

Order PROCELLARIIFORMES

A rather distinct group of some 80–100 species of pelagic seabirds, ranging in size from huge to tiny and in habits from aerial (feeding in flight) to aquatic (pursuit-diving for food), but otherwise with similar biology. About three-quarters of the species occur or have been recorded in our region. They are found throughout the oceans and most come ashore voluntarily only to breed. They are distinguished by their hooked bills, covered in horny plates with raised tubular nostrils (hence the name Tubinarae). Their olfactory systems are unusually well developed (Bang 1966) and they have a distinctly musky odour, which suggest that they may locate one another and their breeding places by smell; they are attracted to biogenic oils at sea, also no doubt by smell. Probably they are most closely related to penguins and more remotely to other shorebirds and waterbirds such as Charadriiformes and Pelecaniiformes. Their diversity and abundance in the s. hemisphere suggest that the group originated there, though some important groups occurred in the northern hemisphere by middle Tertiary (Brodkorb 1963; Olson 1975).

Structurally, the wings may be long in aerial species and shorter in divers of the genera *Puffinus* and *Pelecanoides*, with 11 primaries, the outermost minute, and 10–40 secondaries in the Oceanitinae and great albatrosses respectively. The tail varies in length, being forked in *Oceanodroma*, forked to pointed in other forms, usually with 12 rectrices but up to 16 in fulmars. The tarsi are light and cylindrical in aerial forms; strong and laterally compressed with legs set far back in aquatic ones. The front toes are webbed; hind toe small or absent. The proventriculus is long and glandular; the gizzard small and twisted; and the small intestine often spiral in *Pterodroma*, presumably to aid absorption of the unusual lipids in their food. Chicks are helpless and covered in down, with two coats except in some Oceanitinae. Some larger species have a darker immature plumage, and the female is often darker than the male in the great albatrosses. The male is usually larger than the female, though smaller in the Oceanitinae and some other small species. Otherwise there is little difference in appearance with sex or age, except that young birds may have more pronounced pale or dark edges to the feathers. Many have simple counter-shaded markings that often appear to have given rise to uniformly dark or, less often, to pale derivatives; some species in most groups are dimorphic or polymorphic. The more complex groups have often developed distinctive markings of the extremities.

Breed more or less colonially on offshore islands, coastal cliffs, or on hills and deserts inland, where they perform complex vocal and aerial displays. The nest is a simple scrape or cup in a burrow or natural hole, sometimes under vegetation. The s. albatrosses build large cone-shaped nests in the open; may be lined with any debris available in the area. Smaller species visit it only at night, though larger ones and those breeding on remote islands may come to nests in the open by day. Parents incubate for spells of several days in turn and generally leave the chick alone soon after it hatches, only returning at long intervals to feed it by regurgitation. In consequence the chick is vulnerable to introduced predators and some species are now greatly reduced and at least two are now extinct. Some species also periodically liable to have unsuccessful breeding seasons. Many young or even old birds may be wrecked ashore and die when they meet bad weather or suffer shortage of food on migration or in the winter. Though it has been claimed that they are also vulnerable to all sorts of pollution, the evidence is weak (Bourne 1976). There is at present anxiety about the effect of some fishing methods, such as long-lining, which may be endangering species such as the great albatrosses.

All species feed at sea on a variety of fish, cephalopods and small marine invertebrates, either socially or alone; larger species may scavenge all sorts of offal or prey on other birds. Most, except perhaps *Pelecanoides*, can digest the complex lipids formed by some marine animals (Clarke & Prince 1976), and may eject them to soil the plumage of their enemies with lethal results (Swennen 1974). Some species can digest wax (Obst 1986). Many now take wastes from whaling and fishing operations (Fisher 1952). All have long life-cycles in proportion to their size; they disperse on fledging and then prospect for nest-sites for 2–12 years in their youth. They usually lay a single large white egg annually; though a successful breeding cycle may be completed in less than a year in at least one tropical species, *Puffinus lherminieri*, it may take 2 years in larger southern ones. Before laying, the birds court for weeks or months, then go to sea for feeding. Incubation lasts 6–8 weeks, and fledging 2–9 months. Once the fat chick fledges it fends for itself, even in species that immediately make a long migration, sometimes to the opposite hemisphere.

Tendency for failed breeders and non-breeders to begin moult before successful breeders. Five strategies of wing-moult in breeding adults: (1) In albatrosses, remiges replaced in staffelmauser interrupted while breeding; in nearly all other species, primaries moulted outwards; possibly simultaneously in some diving-petrels. (2) In most subantarctic and temperate species, moult begins soon after breeding and is completed shortly before next breeding season. (3) In most tropical species, moult aseasonal, between breeding attempts; resumption of breeding apparently depends on when moult completed. (4) In trans-equatorial migrants, wing-moult delayed until they reach non-breeding quarters, where it is completed; moult rapid but no satisfactory evidence for flightlessness. In

some species, body-moult also in winter quarters; in others, at breeding grounds. (5) In some species of high latitudes, rapid moult completed in summer when they breed; some begin moult long before breeding finished.

The history of the classification of the Order is very confused, as is seen by comparing Timmermann's (1965) discussion of their Mallophagan parasites with that by Klemm (1969) of their leg muscles and that by Harper (1978) of their proteins, but it is now widely agreed that the Order is best divided into four families: Diomedeidae or large to huge aerial albatrosses; Procellariidae or medium-sized, mainly aerial but sometimes aquatic, petrels, shearwaters and prions; Hydrobatidae or small to tiny, aerial storm-petrels; and Pelecanoididae or small aquatic diving-petrels.

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Family PROCELLARIIDAE fulmars, petrels, prions, shearwaters

The family Procellariidae represents the main radiation of medium-sized 'true petrels', characterized by having united nostrils with a median septum and the outer functional primary at least as long as the next. It tends to be dominant among the birds of the Southern Ocean, though in the n. hemisphere the Charadriiformes are more numerous. The giant-petrels *Macronectes* have also developed as large scavengers and predators, showing some convergence in appearance and behaviour with the Diomedidae. The Procellariidae may be divided into four main groups with some intermediate species, which makes it hard to draw distinctions between them.

(1) The fulmars *Macronectes*, *Fulmarus*, *Thalassoica*, *Daption* and *Pagodroma* consist of seven species of surface predators and filter-feeders of rather varying structure and appearance (Voous 1949) that breed in high latitudes but may migrate along cool currents into much lower ones. *Fulmarus* appears to have colonized the n. hemisphere in the Tertiary. Six of the seven species are essentially confined to our region.

(2) The gadfly-petrels *Pterodroma* are a large series of some 30 agile species; 16 breed in our region and another six occur rarely or rather rarely. Their short sturdy bills are adapted for seizing soft prey at the surface, and their twisted intestines, for digesting marine animals with an unusual biochemistry, which are also found throughout the warmer oceans (Imber 1985). They show complex markings of face and wings that must serve as interspecific recognition-marks (Murphy & Pennoyer 1952). Some species placed in this group have an intermediate structure and intergrade with all other groups distinguished here: *Pterodroma (Lugensa) brevirostris*, which moves S in winter, has distinctly big eyes like *Pagodroma*; *Halobaena caerulea* has a plumage similar to that of prions; *Bulweria* has some structural resemblance to shearwaters. At present it is difficult to determine their precise relationships.

(3) The prions *Pachyptila* are a specialized group of six (perhaps five) very numerous species, all in our region, that show a progressive adaptation of a small, agile, cryptically coloured, fulmarine form for filter-feeding on zooplankton. There has been dispute over their classification (Cox 1980; Harper 1980) but the arrangement discussed by Fleming (1941) seems best except that the Broad-billed Prion *P. vittata* appears to intergrade with Salvin's Prion *P. salvini* through *macgillivrayi* of Ile St Paul; so they may be better treated as subspecies of the same species.

(4) The shearwaters *Procellaria*, *Calonectris* and *Puffinus* include some 20 agile species with long bills adapted to catch prey more or less under water throughout the warmer seas (Kuroda 1954); 13 species breed in our region, some migrating into the n. hemisphere; six others are chance or perhaps regular visitors. From the fossil record (Brodkorb 1963; Olson 1975); they seem to have been particularly common in the great Tethys Ocean of the middle latitudes of the n. hemisphere in the Tertiary, so this development of aquatic habits may have occurred there without competition from penguins with a subsequent return S by the more successful forms.

