PROCELLARIIFORMES

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Introduction

The procellariiformes (commonly referred to as petrels) are a monophyletic group of seabirds containing about 100 species in four families: the albatrosses (Diomedeidae, 13 species), the shearwaters, fulmars, prions, and gadfly petrels (Procellariidae, 65 species), the storm-petrels (Hydrobatidae, 21 species), and the diving-petrels (Pelecanoididae, 4 species). It has recently been suggested that the Diomedeidae and Procellariidae may in fact contain up to 21 species and 79 species, respectively (bringing the total to 125 species), but this remains open to debate and so the more conservative taxonomy has been retained here. Petrels range in body size from the least storm-petrel *Halocyptena microsoma* (wing span 32 cm, body mass 20 g) to the royal albatross *Diomedea epomophora* (wing span 300 cm, body mass 8700 g), but they can all be identified by a single diagnostic feature: the external nares open at the end of a prominent horny tube on the upper mandible (**Figure 1**). They are usually considered a separate and ancient order of birds, probably derived from a late Cretaceous ancestor, although DNA evidence has suggested a more recent origin, with the petrels joining the divers (loons), frigate-birds, and penguins within the Order Ciconiiformes.

Petrels occur from tropical to polar regions in all oceans, but most species breed at cool temperate latitudes, with the highest species richness at 45–60°S for albatrosses and diving-petrels, and 30–45°S for the Procellariidae. However, storm-petrels have highest species richness in warm temperate waters at 15–30°N (**Table 1**). Overall, about 70% of petrel species and probably more than 80% of individuals breed in the southern hemisphere. They generally nest on islands, headlands, or mountains isolated from mammalian predators. About 20% of petrel species are surface-nesters while the rest breed below ground in burrows or beneath boulders and scree. Surface-nesters are either too large to burrow or are smaller, mainly tropical, species without predators at the colony. Burrow-nesters usually return to land only by night, probably as a defense against avian predators. Petrels nest colonially, often in high numbers, with colonies of several species exceeding 2 million breeding pairs. Many species undertake regular annual migrations between breeding colonies and separate locations used outside the breeding season. These often involve transequatorial movements, although some species change latitude without crossing the equator and others move east or west without much change in latitude.

Population Ecology

Demography

Petrels are very long-lived for their size, with some storm-petrels reaching 20 years of age and some albatrosses reaching 80 years. Sexual maturation occurs at 2–13 years of age (later in larger species; **Figure 2**) and all species have only a single-egg clutch. Breeding success is typically about 0.4–0.7 chicks fledged per nest, increasing with age and experience. Most breeding failures occur during incubation and early chick-rearing (especially at hatching), with a secondary peak in losses occurring around fledging in some species, mainly due to naive birds being captured by predators. Most petrels are annual breeders but some albatrosses, which have very long breeding seasons, are biennial, while female Audubon's shearwaters *Puffinus lherminieri* at the Galapagos Islands lay at roughly 9-month intervals. In many species a substantial proportion of breeders (up to 30% in some cases) misses a year occasionally, probably to replenish body reserves depleted during the previous breeding season. Because petrels are long-lived and have low annual reproductive rates, their populations are more sensitive to changes in adult survival than to changes in juvenile survival or breeding success. For instance, in wandering albatrosses *Diomedea exulans*, a reduction of 1% in adult survival would require an increase of 6% in juvenile survival to prevent a decline in population size.

