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 Tubinares). 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 Diomedeidae. 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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Puffinus bulleri Buller's Shearwater

COLOUR PLATE FACING PAGE 625

Puffinus bulleri Salvin, 1888, *Ibis* (5) 6: 354 — New Zealand.

Named in honour of Sir W.L. Buller FRS, 1838–1906, author of *Birds of New Zealand*.

OTHER ENGLISH NAMES Ashy-backed, Grey-backed or New Zealand Shearwater.

Buller's is the name in New Zealand where it breeds endemically and so has precedence over other names.

MONOTYPIC

FIELD IDENTIFICATION Length 46–47 cm; wingspan 97–99 cm; weight 412 g. Large, lightly built shearwater of subtropical Pacific Ocean. Closely resemble Wedge-tailed Shearwater *P. pacificus* in size and shape. Distinctive jizz: long slender dark bill, small head and slender body; long strongly wedge-shaped tail, normally held tightly folded, giving long pointed rear-end; broad wings, with carpals held well forward, outerwing bowed down and gently angled back from carpals; buoyant unhurried flight. Pattern of upperparts striking and unique among shearwaters: light grey with sharply contrasting dark cap, tail and broad dark open M across upperwings. Sexes alike. No seasonal variation. Juvenile inseparable.

DESCRIPTION ADULT. Forehead, crown and nape, blackish-brown, forming dark cap sharply demarcated from white lower cheeks, chin and throat, along nearly straight line from base of upper mandible, through eye to rear of ear-coverts. Dark cap strongly contrasts with uniform light grey of hindneck, mantle, back and shorter scapulars. Penultimate row of scapulars, blackish brown, innermost tipped greyish-white. Rump, dark grey, contrasting with light grey back and upper tail-coverts. Tail, black (except outer two rectrices, light grey but normally concealed), contrasting strongly with light grey upper tail-coverts. Upperwing: outerwing black, except inner primaries frosted with grey and continuous with light-grey secondaries; broad diagonal dark bar across innerwing, from carpal to longest scapulars at base of trailing-edge, contrasting with light grey inner forewing and saddle; behind dark bar, most greater and outer median secondary-coverts, silvery-grey showing as conspicuous broad pale panel curving forward to join leading-edge just outside carpal. Total effect is of bold dark open M across upperwings (joining across dusky rump) contrasting with grey areas in front and behind; when strongly lit, light grey secondaries and silvery grey panel behind dark bar, show as characteristic broad silvery triangle on innerwing. Grey areas of dorsum wear browner. Underparts: grey of hindneck extends downwards behind dark cap to form broad grey patch on sides of upper neck and breast; otherwise clean white, from chin to under tail-coverts; underside of tail, greyish black. Underwing, white, with grey tips to remiges forming narrow grey trailing-edge (slightly broader across tips of outer primaries) and narrow dark leading-edge on outerwing (formed by dark outer web of outermost primary and thin broken blackish margin between carpal and base of outermost primary). Bill, long and slender, with tubed nostrils slightly raised over basal quarter of upper mandible; black, except latericorns greyish-black with bluish-grey cutting edge and ramicorn, bluish-grey; at sea, usually looks dark grey with black tip. Iris, dark brown. Legs and feet, fleshy-pink; outer part of tarsus and outer two toes, black; webs, cream to mauve-grey.

SIMILAR SPECIES Unmistakable; light grey upperparts, with sharply contrasting dark cap, tail and broad open M across upperwings forms striking dorsal pattern unique among shearwaters; striking dorsal pattern, together with extensively white underparts and slow, graceful effortless flight, makes identification straightforward. **Juan Fernandez** *Pterodroma externa*, **White-necked** *P. cervicalis* and **Barau's** *P. baraui* **Petrels** are superficially similar (*q.v.*); see also comments under **Wedge-tailed** and **Streaked** *Calonectris leucomelas* **Shearwaters**.

Widespread in subtropical sw. Pacific Ocean, migrating in non-breeding season through tropics to subtropical and subarctic n. Pacific. Occupy wide range of marine habitats, from well inshore, where commonly seen from land, to shelf-edge zone and over pelagic waters. In light winds, flight buoyant and unhurried, with periods of gentle arcing, banking and turning and long glides low to water interspersed with brief series of slow measured wing-beats; in head-on view, innerwings held so that carpal is above or level with back, while outerwing bowed down, wing-tip falling well below body. In higher winds, arcs higher above surface in graceful effortless progression, with little flapping, wings remaining bowed and held well forward; at all times, flight and jizz closely resemble those of Wedge-tailed Shearwater. Feed by surface-seizing, dipping, occasionally by surface-, shallow- and pursuit-plunging; exceptionally by pursuit-diving. Solitary or gregarious at sea, often forming large feeding flocks; join multispecies feeding flocks. Usually ignore ships, though occasionally follow; occasionally attend trawlers and smaller fishing vessels for scraps. Breed in dense colonies in variety of habitats (usually well-vegetated), only on Poor Knights Is, off n. NZ. Nocturnal and very noisy at colonies, where call in flight and from ground; main calls given are braying and howling sounds; apparently silent at sea.

