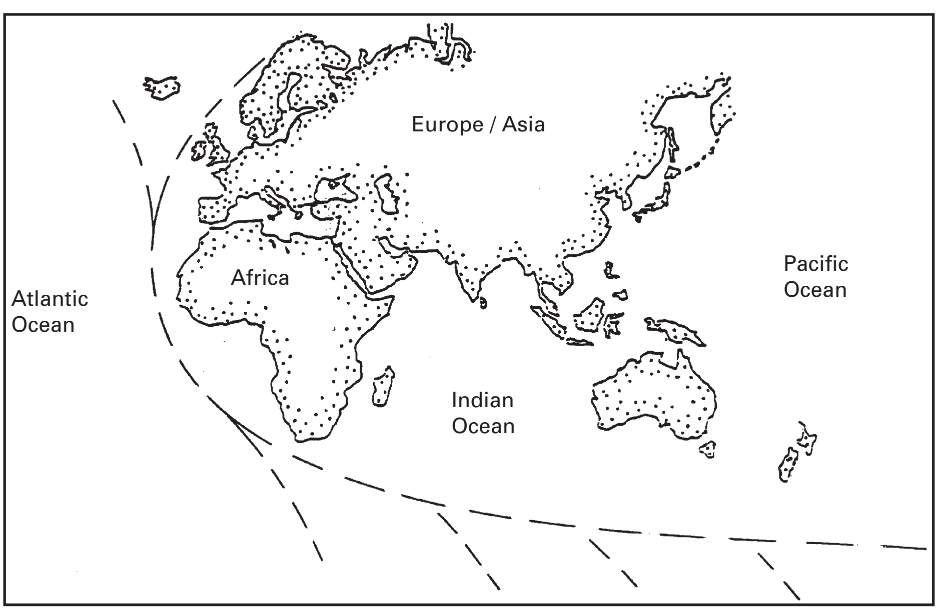

Figure 3 Suggested migration route (dashed lines) to-and-from wintering areas by Arctic Terns breeding in Scandanavia and eastern Canada, from band returns summarized in 1983 by Mead, and from at-sea observations in the Indian Ocean reported in 1996 by Stahl *et al.*

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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doi:10.1006/rwos.2001.0226

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