General features of the family are: body, ovate, or elongate in shearwaters; wings, long and narrow, 11 primaries, p10 longest, p11 minute; 20-29 secondaries, short, diastataxic; tail, short, 12 feathers; bill, heavy (*Macronectes*), slender (shearwaters), broad (prions) or stubby (gadfly-petrels), hooked, formed of several horny plates; nostrils in dorsal tube of varying length; legs set far back, laterally flattened but round in gadfly-petrels; three toes, webbed, hind toe vestigial, raised. Oil-gland feathered. Peculiar musky odour. Sexes similar, male usually larger than female. Plumage, black or grey above, white below, or all dark; light and dark morphs in some species. Juveniles and immatures usually like adults.

Cosmopolitan throughout the oceans, essentially pelagic; more abundant in cool or cold waters rich in plankton and mostly away from ice. Swim well but usually aerial except when feeding or resting. Fly with alternate swooping and flapping action close to the surface but often arcing high in some gadfly-petrels. Gait on land, a shuffling crouch, being unable to walk properly with feet set so far back; generally avoid open areas on land, being thus vulnerable to predators. Nest colonially; for the most part in burrows and cavities in all sorts of terrain, sometimes far from the sea and in mountainous areas but some species, e.g. *Macronectes*, nest on open ground. Hole-nesters usually nocturnal at colonies, when often extremely vocal, though generally silent at sea. Migratory and dispersive. Some species divide the year between s. and n. hemisphere, often migrating in large flocks that may settle on the sea in huge dense rafts. Feed mostly on fish, cephalopods and crustaceans obtained by flight-feeding, plunge-diving, surface feeding, surface-diving and underwater pursuit; hydroplaning (Murphy) is a characteristic method used particularly by prions.

Probably all defend small nesting territories to which they return regularly while undisturbed; certainly so in some hole- and burrow-nesting forms. Agonistic and sexual behaviour of nocturnal, hole-nesting species very poorly known but generally seem to have little specialization for visual displays. Tactile actions such as allopreening and billing used but olfactory and vocal communication is probably important. Breeding is usually seasonal, generally with synchronized laying, often after a pre-laying exodus but some may not nest annually; some have shorter

cycles or nest continually. For the most part, little attempt to make substantial nests. Eggs, ovate, mat, white. Clutch-size, invariably one; single-brooded; no replacement laying. Incubation by both sexes in alternate spells of 1-11 days. Single median brood-patch. Incubation period, 45-55 days. Eggshells probably always trampled in nest. Young, semi-altricial, nidicolous; hatched in down. Rarely left alone in nest for first 1-2 weeks. Cared for and fed by incomplete regurgitation by both parents. Nestling period generally shorter in cliff- and ledge-nesting species than in hole-nesters. Young attain greatest weight, often well above that of adult, some days before fledging, by which time weight has been reduced to about the same as an adult, but no clear evidence that young are totally deserted for last few days in nest. Adults and young of most species liable to eject stomach-oil in defence. Young independent at fledging. Maturity reached at minimum of 3-4 years, in some 6-12 years.

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Pterodroma macroptera Great-winged Petrel

COLOUR PLATE FACING PAGE 401

Procellaria macroptera A. Smith, 1840, *Ills Zool. South Africa, Aves* 2: Pl. 52 — Cape seas.

The generic name is compounded of the Greek πτερόν (feather, winged creature) and δρόμος (running), i.e. the wing-runner; the specific, of μακρός (long) and πτερόν i.e. long-winged.

OTHER ENGLISH NAMES Great-winged, Grey-faced or Long-winged Fulmar or Petrel, Muttonbird.

POLYTYPIC Nominate *macroptera* breeds Gough, Tristan da Cunha, Prince Edward Is, Iles Crozet, Iles Kerguelen, and on islands off sw. Australia; *gouldi* (Hutton, 1869) North Island of New Zealand.

FIELD IDENTIFICATION Length 38–43 cm; wing-span 97–102 cm; weight 460–750 g. Large all-dark gadfly petrel with varying pale face; very similar in size and shape to Providence Petrel *P. solandri*. Typical *Pterodroma* jizz: large chunky black bill, large well-rounded head, thick neck set on thickset body, tapering to longish, gently wedge-shaped tail (usually held folded, appearing pointed); wings, long, narrow, finely pointed, with carpal joints held well forward; strong buoyant arcing flight. Sexes alike. No seasonal changes. Juveniles may be separable by bill-colour and freshness of plumage (see Plumages etc.).

DESCRIPTION Nominate *macroptera*. **ADULT.** Generally, no outstanding markings. Head and neck, blackish brown, slightly paler and greyer round base of bill, on chin

and upper throat, blending into darker plumage of head; face sometimes appears silvery in strong light (recalling *gouldi*). Grey reduced with wear, forehead and lores brownish and chin and throat only faintly paler than rest of head; many appear dark-faced. Upperparts, uniform blackish-brown with indistinct silvery bloom on greater secondary coverts (rapidly lost with wear). Underbody, uniform blackish-brown. Underwing: blackish brown; remiges and greater coverts, slightly paler greyish black, glossy (palest on bases of primaries and greater coverts); in strong light, shows diffuse silvery area on bases of primaries and greater primary coverts, divided by indistinct dark line (dark tips of greater primary coverts). Whole plumage wears browner; white bases of feathers on breast and belly may be exposed with wear, appearing as ir-

regular pale patches or rarely, breast and belly, wholly white. Bill, large and chunky with strongly hooked nail and prominent tubed nostrils; black with varying whitish or horn-coloured patches on bases of unguis. Iris, dark brown. Legs and feet, black. **Subspecies gouldi**. ADULT. Like nominate except pale-grey face more pronounced, better defined and larger, covering whole of forehead, lores, forecheeks, chin and throat; with wear, pale-grey face, smaller and faded; some may appear like fresh *macroptera* but apparently never wholly dark-faced.

SIMILAR SPECIES **Providence Petrel** identical in size, shape and flight but distinguished by (1) steely-grey dorsum with dark M-mark across upperwings and dark hood contrasting with grey saddle and paler grey-brown belly; (2) large clear-cut whitish oval-shaped patch on bases of primaries and greater primary coverts on underwing, clearly divided by dark tips of greater coverts; (3) do not moult remiges in sw. Pacific waters during Feb.–Dec. (D.W. Eades). **Dark-morph Kermadec Petrel** *P. neglecta* slightly smaller with shorter broader wings and shorter squarer tail; bill, smaller more delicate; bold white patch on bases of primaries and greater primary coverts on underwing, clearly divided by dark tips of greater coverts; white shafts of primaries form diagnostic pronounced skua-like flash on upperwing; flight, usually slower, more leisurely, less bounding. **Dark-morph Herald Petrel** *P. arminjoniana* slightly smaller with slimmer body, narrower wings and smaller, more delicate bill; underwing varies: on some, lining wholly dark like Great-winged but normally with narrow white leading-edge to innerwing, often mottled and hard to see; sometimes a little white on bases of greater primary-coverts; as well, others have diffuse silvery area on wing-tip which, unlike Great-winged, continues inward as diffuse tapering silvery line along bases of greater secondary coverts and contrasting strongly with dark lining. **Kerguelen Petrel** *P. brevirostris* about one-third smaller with different jizz: steep forehead, larger head and thicker neck, on slimmer body; wings narrower with carpal joints usually not held so far forward, giving straighter-winged jizz; looks slaty- or brownish-grey with glossy sheen, not blackish brown; head often appears darker than body, giving hooded appearance; underwing very different: pronounced silvery-white band along leading-edge of underwing between carpal joint and body and large silvery wing-tip contrasting strongly with dark of lining; flight similar except for distinctive sustained bouts of gliding, soaring, floating and tern-like circling at great heights during windy conditions; in calm conditions, flight more bat-like and weaving with faster flickering wing-beats. **Dark-morph Soft-plumaged Petrel** *P. mollis* about one-third smaller and more compact with smaller more delicate bill; dark grey above with narrow dark open M-mark; has distinct black patch under eye contrasting with greyer cap; many retain dark chest-band effect of light-morph, which offsets paler chin and throat and contrasts with slightly paler greyish belly, vent and flanks. **Wedge-tailed** *P. pacificus* and **Flesh-footed** *P. carneipes* **Shearwaters**, similarly hold carpals well forward but have less buoyant flight, with more flapping, lower peaks of arcing and fewer, less sudden changes of direction; bill, longer, more slender and paler; less thickset jizz.