HABITAT Marine, pelagic; in subtropical waters. Breeding birds feed in open waters of continental shelf along NZ coast, mainly where water depth <180 m (Jenkins 1974); uncommon less than 2 km (Bartle 1974) and more than 60 km offshore (Jenkins 1974). Abundant in convergence zone of W. Auckland and Westland Currents off NI (Jenkins 1974) and warm waters of Southland Current along SI (Jenkins 1988); s. boundary of distribution along Subtropical Convergence (Vooren 1973). Wind-force and sea conditions influence distribution; birds concentrate in calm waters off capes and peninsulas. Congregate at edges of shoals of fish, especially on down-current side of strong tidal streams (Jenkins 1974). Few found in inshore waters of e. Aust. coast (Milledge 1977). In n.

hemisphere, often found at boundaries of warm and cool currents (Kuroda 1955; Ainley 1976; Wahl 1985). In Californian waters, most abundant when coastal upwelling strong, preceding period of unusually high surface-temperatures (Ainley 1976).

Breed only on Poor Knights Is off NI, NZ; nest in burrows, or on ledges or crevices in cliffs and rock stacks; nest-sites partly protected by trees or shrubs, which may be used for take-off (Falla 1924; Harper 1983).

Foraging birds fly low over surface (Jenkins 1974). May plunge from heights of 1 m, but rarely submerge completely (Jenkins 1974; Brown *et al.* 1978; Wahl 1986); diving to depth of 6 m described by Roberts (1951) exceptional. Breeding birds form rafts on sea surface in late morning and afternoon (Jenkins 1974).

DISTRIBUTION AND POPULATION During breeding season, round coast of NZ, extending W into Tasman Sea, regularly reaching Aust. in small numbers. During non-breeding season, in e. and n. Pacific Ocean. Apparently widespread off Japan and USSR (Kuril Is) from 30°34'N, 150°11'E to 46°15'N, 160°15'E in July, Aug. (Sleptsov 1960; Wahl 1985). Along e. rim of Pacific in Aug., Sept.; rarely to s. coastal Alaska (including Aleutian Is); numerous and regular offshore visitor from British Columbia to central Californian coast; scarce S of Baja Pen. (Harper 1983; Wahl 1985); irregular visitor to offshore Peru and Chile, to *c.* 33°S (Murphy; Johnson 1965; Blake 1977). Also seen W of Galápagos Is (Palmer 1962).

AUST. Regular visitor to e. coast in small numbers, coinciding with NZ breeding season (Holmes 1975). **Qld**. All records from North Stradbroke I.: about seven, Mar. 1973 (Greensmith 1973); three, Jan. 1974 (Corben *et al.* 1974); one, Jan. 1983; two, Dec. 1983 (Qld Bird Rep. 1983); one, Feb. 1984 (Qld Bird Rep. 1984). **NSW**. First recorded Oct. 1954 (Hindwood 1955). Over 39 records, including at least 15 beachcast specimens, since 1954, from Ballina to Eden (Morris *et al.* 1981; NSW Bird Reps 1982–85; Hurley 1988). **Vic.** Only from e. Bass Str.: Jan. 1977 (Aust. Atlas); 3 Feb. 1985 (Vic. Bird Rep. 1985). **Tas.**: one, beachcast, Roaring Beach, Nubeena, Feb. 1974 (Tas. Bird Rep. 1974); one, beachcast, Eaglehawk Neck, Feb. 1977 (Tas. Bird Rep. 1977); one, E of Flinders I., Nov. 1984 (Patterson 1987).

NZ Disperse throughout NZ waters between early Sept. and late May. Recorded from Northland to Foveaux Str. Greatest numbers off coasts adjacent to breeding islands in Northland, Hauraki Gulf and Bay of Plenty during spring. Less frequent off Wairarapa, Auckland West coasts and Cook Str. Also occur in mid- to e. Tasman Sea. During summer, more frequent off N. Canterbury coast, and extend S to Foveaux Str. and Chatham Is. Also disperse in greater numbers into w. Tasman Sea. By autumn, distribution in w. and s. Tasman reduced, with birds more frequent near NZ coasts, but fewer near breeding islands. By May, numbers round colonies increase, preparatory to migration (Jenkins 1988).

