

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: Diomedidae 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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Macronectes halli Northern Giant-Petrel

Macronectes giganteus halli Mathews, 1912, *Birds Aust.* 2: 187 — Iles Kerguelen.

Named in honour of R. Hall, 1867–1949, President RAOU 1912–13.

MONOTYPIC

FIELD IDENTIFICATION Length 80–95 cm; wing-span 150–210 cm; weight: males 5.0 kg, females 3.8 kg. Very large stocky, mostly dark, fulmarine petrel. Adults very close to dark-morph Southern Giant-Petrel *M. giganteus* in size, structure, plumage and jizz; *M. halli* usually has dark tip to pale bill and is darker round face and upper breast. Unlike *giganteus*, no light-phase. Sexes alike, but males markedly larger and heavier-billed. No seasonal plumage differences. Subadult birds have distinct plumage stages.

DESCRIPTION ADULT. Crown and hindneck, freckled brownish-grey, becoming more mottled and lighter with age, but some dark feathers always present, giving capped appearance. Forehead, cheeks, chin and throat, pale, mottled grey becoming white. Mantle, back and upperwings, dark brownish-grey becoming greyer; pale edges of feathers create freckled effect on mantle and wing-coverts. Underparts, grey to pale brown-grey, freckled, normally markedly lighter than upperparts, becoming almost white in old birds (Hunter 1983b; S. Hunter). Underwing, with bases of inner primaries and some secondaries, pale silvery-grey; leading-edge of inner wing may become pale in older birds (Hunter 1983b). Bill, massive, with prominent nasal tube for three-fifths of length; pale pinkish-ochre or horn, with darker nails of both mandibles forming brown, yellow-brown, reddish or pinkish-red tip. Iris, brown, grey-brown, but usually grey to whitish, often flecked with brown; becomes paler with age. Legs and feet, dark grey. **JUVENILE.** Entirely glossy sooty black; bill, usually yellowish; may lack reddish tip. Juvenile plumage rapidly fades to brownish black or grey-brown. With age, cheeks and throat become mottled and lighter.

SIMILAR SPECIES See *M. giganteus*.

Pelagic, marine and coastal; from Antarctic to subtropical waters, mostly subantarctic, but range largely overlaps that of *M. giganteus*. Flight and general behaviour similar. However, almost obligate ship-follower, usually more attracted to ships than *M. giganteus* (Johnstone 1974).

HABITAT Marine, pelagic; mainly in subantarctic waters, but regular in Antarctic waters of sw. Indian Ocean, Drake Passage and W of Antarctic Pen. (Jouventin *et al.* 1982a; Starck & Wyrzykowski 1982; Starck 1985; Stahl 1987). Range extends into subtropical waters mainly in winter–spring. Frequent both pelagic and inshore waters near breeding islands and in non-breeding range (Cox 1976; Milledge 1977; Warham & Bell 1979; Jouventin *et al.* 1982b); during first year, probably mainly continental shelves, slopes and cold e. boundary currents off South America, South Africa, Aust. and NZ (Hunter 1984a; Weimerskirch *et al.* 1985; Woehler & Johnstone 1988); possibly more pelagic from second year on (Hunter 1984a). Attracted to land at sewage outfalls (Aust. Atlas) and scavenge at colonies of penguins and seals (Warham & Bell 1979; Hunter 1987). At S. Georgia, breeding males regularly feed on seal-carrion; females forage more at sea (Hunter 1987).

Breed on subantarctic islands, breeding range extending into Antarctic Zone at S. Georgia. Nest in coastal areas where vegetation or broken terrain offers shelter; sea-facing slopes, headlands; in lee of banks, under or against vegetation clumps, below cliffs or overhanging rocks, or in hollows (Bourne & Warham 1966; Voisin 1968; Warham & Bell 1979; Hunter 1984c). On Campbell I., birds (assumed to be *halli* by location and dates) nest on edge of coastal plateau (Westerskov 1960). Tussock-grass (*Poa*) widespread at many breeding sites (Bourne & Warham 1966; Voisin 1968; Hunter 1984c); on Antipodes I., nest under *Senecio antipoda* (Warham & Bell 1979).

Feed from sea surface while swimming, or dive to 2 m depth (Hemmings & Bailey 1985; Harper 1987).

DISTRIBUTION AND POPULATION Pelagic range circumpolar, usually between 30 and 64°S; imperfectly known because giant-petrels rarely separated at sea. Breed on subantarctic islands and S. Georgia, between 46 and 54°S.

In summer, usually S of 40–45°S in open ocean (Voisin 1980; Jouventin *et al.* 1982a; Mochizuki & Kasuga 1985; Stahl 1987). S. limit of range: sw. Indian Ocean, 64°S (Jouventin *et al.* 1982a; Stahl 1987); se. Indian Ocean, 56°S (Johnstone 1974; Mochizuki & Kasuga 1985); NZ sector, 55–63°S (McQuaid & Ricketts 1984; Wanless & Harris 1988); se. Pacific, off Antarctic Pen., 66°S (Starck & Wyrzykowski 1982). Also in Aust. waters (Johnstone 1974; Aust. Atlas); Humboldt Current to 37°S in Feb. (Weimerskirch *et al.* 1985); possibly farther N on e. coast of South America (Hunter 1984a). In winter and spring, N to 28–30°S in sw. Indian Ocean (Jouventin *et al.* 1982a; J.-C. Stahl). Regular visitor to South Africa (Brooke & Sinclair 1978), and Aust. where arrives c. 1 month earlier than *M. giganteus* (Aust. Atlas). S. limit of range in winter unknown. Immatures recovered N to 23–25°S off sw. Africa; 25°S off WA; 20°S off w. South America; 35°S off e. South America (Hunter 1984a; Weimerskirch *et al.* 1985; Woehler & Johnstone 1988).