Highly pelagic; also common along shelf-breaks and range into outer continental-shelf waters. Occasionally seen well inshore or from land during onshore gales. Flight in high winds, swift and strong, towering well above horizon in characteristic pendulum-like progression. In light winds or calms, flight less bounding, like that of larger *Puffinus*

shearwaters but more buoyant, with less flapping, higher peaks and lazy meandering progression. Periods of gentle arcing and turning broken by short bursts of purposeful flapping when rising into arcs; flapping action strong and steady, with high upstroke recalling that of gulls *Larus* spp; accelerates when flying over breeding places and at sea with urgent powerful action of high upstroke and brief pause before deep downstroke. At breeding places, ride updrafts produced above cliffs in strong to gale-force onshore winds. Rarely follow ships, but often approach beam and turn away. Attend trawlers in large numbers for scraps, following persistently. Feed mainly at night with some scavenging by day; feed by surface-seizing and dipping; associate with cetaceans. Usually solitary at sea except in loose parties at food and round trawlers. In calm conditions, may loaf on sea in flocks (up to 50). When attending trawlers, typically form tight rafts, away from other procellariiforms (D.W. Eades). Swim well, showing characteristic silhouette resulting from buoyant carriage, large well-rounded profile of head, and stubby black bill. Awkward on land, with waddling gait. At breeding grounds, form flocks for courtship or display. Silent at sea; noisy at breeding colonies where main calls include squeaky *kik-kik-kik* in flight, sibilant *si-si-si*, gruff *quaw-er* and braying *eee-aw*.

HABITAT Marine, pelagic; in subtropical, subantarctic and, less often, in open Antarctic waters. Tolerate wide range of sea surface-temperatures (2–24 °C; Bierman & Voous 1950; Szijj 1967; Jenkins 1971), but in A'sian waters, normal feeding and breeding range, subtropical (Imber 1973a); observed by Falla (1937) in Tasman Sea, Southern and Indian Oceans only where sea surface-temperature > 14 °C; in Tasman Sea, may concentrate over intrusions of warm water, 22–24 °C (Jenkins 1971). Widely but sparsely distributed over pelagic waters, exploiting prey at moderate to low densities; not observed to concentrate at upwellings of nutrient-rich water (Imber 1973a); but at Iles Crozet, may be excluded from areas of high food concentration over continental shelf by competition with other petrels, particularly White-chinned *Procellaria aequinoctialis* (Stahl *et al.* 1985). Breed subtropical and subantarctic islands, on islands round NZ coast, on headlands of NZ mainland; on ridges, cliffs, scoria cones, peninsulas and slopes of soil, sand or talus; coastal or inland, and usually below 400 m asl (but on Tristan da Cunha up to 1400 m asl, on Gough I. up to 760 m) (Swales 1965; Richardson 1984). Nest in burrows, scrapes or crevices of rocks under forest, scrub, shrubs, tussock grass or low succulents (Rand 1954; Skegg 1963, 1964; Fullagar 1978; Kolichis & Abbott 1978; Abbott 1981; Schramm 1983; Smith & Johnstone 1987). Fly high above sea, soaring to heights of 18–24 m (Barton 1977); reach heights of 60 m on return flights to breeding islands (Warham 1956). Feed from sea surface (Harper 1987).

On settled breeding islands, may continue to nest near buildings (Fullagar 1978); once incubating on floor of building (Abbott 1978a). On Eclipse I., WA, nest among dense growth of introduced arum lilies (Warham 1956).

DISTRIBUTION AND POPULATION Based on information supplied by M.J. Imber. Pelagic; from mid-S. Atlantic Ocean, s. Indian Ocean, Tasman Sea and sw. Pacific Ocean to as far E as 130°W. (J.A.F. Jenkins; Fleming 1950); usually between 30–50°S in S. Pacific; in Tasman Sea, between 27–47°S (Imber 1976; Harrison 1987; D.W. Eades). Occur regularly off s. tip of Africa; accidentally off e. coast of S. America.



During winter distribution farther N: near Iles Crozet ranges up to 32°S during Sept. compared to 41° S in Feb. (Jouventin *et al.* 1982).

AUST. Seen on all coasts within latitudinal range. **Qld.** Probably moderately common in se. waters; c. 32 beachcast specimens recovered all months except Aug. and Oct. (Roberts 1979). **NSW.** Common visitor, recorded all months, frequently seen Oct.–Dec., beachcast birds most common Oct.–Apr. (Morris *et al.* 1981; M.J. Imber; NSW Bird Rep. 1984). **Vic.** Recorded in all seasons (Vic. Atlas). **Tas.** Common visitor; occasionally beachcast (Green 1989). **SA.** Small numbers (Cox 1976). **WA.** Common, breeding; occurs offshore most months, beachcast birds most common in spring (HASB).

NZ Abundant in N; breeds NI; most common breeding petrel.

BREEDING

Table 1.

Locality	Year	Population (pairs)	Ref.
Prince Edward Is			
Marion I.	1979–80	>60	1
Prince Edward I.		10s of 1000s	2
Iles Kerguelen		100 000–200 000	3
Iles Crozet	1981–82	10s of 1000s	4
Ile de la Possession	1981–82	10s	4
Ile de l'Est	1981–82	10s of 1000s	4
Ile des Pingouins			4
Ile des Apôtres			4
AUST.			
WA			
Recherche Arch.			
Middle I.	1976	c. 50 nests	5

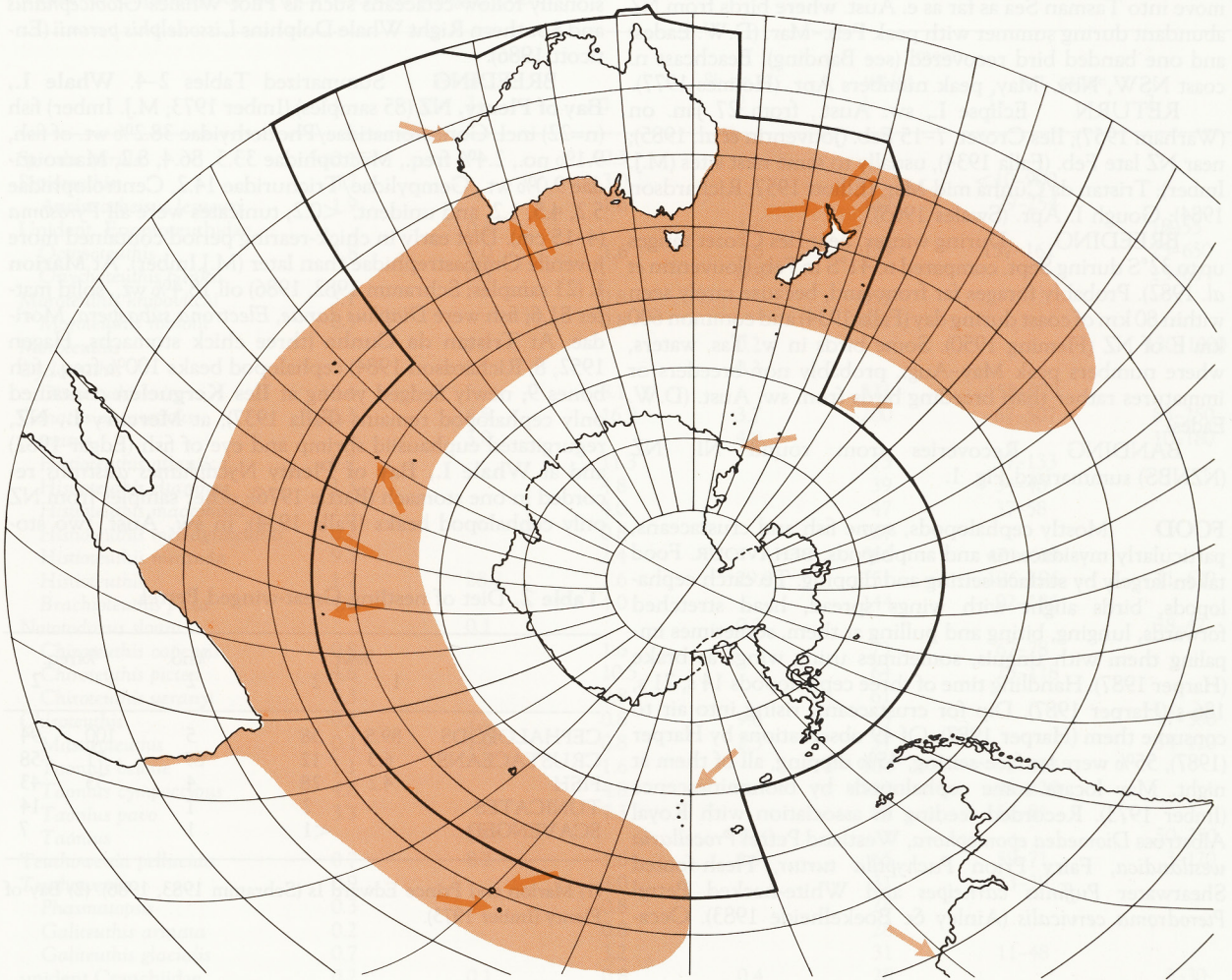
Christmas I.			
Goose I.			
Termination I.			
Boxer I.			4
Figure of Eight I.	1950	>250 nests	6
Hood I.	1981–82	>250 nests	7
Ben Pasley I.		possibly abundant	
Bald I.	1976	abundant	8
Coffin I.	1976–79	c. 2000–3000	9
Gull I.	1977	15–20	10
Rabbit I.			11
Remark I.	1981	few	12
Breaksea I.	1975	few	13
Eclipse I.	1973	10 000–15 000	14
Mistaken I.	1975	possibly	15