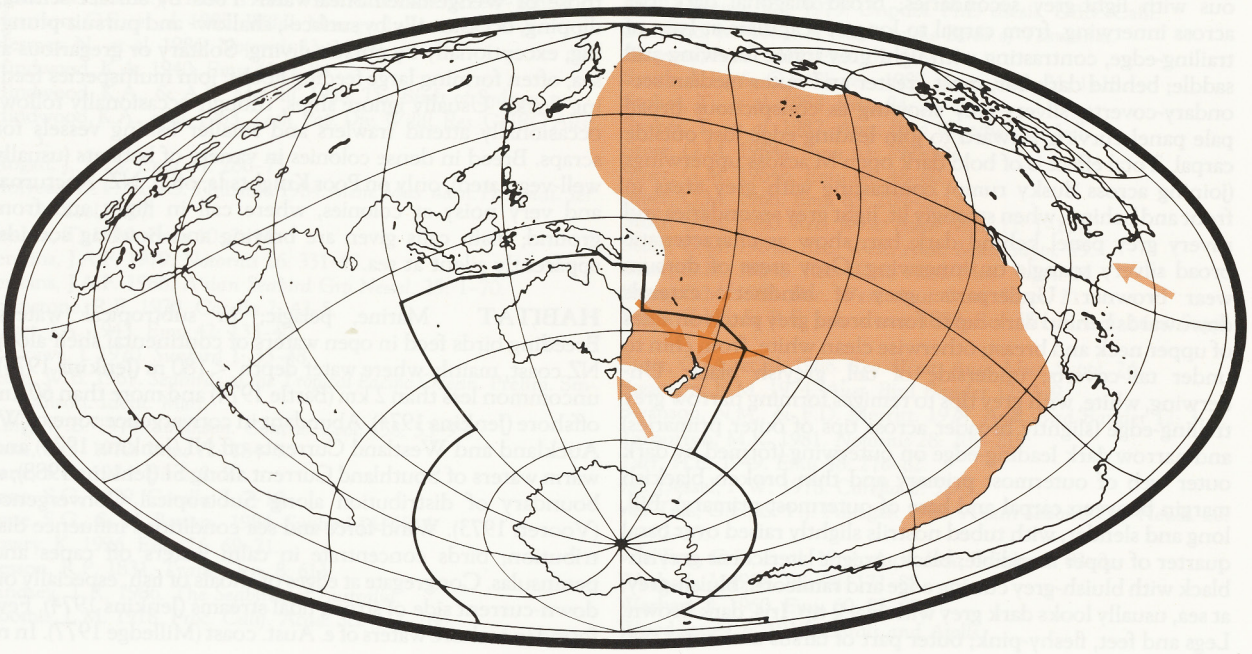
BREEDING, POPULATION Only in NZ, on islands off Northland.

Poor Knights Is (from Harper 1983)
Aorangi
Tawhiti Rahi
five other islets and stacks
Three Kings I. (possible site)
Mayor I. (possible site; Oliver).

Colonies on Aorangi nearly exterminated by feral pigs; recolonized, probably from nearby Tawhiti Rahi, after pigs eradicated in 1936 (Harper 1983). No recent evidence for breeding on Whale I. Populations now increasing: on Aorangi *c.* 100 pairs in 1938; *c.* 200 000 pairs in 1981 (Jenkins 1969; Harper 1983). Total population estimated 2.5×10^6 birds.

MOVEMENTS Trans-equatorial migrant to Subarctic Pacific from breeding ground at Poor Knights Is, NZ, but exact route unknown.