Regular visitor to Iles Amsterdam and St Paul (Roux & Martinez 1987). Occasional to Anvers I. (Parmelee *et al.* 1977); Signy I. (Rootes 1988); Falkland Is (Chater *et al.* 1981); Réunion (Barré *et al.* 1976); Heard I. (photograph in Downes *et al.* 1959).

BREEDING Localities and population estimates in Table 1. Total NZ population, before 1984, 1000–5000 pairs (Robertson & Bell 1984). At S. Georgia and at Ile aux Cochons and Ile de la Possession, Iles Crozet, population has recently increased (Hunter 1984b; Voisin 1984, 1988); at Campbell I., population has decreased (Robertson 1980).

MOVEMENTS Adults usually near breeding colonies throughout year; immatures undertake long and poorly known movements.

DEPARTURE Juveniles leave: S. Georgia, 22 Mar. on average (Croxall & Prince 1987); Iles Crozet, 26 Jan.–14

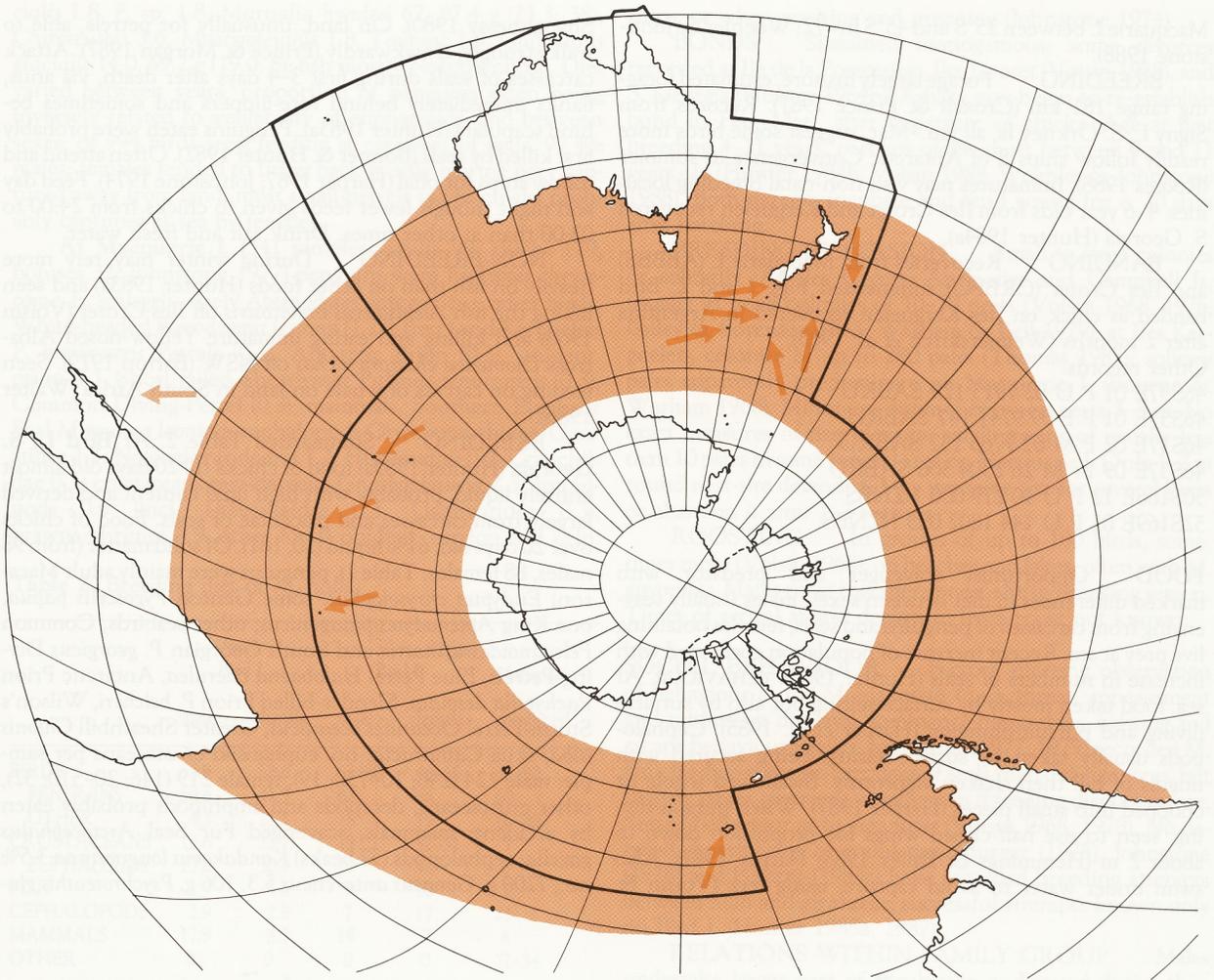


Table 1.