NZ

NI. On headlands and cliff-tops and on most islands and islets from Three Kings Is in N to near New Plymouth (39°10'S) on W coast and near Gisborne (38°30'S) on E coast; larger colonies on Hen and Chickens Grp, Mokohinau Grp, Mercury Grp, Alderman Grp, Whale (30 000–40 000 pairs; Imber 1976) and White Is.

References: (1) Schramm (1983); (2) Williams (1984); (3) Weimerskirch *et al.* (1989); (4) Jouventin *et al.* (1985); (5) Tingay & Tingay (1982a); (6) Lane (1982); (7) Tingay & Tingay (1982b); (8) van Tets & Fullagar (1984); (9) Smith & Kolichis (1981); (10) Kolichis & Abbott (1978); (11) Aust. CL; (12) Lane (1982); (13) Abbott (1978a); (14) Fullagar (1978); (15) Abbott (1978b).

Extralimital: breed Tristan da Cunha and Gough I. Now extinct on Ile de la Possession and Ile aux Cochons, Iles Crozet; on Major I., NZ, and possibly on Little Barrier I. (Weimerskirch *et al.* 1989; M.J. Imber).



POPULATION Possibly increased in last 20 years in A'sian region because collection of muttonbirds has declined as has occurred on White I. and Whale I. (M.J. Imber). Suffer heavy predation by feral cats on Marion, Kerguelen and Little Barrier Is., breeding in winter when other food for cats scarce (Imber 1973b; Schramm 1983; Weimerskirch *et al.* 1989); colony on Little Barrier I. almost eliminated (Imber 1973b). Black Rats *Rattus norvegicus* eat neglected eggs on Whale I. (Imber 1984).

MOVEMENTS Dispersive or migratory, though seen near breeding islands throughout year.

DEPARTURE Young fledge from Ile de l'Est, Iles Crozet, 4 Nov. (14 days; 16 Oct.-11 Dec.; 3 days; Jouventin *et al.* 1985); Tristan da Cunha, mid-Nov. (Elliott 1957; Richardson 1984); Iles Kerguelen, late Nov. (Falla 1937); Eclipse I., WA, late Nov. (Warham 1956; Cheah & Hansen 1970); Whale I., NZ, after 6 Dec., mostly in last 10 days of Dec. (Imber 1976). Immatures may leave Tristan da Cunha first week Aug. (Richardson 1984).

NON-BREEDING Absent from Iles Crozet, mid-Dec. to early Feb. (Jouventin *et al.* 1985) though population still concentrated nearby (Stahl *et al.* 1985; Jouventin *et al.*

1982). Moulting non-breeders and probably failed breeders thought to move to s. edge of range in NZ waters (about 45°-48°S) Nov.-Dec. (M.J. Imber) and peak numbers beachcast NZ beaches Jan.-Feb., possibly inexperienced juveniles (Powlesland 1987). Much of NZ population, however, appears to



Fig. 1. 37S 176E 10X10 NZNBS

move into Tasman Sea as far as e. Aust. where birds from NZ abundant during summer with peak Feb.-Mar. (D.W. Eades) and one banded bird recovered (see Banding). Beachcast n. coast NSW, Nov.-May, peak numbers Apr. (Holmes 1977).

RETURN Eclipse I., sw. Aust., from 27 Jan. on (Warham 1957); Iles Crozet, 7-15 Feb. (Jouventin *et al.* 1985); near NZ late Feb. (Falla 1934), usually to same nest sites (M.J. Imber); Tristan da Cunha mid-Mar. (Elliott 1957; Richardson 1984); Gough I. Apr. (Swales 1965).

BREEDING During winter, near Iles Crozet ranges up to 32°S during Sept. compared to 41°S in Feb. (Jouventin *et al.* 1982). Probably forages far from land, because rarely seen within 80 km of coast during day (Falla 1934) and common 600 km E of NZ (Fleming 1950). Some birds in w. Tas. waters, where numbers peak May-Aug., probably non-breeders or immatures rather than breeding birds from sw. Aust. (D.W. Eades).

BANDING Recoveries from round NI, NZ (NZNBS) summarized Fig. 1.

FOOD Mostly cephalopods, some fish and crustaceans, particularly mysidaceans and amphipods. **BEHAVIOUR.** Food taken largely by surface-seizing and dipping. To catch cephalopods, birds alight with wings spread, head stretched forwards, lunging, biting and pulling at them, sometimes impaling them with unguis, sometimes using wings as brake (Harper 1987). Handling time of three cephalopods 14 s, 71 s, 186 s (Harper 1987). Dip for crustaceans, rising into air to consume them (Harper 1987). Of 49 observations by Harper (1987), 55% were surface-seizing, 45% dipping, all of them at night. May locate some cephalopods by bioluminescence (Imber 1973). Recorded feeding in association with Royal Albatross *Diomedea epomophora*, Westland Petrel *Procellaria westlandica*, Fairy Prion *Pachyptila turtur*, Flesh-footed Shearwater *Puffinus carneipes* and White-necked Petrel *Pterodroma cervicalis* (Ainley & Boekelheide 1983). Occa-

sionally follow cetaceans such as Pilot Whales *Globicephalus* and Southern Right Whale Dolphins *Lissodelphis peronii* (Enticott 1986).

BREEDING Summarized Tables 2-4. **Whale I., Bay of Plenty, NZ** (85 samples) (Imber 1973; M.J. Imber) fish (n=22) incl. Gonostomatidae/Photichthyidae 38.2% wt. of fish, 9.1% no., 2.4% freq., Myctophidae 33.5, 86.4, 8.2, Macrouridae 9.0% wt., Gempylidae/Trichuridae 14.2, Centrolophidae 5.2, 4.5, 1.2, and unident. <0.2; tunicates were all *Pyrosoma* (4-15 cm). Diet early in chick-rearing period contained more juvenile Ommastrephidae than later (M.J. Imber). At **Marion I.** (21 samples; Schramm 1982, 1986) oil 18.4% wt., solid matter 81.6; fish were *Diaphys danae*, *Electrona subaspera*, Moridae. At **Tristan da Cunha** (three chick stomachs, Hagen 1952; 8, Richardson 1984) cephalopod beaks 100% freq., fish bones 9; newly fledged young at **Iles Kerguelen** contained only cephalopod remains (Falla 1937); at **Mercury I., NZ**, regurgitated euphausiid shrimp and eye of fish (Edgar 1962) and at **Whale I., Bay of Plenty** *Nyctiphanes australis* recorded in one stomach (Bartle 1976); other samples from NZ only cephalopod beaks (Falla 1934); in **sw. Aust.** two sto-

Table 2. Diet of nestling Great-winged Petrel.

	%wt.		%no.		%freq.	
	1	2	2	1	2	
CEPHALOPODS	89.5	58	5	100	94	
CRUSTACEANS	6.3	12	89	71	58	
FISH	4.2	28	4	33	43	
TUNICATES		2	1		14	
SCAVENGED		<1	1		7	

(1) Marion and Prince Edward Is (Schramm 1983, 1986). (2) Bay of Plenty (Imber 1973).

Table 3. Crustaceans in diet of Great-winged Petrel.