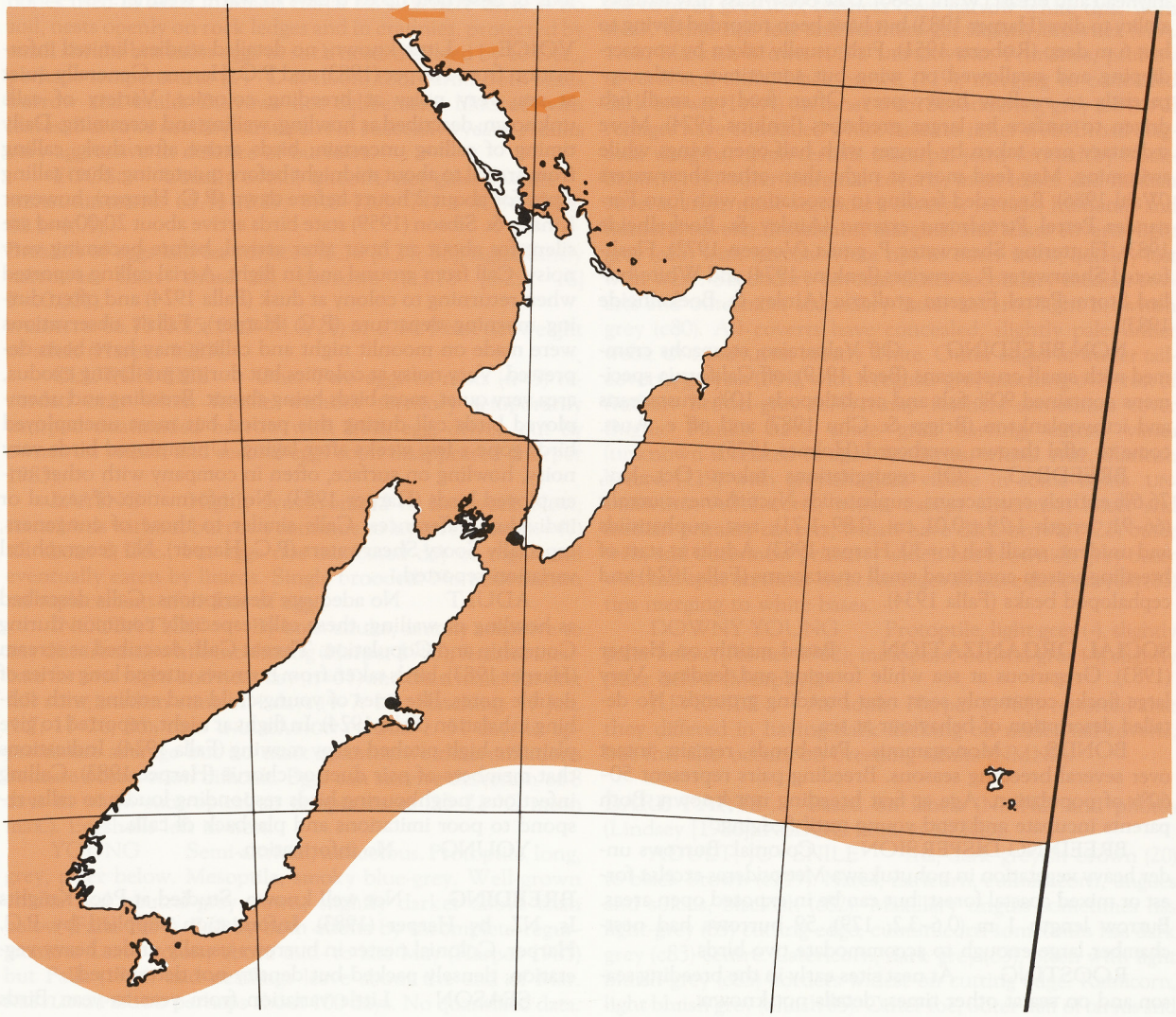
DEPARTURE Young and breeding adults depart breeding colonies mid-late May (Harper 1983), probably not late Mar. as suggested by Falla (1934).



NON-BREEDING Recorded Tongan waters (Cheshire 1974; Jenkins 1980) only during n. migration but not often; main path believed to be further E (Jenkins 1980). May move up w. side of Pacific (Kuroda 1957) but more likely to travel direct to n. feeding grounds like Sooty and Short-tailed Shearwaters. Main arrival in Subarctic occurs in June with many N of North Tropical Convergence by July (Nakamura & Hasegawa 1979) after which spread slowly N, possibly following the Subarctic Current W to E to Gulf of Alaska and ne. Pacific where records before Aug. few (Wahl 1975). Adults may return direct to breeding grounds from ne. Pacific though concentrations of birds off s. California in Aug. thought to be adults about to return to breed (Ainley 1976). Immatures and pre-breeders move S down American coast Aug.–Nov.: considered regular autumn migrant off British Columbia (Campbell 1971) and most numerous off n. California Aug.–Oct. (recorded Apr.–Dec.; Briggs *et al.* 1987) with numbers there highest during periods of above-average abundance of plankton (Ainley 1976) or when warm water approaches coast (Briggs *et al.* 1987). Small numbers also still in nw. Pacific at this time (Nakamura & Hasegawa 1979), when few observations have been made, which suggests that birds remaining in N. Pacific concentrate in areas of high abundance of food (Wahl 1985).

RETURN Breeders return to NZ, early Sept.; first seen at sea near NZ 10.5 Sept. ± 5.5 days (2–19 Sept.; 11) (Edgar 1962; Jenkins 1974, 1988) and first bird observed at nest 10 Sept. with most present by 18 Sept. (1981 only; Harper 1983). Migrate in small groups ≤5 birds (Jenkins 1974) at 40–45 km/h (Jenkins 1988). Pre-laying exodus by both breeders and non-breeders late-Oct. to late Nov., males probably returning 1–2 days before females, non-breeders a few days after (Harper 1983).