LOCALITY	YEAR OF ESTIMATE	ESTIMATE (pairs)	REF.
Prince Edward Is	<1984	310	1
	1984	500	2
Iles Crozet	1981-82	1313 +	3
Iles Kerguelen	1984-87	1450-1800	4
Macquarie I.	1977	1000	5
Campbell I.	1958	100	6
Auckland Is			7
Antipodes Is.	1969	320	8
Chatham Is.			7
Nelly I. (off Stewart I.)			9
S. Georgia	<1984	3000	10

References: (1) Williams (1984); (2) S. Hunter; (3) Jouventin *et al.* (1984); (4) Weimerskirch *et al.* (1989); (5) Rounsevell & Brothers (1984); (6) Bailey & Sorensen (1962); (7) Robertson & Bell (1984); (8) Warham & Bell (1979); (9) NZRD; (10) Croxall *et al.* (1984).

Mar. with 80% leaving 10 Feb.-3 Mar. (Voisin 1976); Iles Kerguelen, Feb.-Mar. (Paulian 1953); Macquarie I., mid-Mar. (Woehler & Johnstone 1988); Antipodes Is, probably early

Feb. (Warham & Bell 1979).

NON-BREEDING, BANDING

Adult movements in winter poorly known, but recovery in South Africa of bird that had bred at Marion I. suggests some travel widely (Gartshore *et al.* 1988). Juveniles apparently undertake circumpolar movements. Chicks banded at Macquarie I. have been recovered progressively later eastwards: NZ, Mar.; South America, May; South Africa, June; and Aust., July (Woehler & Johnstone 1988). Birds banded Iles Kerguelen and Crozet may also follow prevailing w. winds, though recoveries in Chile three months and Argentina 2 months after banding suggest movement may also be in opposite direction (Weimerskirch *et al.* 1985). Birds banded S. Georgia also appear to travel E, though no recoveries from South Africa, which suggests rapid movement across Southern Ocean, at least as far as Aust. (Hunter 1984a). Sightings associated with cold fronts passing across South Pacific suggest trans-oceanic journeys, particularly by immatures, probably wind-assisted (Harper 1987). High recovery rates in Aust. waters during winter (Woehler & Johnstone 1988) suggest that these may be important wintering areas for Macquarie I. birds but immatures from S. Georgia may be more likely to cross Pacific to South America to winter (Hunter 1984a). No recoveries S of 50°S, which suggests that Antarctic Convergence represents s. extent of range (Johnstone 1974); 95% of banding recoveries from

Macquarie I. between 25°S and 45°S (n=72; Woehler & Johnstone 1988).

BREEDING Forage largely inshore, estimated foraging range 181 km (Croxall & Prince 1987). Records from Signy I., S. Orkney Is, all Jan.-Mar. suggest some birds more readily follow ships S of Antarctic Convergence in summer (Rootes 1988). Immatures may visit non-natal breeding localities: 4-6 year olds from Iles Crozet and Kerguelen recovered S. Georgia (Hunter 1984a).

BANDING Recoveries from Macquarie I. (ABBBS) and Iles Crozet (CRBPO) summarized Figs 1 and 2. Bird banded as chick on Iles Kerguelen recovered in Argentina after 2 months (Weimerskirch *et al.* 1985).

Other records:

46S37E 01 P U 02 7913 129 SABRU
46S37E 01 P F 09 9741 147 SABRU
46S37E 02 P M 02 7765 132 SABRU
46S37E 09 1+ M 26 2304 306 SABRU
50S166E 12 P U 10 279 000 NZNBS
52S169E 01 P U 144 1802 023 NZNBS

FOOD Opportunist scavenger and predator with marked differences in diet between sexes, males usually scavenging from carcasses of penguins and seals, females obtaining live prey at sea. Recent increase of population correlated with increase in numbers of seals (Hunter 1985). **BEHAVIOUR.** At sea, food taken mostly by surface-seizing but also by surface-diving and pursuit-plunging (Harper *et al.* 1985). Cephalopods usually taken by surface-seizing, being secured with unguis of bill then shaken vigorously. Swallowed whole or chopped into small pieces (Harper 1987). When pursuit-diving, seen to use half-closed wings for propulsion down to about 2 m (Hemmings & Bailey 1985; Harper 1987). Also swim under water to avoid capture, using feet (Voisin &

Shaughnessy 1980). On land, unusually for petrels, able to walk strongly, if awkwardly (Prince & Morgan 1987). Attack carcasses of seals during first 3-4 days after death, via anus, flanks immediately behind fore-flippers and sometimes behind scapulars (Hunter 1983a). Penguins eaten were probably first killed by seals (Bonner & Hunter 1982). Often attend and follow ships for offal (Harper 1987; Johnstone 1974). Feed day and night though fewer feeds given to chicks from 24:00 to 03:00 than at other times. Drink salt and fresh water.