	% wt.		% no.		%freq.	
	1	2	1	2	2	
MYSIDACEANS						
<i>Gnathopausia gigas</i>	48.7	0.7	22.2	0.1	1.2	
<i>Gnathopausia ingens</i>		27.6		0.6	10.6	
AMPHIPODS						
<i>Vibilia</i>		<0.4		3.5	3.5	
<i>Eurythenes obesus</i>	38.5			44.4		
EUPHAUSIID						
<i>Euphausia recurva</i>		9.6		49.5	3.5	
<i>Nyctiphanes australis</i>		7.7		45.5	1.2	
DECAPODS						
<i>Gennades</i>		0.4		0.2	3.5	
<i>Sergestes</i>	6.0	2.2	16.7	0.2	5.6	
<i>Parapasiphae</i>	6.8	14.0	16.7	0.1	16.5	
unident. Pasiphaeidae		1.8		0.1	1.2	
<i>Acanthephyra quadrispinosa</i>		16.2		1.5	22.4	
<i>Notostomus</i>		16.5		0.6	10.6	
<i>Oplophorus novaeseelandiae</i>		1.5		0.2	1.2	
<i>Systellaspis debilis</i>		1.8		0.3	4.7	
Total number			18	1496		

(1) Marion and Prince Edward Is (Schramm 1986). (2) Bay of Plenty (Imber 1973).

Table 4. Cephalopods in diet of Great-winged Petrel.

	% wt.		% no.		mean		2
	1	2	1	2	wt.(g)	wt. range	
<i>Spirula spirula</i>	<0.1		0.3				
<i>Sepioteuthis</i>	6.7		3.0			<10-900	
<i>Ancistrocheirus lesueuri</i>	1.9		1.6		167	79-254	
Unident. Enoploteuthidae		0.6		1.6			18-55
<i>Octopoteuthis</i>	1.8	6.0	1.6	2.6	159	157-161	25-650
<i>Onychoteuthis banksi</i>		0.3		0.8			15-65
<i>Moroteuthis knipovitchi</i>	3.1		0.8		555		
<i>Moroteuthis robsoni</i>	6.3		0.8		1131		
<i>Moroteuthis</i>		1.3		0.2			130-1000
<i>Cycloteuthis</i>		<0.1		0.3			
<i>Discoteuthis</i>	18.4		8.1		331	158-979	
<i>Gonatus antarcticus</i>	23.3	6.5	16.9	3.7	200	67-507	85-250
<i>Gonatus</i>		3.8		4.9			10-180
<i>Histioteuthis atlantica</i>	5.7		11.3		73	37-133	
<i>Histioteuthis eltaninae</i>	1.3		4.8		39	34-40	
<i>Histioteuthis macrohista</i>	1.3		4.0		47	37-58	
<i>Histioteuthis meleagroteuthis</i>	0.7		0.8		127		
<i>Histioteuthis miranda</i>	9.3		2.4		561	471-639	
<i>Histioteuthis</i>	1.7	28.7	1.6	29.9	151	106-196	11-620
<i>Brachioteuthis picta</i>	4.0		4.0		144	92-186	
<i>Nototodarus sloani</i>		0.1		0.3			38-42
<i>Chiroteuthis capensis</i>	0.8		1.6		73	67-78	
<i>Chiroteuthis picteti</i>	4.6		10.5		64	25-118	
<i>Chiroteuthis veranyi</i>	0.3		0.8		61		
<i>Chiroteuthis</i>	0.2	7.2	0.8	9.8	35		17-360
<i>Mastigoteuthis</i>	0.2	1.9	0.8	2.3	34		34-120
<i>Taonius belone</i>	1.1		1.6		101	99-103	
<i>Taonius cympoctypus</i>	4.8		4.8		143	99-220	
<i>Taonius pavo</i>	3.3		7.3		67	54-81	
<i>Taonius</i>		19.6		14.0			50-350
<i>Teuthowenia pellucida</i>	0.7	8.2	1.6	1.9	65	59-71	3-120
<i>Teuthowenia</i>	0.9		4.0		31	23-39	
<i>Phasmatopsis</i>	0.3		0.8		28		
<i>Galiteuthis armata</i>	0.2		0.8		28		
<i>Galiteuthis glacialis</i>	0.7		3.2		31	11-48	
unident. Cranchiidae	0.2	0.1	0.8	0.4	28		5-30
<i>Vampyroteuthis infernalis</i>		<0.1		0.3			
Amphithetridae		<0.1		0.8			
<i>Argonauta nodosa</i>		8.8		10.0			<10-350
<i>Argonauta</i>		0.1		0.4			10-60
<i>Alloposus mollis</i>	3.0		1.6		267	164-364	
unident. Alloposidae		<0.1		0.4			
Total number beaks			124	907			

(1) Marion and Prince Edward Is (Schramm 1986). (2) Bay of Plenty (Imber 1973).

machs contained cephalopod beaks (Cheah & Hansen 1970). Stomach contents of one bird 7.5% lipid though stomach oil only 1.7% lipid (Horgan & Barrett 1985). Stomach oil from chick largely glycerides, about 6% wax esters (Cheah & Hansen 1970).

INTAKE At Iles Crozet visited on 33.2% of nights (12.3; 11.1-55.6; 25 chicks) with 3.25 days between visits (1.61; 1.50-8.74; 222 weighings), chicks gaining 56.7 g (44.1; 0-200; 72) per 24 h weighing period (Jouventin *et al.* 1985); in NZ, fed on 26% of nights at 4-6 weeks old (Imber 1976) and in sw. Aust. on 14.3% nights in latter half of nestling stage (Warham 1956). Mean weight of contents of chicks' stomachs at Marion I., 15.3 g (n=21; Schramm 1986).

SOCIAL ORGANIZATION Usually solitary at sea; form loose parties at sources of food and round trawlers; when calm, sometimes loaf in flocks (up to 50) on sea by day; birds attending trawlers typically form tight monospecific rafts away from other procellariiforms (D.W. Eades). More gregarious at breeding grounds, forming flocks for courtship and display.

BONDS Monogamous; sustained or long-term. If pair repeatedly unsuccessful, may divorce. Earliest age of first pairing recorded, 6 years (M.J. Imber). Courting starts soon after arrival at breeding grounds; on Eclipse I., WA, first aerial chase on 21 Jan. (Warham 1957); in NZ, in Apr. and early May, birds mate, then feed at sea for about 2 months. Male spends

more time than female at colony. Both parents incubate and feed young (M.J. Imber).

BREEDING DISPERSION Colonial. Density varies depending on substrate; friable well-drained, rather deep soil preferred. At Eclipse I., WA, highest density was 23 occupied sites in 400 m² (Fullagar 1978). Defend burrow only.

ROOSTING Infrequently loaf or sleep by day on calm seas, usually in small parties; probably sleep on the wing (M.J. Imber). During breeding, when occupying burrows, sleep all day (M.J. Imber) tucking bill into scapulars (Warham 1956).

SOCIAL BEHAVIOUR Little studied; account based on observations by M.J. Imber. Observation can be difficult as active at night and breed in burrows; incubating birds docile when handled. Displays typical of genus. Occasionally have curious habit of following close behind, and flying in tandem with, other dark procellariiforms, e.g. Northern Giant-Petrel *Macronectes halli*, as if in display (D.W. Eades).

AGONISTIC BEHAVIOUR Non-breeders sometimes settle in burrow of breeding pair, leading to conflict when owners return. Defend burrow against intruders (e.g. other petrels, rabbits) by **THREATENING** with calls; bird lunges towards intruder, exposing pink buccal cavity, and will use its sharp bill to grapple (Warham 1957). Usually, unsuccessful birds retreat but threats can intensify to **FIGHTING**, which may lead to death in serious encounters (M.J. Imber). When **ALARMED** at nest, call repeatedly with *si-si-si* call and body pulsating continually (Warham 1956).

SEXUAL BEHAVIOUR Display begins when birds return to colony and continues until soon after hatching finished (M.J. Imber); in WA, last date of hatching recorded as 9 Sept. (Warham 1957). **Aerial Displays**, apparent pursuit-flights, involve small groups of birds, flying noisily in pairs or trios at high speed and often close together; calls by both groups; occur at dusk or during night (Warham 1956; M.J. Imber). At night, during **PAIR-FORMATION** or **COURTSHIP** of established pair, male and female may **MUTUALLY PREEN** each others' heads, necks, shoulders and occasionally folded wings and along edges of folded wings; also fence with bills; accompanied by braying or *si-si-si* call (Warham 1957). **COPULATION** occurs late Apr. or early May, average 64 days before laying (M.J. Imber). As indicated by Imber (1976) and subsequently shown for other petrels by Hatch (1983), females retain viable spermatozoa in reproductive tract till ovulation at least 25 days after mating (M.J. Imber); achieved by sperm-storage gland in utero-vaginal part (Hatch 1983).