BREEDING During summer remain N of Subtropical Convergence (Vooren 1973; Jenkins 1988) and S of 33°S, the northernmost extent of the NZ continental shelf (Jenkins 1988). Most breeding adults appear to forage along ne. and nw. coast of NI, many flying round top of North Cape in morning, returning in afternoon (Jenkins 1988). Birds of unknown status but assumed to be non-breeders spread slowly across Tasman Sea as far W as Aust. (Holmes 1971; D.W. Eades) and down e. coast of SI from Oct.–Jan., returning in Feb. to concentrate in NZ coastal waters, particularly off e. coast of SI until late Apr. (Jenkins 1974, 1988). Birds recorded 800 km E



of NI (Fleming 1950) and at Chatham Is at this time also probably non-breeders (Jenkins 1988). Significant numbers of non-breeders remain along American coast between British Columbia and s. California until late Oct. to early Nov. but many eventually return to NZ waters, summer storm-driven birds in NZ being non-breeders in worn plumage. Non-breeders also frequent at breeding colonies but depart in late Dec. (Harper 1983) and have been recorded in Humboldt Current off Chilean coast during late Feb. and early Mar. (Murphy).

BANDING

36S150E 10 1+ U 62 1125 017 ABBBS
35S 174E 01 1+ U 119 162 293 NZNBS

FOOD During breeding season chiefly crustaceans and fish but few data. BEHAVIOUR. Mostly surface feeder; recorded surface-seizing, surface-filtering, contact-dipping, dipping, pursuit-plunging and pursuit-diving. Quantified observations: contact-dipping or surface-seizing 100% frequency, pursuit-plunging <0.1 (453 observations; Harper 1983; P.C. Harper); dipping 80%, pursuit-plunging 20% (28 observations; Ainley & Boekelheide 1983). Also seen upending like ducks or swimming with head submerged and swinging from side to side (Jenkins 1974) and flopping into water, briefly submerging head and breast (Wahl 1986). Low body-mass may hamper ability to dive (Harper 1983) but have been recorded diving to bait 6 m deep (Roberts 1951). Fish usually taken by contact-dipping and swallowed on wing but sometimes settle, apparently to swallow heavy prey. Often feed on small fish driven to surface by larger predators (Jenkins 1974). More sedentary prey taken by lunges with half-open wings while swimming. May feed more at night than other shearwaters (Wahl 1986). Recorded feeding in association with Juan Fernandez Petrel *Pterodroma externa* (Ainley & Boekelheide 1983), Fluttering Shearwater *P. gavia* (Vooren 1972), Flesh-footed Shearwater *P. carneipes* (Jenkins 1974) and White-bellied Storm-Petrel *Fregetta grallaria* (Ainley & Boekelheide 1983).

NON-BREEDING Off Valparaiso, stomachs crammed with small crustaceans (Beck 1919); off California specimens contained 90% fish and cephalopods, 10% crustaceans and icthyoplankton (Briggs & Chu 1987) and off e. Aust. come to offal thrown overboard (Holmes 1975).

BREEDING Of regurgitations taken Oct.–Jan., 76.6% entirely crustaceans, euphausiids *Nyctiphanes australis* (66–91, length 1.29 ± 0.01 cm, 0.89–1.71); rest, euphausiids and unident. small fish (n=30; Harper 1983). Adults at start of breeding season contained small crustaceans (Falla 1924) and cephalopod beaks (Falla 1934).

SOCIAL ORGANIZATION Based mainly on Harper (1983). Gregarious at sea while foraging and feeding. Very large flocks commonly seen near breeding grounds. No detailed description of behaviour at sea.

BONDS Monogamous. Pair-bonds remain intact over several breeding seasons. Breeding pairs represent 50–60% of population. Age at first breeding not known. Both parents incubate and tend young until fledging.

BREEDING DISPERSION Colonial. Burrows under heavy vegetation in pohutukawa *Metrosideros excelsa* forest or mixed coastal forest, but can be in exposed open areas. Burrow length 1 m (0.6–3.2; 179); 59 burrows had nest-chamber large enough to accommodate two birds.

ROOSTING At nest sites early in the breeding season and on sea at other times; details not known.

SOCIAL BEHAVIOUR Not well known. Little communication at sea, but noisy on ground and when in flight at breeding grounds. Departs burrow before sunrise and returns shortly after sunset; does not visit breeding grounds during day. Skilled tree climber; birds climb rough-barked trees into canopy, sometimes 10 m from ground. Light body weight, broad wings and long tail also enable agile and rapid passage over ground. Proficient digger of burrows.

AGONISTIC BEHAVIOUR Pre-laying exodus *c.* 30 days. Fierce defender of territory against inquisitive non-breeding birds and Tuataras *Sphenodon punctatus*. Antagonistic behaviour between birds on ground away from nest-sites during evening; includes gaping and sparring with bill; fights rare. Birds crowding about departure trees and other prime sites in early morning mostly ignore each other. Acutely sensitive to human disturbance of nests.

SEXUAL BEHAVIOUR ALLOPREENING, chiefly to head and neck areas, common between mated pairs. Non-breeders explore burrows, sit and sleep or gather in groups of two or three for mock nest-building and mutual howling.

RELATIONS WITHIN FAMILY GROUP Parents share incubation equally. Males usually incubate first; median incubation shift 4 days (4–7; 18). Eggs can survive periods of desertion up to 8 days in warm weather.