NON-BREEDING During winter may rely more heavily on fish than on other foods (Hunter 1983a) and seen taking the fish *Alepisaurus brevirostris* off Iles Crozet (Voisin 1968) and killing and eating immature Yellow-nosed Albatross *Diomedea chlororhynchus* off NSW (Barton 1979). Seen feeding on carcass of whale on land in South Africa (Walter 1986).

BREEDING Summarized Table 2. At Bird I., S. Georgia (Hunter 1983a) food of chicks till 20 days old almost entirely liquid, probably with high lipid content and derived largely from carcasses and placentae of seals. Food of chicks over 20 days old, 61% liquid (20, 181). Of solid matter (from 98 males, 88 females; Table 1), penguins were mainly adult Macaroni *Eudyptes chrysolophus*, some Gentoo *Pygoscelis papua*, one King *Aptenodytes patagonicus*; other seabirds, Common *Pelecanoides urinatrix* and South Georgian *P. georgicus* Diving-Petrels, Blue Petrel *Halobaena caerulea*, Antarctic Prion *Pachyptila desolata*, Slender-billed Prion *P. belcheri*, Wilson's Storm-Petrel *Oceanites oceanicus*, Greater Shearwater *Chionis alba*, skua *Catharacta*; no. euphausiid crustaceans per sample: male 224 (246; 10-750; 19), female 219 (146; 20-510; 32), other crustaceans, decapods and amphipods probably eaten by accident; mammals, scavenged Fur Seal *Arctocephalus gazella*; cephalopods (57 beaks) *Kondakovia longimana* 3.5% no., 7200 g, *Gonatus antarcticus* 5.3, 106 g, *Psychroteuthis gla-*

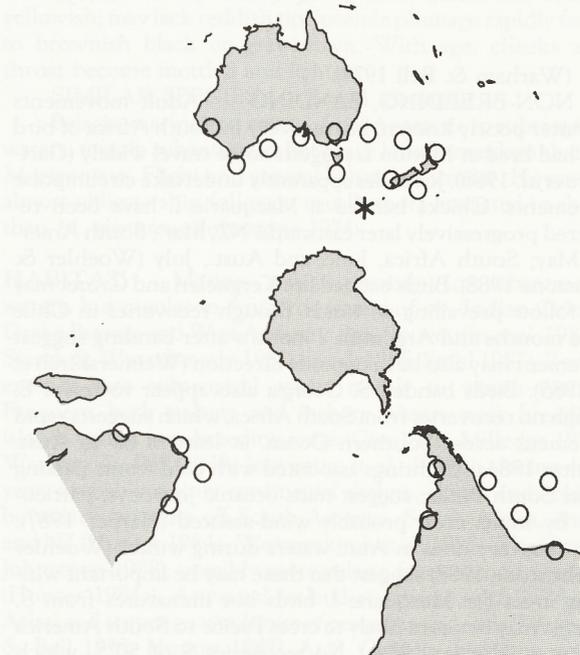


Fig. 1. 54S 158E 10X10 ABBBS

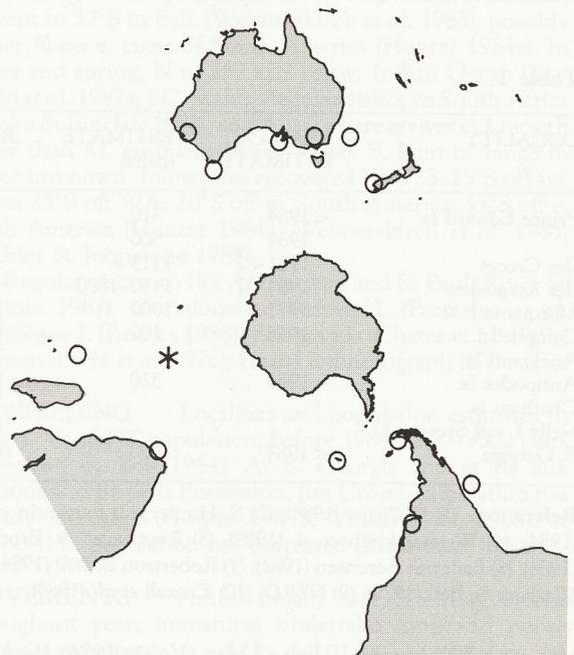


Fig. 2. 46S 51E 10X10 CRBPO

cialis 1.8, *P. sp.* 1.8, *Martialia hyadesi* 67, 87.4 g (23.3; 38), *Chiroteuthis* 3.6, *Mastigoteuthis* 1.8, *Taonius* 1.8, *Galiteuthis glacialis* 14.0, 69.2 g (19.0; 8); fish mostly Nototheniidae. Diet varied between years, proportion of penguins eaten being inversely related to availability of euphausiids, and between sexes; of 994 birds seen feeding at carcasses of seals, 97.4% males; females tended to bring back mostly marine prey captured away from land; most small petrels fed to chicks probably captured at sea by females.