Regulation of Population Size

Under normal circumstances, some petrel populations may be regulated in a density-dependent manner by intraspecific competition for food or breeding space. Although there is little direct evidence of prey depletion, the large size of many petrel colonies implies a strong potential for foraging success to be reduced by competition for food, and the notion

Figure 1 Examples of Procellariiform Seabirds. (1) Wandering albatross (*Diomedea exulans).* Adult. Length: 115 cm; wingspan: 300 cm; approximate body mass: 8750 g. Range: Most ocean areas south of 30 S. (2) Mottled petrel (*Pterodroma inexpectata*). Other names: scaled petrel, Peale's petrel. Length: 34 cm; wingspan: 74 cm; approximate body mass: 330 g. Range: Pacific Ocean. (3) Sooty shearwater (*Puffinus griseus*). Length: 44 cm; wingspan: 99 cm; approximate body mass: 780 g. Range: North and South Pacific Ocean, North and South Atlantic Ocean, Southern Ocean. (4) Common diving-petrel (*Pelicanoides urinatrix*). Other names: sub-antarctic diving-petrel. Length: 22 cm; wingspan: 35 cm; approximate body mass: 135 g. Range: Southern oceans. (5) Cape petrel (*Daption capense*). Other names: Cape pigeon, pintado petrel. Length: 39 cm; wingspan: 86 cm; approximate body mass: 450 g. Range: most ocean areas south of 30 S. (6) Wilson's storm-petrel (*Oceanites oceanicus*). Length: 17 cm; wingspan: 40 cm; approximate body mass: 35 g. Range: North and South Atlantic Ocean, Southern Ocean.

Table 1 Species richness of breeding petrels by latitude

	Number of species				
*Latitude (*deg)	*Diom*	*Procel*	*Hydro*	*Pelec*	*Total*
75.1–90N	0	1	0	1	1
60.1–75N	0	2	2	0	4
45.1–60N	0	2	3	0	5
30.1–45N	2	10	7	0	20
15.1–30N	2	15	9	0	27
0–15N	0	3	1	0	4
0–15S	1	9	4	1	15
15.1–30S	0	17	5	1	23
30.1–45S	6	32	4	2	44
45.1–60S	9	21	4	3	37
60.1–75S	0	6	2	0	8
75.1–90S	0	2	1	0	3

Taxonomy follows Warham (1990) except that Levantine shearwater *Puffinus yelkouan* (previously regarded as a Mediterranean subspecies of *P. puffinus*) is given full specific status, raising the number of Procellariidae breeding at 30.1–45°N from 9 to 10. Diom = Diomedeidae, Procel = Procellariidae, Hydro = Hydrobatidae, Pelec = Pelecanoididae.

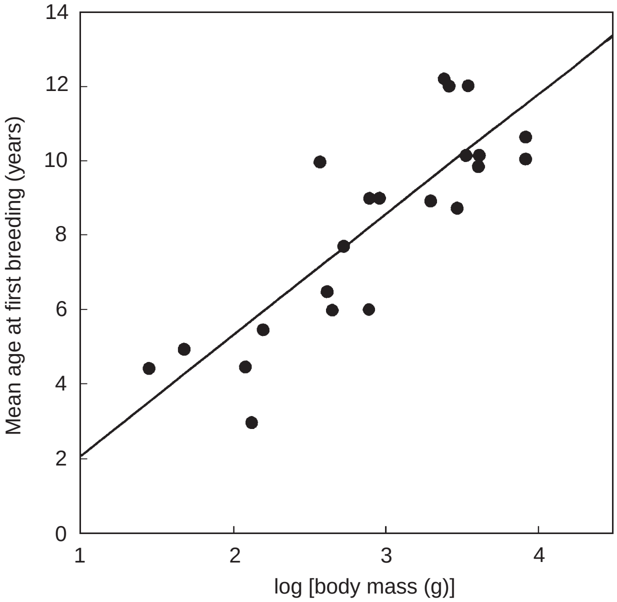

Figure 2 The relationship between body mass and mean age at first breeding in 22 species of petrel. (Data from Table 15.4 in Warham (1990) and Table 1.3 in Warham (1996).)

of competitive exclusion is supported by segregation of feeding zones between sexes, age classes, and populations of some species, particularly southern albatrosses. However, the large foraging ranges of petrels and their wide dispersal at sea reduce the likely importance of prey depletion in most cases, and direct interference competition is unlikely to have a major influence on foraging success except under particular circumstances such as when scavenging behind fishing vessels. Shortage of space may be an important regulatory factor for some species, especially burrow-nesters, when competition for nests may delay the age of first breeding and hence reduce recruitment. Predation at the colony seems to have little impact on petrel populations under natural conditions, although introduced alien predators can have large impacts (see Conservation below).

