

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.

References

- Bang, B.G. 1966. *Acta anat.* 65: 305-415.
 Bourne, W.R.P. 1976. Pp 403-502. In: Johnston 1976.
 Brodkorb, P. 1963. *Bull. Flor. St. Mus. biol. Sci.* 7: 179-293.
 Clarke, A., & P.A. Prince. 1976. *J. Exp. mar. Biol. Ecol.* 23: 15-30.
 Fisher, J. 1952. *The Fulmar*.
 Harper, P.C. 1978. *NZ J. Zool.* 5: 509-549.
 Johnston, R. (Ed.). 1976. *Marine Pollution*.
 Klemm, R.D. 1969. *S. Ill. Univ. Monogr. Sci. Ser.* 2.
 Obst, B.S. 1986. *Wilson Bull.* 98: 189-95.
 Olson, S.L. 1975. *Smithson. Contr. Paleobiol.* 23.
 Swennen, C. 1974. *Ardea* 62: 111-117.
 Timmermann, G. 1965. *Abh. Verh. naturwiss. Vereins Hamburg NF* 8, Suppl. 1-249.

Family DIOMEDEIDAE albatrosses

The albatrosses are a small group of some 13-16 large petrels with long wings adapted for gliding flight and with long powerful beaks adapted for seizing prey at the surface; nine species breed in our region and one other has been recorded as a vagrant. Because they are so large, they must breed in the open, where they walk well for petrels. Most s. species build substantial conical nests but n. ones, breeding in warm climates, make only scrapes. Young birds in some species have a drab plumage but adults of many species develop bolder markings with brightly coloured stripes on the bill, used in social displays when breeding. Three distinct groups occur in the Southern Ocean but the distinction between two is blurred by intermediate forms that occur in North Pacific:

(1) The great albatrosses are huge, long-winged, long- and pale-billed, short-tailed birds that glide round the world in Southern Ocean. Until recently, there were thought to be two species: the more pelagic Wandering Albatross *D. exulans* breeding on most of the subantarctic islands, which is dark with a white underwing when young, becoming more or less white with dark wing-tips when adult; and the more coastal Royal Albatross *D. epomophora*, breeding round NZ, which resembles the extreme white adult Wanderer throughout its life but has a dark cutting-edge to the upper mandible. A few birds breeding in extreme immature *exulans*-type of plumage on Ile Amsterdam in the Indian Ocean have recently been described as a third species *D. amsterdamensis* but there is continuing debate whether this is justified owing to the occurrence of similar populations in South Atlantic and round NZ (Bourne 1989).

(2) The medium-sized albatrosses *Diomedea* (*Thalassarche*), often called mollymawks, are a compact group of white-bodied, dark-backed species with brightly marked bills in adults, all five species being found in our region. They consist of two comparatively coastal species, the Black-browed Albatross *melanophrys* with main breeding colonies round South America, and the Shy *cauta* with 3-4 rather well-defined subspecies, sometimes treated as separate species, breeding in A'asia. There are also three pelagic species: Grey-headed *chrysostoma* to the south, Yellow-nosed *chlororhynchus* in subtropical South Atlantic and Indian Oceans, and Buller's *bulleri* in equivalent parts of South Pacific.

The differences between Groups (1) and (2) are rather marked and they would doubtless be treated as distinct genera if it were not that four other albatrosses with intermediate characters breed in North Pacific: Black-footed *nigripes* with plumage resembling that of sooty albatrosses, though shape differs; Laysan *immutabilis* with plumage like that of the medium-sized albatrosses (Group 2); Short-tailed *albatrus* with a sequence of plumages rather like those of Wanderer, though smaller; and the Waved *irrorata* with dark plumage except for pale head, neck and underwing. Because it is hard to make any clear distinction between these birds they are normally all included in an unusually wide genus *Diomedea*.

(3) The sooty albatrosses *Phoebastria*. Two extremely aerial, highly pelagic and rather aggressive or predatory species with fairly small bills with a groove along the lower mandible; long wings; long pointed tails; and dark plumage; nest on steep places and have vocal aerial displays.

General characters are: body, short and broad; head, large; neck, short. Wing, long and narrow, folded in three almost equal parts, 11 primaries, p10 longest, p11 minute; up to about 40 secondaries, diastataxic. Tail, short and square in *Diomedea*, longer and wedge-shaped in *Phoebetria*, 12 feathers. Bill, heavy and composed of several horny plates; hooked; nostrils in tubes on either side. Legs, strong; three front toes joined by web; hind toe absent or vestigial. Oil gland, feathered. Sexes similar; male larger on average. Plumage mainly white except in *Phoebetria*, in which it is dark grey. Juveniles and immatures generally separable but mostly not very different from adults except in *D. exulans* and *D. albatrus*; fully adult plumage attained only after several years. Stance upright and able to walk much better than most other Procellariiformes. Swim and rest on sea buoyantly with head held high. Feed mostly on fish and squid by surface-seizing or shallow diving, but sooty albatrosses also take birds. Follow ships for scavenging.