VOICE Little known; no detailed studies; limited information from Harper (1983) and P.C. Harper. Generally quiet at sea; very noisy at breeding colonies. Variety of calls unknown; described as howling, wailing and screaming. Daily timing of calling uncertain: birds arrive after dusk, calling from arrival to about midnight before quietening; then calling again for about 2 hours before dawn (P.C. Harper); however Kinsky & Sibson (1959) state birds arrive about 20:00 and are silent for about an hour after arrival, before becoming very noisy. Call from ground and in flight. Aerial calling reported when returning to colony at dusk (Falla 1924) and often during morning departure (P.C. Harper); Falla's observations were made on moonlit night and calling may have been depressed. Very noisy at colonies but during pre-laying exodus, area very quiet, most birds being absent. Breeding and unemployed birds call during this period but most unemployed birds gone a few weeks after laying. Unemployed birds very noisy, howling on surface, often in company with other unemployed birds (Harper 1983). No information of sexual or individual differences. Calls similar to those of congeners, especially Sooty Shearwaters (P.C. Harper). No geographical variation reported.

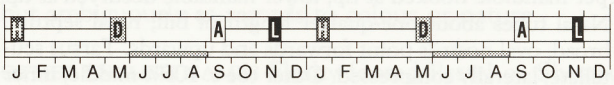
ADULT No adequate descriptions. Calls described as howling or wailing; these calls especially common during Courtship and Copulation. **Threat Call**: described as scream (Harper 1983); birds taken from burrows uttered long series of double notes, like cries of young child and ending with sobbing inhalation (Falla 1924). In flight at night, reported to give plaintive high-pitched raspy mewing (Falla 1924). Indications that members of pair duet or chorus (Harper 1983). Calling infectious, neighbouring birds responding loudly to calls; respond to poor imitations and playback of calls.

YOUNG No information.

BREEDING Not well known. Studied at Poor Knights Is, NZ, by Harper (1983). Information supplied by P.C. Harper. Colonial nester in burrows usually under heavy vegetation; densely packed but density not determined.

SEASON Little variation from year to year. Birds

arrive at colonies about 10 Sept.; colonies almost fully occupied by 18 Sept.; copulation widespread, 26 Oct.; dramatic pre-laying exodus by all age-groups follows for about 30 days (18 days needed for yolk formation); laying begins 26 Nov., ends 30 Nov.; most fledglings gone mid-late May (Harper 1983; C.R. Grau; P.M. Sagar).



SITE Burrows in ground among tree-roots or in earth-floored caverns under rock slabs, under pohutukawa or regenerating mixed coastal forest; sometimes in exposed open areas; also in rock crevices, caves, holes in Maori walls.

NEST, MATERIALS Burrows 1.01 m long (0.2; 0.6–3.2; 179). Nest chamber (n=59) large enough to take two birds; in crevices (n=129) lined with stone fragments; in earth burrows (n=26 *ex* 59), lined with twigs, stiff leaves of pohutukawa, karo *Pittosporum crassifolium* or swordlike leaves of Poor Knights Lily *Xeronema callistemon;* also of kohekohe *Dysoxylon spectabile* and taupata *Coprosma repens,* which are important requirements of habitat where they occur. Human bones used in nests in Maori burial cave. Where there is no soil, nests openly on rock ledges and in crannies, protected by small shrubs but most eggs in such nests deserted by 10 Dec., perhaps temperatures (24 °C at noon) too warm. Both sexes burrow and build. Burrows not deliberately blocked with leaves. Burrows used by same pairs in successive years. Adults very aggressive in defence of burrows.

EGGS Usually ovoid; smooth, not glossy; white.
MEASUREMENTS: 65.44 (0.29; 59.0–72.3; 74) x 42.96 (0.22; 40.1–46.1).
Breadth of eggs laid on surface (42.38 [0.21; 33]) significantly narrower than those in burrows (43.78 [0.29; 18] $P<0.001$).
WEIGHTS: 66.76 (0.85; 59.0–74.0; 27) or *c.* 16.4% of net weight of adult (Harper 1983).

CLUTCH-SIZE One. Two eggs in nests (n=5) recorded only when female without territory temporarily usurped unattended burrow with fresh egg; driven out by owner on return and second eggs soon disappeared (Harper 1983).

LAYING Highly synchronized in last week Nov.; some birds without burrows continue to lay on surface (n=47) till about 3 Dec., but eggs not incubated day or night and eventually eaten by lizards. Single brooded. No information on replacement after loss of egg.

INCUBATION By both adults; acutely sensitive to any disturbance while incubating (Harper 1983); females incubate for first night and next day (n=37) and then males for first full stint; median stint of 4 days (4–7; 18). Hatching: 19 Jan. (1.7; 17–26; 86); thus INCUBATION PERIOD *c.* 51 days as approximate average but no exact quantitative determinations because observation difficult. Eggs can survive desertion of 8 days in warm subtropical air temperatures (16–21 °C mean max.). Eggshells left in nest.