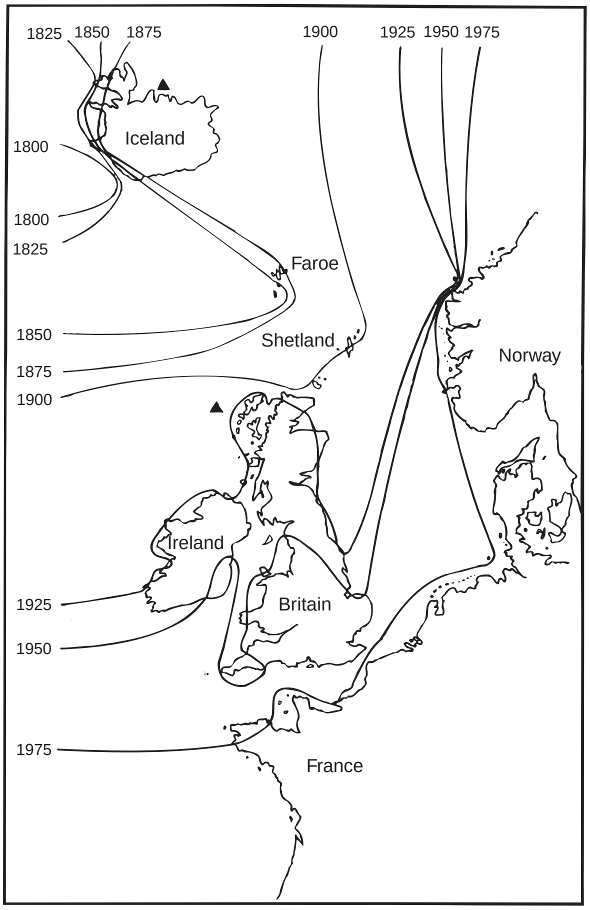

Figure 3 The spread of northern fulmars in the eastern Atlantic Ocean. Contours are at 25-year intervals. The triangles show the position of the two preexpansion colonies at Grimsey, north of Iceland and St. Kilda, west of Scotland. (Redrawn from Williamson (1996) with permission.)

Changes in Distribution

Most petrel species have fairly stable geographical distributions. However, one major exception to this is the northern fulmar *Fulmarus glacialis*, which has undergone a massive range expansion in the northeast Atlantic Ocean during the past 150 years (**Figure 3**). Historically, its breeding distribution was restricted to Arctic regions, with only two fulmar colonies in the temperate North Atlantic, one on the island of Grimsey about 40 km north of Iceland, the other at St Kilda, about 50 km west of NW Scotland. Fulmars spread to the Westman Islands off the south coast of Iceland sometime between 1713 and 1757, then to Faroe and Britain, colonizing the island of Foula, Shetland, in 1878. By 1975 their range included France, Germany (Helgoland), and Norway, and there are now colonies in Greenland, Labrador, and Newfoundland. The most likely cause of this spread was the appearance of a novel food supply in the form of offal and discards, first from Arctic whalers then from industrial and commercial trawlers. In keeping with this view, fulmars at high Arctic colonies appear less reliant on fishery discards than individuals at more southerly colonies. However, the latter also consume many other types of prey which they catch for themselves. These include fast-growing planktonivorous fish such as sand eels *Ammodytidae* and sprat *Sprattus sprattus*, which increased during the second half of the twentieth century following overfishing of predatory fish such as herring *Clupea harengus* and mackerel *Scomber scombrus*. Commercial fishing may thus have benefited fulmars in recent years almost as much by causing these dramatic changes in marine ecosystem structure as by the direct provision of discards.