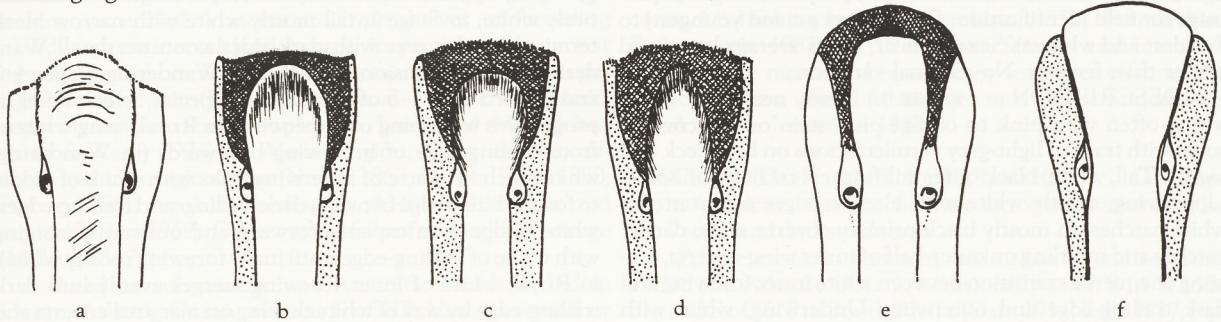


Fig. 1 Dorsal view of base of bill of small *Diomedea*

Fig. 1a Black-browed Albatross *D. melanoprys*

Fig. 1b Grey-headed Albatross *D. chrysostoma*

Fig. 1c Yellow-nosed Albatross, *D. chlorohynchos*, subspecies *chlorohynchos*

Fig. 1d Yellow-nosed Albatross, *D. chlorohynchos*, subspecies *bassi*

Fig. 1e Shy Albatross *D. cauta*

Fig. 1f Buller's Albatross *D. bulleri*

Long-lasting monogamous pair-bond. Breed colonially, pairs often returning to same site. Defend small nest-territories. Perform spectacular agonistic and sexual displays at nest in *Diomedea*; vocal aerial displays in *Phoebetria*. Eggs, white, minutely spotted reddish. Clutch-size; one; no replacement laying. Incubation by both sexes in long alternate spells. Incubation period, 2 or more months. Nestling, semi-altricial, nidicolous; hatched in down. Brooded for a short time after hatching; then left alone in nest, parents returning only to feed chick by incomplete regurgitation. Nestling period long, up to 12 months, and so in some species successful adults cannot breed annually. Young independent on fledging. Maturity reached only after several years. Some populations were reduced in the past, notably by egg-collecting, but there appear to be few threats now except that some great albatrosses are caught by long-line fishing.

REFERENCES

Bourne, W.R.P. 1989. *Gerfaut* 79: 105-16.

Diomedea exulans Wandering Albatross

COLOUR PLATE FACING PAGE 272 273

Diomedea exulans Linnaeus, 1758, *Syst. Nat.*, ed. 10, 1: 132; based chiefly on 'The Albatross' of Edwards, 1747 — Cape of Good Hope ex Edwards.

The genus is named after Diomedes, King of Argos, next to Achilles the bravest hero in the Greek army at Troy. When he died, his companions were inconsolable and were metamorphosed into birds (*aves Diomedae*). The specific name refers to the wandering habits of the species (*exsulans*, living as an exile).

OTHER ENGLISH NAMES Cape Sheep; Man-of-War Bird; Great Wandering, Snowy or White-winged Albatross.

POLYTYPIC Nominate *exulans* Linnaeus, 1758, Tristan da Cunha & Gough I.; *chionoptera* Salvin, 1896, S. Georgia, islands in s. Indian Ocean and Macquarie I.; perhaps two other subspecies on Antipodes Is and Auckland and Campbell Is (Robertson & Bell 1984).

FIELD IDENTIFICATION Length 110–135 cm; wingspan 250–350 cm; weight 6–11 kg. Huge full-bodied albatross with extremely long wings and short, gently wedge-shaped tail; bill, huge and pink with bulbous tip. Similar only to other great albatrosses — Royal *D. epomophora* and Amsterdam *D. amsterdamensis*. Much larger than the black-backed albatrosses (mollymawks). Juveniles have mostly dark plumage which gradually whitens over a long period. Extent of white of breeding adults varies between individuals, sexes and geographically (n. populations tend to be darker). Harrison (1979, 1985, 1987; on which account based) proposed stages of plumage for field identification; from 1 (darkest and youngest) to 7 (oldest and whitest). Sexes similar; males average larger and whiter than females. No seasonal variation.

DESCRIPTION **STAGE 7.** Head, neck and body, white; often with pink to orange-pink stain on ear-coverts; some with trace of light-grey vermiculations on hindneck and saddle. Tail, white; black outer tail-feathers retained on some. Upperwing, mostly white with black remiges and scattered white patches on mostly black primary coverts; some darker patches and mottling on outer-half of inner wing-coverts, creating chequered transition between white inner forewing and dark trailing-edge and outerwing. Underwing, white with black remiges forming thin dark trailing-edge and large dark tip. **STAGE 1 (JUVENILE).** Head, neck, body and tail, wholly chocolate-brown except for conspicuous white mask. Underwing, as adult except for thin black margin between carpal joint and base of outermost primary and chocolate-brown pre-axillary notch, conspicuous at base of inner leading edge of wing. **STAGE 2.** Like Stage 1 but with white mottling appearing on hindneck, saddle, rump, upper tail-coverts and centre of inner upperwing behind elbow. Belly and flanks, mostly white with brown breast-band and under tail-coverts. **STAGE 3.** Head and neck, mostly white except for brownish crown and mottling on sides of neck. Body, mostly white with brown and grey vermiculations on saddle and flanks and indistinct breast-band. Tail, white with black sides and tip. Upperwing, mainly blackish brown with small whitish patch on centre of innerwing behind elbow. Underwing, as Stage 1 and 2; pre-axillary notch still present but may be paler. **STAGE 4.** Like Stage 3 but head and body whiter and breast-band paler, greyer and less distinct; tail, whiter with dark sides and tips of outermost feathers usually retained. Underwing, like Stage 3 but lacks pre-axillary notch. **STAGE 5.** Like Stage 4 except head and body mostly white; tail mostly white, usually with dark outer feathers. On upperwing, white central patch behind elbow linked to white of back, forming white wedge extending from body into innerwing, leaving broad black leading- and trailing-edges. Underwing, as Stage 4 but black leading-edge between carpal joint and base of outermost primary, thinner and not continuous. **STAGE 6.** Like Stage 5 except dark leading-edge of upperwing heavily blotched with white or mainly white; white central wedge extends forwards and outwards, merging with white of leading-edge. Unlike in Stage 7, usually retain some dark inward of carpal joint, thus less white on innerwing; transition between white of forewing and dark of trailing-edge and outerwing chequered, as on Stage 7. Tail usually retains some dusky markings though some birds have wholly white tail. **Bare parts of all birds.** Bill, large, with bulbous maxillary unguis; pinkish horn with yellowish-horn unguis forming contrasting paler tip; flushes to brighter pink, especially in breeding birds. Nostrils, small, on sides of bill, opening slightly upwards. Iris, brown. Legs and feet, flesh-pink with bluish-coloured webs and horn-col-

oured claws. Feet project well beyond tip of tail in flight; sometimes tucked forward into belly feathering.