YOUNG Semi-altricial, nidicolous. Protoptile, long, grey, paler below. Mesoptile, smoky blue-grey. Well-grown chicks had neutral-grey down, slightly darker above than below (Falla 1934). Fed by both adults by incomplete regurgitation. Leave colony about mid- to late May (Harper 1983) but Falla (1934) said nestlings leave about the end of Mar. NESTLING PERIOD perhaps about 100 days. No quantified data. No further information.

GROWTH No information.

SUCCESS No information. Till 1823, much prized as food by the Maori, who called the bird *rako.* After extinction of Maori population on Poor Knights Is, preyed on heavily by feral pigs, which were exterminated in 1936; now no major predator on Poor Knights Is. Swamp Harriers *Circus approximans* may take some adults. Tuataras *Sphenodon punctatus* are also potential predators. Some adults accidentally become jammed under rocks, entangled by legs or wings in saplings, e.g. of mahoe *Melicytus ramiflorus.*

PLUMAGES

ADULT Definitive basic. Age attained and age of first breeding unknown. HEAD AND NECK. Forehead, crown, nape and most of hindneck, dark brown (121). Ear-coverts and lowermost hindneck, light greyish (c85). Lores, brown-grey (79) mottled white; feathers, brown-grey (79) with white tips. Chin and throat, white. UPPERPARTS. When fresh, mantle, back and shorter scapulars, uniform grey (c84); feathers have concealed whitish bases. With wear, feathers fade to brown (119A) with frosted light-brown (119C) fringes. Longest scapulars, blackish brown (c119). Rump and upper tail-coverts, grey (84); feathers have narrow white tips. With wear, white tips lost and feathers get slightly browner (c79). TAIL, blackish brown (119). UPPERWING. Primaries, primary coverts and alula, black-brown (119), merging to concealed dark brown (119A) on inner web. Secondaries, grey (c84). All remiges have concealed white bases to inner web. Broad diagonal wing-bar from tertials to carpal joint formed by black-brown (119) outer marginal coverts, most lesser and median coverts, innermost secondary coverts, tertials, humerals and humeral coverts. Innermost marginal and lesser coverts, light grey (c85) with narrow white tips to outer webs, quickly lost with wear. Secondary coverts, outer secondary median coverts and outermost secondary lesser coverts, light brownish grey (c80). All coverts have concealed, slightly paler inner webs. UNDERPARTS, mostly white. Outer edges of under tail-coverts, greyish (c84), with irregular grey mottling over rest of feather. Brown-grey (c79) rump feathers sometimes cover thighs. Flanks have some grey barring; extent varies (unknown if related to age). Axillaries, white. TAIL, blackish brown (119) with greyish gloss visible in some lights. UNDERWING. All coverts, white, except outermost lesser and median primary coverts, which have dark brown (121) outer web, and outermost primary, which has brownish grey outer web and spot on inner web. Remiges all have dark greyish (83) tips merging to white bases.

DOWNY YOUNG Protoptile, light grey (-), slightly paler below (Palmer 1962); mesoptile, neutral grey (-), slightly paler below (Murphy).

JUVENILE As adult. Harper (1983) reported that they differed in having dark flecking on under tail-coverts, but this also occurs on breeding adults (NMNZ).

BARE PARTS Based on labels (NMNZ) and photos (Lindsey [1986]; NZDOC library; NZRD).

ADULT, JUVENILE Iris, dark greyish brown (20) to black brown (c119). Nares, naricorn, culminicorn, ungues and sulcus, blackish (c82). Maxillary unguis sometimes has light-grey (85) cutting edge; culminicorn sometimes has dark grey (c83) centre. Latericorn, dark grey (83), often with light bluish-grey (c85) borders widest on cutting edge. Ramicorn, light bluish grey (bluish 85). Outer toe, outer half of tarsus and

middle toe, dark grey (83), sometimes with brown tinge. Inner toe and inner half of middle toe, light flesh-pink (pale 7). Webs, light flesh-pink (pale 7) with greyish (c85) borders broadest near tip.

DOWNY YOUNG In mesoptile: bill and feet coloured as adults, but paler, with less pigment in darker parts of skin (Falla 1934; Murphy).

MOULTS

ADULT POST-BREEDING Pre-basic. Assumed to take place between May and Sept., because adults do not moult on breeding grounds (NMNZ). Unknown if any moult of remiges occurs during migration.

POST-JUVENILE, SUBSEQUENT MOULTS Birds moulting their quills collected late Feb. and early Mar. off Valparaiso, Chile (Murphy). Bird of unknown age collected at sea W of Chathams (NMNZ) in late Jan. was completing primary moult; $N^9 4^1$. Non-breeding birds of unknown age beachcast in NI, NZ, in late Feb. were in body-moult but not in moult of remiges. Birds aged as adults (criteria unknown) beachcast in Apr. in full moult (Kinsky 1968).