At **Macquarie I.** (341 samples, adults 99, chicks 179, boluses 32; Johnstone 1977) penguins were *Eudyptes chryso- come*, *E. schlegeli*, rarely *Aptenodytes patagonicus*; other birds, White-headed *Pterodroma lessonii* (1.2% freq.) and Kerguelen *P. brevirostris* Petrels (0.3), Antarctic Prion (0.3), unident. prion 0.3, Short-tailed Shearwater *Puffinus tenuirostris* (0.3), Common Diving-Petrel (0.3); mammals, Southern Elephant Seal *Mirounga leonina*; cephalopods Onychoteuthidae/Gon- atidae 1.2, *Nototodarus sloanii* 1.2, *Histioteuthis* 0.9, Cranchii- dae 0.3; crustaceans mysidaceans *Gnathophausia* 2.3, amphip- ods 0.6 (incl. Lysianissidae 0.3, Gammaridea 0.3), prawns/shrimps 0.9; other foods unident. carrion and kelp.

Table 2. Breeding diet of *M. halli*.

	%wt. Bird I.		%freq. Bird I.		Macquarie I. combined
	male	female	male	female	
BIRDS	63.9	52.6	62-80	46-65	60-80
PENGUINS	59.6	41.5	62	46	60
OTHER	4.3	11.1	18	19	16-20
CRUSTACEANS	13.6	31.7	19	42-51	5
EUPHAUSIIDS	13.6	30.4	19	42	0
FISH	1.9	4.6	9	10	7
CEPHALOPODS	2.9	2.8	7	17	21
MAMMALS	17.9	8.3	19	7	6
OTHER	0	0	0	0	32-34

Bird I. (Hunter 1983a); Macquarie I. (Johnstone 1977).

INTAKE Total food fed to chicks differed between sexes: male chicks received 63.5 kg (n=30), females 51.5 kg (n=26); though both sexes were fed meals of similar size, frequency of meal declined more rapidly for female chicks than males; see Table 3.

Food at Bird I., S. Georgia, abundant enough during summer to allow breeding and moult to occur simultaneously (Hunter 1984b).

Table 3. From Hunter (1983a).

AGE (days)	MEAN MEAL WT BOTH SEXES (g)	N	meals/day	
			MALE	FEMALE
0-20	94	61	2.21 (0.89; 14)	2.33 (0.98; 12)
21-40	180	140	2.69 (0.87; 38)	2.26 (0.93; 19)
41-60	311	82	2.00 (0.96; 38)	1.81 (0.82; 36)
61-80	335	95	2.22 (0.94; 18)	1.53 (1.12; 19)
81-100	345	49	2.10 (1.20; 10)	1.44 (0.88; 9)

SOCIAL ORGANIZATION Gregarious on breeding grounds, but also nesting solitarily at Macquarie I. (Bourne & Warham 1966). Congregate round food, when following

ships, or when washing and preening (Johnstone 1974).

BONDS Sustained monogamous; some divorces recorded at Ile de la Possession, Iles Crozet (Voisin 1988), and S. Georgia (Hunter 1984b). Adults may begin to re-establish bond in Feb.-Mar., after departure of chicks. Age at first breeding 4-11 years, perhaps older; most between 9 and 11 years old (Hunter 1984b; Voisin 1988; Woehler & Johnstone 1988). Both parents incubate and tend young for c. 20 days after hatching.

BREEDING DISPERSION Small to large colonies or solitarily. At Iles Crozet, Antipodes and Campbell Is, usually in small colonies of 10-20 nests (Voisin 1968, 1976; Bailey & Sorensen 1962; Warham & Bell 1979); at Iles Kerguelen, colonies of up to 280 pairs (Thomas 1983); solitary pairs apparently predominate on Macquarie I. (Bourne & Warham 1966). Minimum distance between nests 3-5 m. No exact measures of nest density; small groups of usually less than 10 pairs in same general area on Macquarie I. Only 1-2 m round nest-site defended. May use same site for several years or abandon it after 1-2 seasons.

ROOSTING In groups of up to 100 birds, sometimes more (Voisin 1968), on beaches and lakes, often with *M. giganteus*. Mates roost together at nest-site in breeding season. Times of arrival at and departure from roost not known.

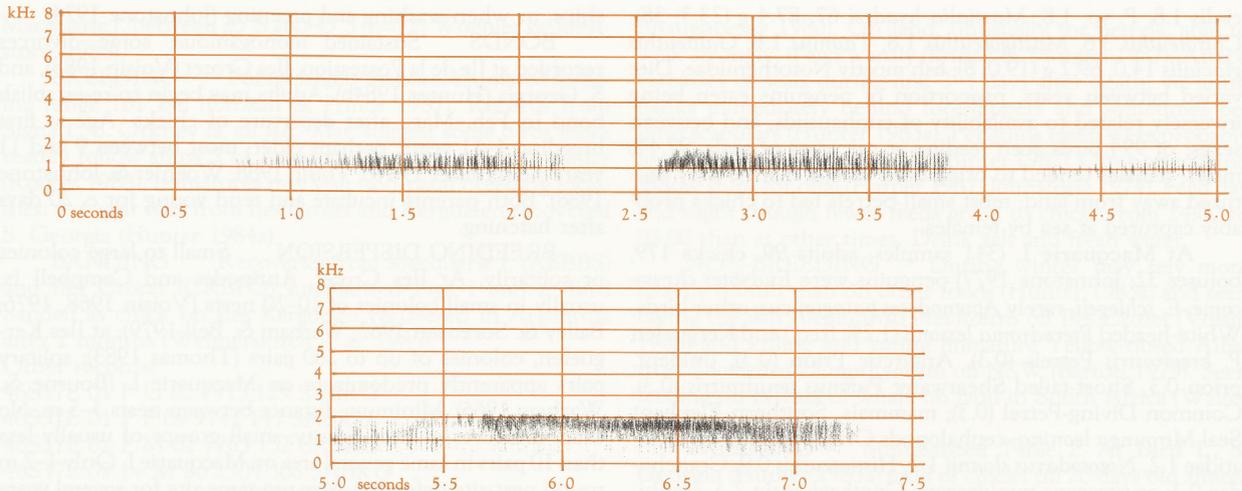
SOCIAL BEHAVIOUR Factors affecting observation of behaviour as for *M. giganteus* (q.v.); threat, appeasement and submissive displays, dominance hierarchies, fighting and escape behaviour similar. Johnstone (1977, 1979) recorded *M. halli* feeding more on carcasses of seals than did *giganteus*, but slightly larger *giganteus* usually won if feeding disputes arose. Sexual behaviour as in *giganteus* (Voisin 1968, 1978). No detailed descriptions of copulation. Burger (1978), Johnstone (1978) and Hunter (1983a) have recorded breeding attempts between *halli* and *giganteus*; successful attempts known only on Bird I. (Hunter 1983a, 1987).