RELATIONS WITHIN FAMILY GROUP Chicks fed by both parents independently, by incomplete regurgitation; during feeding bills crossed at right angles, chick's bill inside that of adult; feeding bout may have 15 feeds. Chicks gape and lunge with beak in self-defence but do not spit oil or

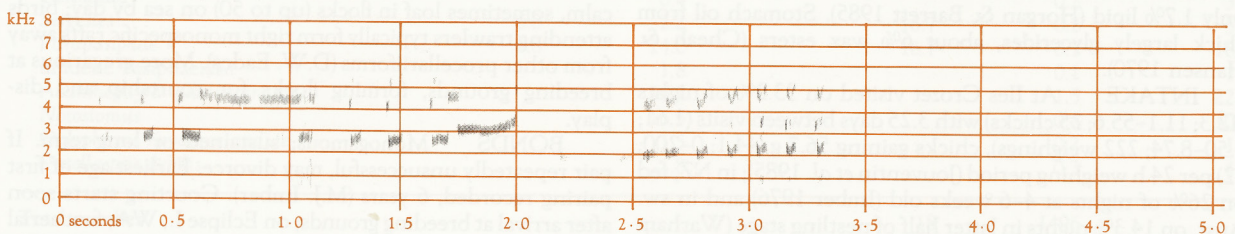
very little; young chicks often disgorge food when handled (Warham 1956). After hatching, chick attended by only one parent (usually female) for 3 days at most; then usually parents visit only during feeding. Older chicks leave burrows to exercise wings, excrete and explore for several nights before departure. Young dependent until departure from colony; parents visit until, or even after, chick leaves (Imber 1976).

VOICE No detailed studies; information from Eclipse I., WA (Warham 1956) and NZ (M.J. Imber, who supplied information). Silent at sea; noisy at night at breeding colonies, mostly in flight but also from ground; will call from burrows during day when observers walk over burrows. Utter several calls; from soft and quiet to loud and harsh. Call from start of breeding season, stopping soon after hatching. In WA, most calling in early evening, just after dark, decreasing later when most birds on ground, though calling continued through night. Calls similar to those of White-headed Petrel *P. lessonii*. Sexual differences have been suggested but not studied. No information on individual differences. Apparently some geographical variation between WA and NZ birds, especially in Flight Call over colonies; no differences reported between NZ colonies (M.J. Imber).

ADULT Flight Call: main call at colonies; in WA, described as sharp squeaky *kik-kik-kik*, each syllable repeated c. 3 times/s (though varying; see sonagram A); variations described as *kee-ik kee-ik* and *kee-ik kukee-ik*; in NZ, main flight call described as *ohi* or *o-hee* or *aw-hee*, first part almost like cooing of pigeon, second part, shrill. Call in NZ reflected in Maori name: *Oi* or *Ohi* (NZCL). **Other calls.** Similar in WA and NZ. (1) Gruff slurred *quawer* (WA) or *bor-r-r* (NZ) while in flight or on ground; given by solitary birds (possibly males); (2) repeated *kek* and squeaks or shrieks by interacting pairs or parties in flight; (3) sibilant *si-si-si* used to threaten intruders (other petrels, rabbits, etc.) or when alarmed; can be repeated between 12 and 20 times; also given during courtship and greeting at nest; heard sometimes during daylight when observers walk over burrows; (4) courting pairs (possibly only male) also give clear braying *eee-aw* (Warham 1956); (5) also loud screeches when intruders enter burrows (see 3).

YOUNG Generally silent. Small chicks beg with chirruping call; older chicks (>60 days) use variation of the *si-si-si* call and hiss when threatened (Warham 1956).

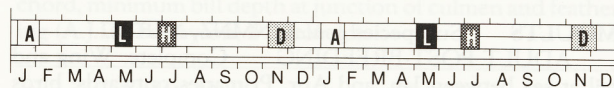
BREEDING Quite well known. Studied by Warham (1956, 1957) in WA, Imber (1976) and Johnstone & Davis (1990) in NZ and Schramm (1983) on Marion I.; also Jouventin *et al.* (1985) on Iles Crozet. Information supplied by M.J. Imber. Colonial breeder, often sharing burrows with Flesh-footed Shearwaters (WA, NZ islands), Sooty Shearwaters and Little Penguins *Eudyptula minor* (NZ islands), all of which breed in summer in contrast to, or in alternation with, winter-



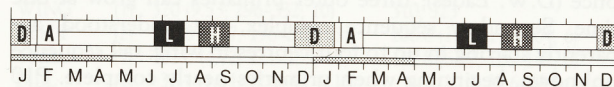
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breeding Great-winged Petrels.

SEASON Autumn-winter breeding; broadly late Feb. to mid-Jan. Birds arrive at colonies: WA, late (27) Jan.; NZ, Feb. (Falla 1934); having been absent for only about 2 months. Pre-laying exodus: WA, no data; NZ, 50–55 days (males), c. 64 (60–80) days (females). Females usually return first after exodus (Johnstone & Davis 1990). Immatures and non-breeders do not show an exodus. Laying: in WA, first week to end May; in NZ, June–July; Marion I., late May. Breeding birds and fledgelings leave: WA, Nov.–early Dec.; NZ, 7 Dec. to c. 20 Jan. with peak 20–30 Dec. Immatures and non-breeders leave: WA, during Aug.; NZ, Sept.–early Oct. (Warham 1956, 1957; Imber 1976; Schramm 1983; M.J. Imber).



a) WA



b) NZ

SITE Burrows in coastal forest, in subantarctic tundra on subantarctic islands. Also on surface under bushes, roots or in niches between rocks, in places in sunlight at some time of day in WA. On Eclipse I., WA, from sea-level to highest point of island; on Whale I., NZ, mostly on dormant volcanic cone, 355 m high. Burrows, 60–125 cm long on Eclipse I., 50–200 cm on Whale I.; on Marion I.; length averaged 1.5 (0.6–2.9) m, diameter of entrance, 14–19 cm, and depth below surface, 53 (30–120) cm. Traditionally used from year to year. Same burrows used by other species breeding in summer (see above). Cave Metas (Orthoptera) usual in burrows in NZ; King Skinks *Egernia kingii* use burrows in WA. If rabbits on breeding islands, they may usurp burrows (see below). Males usually reoccupy and clean burrow first, thus probably selecting it. New burrows rarely dug in established colonies; no data on process of excavation. Density of 23 occupied burrows in 400 m² on Eclipse I. (Fullagar 1978).

NEST, MATERIALS In enlarged chamber at end of burrow. Bowl-shaped structure of twigs, leaves, grass, stems of pigface, Casuarina needles, often substantial but amount varies greatly; sometimes almost none and egg laid on soil. On Eclipse I., entrances to some burrows surrounded with casuarina needles to form sort of collar. Male adds material to nest during courtship-mating period and female does so at start of her main incubation shift, when most building may occur. Material collected at night within 1 m of entrance, being plucked and passed back over shoulder towards entrance, carried in bill later to nest.

EGGS Oval with some degree of pointedness; smooth-shelled, not glossy; white.

MEASUREMENTS.

WA: 66 (64–68; 10) x 47 (46–49)

NZ: 67.5 (60.2–75.3; 79) x 48.3 (45.0–50.7)

Marion I.: 65.6 (2.46; 62.1–69.8; 16) x 48.6 (2.24; 45.4–55.9)

WEIGHTS. NZ: 87.0 (62–103; 159) (M.J. Imber) or 15.5% of post-laying weight of female; Marion I.: 80.8 (5.94; 74.0–90.5; 16).

CLUTCH-SIZE One. Single brooded. No replacement laying.

LAYING WA: no specific dates (see above); NZ, 21 June to 29 July (M.J. Imber), median date varies from 1 to 10 July, averages c. 4 July (Imber 1976; M.J. Imber; D.J. Bettlesworth; R.M. Johnstone). Thus, laying roughly 6–7 weeks earlier in WA (also Marion I. above) than in NZ. Laying at night, nearly always on night of return by female. In NZ, 3–6% of burrows laid in by more than one female (Imber 1976).