MEASUREMENTS From throughout range. (1) Definitive skins (NMNZ). (2) Skins; flattened chord, tarsus and toe methods unknown (Loomis 1918). (3) Recently dead (NMNZ).

		MALES	FEMALES
WING	(2)	297.1 (6.24; 285–309; 12)	298.0 (5.00; 293–303; 2)
	(3)	293.1 (3.93; 287–298; 8)	289.9 (6.74; 275–295.5; 9)
8TH P	(1)	182.6 (3.26; 177–188;11)	179.7 (3.96; 173–186; 15)
TAIL	(2)	127.9 (4.11; 120–135; 12)	127.0 (7.48; 119–137; 3)
	(3)	126.8 (3.15; 124–132; 8)	126.9 (4.84; 117–134;9)
BILL	(2)	41.8 (1.22; 40.4–45.0; 12)	41.8 (1.00; 40.7–43.1; 3)
	(3)	42.5 (1.32; 40.6–44.6; 8)	40.1 (1.10; 37.7–41.2; 9)
TOE	(2)	62.0 (1.34; 58.9–63.7; 12)	62.1 (0.48; 61.7–62.8; 3)
	(3)	61.3 (2.52; 58.1–65.4; 8)	60.8 (2.06; 58.6–65.4; 9)

(4) Live; methods unknown (P.C. Harper).

		UNSEXED
WING	(4)	287.2 (12.12; 275–309; 28)
TAIL	(4)	125.4 (7.41; 119–138; 28)
BILL	(4)	49.4 (5.29; 47–53; 28)
TOE	(4)	62.5 (4.76; 59.8–66.0; 28)

WEIGHTS Poor Knights Is; weights on arrival in evening when proventriculus contains food, 16 Jan.: 452.0 (20.54; 408–488; 30); 21 Jan.: 452.5 (28.70; 385–490; 30). Weights in morning, when proventriculus probably empty, 19 Jan.: 406.8 (40.59; 339–499; 30); 22 Jan.: 416.7 (32.21; 380–480; 30) (Harper 1983). NZ beachcasts: males 345 (38.4; 290–380; 5) (NMNZ); females 306.5 (22.1; 278–335; 8) (NMNZ).

STRUCTURE Eleven primaries, p10 longest, p11 minute, p9 1–5, p8 14–20, p7 30–37, p6 49–58, p5 71–78, p4 92–99, p3 113–122, p2 130–141, p1 144–157. Twenty secondaries, five of tertial form. Four short humerals. Tail, wedge-shaped; 12 feathers, t1 42–51 longer than t6. Bill long, rather slender, depth at culminicorn about one-quarter length. Upper mandible hooked at tip, lower mandible decurved at tip. Nasal tubes about one-quarter length of bill; nasal septum, broad; oval nostrils point forwards and upwards. Tarsus scutellate, laterally compressed. Outer toe *c.* 105% middle, inner toe *c.* 80%.

DIR

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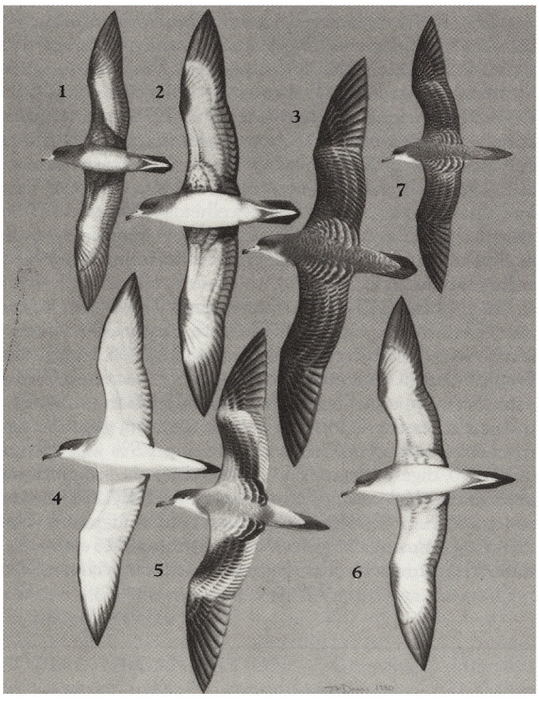

Volume 1 (Part A), Plate 46

Pink-footed Shearwater *Puffinus creatopus*
1. Adult, dark morph, ventral
2. Adult, light morph, ventral
3. Adult, dorsal

Buller's Shearwater *Puffinus bulleri*
4. Adult, ventral
5. Adult, dorsal

Wedge-tailed Shearwater *Puffinus pacificus*
6. Adult, light morph, ventral
7. Adult, light morph, dorsal