RELATIONS WITHIN FAMILY GROUP Males undertake larger part of incubation and guard duties than females (Mougin 1975; Hunter 1987). At S. Georgia, mean brood-stage, 19.7 days and mean guard-stage 12.5 days (Hunter 1984b; see Breeding). No proper period of desertion; chicks may be fed up to day of fledging (S. Hunter). Begging behaviour of chick and feeding by adults same as for *giganteus*.

VOICE No detailed study. Calls apparently similar to those of *M. giganteus*, but display call thought to be harsher and pitched lower than that of *giganteus* (Voisin 1968). Sonagram A shows Whinnying call.

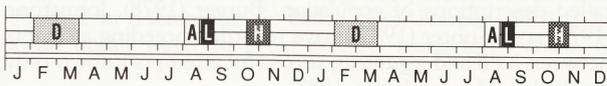
BREEDING Fairly well known. Studied at Iles Crozet (Voisin 1968, 1976; Mougin 1975) and S. Georgia (Hunter 1984b); Macquarie I. study (Warham 1962) made before separation of species. Information supplied by J.-C. Stahl. Colonial or solitary breeders on subantarctic islands and S. Georgia.

SEASON Arrival at colonies: Iles Kerguelen, Aug. (Paulian 1953); S. Georgia, early Aug. (Croxall & Prince 1987); at Iles Crozet, attendance at colonies varies throughout non-breeding season. Pre-laying period little known. At Iles Crozet, numbers in colonies decrease sharply second half July, increase again early Aug. when first copulation observed. Laying: Marion I., 10 Aug.-1 Sept. (Burger 1978); Iles Crozet, 16 Aug.-5 Sept.; 43% lay 20-27 Aug.; Iles Kerguelen, starts 17-



A J. Kendrick; Auckland Is, NZ, Feb. 1966; P26

24 Aug. (Paulian 1953; Thomas 1983); Campbell I. starts mid-Aug. (Bailey & Sorensen 1962); Macquarie I., 11 Aug.–6 Sept. (Johnstone 1978); Antipodes Is, late Aug.–early Sept. (Warham & Bell 1979); S. Georgia, mean 2–3 Oct. (2.3–7.1; 23 Sept.–10 Oct.; 2 years). Departure of young: Iles Crozet, 26 Jan.–14 Mar., 80% 10 Feb.–3 Mar.; Iles Kerguelen, Feb.–Mar. (Paulian 1953); Macquarie, Feb.; Antipodes Is, most early Feb. (Warham & Bell 1979); S. Georgia mean fledging date 22 Mar. (Croxall & Prince 1987).



(I. Kerguelen)

SITE Nests established usually at low altitude and near sea; on densely vegetated flats, slopes, sand-dunes, beach terraces, headlands on edges of plateaux overlooking sea. Nests sheltered by clumps of tussock, rock, overhang or in lee of sand-dunes. At Iles Crozet and Kerguelen, locations of colonies show marked changes from year to year, and breeding pairs usually not bound to traditional nest-site (Voisin 1968, 1984; Thomas 1983). May breed with *M. giganteus* at S. Georgia and Iles Crozet, but *M. halli* usually in dense tussock vegetation.

NEST, MATERIALS Nest cup-shaped, size depending on availability of material. Material includes tussock-grass, *Acaena* twigs, fern, branches of *Coprosma*, green leaves, and dead flower-stalks of *Chrysobactron rossii* at Campbell I. (Bailey & Sorensen 1962). At Iles Kerguelen, nests usually simple depression scratched in sandy soil, with some *Acaena* twigs (Paulian 1953). External diameter 60–150 cm; height c. 15 cm; diameter of cup 30 cm, depth of cup 10–25 cm. Nest maintained during incubation. Building activity from Feb. to egg-laying (Voisin 1968).

EGGS Elliptical to oval; rough-textured; white.