SIMILAR SPECIES Most likely to be confused with **Royal Albatross**. At close quarters, Royal recognized by dark cutting-edge of upper mandible. Head and body always clean white except for a little brown mottling on cap of some immatures (*sanfordi* only) and black speckling on lower back and rump in juveniles; never has brownish body plumage and vermiculations of Wandering Albatross Stages 1–4 nor greyish vermiculations of Wandering Stages 5–6 (sometimes 7) that give dirty appearance to body. In Royal Stages 2–5, tail entirely white; in Stage 1, tail mostly white with narrow black terminal band, never with dark sides as on nearly all Wandering. Main confusion lies between Wandering Stages 4–7 and Royal Stages 1–5 of southern subspecies, which differ in progressive whitening of upperwing: in Royal, wing whitens from leading-edge of innerwing backwards (in Wandering, white patch in centre of innerwing links with white of saddle to form white wedge between dark leading- and trailing-edges; white wedge then expands forward and outwards, merging with white of leading-edge until inner forewing mostly white); in Royal, white of inner forewing merges evenly into dark trailing-edge by way of white dusting on marginal coverts and delicate white fringing to lesser and median secondary coverts (in Wandering, transition between white of forewing and dark of trailing-edge and outerwing, heavily blotched giving more chequered appearance). Separation of Royal and Wandering in whitest stages (5 and 7 respectively) difficult because upperwing pattern very similar; apart from diagnostic black cutting-edge of bill in Royal, black in tail indicates Wandering. Subtle distinctions in jizz often helpful: Royal has longer bill and more sloping, less angular forehead profile giving more rounded, slender-headed appearance (Wandering tends to look flatter-crowned with shorter, often pinker bill). Very rare **Amsterdam Albatross**, similar to Wandering Stages 1–3 but has diagnostic dark-brown cutting-edge to upper mandible, which appears black at distance, and greenish-brown unguis, forming dusky tip contrasting with rest of bill. All **other albatrosses** of s. oceans have black backs; are much smaller with proportionately smaller bill and shorter wings; feet do not project beyond tail; black leading-margin on inner underwing. Much greater size, mostly white underwing, white mask and pink bill separate brown-bodied Wandering Albatrosses from **giant-petrels** *Macronectes* spp and **sooty albatrosses** *Phoebastria* spp.

Circumpolar in s. oceans; adult females, juveniles and immatures occur farther N than adult males which tend to range in higher latitudes. Occupy wide range of marine habitats; occur in pelagic waters but also concentrate in shelf-break and continental shelf waters. Commonly seen from land. Graceful in flight: long sweeping glides and soaring on stiff outstretched wings, rarely flapping except in calm conditions, when flight laboured with deep pliable wing-beats. On calm days, spend much time sitting on sea. Take-off and flight in light winds, laboured; long run-off before becoming airborne, heavy flapping to stay aloft. Feed by surface-seizing, occasionally surface-plunging, pursuit-plunging and surface-diving. Habitually follow ships; attend fishing vessels, squabbling over offal. Solitary or gregarious at sea. Give harsh croaking at sea and croaking, groaning and whining calls at colonies.

HABITAT Marine, pelagic and aerial. In Antarctic, occur in open water, rarely entering belt of icebergs (Falla 1937;

Hicks 1973), but in late summer birds may approach edge of pack-ice (Darby 1970); in winter, uncommon S of Antarctic Convergence indicating northward shift in distribution (Sziij 1967). At Iles Crozet, males feed over Antarctic waters; females and immatures in Subtropics (Weimerskirch & Jouventin 1987). Observed over waters with surface-temperatures from -2 to 24°C (Bierman & Voous 1950; Grindley 1981); in s. Indian Ocean prefer waters of 6.3-7.7 °C (Rand 1963); off South America, 8-12 °C (Jehl 1973); in South Atlantic Ocean, two zones of increased abundance at 0 °C and 9-20 °C (Bierman & Voous 1950). Versatile feeders in shelf or pelagic waters; some birds concentrate over shelves off breeding islands or continental land masses, in productive waters at upwellings and boundaries of currents; others remain in pelagic waters all year (Weimerskirch *et al.* 1985). In Antarctic, concentrate near submarine plateaux, banks and ridges (Johnstone & Kerry 1976). In A'sian region, occur inshore, offshore and in pelagic waters (Norris 1967; Barton 1979, 1980; Blaber 1986), regularly feeding in sheltered harbours and straits (Secker 1969). Gather at outfalls of unmodified sewage (Milledge 1977).

Breed on subantarctic and Antarctic islands in Indian Ocean, Atlantic Ocean and seas S of NZ. Nest on coastal or inland ridges, slopes, plateaux and plains, often on marshy ground (Falla 1937; Bailey & Sorensen 1962; Rand 1954,

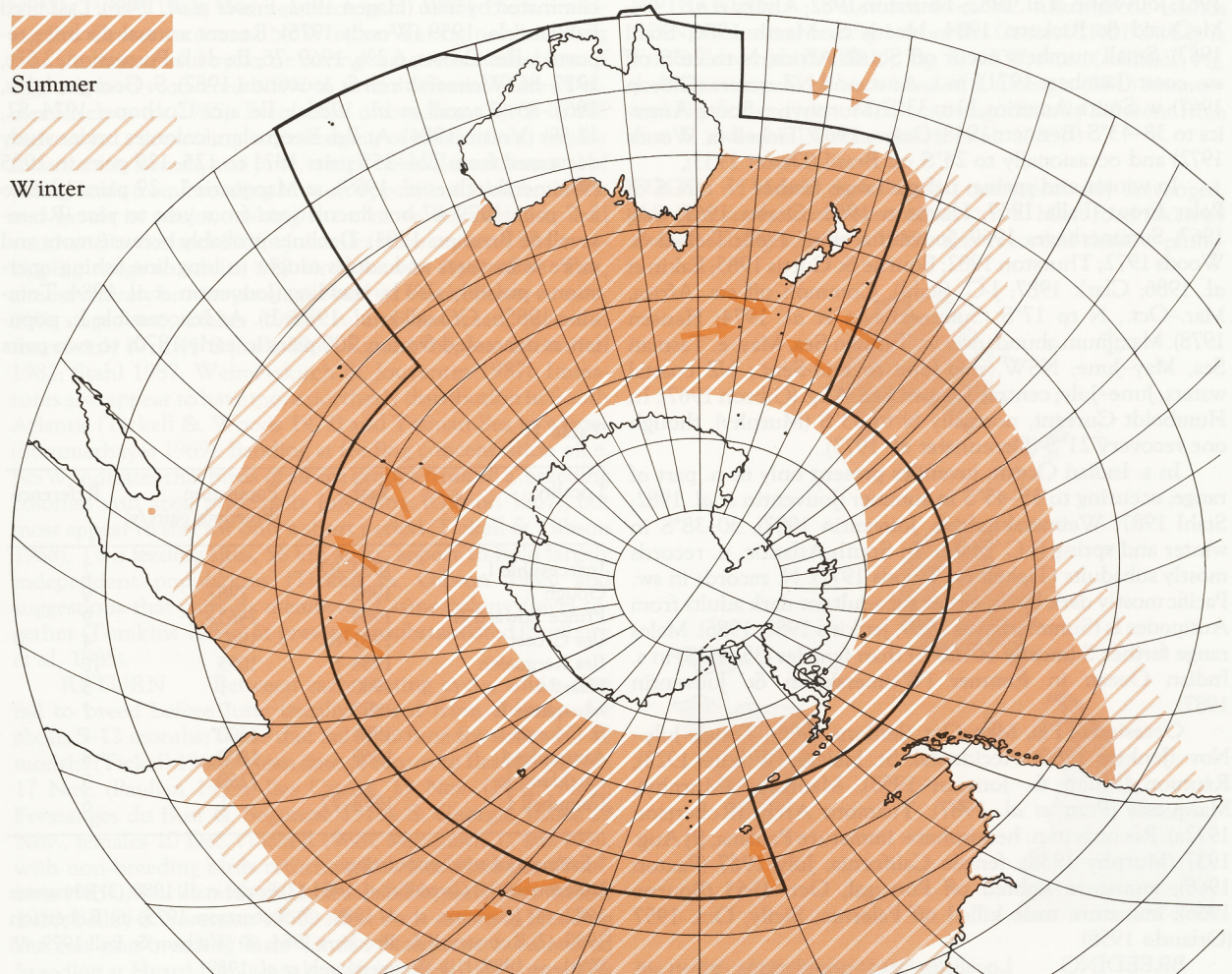
1963; Warham & Bell 1979; Weimerskirch *et al.* 1986). Prefer open or patchy vegetation (tussock, fern or shrubs) for easy access, near exposed ridges or hillocks for take-off (Warham & Bell 1979).