INCUBATION Incubation by both sexes, starting with female for c. 4 days on average (0–14) unless male waiting or arrives at time of laying. Three main shifts, averaging 17 days (13–21+), first and third by male, second by female. Loss of weight (8g/day) during shifts, same for both sexes. Sitting bird often remarkably docile, not reacting violently to handling or being touched (Warham 1956). Hatching usually occurs at end of male's second shift; if not, female takes another short shift. Females usually arrive shortly before hatching, having been away for 16.5 days (2.1; 12–21; 15) and apparently can adjust length of absence to time of hatching (Johnstone & Davis 1990). Incubation usually uninterrupted but desertions of up to 5 days recorded, accordingly prolonging incubation period. Once reported to move egg 50 cm from exposed to better hidden site (Warham 1956). When two eggs laid in same burrow, some evidence that birds recognize own egg, perhaps by smell. Pipping to hatching takes c. 5 days on average, longest time 8 days. Egg-shells trampled in nest; unhatched eggs scratched out of nest or buried in fresh digging if rotten (Imber 1976). **INCUBATION PERIOD.** WA, one estimate of 53 ± 1 days; NZ: 54.6 (53–57; 36) (Imber 1976) and 54 (1.77; 51–58; 23) (Johnstone & Davis 1990); Marion I. (n=2): 55 and 57 days. Eggs may be neglected during incubation, often between laying and arrival of mate, for 3.4 days (1–6; 11) (Johnstone & Davis 1990); this lengthens period from laying to hatching. Addled eggs incubated well beyond period but not recorded for how long. Some tendency (10%) to desert nests if handled (Imber 1976).

NESTLING Semi-altricial, nidicolous. Hatched in sooty protoptile with black bill and grey feet with pinkish webs; replaced by rather dark teleoptile, feet gradually becoming grey-black; eyes open very early. No further information on development of plumage. **NESTLING PERIOD.** WA: 128, 123 days (n=2); NZ: 118 days (108–c. 128; 28). Brooded by parent for only few hours after hatching (Johnstone & Davis 1990; M.J. Imber); report of 2–3 days of brooding (Warham 1956) probably refers to guarding; in NZ, guarding lasts for c. 12 h to 3 days or average 1.4 days (0.5; 0.5–2; 18) (Johnstone & Davis 1990). Chicks gape and lunge with beak in self-defence but do not spit oil or very little (Warham 1956). Fed by both parents independently, by incomplete regurgitation; during feeding, bills crossed at right angles, chick's bill inside that of adult; feeding bout may have 15 feeds. In first 10 days after hatching, chicks visited every 3.1 nights (2.13; 1–10; 16) (Johnstone & Davis 1990). In WA, feeding very irregular when chicks c. 65 days old, averaging once every 7.2 days (2–10); in NZ, one feeding bout every 3.9 nights on average or only on c. 26% of nights during growth until c. 4–6 weeks old; size of meals 97 g (40–160). No period of starvation before fledging. No nest sanitation by small chicks; when older, excrete outside burrow.

GROWTH No weights at hatching. In NZ, average 490 g (313–604; 12) between 25 Oct. and 1 Nov.; 622 g (470–828) on 8–9 Dec. but no weights available for last half Nov.

when most chicks may be heaviest; weight at fledging 542 g (470–605; 23) or 102% of av. adult weight. Partial growth curves for tarsi, culmina, wings and tail in Schramm (1983).

FLEDGING TO MATURITY Chicks may emerge from burrows for 7 to 10 days before leaving, to exercise wings and find departure points. Leave at night, able to fly right away and totally independent of parents. First pair at 6 years old or later; first breeding, 7 years old or later (M.J. Imber).

SUCCESS WA, no data; Whale I., NZ: evidence from c. 100 burrows, observed from 1969 to 1986, in which 80–85 eggs laid annually; successful fledging ranged from 0 to c. 40%. Years of total failure attributable to heavy predation of eggs and chicks by Black Rats *Rattus norvegicus* but desertion a major cause of failure, by early departure of sitting bird, usually male (Johnstone & Davis 1990). At Marion I. in two seasons, total failure of all 57 eggs laid (Schramm 1983). Birds live for more than 18 years; survival of breeding adults, at least 94% per annum; no data for immatures and non-breeders (M.J. Imber). **PREDATORS:** WA, King Skinks take eggs and small chicks (HASB); NZ, Black Rats (as above); formerly on Little Barrier I., feral cats took adults and fledgelings; on Subantarctic islands, skuas *Catharcta* kill adults and fledgelings; rabbits, where introduced, take over burrows, modify them and drive Petrels out, e.g. Whale I. formerly. On Marion I., feral cats are menace, seriously affecting breeding success (Schramm 1983), as probably also on Iles Kerguelen (P. Jouventin). Taking for food by humans (muttonbirding) declining in NZ and stopped on Whale I. after 1964. Chicks sometimes heavily infested with fleas but no effect on survival known.

PLUMAGES *Subspecies gouldi.*

ADULT Definitive basic. Age of first breeding 7 years or older (M.J. Imber). **HEAD AND NECK.** Mostly black-brown (greyish 19), with sooty-brown (119) patch in front of eye. Forehead, front of lores, chin and throat pale brownish grey, forming pale patch in which poorly defined margin with darker foreneck occurs 1–3 bill-lengths from base of bill. Bases of feathers of chin and throat, white; of lores and forehead, dark brown (119A); forehead can appear slightly scalloped when feather bases exposed by wear. **UPPERPARTS,** blackish-brown (c119) when fresh, fading slightly to dark brown (c21) when worn; concealed bases of feathers, grey-white. **TAIL,** dark grey-brown (dark 19). **UPPERWING.** Coverts, blackish brown (c119) when fresh, fading slightly to dark brown (c21) when worn; secondary coverts have light-grey (c85) bloom when fresh. Remiges, black-brown (121); primary shafts, grey-black (82). **UNDERPARTS,** uniform dark brown (c121), appearing slightly greyer when very fresh; concealed bases of feathers, white. **UNDERWING.** Innermost lesser and marginal coverts, black-brown (119). Other coverts, dark greyish-brown (119A–119B), appearing slightly grey when very fresh; greater under wing-coverts can appear paler in some direct light. Remiges, dark grey-brown (c20), reflecting pale in some lights, as pale as light grey (c85).

DOWNY YOUNG Protoptile, brown-black (c20). Mesoptile, brown-grey (brownish 44).

JUVENILE Similar to adults. In some, pale grey-brown on head restricted to forehead, but extremely varying. In nominate *macroptera*, juveniles have less grey on face than adult (Falla 1937 *contra* Harrison 1983).

ABERRANT PLUMAGES Partial albino recorded (NMNZ). In fledgeling with feather deformity (described in Westland Petrel plumages), white bases of underpart feathers exposed by wear.

BARE PARTS

ADULT Iris, dark brown (121A) to black-brown. Bill, black; bases to unguis have varying horn-white band with distinctive rough texture. Legs and feet, grey-black (c82).

DOWNY YOUNG In mesoptile, iris, black-brown. Narrow ring of whitish skin round eye. Bill, grey-black (82) with pink-white rictus and lower tomtia. Tarsus and feet: scales, brownish grey, narrow areas of skin between, white (NZDOC slide library). In protoptile, feet of *macroptera* at Gough I., blue-grey with pinkish webs (Elliott 1957).

JUVENILE Before leaving colony, and in first summer at sea, bill, black, without pale markings at base of unguis. Unknown when these markings develop, or whether extent continues to increase with age.

MOULTS *Subspecies gouldi* (NMNZ, NZRD).

ADULT POST-BREEDING Complete. Wing and tail at sea between Jan. and Apr. Primaries outwards; birds typically observed with four or five inner primaries missing at once (D.W. Eades); three outer primaries can grow at one time. Secondary sequence complex, not understood, apparently starting in up to four centres in wing; tail sequence unknown, beginning when primaries nearly complete. P10 sometimes still growing at start of breeding season (M.J. Imber). During beachwreck in Apr., birds entering breeding condition were growing p10 (Kinsky 1968). Body-feathers replaced gradually after breeding; may not all be replaced until incubation period of next breeding season. In se. Aust. waters, in active primary moult, Nov.–Apr. (D.W. Eades).

POST-JUVENILE, SUBSEQUENT PRE-BASIC MOULT No information on post-juvenile moult. Failed breeders begin body-moult as early as Sept., while still visiting breeding grounds. Occasionally birds seen moulting in winter months (D.W. Eades).