MEASUREMENTS:

S. Georgia 104.3 (3.5; 96.2–112.4; 46) x 65.4 (1.8; 61.4–70.7)

Iles Crozet 104.7 (98–115; 15) x 66.1 (60–79)

Iles Kerguelen 104.5 (101–111; 4) x 66.7 (64–69) (Paulian

1953)

Chatham Is 101.5 x 64.0 (n=1) (Oliver)

Auckland Is 101.6 x 67.6 (n=1) (Oliver)

WEIGHTS:

S. Georgia: 256.4 (17.9; 236–284; 8)

Campbell I.: 228 (205–255; 7) (Bailey & Sorensen 1962)

CLUTCH-SIZE One. No replacement laying; at S. Georgia, 37.3% of breeders did not nest again in following season.

LAYING Fairly well synchronized. Dates given above.

INCUBATION By both sexes. At Iles Crozet, average 8 shifts (5–10), male takes 54% of share; shortest shift, first by female, 2–8 days; longest, fourth by male and fifth by female, 11.3 days. At S. Georgia, mean length of five last shifts 2.9 days, male takes greater share than female. **INCUBATION PERIOD:** Iles Crozet, 59 days (57–62; 15); S. Georgia 60.1 days (1.1; 59–62; 8).

NESTLING At hatching: upperparts ashy grey, underparts white; grey crown in marked contrast with white forehead and facial area (Voisin 1968). **NESTLING PERIOD:** S. Georgia, males 114.3 days (2.8; 108–120; 30), females 109.8 days (2.1; 106–115; 26). At Macquarie I., 110–120 days (Johnstone 1977). Chipping up to 4 days before hatching (Hunter 1984b). Chick attended by both parents. **Brood-stage:** Iles Crozet, 17 days (16–18); S. Georgia, 19.7 days (2.5; 14–24; 31). **Guard-stage:** S. Georgia, 12.5 days (7.7; 0–20; 31); Iles Crozet, 6–20 days. **Brooding shifts:** Iles Crozet 3 days (1–10).

GROWTH At S. Georgia, weight at hatching: males 172.8 g (13.0; 152–193; 14), females 176.0 g (13.0; 155–193; 8); maximum weight: males, 6420 g (129% adult weight), females 4810 g (127%) after 90–100 days; weight at fledging: males 5070 g (102%), females 4160 g (110%). At Iles Crozet, maximum weight: 6180 g (146%), weight at fledging: 5170 g (122%). **Wing, culmen and tarsus at fledging** c. 95% adult length (Hunter 1984b).

FLEDGING TO MATURITY Independent of parents at fledging. Youngest-known birds returning to Ile de la Possession, where banded as chicks, 3 years old (Voisin 1988). **Age at first breeding:** S. Georgia minimum, 6 years for males; Macquarie I., minimum 6 years, peak 9–11 years (Woehler & Johnstone 1988); Ile de la Possession, 4–11 years, perhaps

more (Voisin 1988).

SUCCESS Iles Crozet: hatching 36.7% (18.5; 25.3–66.7; 147 in three seasons), fledging 77.8% (7.5; 66.7–84.2; 54 in three seasons), total success 28.6% (15.1; 21.3–53.3; 147 in three seasons). Campbell I.: total success c. 25% (Bailey & Sorensen 1962). S. Georgia: hatching 91.0% (7.3; 82.6–95.9; 108 in 3 years), fledging 90.4% (5.8; 84.2–95.7; 100 in 3 years), total success 73.1% (18.3; 51.9–90.4; 2598 eggs in four seasons). Ile de la Possession: breeding failure 1966–77, 29.4–87.8% (Voisin 1988). Mean annual adult survival: S. Georgia 88–93%; Ile de la Possession, 92.3% (Voisin 1988). Most loss of eggs in first 10 days of incubation; main causes: snow-storms, desertion, predation by skuas and sheathbills, infertility, damage by incubating bird. Most chicks lost within 10 days of hatching; main causes: starvation, exposure, trampling by adults, predation by skuas. High breeding failure on Ile de la Possession, 1975–77, probably caused by disturbance at colonies (Voisin 1988). Increase of S. Georgian population probably because breeding success has improved after increase of carrion from seals (Hunter 1984b).

PLUMAGES For diagrammatic representation of morphs, see figure in Conroy *et al.* (1975). Plumage similar to *M. giganteus* but no white morph. At S. Georgia and Macquarie I., age of first breeding 6 years (Hunter 1984b; Woehler & Johnstone 1988).

ADULT Similar to dark morph of *M. giganteus*; differs in: **HEAD AND NECK.** Extent of white plumage varies (see figure in Johnstone [1974]). Chin to lower throat, white; from lower throat to base of foreneck, feathers have broad subterminal dull-white patches on webs, with open pennaceous dark-brown (121) tips. Breast similar, but feathers suffused pale dark-brown (121).

DOWNY YOUNG Protoptile. Ash-grey cap contrasting with white forehead, face and sides of head; rest, white. Mesoptile, uniform grey (illustration in Voisin 1968).

JUVENILE, IMMATURE Similar to *M. giganteus*; no juvenile white morphs.

SUBSEQUENT PLUMAGES Progressive whitening round head and throat only (Johnstone 1974).

BARE PARTS Based on photos in NZRD, Lindsey (1986) and NZDOC Library, except where stated.