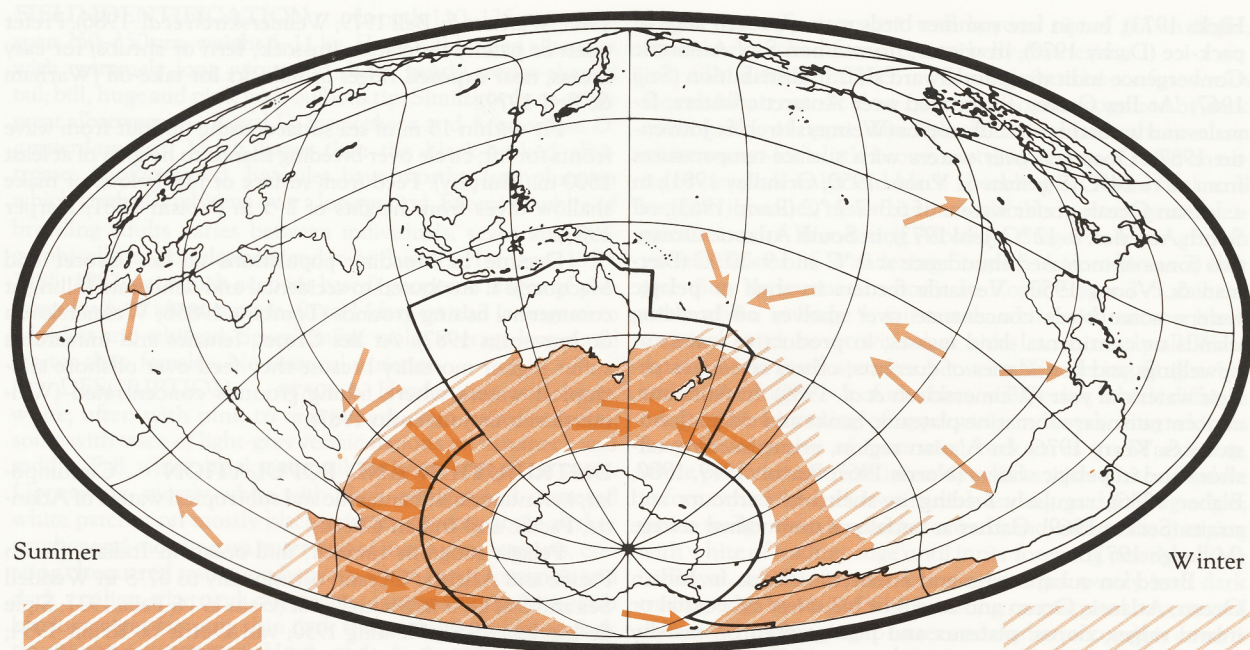
Fly within 15 m of sea surface, using updraft from wave fronts for lift; circle over breeding islands to heights of at least 1500 m (Murphy). Feed from surface or just below, or make shallow dives from heights of 2-5 m (Voisin 1981; Harper 1987).

Decline in breeding populations at Iles Crozet and Macquarie I. attributed to accidental and deliberate killing at commercial fishing grounds (Tomkins 1985b; Weimerskirch & Jouventin 1987). At Iles Crozet, females and immatures suffer higher mortality because they feed over offshore subtropical waters where fishing grounds concentrated (Weimerskirch & Jouventin 1987).

DISTRIBUTION AND POPULATION Circumpolar; in Antarctic, subantarctic and subtropical waters of Atlantic, Pacific and Indian Oceans.

Pelagic range in summer, mid-ocean in Indian, South Pacific and Atlantic Oceans; occasionally to 67°S in Weddell Sea and S of 68°S in South Pacific (Gain 1914; Falla 1937; Siple & Lindsey 1937; Fleming 1950; van Oordt & Kruijt 1954; Holgersen 1957; Dell 1960; Gill 1967; Ozawa 1967; Darby





1970; Tickell & Woods 1972; Johnstone & Kerry 1976; Zink 1981; Jouventin *et al.* 1982; Thurston 1982; Ainley *et al.* 1984; McQuaid & Ricketts 1984; Meeth & Meeth 1986; Stahl 1987). Small numbers occur off South Africa, N to 26°S off sw. coast (Lambert 1971); in s. Aust. and NZ waters (Gibson 1967); w. South America, N to 33°S (Murphy); e. South America to 38–43°S (Bennett 1948; Ozawa 1967; Tickell & Woods 1972) and occasionally to 24°S off Brazil (Dixon 1933).