P.m. macroptera. First arrivals at Tristan da Cunha, moulting birds (Elliott 1957). Hagen (1952) found birds in 'advanced stage of moult' in Mar. At Gough I.; bird caught 30 Apr. starting to moult (Swales 1965).

MEASUREMENTS Nominate *macroptera*. (1) From breeding localities and Cottlesloe Beach, WA, skins (NMNZ, WAM). (2) Eclipse I., breeding adults, live birds; unflattened, unstraightened wing measured with a tape passed over top of wing, from carpal joint to tip of longest primary; bill length from junction of culmen and feathering to tip of maxillary unguis (which is not always most distant point on unguis) (Fullagar & van Tets 1976). (3) Iles Kerguelen, live birds; methods unknown (Weimerskirch *et al.* 1989). (4) Iles Crozet, live birds (Jouventin *et al.* 1985). (5) Marion I., live birds; methods unknown (Schramm 1983).

UNSEXED	
WING	(1) 304 (5.90; 297–315; 7)
	(2) 309 (5; 304–314; 10)
	(3) 317.5 (8.3; 302–323; 23)
	(4) 306 (7; 293–320; 29)
	(5) 307 (6.8; 289–321; 52)
8TH P	(1) 186.8 (6.72; 176–194; 7)
	(2) 122.3 (3.90; 116–128; 7)
TAIL	(1) 125 (5; 110–128; 5)
	(2) 125 (5; 110–128; 5)
BILL	(1) 34.8 (1.18; 33.1–36.0; 6)
	(2) 34.9 (1.3; 32.7–36.6; 10)
	(3) 36.9 (1.3; 34.5–40.9; 22)
	(4) 36.2 (1.2; 33.5–38.8; 29)

	(5)	36.3 (0.98; 33.6–38.8; 54)
TARSUS	(1)	43.9 (0.99; 42.5–44.8; 6)
	(2)	44.2 (0.7; 43.3–45.6; 10)
	(3)	43.0 (1.5; 40.1–45.9; 23)
	(4)	43.8 (1.4; 41.2–48.0; 29)
	(5)	44.4 (1.09; 42.2–46.7; 53)
TOE	(1)	57.6, 62.1

P.m. gouldi. (1) From breeding localities and NZ beaches, juveniles excluded, recently dead (NMNZ). (2) From breeding localities and NZ beaches, juveniles excluded, skins (NMNZ). (3) Whale I., breeding adults (Johnstone & Niven 1989). (4) Whale I., breeding adults; width of bill taken at gape, at widest point (Imber 1973). (5) Stanley I., Mercury Grp; maximum chord, minimum bill depth at junction of culmen and feathering (A.J.D. Tennyson; P. Scofield).

	MALES	FEMALES
WING	(1) 320 (9.53; 296–332; 10)	310, 323
8TH P	(2) 202.8 (4.37; 196–210; 13)	200.8 (2.34; 197–204; 6)
TAIL	(1) 132.0 (4.72; 121–139; 18)	132.8 (6.07; 126–144; 6)
BILL	(1) 37.4 (1.84; 32.9–40.4; 18)	36.9 (1.16; 35.6–38.8; 6)
	(3) 37.2 (1.25; 34.0–39.3; 56)	36.6 (1.29; 34.3–39.5; 52) *
	(4) 37.4 (0.97; 33.8–39.5; 116)	36.6 (1.07; 34.4–40.2; 95) **
BILL W	(4) 18.0 (0.53; 16.5–19.1; 111)	17.1 (0.58; 15.9–18.9; 92) **
TARSUS	(1) 46.0 (2.18; 41.9–51.2; 17)	44.5 (1.75; 41.9–47.4; 6)
TOE	(1) 62.5 (2.11; 56.5–67.0; 18)	61.5 (1.08; 59.5–62.7; 6)
	UNSEXED	
WING	(5) 317 (6.10; 305–327; 15)	
TAIL	(5) 127.1 (6.13; 111.1–136.8; 15)	
BILL D	(5) 17.1 (0.44; 16.2–17.9; 17)	
TARSUS	(5) 44.2 (1.07; 41.5–46; 28)	
TOE	(5) 63.5 (2.20; 60.2–67.1; 12)	

Adult size not always reached at fledging (Jouventin *et al.* 1985).

WEIGHTS *P.m. macroptera*. Eclipse I., WA, breeding adults 478 (21; 440–500; 10; Fullagar & van Tets 1976). At Iles Kerguelen, 581 (58; 480–680; 23; Weimerskirch *et al.* 1989). At Iles Crozet, 560 (58; 455–680; 28; Jouventin *et al.* 1985). At Marion I., adults 587 (69.1; 460–745; 61; Schramm 1985).

P.m. gouldi: males, at start of first incubation shift 668 (35; 595–740; 52) (Imber 1976). Mean weight loss per day during incubation 8.0 (n=21), so estimated mean weight after 17 days incubation (av. duration) 532 (Imber 1976). Females, at egg laying 523 (74; 385–710; Johnstone & Niven 1989). At start of main incubation shift, about 17 days later, 667 (39; 595–760; 30; Imber 1976). Mean weight loss per day 8.1, so estimated average weight at end of 17 days incubation shift 529 (Imber 1976). At time of abandoning egg, when not relieved by males 467 (435–500; 8; Imber 1976). NZ beachcasts, males 471 (72.1; 324–574; 14), females 487 (38.9; 422–520; 6) (NMNZ).

STRUCTURE *P.m. gouldi*. Wing, long and narrow. P11 minute, p10 longest, p9 0–6, p8 9–19, p7 26–39, p6 55–72, p5 72–92, p4 100–119, p3 129–146, p2 156–172, p1 181–196. About four humerals. Tail, strongly rounded, 12 feathers, t1–t6 27–37. Bill, deep, nostrils about one-quarter length of bill; maxillary unguis, hooked; mandibular unguis, decurved. Tarsus, rounded. Outer and middle toes about equal, inner c. 80%.

SEXING Males tend to have more conspicuous white

filoplumes in crown than females (Imber 1971). Johnstone & Niven (1989) discuss use of discriminant analysis of measurements and weight.

GEOGRAPHICAL VARIATION Nominate *macroptera* slightly smaller than *gouldi* (see Measurements), with shorter maxillary unguis (Murphy; Murphy & Pennoyer 1952). Pale brownish grey (c79) at base of bill of *macroptera* less extensive, though overlaps with juvenile *gouldi*. In palest *macroptera*, pale brownish-grey occupies upper throat, extending ventrally about one bill-length from base of bill. In darkest birds, pale brownish-grey restricted to chin. DIR

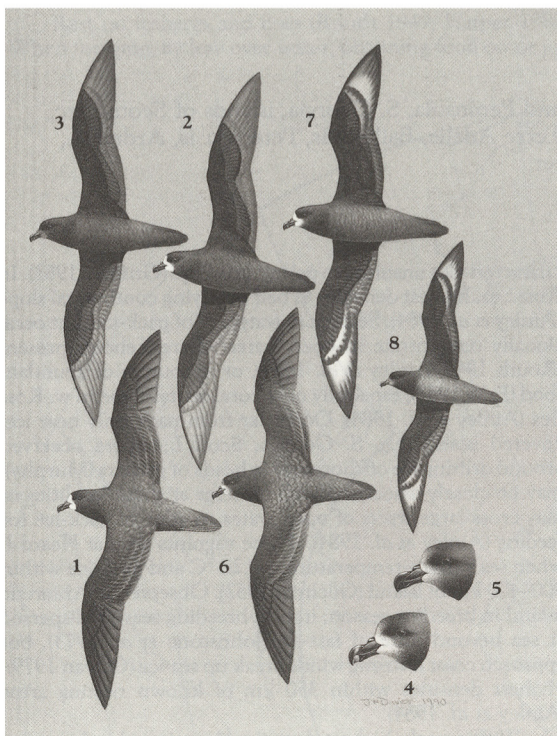
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Volume 1 (Part A), Plate 28

Great-winged Petrel *Pterodroma macroptera*

- 1. Adult, subspecies *gouldi*, dorsal
- 2. Adult, subspecies *gouldi*, ventral
- 3. Adult, subspecies *macroptera*, ventral
- 4. Adult, subspecies *gouldi*
- 5. Juvenile, subspecies *gouldi*

Providence Petrel *Pterodroma solandri*

- 6. Adult, dorsal, fresh
- 7. Adult, ventral, fresh
- 8. Adult, ventral, worn

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