Another species currently expanding its geographical range is the Laysan albatross *Diomedea immutabilis*. Following increases in populations on small islands in Hawaii, this species has established (or possibly reestablished) colonies on the main Hawaiian Islands since 1970 and has recently founded a number of new colonies in western Mexico. Two species undergoing lesser range expansions are the Manx shearwater *Puffinus puffinus*, which spread from NW Europe to establish a breeding colony in Newfoundland during the 1970s, and the shy albatross *D. cauta* which recently colonized the Crozet Islands, far from its nearest colony in the Bass Strait, Australia.

Food and Foraging

With the exception of diving-petrels, which forage close inshore, all petrels are pelagic feeders. During the breeding season, some albatrosses may travel up to 3000 km or more on a single foraging trip lasting several days, while trips by northern fulmars may be as short as 6 hours. Most species exploit a variety of epipelagic fish, squid, and crustacea, with a greater reliance on fish and squid by most albatrosses, shearwaters, fulmars, and gadfly petrels (most of the latter relying mainly on squid), and a greater reliance on crustacea by storm petrels, diving-petrels, and prions. In the Southern Ocean, a number of petrels prey extensively on the swarming crustacea *Euphausia superba* and *E. chrystallorophias* (krill). Most petrels exploit carrion when available, especially discards from industrial and commercial fishing vessels. Some species, notably northern fulmars, also include other prey such as polychaete worms and medusae in their diet at some colonies. Diets can differ markedly between breeding and nonbreeding seasons, especially in migratory species. For instance, short-tailed shearwaters *Puffinus tenuirostris* consume a mixture of krill, fish, and squid during the breeding season in the Southern Ocean, but during the nonbreeding season in Alaska they prey almost exclusively on the euphausiid crustacean *Thysanoessa raschii*. In most petrels the diets of males and females are similar. However, in giant petrels, *Macronectes giganteus* and *M. halli*, males primarily scavenge for carrion from penguin and seal colonies while females feed primarily at sea.

About 80% of petrel species obtain food by seizing it from the surface of the water, usually while in flight but sometimes while swimming. Other species dive below the surface and some pursue prey underwater, sometimes at great depth (up to 71 m in short-tailed shearwaters). Feeding often occurs in association with dolphins, tuna (*Thunnus* spp.), and other marine predators that force prey toward the surface. Some species also forage extensively at tidal fronts, or at polynyas in polar regions, where prey tend to aggregate.

Stomach Oil

With the exception of diving-petrels, most petrels alter the chemical composition of captured prey during transport to the nest by differential retention of the aqueous and lipid fractions of the digesta within the proventriculus: following liquefaction of the food, the denser aqueous fraction passes into the duodenum first, leaving a lipid-rich liquid termed stomach oil in the proventriculus. Stomach oil has a much higher caloric density than the prey (up to 30 times higher in some cases) and may be essential in some species to allow adults to carry enough energy back to the chick. The extent to which adults form stomach oil increases with foraging range and trip duration.

Breeding Ecology

Petrels are socially monogamous and form long-lasting pair bonds, although they do switch partners on occasion, particularly after an unsuccessful breeding attempt. Pairing usually takes place at the colony and involves elaborate visual displays in diurnal species or auditory displays in nocturnal species. Young prebreeding birds return to the colony progressively earlier each year to display, pair off, and establish a breeding territory. This process takes several years and initial breeding attempts mostly fail.