In winter and spring, pelagic range farther N: rare S of Polar Front (Falla 1937; Harrison 1962; Ozawa 1967; Szijj 1967; Summerhayes 1969; Jouventin *et al.* 1982; Tickell & Woods 1972; Thurston 1982; Bourne & Curtis 1985; Eakin *et al.* 1986; Clark 1987; J-C. Stahl). Common off sw. Africa, Mar.–Oct., N to 17°S (Summerhayes *et al.* 1974; Hansen 1978). Maximum abundance: w. Tasman Sea, May; e. Tasman Sea, May–June; NSW, mid-June to mid-Sept.; NZ coastal waters, June–July; central Tasman Sea, Aug. (Gibson 1967). In Humboldt Current, normally N to 33°S (Murphy), though one recovery 21°S (Derenne *et al.* 1972).

In s. Indian Ocean, juveniles present only in n. part of range; occurring to 35–45°S in summer (Jouventin *et al.* 1982; Stahl 1987; Weimerskirch & Jouventin 1987), 30–38°S in winter and spring (J-C. Stahl). In South Atlantic, n. records mostly subadults (Tickell & Woods 1972). N. records in sw. Pacific mostly dark birds, either subadults or dark adults from Antipodes Is (Summerhayes 1969; Jenkins 1980, 1986). Males range farther S (mostly 50–60°S) than females (35–45°S) in s. Indian Ocean in summer (Weimerskirch & Jouventin 1987).

Occasional: Fiji, May–Oct. (Jenkins 1986); Tonga, July–Nov. (Jenkins 1980). Accidental: St. Helena (Wilkins 1923), Réunion (Milon & Jouanin 1953), Mauritius (Murphy), Marquesas (Pratt *et al.* 1987), Tuamotu Arch. (Robertson 1972a). Records in n. hemisphere: immature Panama, [?] Aug. 1937 (Murphy 1938); female California, July 1967 (Paxton 1968); immature sighted off Portugal, Oct. 1963 (Bourne 1966); immature male killed off Palermo, Sicily, Oct. 1957 (Orlando 1958).

BREEDING Localities and populations given in

Table 1. Last bred Tristan da Cunha in 1907, almost certainly eliminated by man (Hagen 1952; Fraser *et al.* 1988). Last bred Falkland Is, 1959 (Woods 1975). Recent annual declines reported: Iles Crozet, 6.2%, 1969–76; Ile de la Possession, 2.5%, 1977–86 (Weimerskirch & Jouventin 1987); S. Georgia, 1.1%, 1961–86 (Croxall *et al.* 1988a); Ile aux Cochons, 1974–82, 12.5% (Voisin 1984). At Iles Kerguelen, colonies under study decreased from 224–255 pairs 1971 to 125–129 pairs in 1985 (Weimerskirch *et al.* 1989); at Macquarie I., 29 pairs 1968 to 5–7 pairs 1979–82 but fluctuations from year to year (Rounsevell & Brothers 1984). Declines probably because more and more immatures and adults caught in long-line fishing operations; possibly also by trawling (Jouventin *et al.* 1984; Tomkins 1985b; Croxall *et al.* 1988a,b). At Inaccessible I., population decreased from c. 200 pairs in early 1870s to two pairs

Table 1.

Locality	Year	Population (breeding pairs/y)	Reference
Inaccessible I.	1982–87	3	2
Gough I.	1982	798+	9
Prince Edward Is	1984	2461+	9
Iles Crozet	1981–82	1962	4
Iles Kerguelen	1984–8	1095	10
Heard I.	1980	1	3
Macquarie I.	1982	7	7
S. Georgia	<1984	4300*	1
Antipodes I.	1969	1000	8
Auckland Is		7250	5
Campbell I.	1975–77	1	6

* Estimate of total population.

References: (1) Croxall *et al.* 1984; (2) Fraser *et al.* 1988; (3) Johnstone 1982; (4) Jouventin *et al.* 1984; (5) Robertson 1975; (6) Robertson 1980; (7) Rounsevell & Brothers 1984; (8) Warham & Bell 1979; (9) Watkins 1987; (10) Weimerskirch *et al.* 1989.

1938, because pigs took eggs and chicks; population stable at very low level since (Fraser *et al.* 1988).

MOVEMENTS Migratory or dispersive.

DEPARTURE Chicks fledge: Iles Crozet, 25 Nov.–2 Feb. (Fressanges du Bost & Segonzac 1976); Iles Kerguelen, 21 Nov.–5 Jan. (Paulian 1953); S. Georgia, 17 Nov.–18 Jan. (Tickell 1968; Croxall & Prince 1987); Marion I., mid-Dec–mid-Jan. (van Zinderen Bakker 1971); Campbell I., late Dec–mid-Feb. (Bailey & Sorensen 1962); Gough I., Jan–early Feb. (Swales 1965); Auckland Is, mid-Jan–mid-Feb (Bailey & Sorensen 1962); Antipodes Is, late Jan.–Mar. (Warham & Bell 1979). Non-breeders leave Macquarie I., early Jan.–early Apr., failed breeders leaving within a few days of failure (Tomkins 1985a).

NON-BREEDING Banding returns suggest adults and young disperse or migrate E (Tickell 1968; see Banding). Birds from Gough I. apparently confined to South Atlantic and South African waters; chicks recovered off Cape (one) and Tripp Seamount 30°S 14°E (one); one adult Port Elizabeth (Cooper 1988) and those breeding Antipodes, Auckland and Campbell Is apparently restricted to Tasman Sea and South Pacific Ocean (Robertson 1972a,b, 1973; Warham & Bell 1979; see Banding). Movements of birds from s. breeding sites probably circumpolar, but definite proof still lacking. Some birds breeding S. Georgia and Iles Crozet migrate regularly to NSW (Tickell 1968; Weimerskirch *et al.* 1985). Birds breeding Iles Crozet recovered NSW either during non-breeding year after successful cycle, or during same season after loss of egg; one bird recovered NSW in seven different years (Weimerskirch *et al.* 1985). Frequency of beachcast birds in NZ highest Jan., coinciding with fledging of chicks from nearby subantarctic islands, and June, which coincides with arrival of young birds from breeding sites on opposite side of Antarctic and moult in adults, making them more vulnerable to bad weather (Powlesland 1985). Juveniles have separate but overlapping range to adults; 177 birds seen in Apr. off se. Tas., almost entirely brown-plumaged birds (15% chocolate-brown, 85% stages 4–6; Blaber 1986). In Indian Ocean, juveniles found only N of 45°S (Falla 1937; Rand 1963; Jouventin *et al.* 1982; Stahl 1987; Weimerskirch & Jouventin 1987). Immatures also appear to have more northerly distribution in South Atlantic (Tickell & Woods 1972) and Tasman Sea in winter (Summerhayes 1969). Banding at feeding concentration off e. NSW indicates that birds of all age groups from all s. breeding colonies visit area, principally July–Nov. (Gibson 1967), but most appear to stay for only a short period (Tickell & Gibson 1968). Two feeding sites, 56 km apart, appear to hold largely independent populations (Tickell & Gibson 1968) and suggestions that pairs or members of same colony travel together (Tomkins 1984a) at present unsubstantiated (Sudbury *et al.* 1985).