ADULT Iris, pale grey (86); varies from brown to grey (Johnstone 1971, 1974). Asymmetry in colour of iris occurs: one grey, other flecked black (Warham 1962; Warham & Bell 1979), but not mentioned in Conroy *et al.* (1975); unknown at what rate colour of iris changes; for details of frequency of colours at Macquarie I., see Johnstone (1974). Bill and nostrils, dull pink (5); unguis, pink (3) contrasting with rest of bill; typically, small dusky patch on cutting edge of mandibular unguis. Legs and feet, similar to *M. giganteus*.

DOWNY YOUNG Similar to *M. giganteus*; reddish tip to unguis evident at 2–3 weeks (Johnstone 1974).

JUVENILE, IMMATURE Similar to adult (Voisin 1968; Johnstone 1974).

ABERRANT BARE PARTS Hybrids between *halli* and *giganteus* at S. Georgia have wholly pale bills, without dark red tip of *halli* or pale green tip of *giganteus*.

For further details of bare parts see Johnstone (1971, 1974) or Conroy *et al.* (1975).

MOULTS Based on Hunter (1984c). Pattern of moult is

generally similar to *M. giganteus* (*q.v.*) (Warham & Bell 1979; Hunter 1984c). Differs in timing of primary moult: some males start midway through incubation but others delay until hatching; females do not start wing-moult until 3 weeks into chick-rearing period. Two males showed suspended moult; no suspended moult found in females. Estimated duration of primary moult in breeders: males 183 days, females 168 days.

MEASUREMENTS (1) Iles Crozet; methods unknown (Voisin 1968). (2) Macquarie I., breeding adults, live; wing measurement not specified (Johnstone 1977). (3) S. Georgia, adults; methods unknown (Hunter 1984c).

	MALES	FEMALES
WING	(1) 526.1 (4.15; 495–562; 19) (2) 529.0 (11.0; 515–544; 6) (3) 538.5 (9.25; 521–564; 33)	499.1 (3.9; 473–528; 13) 499.0 (9.4; 487–510; 4) 505.6 (8.55; 482–522; 35)
BILL	(1) 101.2 (0.50; 97–106; 29) (2) 101.5 (2.58; 95.7–107.9; 95) (3) 103.3 (3.02; 96–110.5; 44)	88.2 (0.36; 84–93; 16) 88.2 (2.24; 81.7–93.6; 95) 89.4 (2.54; 85–96; 46)
BILL D	(3) 36.5 (1.16; 34.4–38.4; 41)	31.9 (1.08; 29–34.1; 41)
TARSUS	(1) 104 106	90.8 (87–96.5; 3)

Before Bourne & Warham's (1966) separation of *halli* from *giganteus*, only one species of giant-petrel recognized. Carrick & Ingham (1970), and others, confirmed separation. Measurements before 1966 of little use unless of white morphs or from allopatric breeding localities. Post-mortem measurements of skins after 9 years preservation do not significantly alter, except for slight shrinkage of wing (Warham & Bell 1979). Additional measurements in Lowe & Kinnear (1930) and Westerskov (1960). For details of growth rates of chicks, see Hunter (1984c).

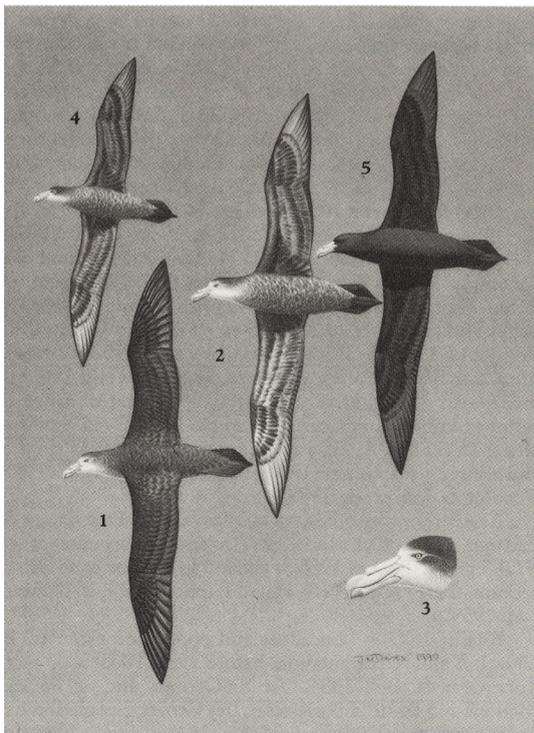
WEIGHTS At Iles Crozet, no date, unknown status: males 4711.1 (96.0; 4250–5400; 18); females 3370.8 (121.0; 2900–4200; 12) (Voisin 1968). At Macquarie I., adults during guard-stage: males 4790 (330; 4100–5450; 57); females 3580 (300; 3100–4450; 49) (Johnstone 1977). At S. Georgia, adults, summer: males 4902 (391.0; 4150–5800; 56); females 3724 (313.0; 3050–4500; 43) (Hunter 1984c).

STRUCTURE Similar to *M. giganteus*. RMO

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Volume 1 (Part A), Plate 26

Northern Giant Petrel *Macronectes halli*

- 1. Adult, dorsal
- 2. Adult, ventral
- 3. Adult head
- 4. Immature, ventral
- 5. Juvenile, ventral

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