In established breeders, the period between arrival at the colony each year and egg-laying is generally 30–40% of the whole reproductive cycle, except in albatrosses where it comprises 7–14% of the total. Sedentary species, which occur in all families except the Diomedeidae, may also visit the colony outside the breeding period. Precopulatory behavior may be complex (as in albatrosses) or simple (as in diving petrels) but generally involves mutual preening of the head, nape, cheek, and throat. Copulation takes place on the ground, usually at the nest. Individuals may copulate many times and females sometimes solicit or accept copulations from males other than their partner, although these seldom result in extra-pair paternity. For instance, in a study of northern fulmars, females copulated up to 54 times with their male partner and up to 17 times with an extra-pair male. The final copulation was always with the pair male and there was no evidence of any extra-pair paternity. In all petrels, after copulating there is a period of several days to several weeks, termed the prelaying exodus, when some or all of the established breeders return to sea during egg formation. This may allow birds access to highly productive waters distant from the colony. Females stay away longer than males and in some species only the females leave.

After returning to the colony, the female almost immediately lays a single egg weighing 5–30% of her own body mass (heavier than in other birds that lay a single-egg clutch) with a relatively large yolk. The embryo within the egg grows slowly, resulting in a long incubation period (about 39–79 days depending largely on body mass). The male is responsible for the first long incubation shift and thereafter the two parents alternate between incubating the egg and foraging at sea, at average intervals of about 1–20 days (generally longer in larger species but shortest in diving-petrels and longest in some gadfly petrels and albatrosses of intermediate body mass; **Figure 4**). The two sexes usually spend about the same amount of time incubating, although in some species the male spends longer. In both cases, incubation shifts by both sexes shorten toward the end of incubation, which increases the probability that the incubating bird has food for the chick when it hatches.

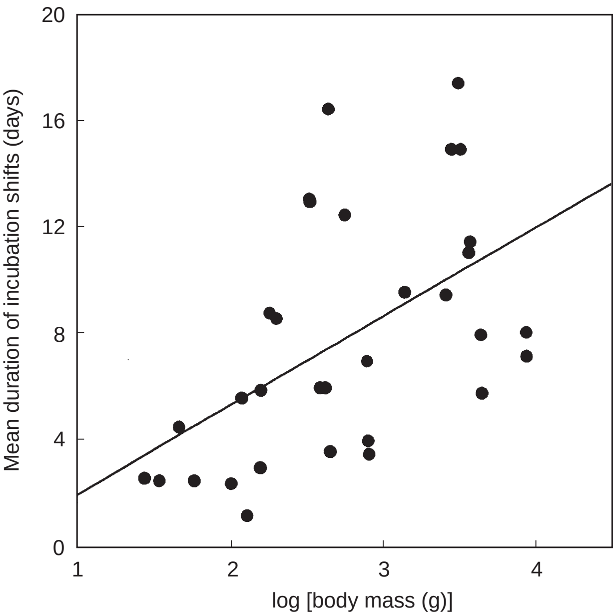

Figure 4 The relationship between body mass and incubation shift length in 32 species of petrel. (Data from Table 14.1 and 15.4 in Warham (1990).)

If for whatever reason the foraging bird does not return sufficiently quickly, the incubating bird may head to sea before its partner returns, leaving the egg unattended. Such eggs are vulnerable to predators, especially in surface-nesters, but they can remain viable for many days without further incubation (up to 23 days in Madeiran storm-petrel *Oceanodroma castro* at the Galapagos Islands). This resistance to adverse effects of chilling may be a major adaptation of petrels to pelagic foraging, permitting them to nest far from their main food sources. However, cooling of the embryo does retard growth, resulting in a delay in hatching.

Like embryos before hatching, petrel chicks grow slowly for their size. This results in petrels having very long breeding seasons, with two extremes for the period from egg-laying to chick-fledging being 125 days in snow petrels *Pagodroma nivea* and 380 days in wandering albatrosses. Petrel chicks also accumulate very large quantities of nonstructural body fat during posthatching development (up to 30% of body mass in northern fulmars). This results in chicks attaining peak body masses far in excess of adult body mass (up to 170% of adult mass in yellow-nosed albatross *Diomedea chlororhynchos*) before losing mass prior to fledging.