RETURN Between each nesting cycle, adults that fail to breed before June usually absent from colonies for about 5–12 months; those that fail after June for about 12–17 months (Tickell 1968). Mean date of return to Iles Kerguelen, 17 Nov. (Paulian 1953); Iles Crozet, 19 Nov. (14–23 Nov.; Fressanges du Bost & Segonzac 1976); S. Georgia, males 29 Nov., females 10 Dec. (Tickell 1968); Macquarie I., late Nov. with non-breeding birds returning late Nov.–late Jan. (Tomkins 1985a); Auckland Is and Inaccessible I., early Dec. (Elliott 1957; Bailey & Sorensen 1962). Most birds return to breeding site but non-breeding male banded Macquarie I. recovered breeding at Heard I. 13 years later (Johnstone 1980); juveniles

from Marion I., and juveniles and adults from Iles Crozet recovered at other breeding localities (Weimerskirch *et al.* 1985; Gartshore *et al.* 1988). Only known instance of gene-flow between populations, one fledgeling from Iles Crozet breeding at Marion I. three years later (Mougin 1977).

BREEDING Travel up to 15 200 km between incubation bouts. One bird from Iles Crozet tracked by satellite recorded flying SW to Antarctica and back past Heard and Kerguelen Is; another flew 3664 km to NW, travelling at 62.7–81.2 km/h, mostly (87.1–90.9%) during daytime. Distance travelled related to wind speed; birds were almost stationary in centre of high-pressure zones for 1–7 days. After hatching, foraging distance 330 and 381 km for one male (Jouventin & Weimerskirch 1990). Other records: adult with young on Iles Crozet recovered 1800 km N (Weimerskirch & Jouventin 1987); incubating bird dyed on Iles Kerguelen seen 1420 km S (Weimerskirch *et al.* 1988); adult with young on S. Georgia sighted off Falklands and Argentinian coast (Croxall *et al.* 1988b); birds banded Macquarie I. recaptured 1600 and 2240 km N during breeding season (Tomkins 1985a); estimated foraging range from S. Georgia 1478 km (Croxall & Prince 1987). However birds breeding Iles Crozet frequently forage over neritic waters (Weimerskirch *et al.* 1986). Tropical cephalopods in diet of S. Georgian birds suggest most foraging N of Island (Prince & Morgan 1987); fish taken all characteristic of S. Georgian shelf (Croxall *et al.* 1988b).

BANDING Returns from NZ subantarctic islands (NZNBS) summarized Fig. 1; from Iles Crozet (CRBPO), Fig. 2; Prince Edward Is (SABRU), Fig. 3; NSW, Aust. (ABBBS), Fig. 4. Asian returns of birds banded S. Georgia (BBL) summarized Fig. 5. Recovery of adults not significantly different from that of juveniles (Weimerskirch *et al.* 1985).

FOOD Mostly cephalopods, many probably scavenged, also fish, rarely crustaceans. **BEHAVIOUR.** Most food taken by surface-seizing (Griffiths 1982), also recorded shallow-plung-



Fig. 1. 34S 151E 10X10 % ABBBS



Fig. 2. 41S 176E 10X10 NZNBS

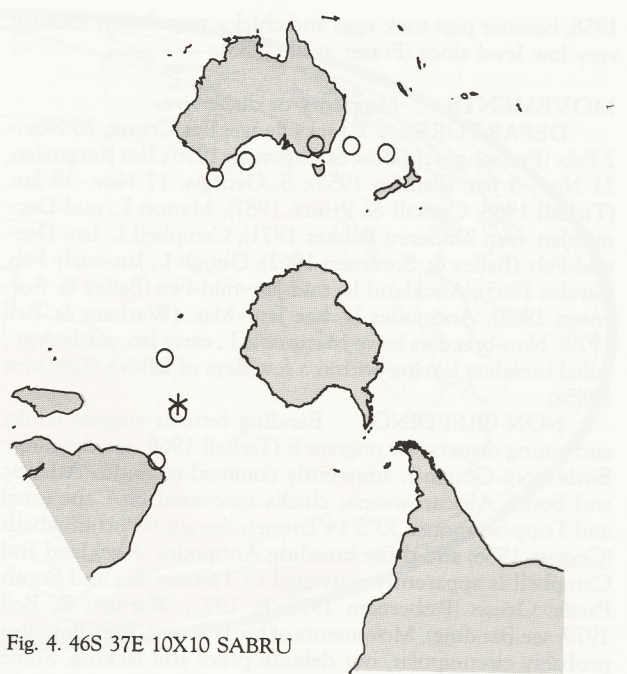


Fig. 4. 46S 37E 10X10 SABRU



Fig. 3. 46S 51E 10x10 CRBPO



Fig. 5. 54S 38W 10X10 BBL

ing and pursuit-plunging (Harper *et al.* 1985). Usually alight near food and swim towards it with outstretched neck and partly open wings; if food sinks, try to retrieve it by partially upending like ungainly duck (Harper 1987). Usually hunt for cephalopods at night, in winds >15–20 knots gliding low over surface and dropping on prey, occasionally maintaining height by pattering feet along surface. In still conditions, sit quietly with wings closed, snapping suddenly at prey that appears nearby. Have been recorded pursuit-plunging from about 2 m with folded wings, then swimming under water using wings for propulsion (Voisin 1981) or plunging from 5

m to just beneath surface so that only wing-tips visible (Gibson & Sefton 1959); immature twice seen dropping from about 3.5 m and completely disappearing underwater (Harper 1987). Of 261 observations of feeding, 98.1% were surface-seizing, 1.1 surface-diving, 0.8 shallow-plunging, 78.9 during day, 21.1 at night; of natural prey not originating from observation vessel, 93.3% of 119 observations were at night and only 6.7% during day (Harper 1987); have also been seen carrying wild-caught cephalopods at night off NSW (Barton 1979). Cephalopods killed and eaten in 30.1 s (14.5–156; 11). Often feed in association with other seabirds (Jenkins 1979;

Table 2. Cephalopods in the diet of the Wandering Albatross.

	% Weight			% Number			
	1	2	3	1	2	3	4
<i>Loligo</i>	0.1			0.3			
<i>Ancistrocheirus lesueuri</i>		1.5	0.3		1.4	0.1	0.7
unident. Enoploteuthidae	0.1		1.1				
<i>Octopoteuthis rugosa</i>		0.3	<0.1		1.5	<0.1	
<i>Octopoteuthis</i>	2.1			2.5			0.7
<i>Taningia</i>	2.5	5.5	2.6	0.7	1.3	0.5	0.6
<i>Onychoteuthis banksi</i>	<0.1		0.1	0.4		0.1	
<i>Moroteuthis ingens</i>	21.8		4.0	3.5		0.7	1.9
<i>Moroteuthis knipovitchi</i>	1.2	0.1	2.3	1.1	0.6	1.8	35.9
<i>Moroteuthis robsoni</i>	3.3	2.0	0.5	1.1	1.9	0.2	0.7
<i>Kondakovia longimana</i>	11.0	81.1	58.6	0.7	40.0	10.0	14.1
Unident. Onychoteuthidae							0.2
<i>Cycloteuthis sirventi</i>							1.3
<i>Cycloteuthis</i>	5.2			1.4			
<i>Discoteuthis discus</i>							0.2
<i>Discoteuthis</i>			0.1			0.4	
<i>Gonatus antarcticus</i>	0.5	0.8	1.1	1.1	3.6	2.5	2.5
<i>Gonatus</i>	1.1		2.1	1.8			
Unident. Gonatidae	1.0	5.3					
<i>Psychroteuthis glacialis</i>		0.3			2.0	0.7	
<i>Psychroteuthis</i>	0.5			0.4			
<i>Lepidoteuthis grimaldii</i>		0.8	0.6		0.9	0.1	
<i>Pholidoteuthis boschmai</i>			<0.1			<0.1	
<i>Architeuthis</i>	2.6		1.2	0.4		<0.1	0.4
<i>Histioteuthis</i>	22.5	1.6	17.6	52.9	14.4	7.6	15.3
<i>Alluroteuthis antarcticus</i>			3.2			4.8	
<i>Batoteuthis skolops</i>			0.1			2.5	
<i>Illex</i>			13.1			23.8	
<i>Todarodes</i>		0.1			0.4		
<i>Martialia hyadesi</i>			3.5			2.1	0.2
unident. Ommastrephidae	1.2		0.4				
<i>Chiroteuthis imperator</i>			<0.1			0.1	
<i>Chiroteuthis macrosoma</i>							0.6
<i>Chiroteuthis picteti</i>							0.4
<i>Chiroteuthis veranyi</i>	0.2	<0.1		0.2	1.0		
<i>Chiroteuthis</i>	8.3		<0.1	7.8		0.7	3.4
<i>Mastigoteuthis</i>	0.9	0.7	0.7	2.1	2.8	1.8	0.2
<i>Taonius belone</i>							0.2
<i>Taonius cympoctypus</i>							2.3
<i>Taonius pavo</i>	12.6	3.4	0.3	10.3	16.8	0.5	0.4
<i>Taonius</i>			0.6			1.5	
<i>Egea inermis</i>			<0.1			<0.1	
<i>Teuthowenia pellucida</i>		0.2			0.7		
<i>Teuthowenia</i>		0.1			0.1	9.7	
<i>Megalocranchia maxima</i>							0.2
<i>Megalocranchia</i>			<0.1			<0.1	
<i>Helicocranchia</i>			<0.1			0.1	
<i>Galiteuthis armata</i>							0.7
<i>Galiteuthis</i>			<0.1			0.1	
<i>Mesonychoteuthis hamiltoni</i>		0.4	<0.1		0.2	0.1	0.2
Unident. Cranchiidae	0.1	0.9		0.4	8.0		
<i>Vampyroteuthis infernalis</i>			<0.1			<0.1	
<i>Argonauta nodosa</i>	0.4			1.1			
<i>Argonauta</i>	0.3			0.4			
<i>Alloposus mollis</i>		1.0	1.0		1.7	1.1	0.2
Unident. cephalopods	0.5	0.5	0.4	0.4	1.2	0.4	
Number of beaks				281	527	3421	515
Number samples				7	18	78	6

(1) Near NZ (Imber & Russ 1975); (2) S. Georgia (Clarke et al. 1981); (3) (Rodhouse et al. 1987); (4) Imber & Berruti (1981).

Harper 1987), repelling all competitors (Weimerskirch *et al.* 1986) except flocks of White-chinned Petrels *Procellaria aequinoctialis*, which distract Wanderer Albatrosses by dive-bombing, then stealing food (Harper 1987), and occasionally giant-petrels *Macronectes* spp (9% of 64 observations; Weimerskirch *et al.* 1986). Also follow schools of dolphins, feeding on remnants of their prey (Gibson & Sefton 1955) as well as Southern Right Whales *Balaena glacialis*, Pilot Whales *Globocephala* and Southern Right Whale Dolphins *Lissodelphis peronii* (Enticott 1986).

NON-BREEDING Diet of non-breeding birds poorly known. Off e. NSW, appear to concentrate on large cephalopods *Sepia apama*, which caught alive or scavenged (Gibson & Sefton 1955, 1959; Gibson 1967); two from Drake Passage contained many cephalopod beaks with some fish and *Euphausia superba* (Linkowski & Rembiszewski 1978).

BREEDING At Bird I., S. Georgia (79 samples; Croxall & Prince 1987; Prince & Morgan 1987) fish 41.5% wt., cephalopods 39.5, crustaceans 0.2 and higher proportion of penguin and seal carrion 18.8 than for any other albatross as well as many cephalopods that were probably too large to have been caught alive.

At Iles Crozet, cephalopods predominated in 68% of 31 regurgitated samples (actual freq. 71.0%, mostly Onychoteuthidae; Weimerskirch *et al.* 1986) with rest mostly fish 32 (35.5); carrion (3.2) was penguin feathers (Voisin 1969; Mougin 1970). Cephalopod diet described in Table 2.