Newly hatched petrel chicks are unable to regulate their own body temperatures and they are brooded more or less continuously for the first few days after hatching. Small chicks also have limited gut capacity and so, during this period, they are fed small meals several times a day by the attending

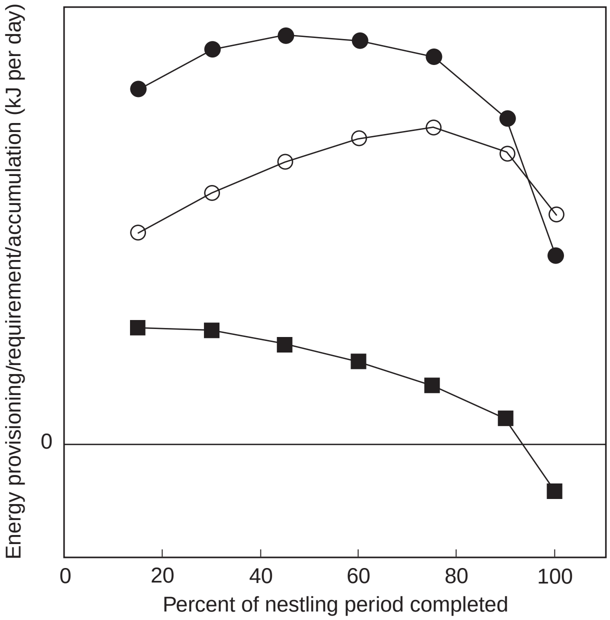

Figure 5 A generalized scheme for the relationship between food provisioning and growth of petrel chicks. Solid circles indicate mean energy provisioning rate (more or less independent of chick age except at the end of the nestling period): open circles indicate mean daily energy requirement (determined by body mass and structural (lipid-free) growth rate, and reaching a maximum after about 75% of the nestling period): solid squares indicate net rate of accumulation of energy within the body (about 70% of the difference between provisioning rate and requirement when growth is positive; $>100\%$ of the difference when growth is negative). N.b. In some species, despite a drop in energy provisioning rate at the end of the nestling period, supply does not fall below energy requirement, and so chicks continue to accumulate energy, principally as body fat, until fledging.

parent. Once chicks gain thermal independence, they are left unattended for most of the time while both parents forage simultaneously at sea. This change in parental attendance is accompanied by an increase in meal size and a decrease in feeding frequency. For most of the nestling period, parents deliver meals weighing 5–35% of adult body mass (proportionately smaller in heavier species) to the chick. Overall feeding frequency, resulting from provisioning by both parents, is generally between one meal every two days and two meals per day (higher in fulmars and diving petrels than in other species). Feeding frequency then declines at the end of the nestling period, so that in most cases total food delivery is insufficient to meet the chick's nutritional requirements (**Figure 5**). Chicks thus enter negative energy balance and lose mass as they presumably deplete their fat stores. However, northern fulmar chicks continue to accumulate fat until fledging, and their prefledging drop in body mass is due entirely to the loss of water from embryonic tissues as they attain full size and functional maturity. Grey-headed albatrosses *Diomedea chrysostoma* show a similar pattern, and further data are required to determine how prefledging declines in body mass relate to changes in body fat in other species.

Large fat stores were until recently thought to provide chicks with an energy reserve to tide them over long intervals between feeds. However, in many species, the intervals between feeds are too short to account for the quantities of fat stored, and the combined cumulative effects of variability in both feeding frequency and meal size are probably more important than long intervals *per se*. Fat stores may also be important to chicks after fledging, while they learn to forage for themselves, and this view is supported by the fact that northern fulmars have larger fat stores at fledging than at any previous time. In addition to body fat, petrel chicks also store large quantities of stomach oil, which acts as a convenient energy store and is metabolically more efficient than converting the oil into body fat.

Reproductive Effort

Petrels are long-lived and so they need to balance the requirements of current and future reproduction in order to maximize their lifetime reproductive output. During chick-rearing, they need to judge how much energy to invest in the chick without impairing their own ability to breed again. In species that make long foraging trips and feed their chick comparatively infrequently, this seems to be achieved by adults delivering food according to an intrinsic rhythm that is sensitive to changes in the parent's body condition but not to changes in the chick's nutritional requirements. Other species that make shorter trips on average appear to monitor the chick's nutritional status and will reduce subsequent food delivery to a well-fed chick. However, experimental evidence indicates that they either cannot or do not increase food delivery to a chick in poor condition. Moreover, experimental manipulations that increase the work that adults need to perform to obtain food generally result in a reduction in the rate of food provisioning of the chick rather than a decline in the parent's nutritional reserves. In some species, adults also adopt a dual foraging strategy, in which comparatively short trips undertaken to obtain food for the chick are interspersed with less frequent long trips on which adults obtain food for themselves. The switch between short and long trips seems to be determined by a threshold body condition, below which adults forage only for themselves. In some cases the areas of ocean visited on short and long trips are far apart. For instance, short-tailed shearwaters breeding in SE Australia forage comparatively close to the colony to obtain food for their chick but obtain food for themselves in the highly productive waters of the Polar Frontal Zone at least 1000 km away.

Conservation

Petrels are adversely affected by a wide range of factors related to human activities, including ingestion of plastic particles and exposure to a wide variety of marine pollutants, but, historically, introduction of alien mammals to remote breeding colonies has been perhaps the greatest threat to petrel populations, with the greatest impacts being due to introductions of cats *Felis catus* and rats *Rattus* spp. Small species of petrels have been particularly affected, but even large species such as albatrosses have not been immune. Eradication programs have been developed to remove introduced mammals from a number of islands where petrels breed, especially in the southern hemisphere, and these have met with some success. For instance Marion Island, in the sub-Antarctic Indian ocean, was cat-free prior to 1949, when five cats were introduced as pets. By 1975 the cat population had risen to about 2000 individuals consuming 450 000 burrowing petrels annually. An eradication program was started in 1977, when the cat population was over 3000 individuals, and by 1993 there were no signs of live cats on the island. The elimination of cats resulted in a marked increase in the breeding success of several species of petrel, although a combination of small populations and delayed maturity has resulted in only slow population recoveries. It should also be noted that on islands that have been colonized by more than one species of predator, eradication of one species could lead to a disproportionate increase in other species, to the detriment of petrels. This is likely to be a particular problem with eradication of cats from islands that have also been colonized by rats.

One of the major current threats to petrel populations, especially in the southern hemisphere, is longline fishing using baited hooks to catch demersal and pelagic fish, particularly tuna and Patagonian toothfish *Dissostichus eleginoides*. Petrels can be drowned after striking at baited hooks and, while the rate of by-catch is generally very low, the large number of hooks set means that total mortality can be sufficient to reduce population sizes of some species. For instance, the Japanese pelagic longline fishery for southern bluefin tuna *T. maccoyi* deployed up to 100 million hooks or more annually during the 1990s. In Australian waters, the average rate of sea bird by-catch from this fishery was 1.5 birds per 10 000 hooks set, but this resulted in an annual mortality of up to 3500 birds per year. Longline fishing operations have been implicated in serious population declines of a number of albatrosses, including wandering albatross, grey-headed albatross, black-browed albatross *Diomedea melanophrys*, yellow-nosed albatross, and light-mantled sooty albatross *Phoebetria palpebrata*. Some populations have declined by as much as 90% and are facing imminent extinction if current catch rates are not reduced.

See also

Ecosystem Effects of Fishing. Fishery Management, Human Dimension. Fishing Methods and Fishing Fleets. Fisheries: Multispecies Dynamics. Krill. Network Analysis of Food Webs. Seabird Foraging Ecology. Seabird Migration. Seabird Population Dynamics. Seabird Reproductive Ecology. Seabirds and Fisheries Interactions.

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