At Bird I., S. Georgia (Rodhouse *et al.* 1987) cephalopods estimated to constitute 35% of diet by wt. *Loligo* 0.18–0.30 cm lower rostral length, *Ancistrocheirus lesueurii* 0.62–0.82, *Octopoteuthis rugosa* 0.95, *Taningia danae* 0.90–1.57, *Onychoteuthis banksi* 0.32–0.67, *Moroteuthis ingens* 0.90–1.32, *Moroteuthis knipovitchi* 0.52–1.53, *Moroteuthis robsoni* 0.76–0.85, *Kondakovia longimana* 0.23–2.00, *Discoteuthis* 0.41–0.78, *Gonatus antarcticus* 0.49–0.81, *Psychroteuthis glacialis* 0.35–0.66, *Lepidoteuthis grimaldii* 0.91–1.58, *Pholidoteuthis boschmai* 0.27, *Architeuthis* 1.33, *Histioteuthis atlantica* 0.25–0.67, *Histioteuthis eltaninae* 0.25–0.45, *H* sp. 0.29–0.53, *Alluroteuthis antarcticus* 0.40–0.60, *Batoteuthis skolops* 0.29–0.54, *Illex* 0.33–0.82, *Martialia hyadesi* 0.35–0.88, *Chiroteuthis imperator* 0.52–0.61, *C. spp* 0.34–0.82, *Mastigoteuthis* 0.48–0.79, *Taonius pavo* 0.70–1.05, *Taonius* 0.65–1.10, *Egea inermis* 0.51, *Teuthowenia* 0.70–0.90, *Megalocranchia* 0.82, *Helicocranchia* 0.30–0.35, *Galiteuthis glacialis* 0.32–0.64, *Galiteuthis* 0.40–0.42, *Mesonychoteuthis hamiltoni* 0.59–1.00, *Vampyroteuthis infernalis* lower hood length 0.70, Octopodidae 0.48–1.14, *Alloposus mollis* 0.35–2.10. Differences noted between years: more Ommastrephidae and number of cephalopod species in winter of 1984 than 1983 and fewer Onychoteuthidae and Antarctic species, at time when krill populations in region declined. Some deep-water cephalopods may be caught only when they come to surface, spawn and die.

Composition of fish diet at S. Georgia by weight: *Pseudochaenichtys georgianus* 54.5% (length 377 mm [127; 225–634]), *Chaenocephalus aceratus* 25.3% (469 [88; 319–604]), *Muranolepsis microps* 13.0% (237 [40; 241–389]), *Notothenia gibberifrons* 4.2% (322 [27; 294–358]), plus five other species. Fish taken were pelagic and benthic-demersal species characteristic of S. Georgian shelf; species taken by commercial fisheries poorly represented, which indicates that most fish probably taken naturally (Croxall *et al.* 1988b).

Samples from near NZ (Imber & Russ 1975) also contained otoliths of fish *Halargyreus johnsonii* and *Macruronus novaezelandiae*. Near Iles Crozet also seen feeding on jellyfish

(Weimerskirch *et al.* 1986).

INTAKE Chicks may consume up to 100 kg of food during rearing period (Rodhouse *et al.* 1987). At S. Georgia, size of meals 750 g and weight gain 56 g/day (Tickell 1968) at rate of 0.36 meals/day (Croxall & Prince 1987) or every 5–6 days/adult (Croxall & Prince 1980). At Ile de la Possession, Iles Crozet, gain 85 g/day (Weimerskirch *et al.* 1986) with 0.35 meals/day (Mougin 1970). Between end of brooding and fledging chicks receive a total of about 80 meals of 1–2 kg (0.11–2.11 kg) (Tickell 1968).

SOCIAL ORGANIZATION At sea, usually solitary or in small groups (2–10 individuals) at food near vessels; occasionally up to 50 birds together (Dixon 1933; Gibson 1967). Gregarious on breeding grounds. Associate with other procellariiforms at food and when following cetaceans (Griffiths 1982; Enticott 1986).

BONDS Monogamous, lifelong; no known divorces (Tickell 1968). At Macquarie I. and Iles Crozet, sex-ratio probably imbalanced in favour of males, survival of males being higher than that of females (Tomkins 1985a; Weimerskirch & Jouventin 1987); at Iles Crozet, sex-ratio of non-breeding birds 1 female:2.5 males (Weimerskirch & Jouventin 1987). Age at first return to colonies: Iles Crozet 7.8 years old (4–14; 187) (Weimerskirch & Jouventin 1987); S. Georgia 3–11 years old,

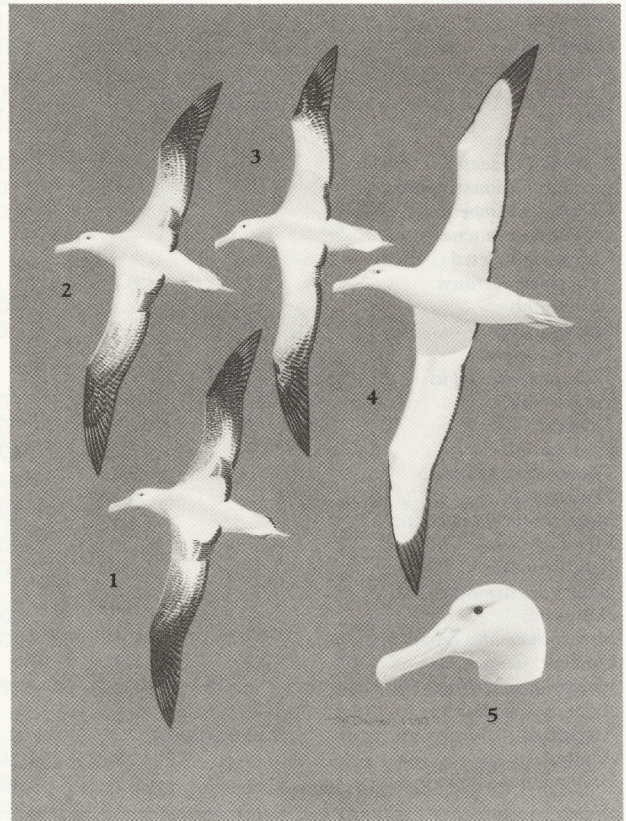


Plate 13

Wandering Albatross *Diomedea exulans*

1. Dorsal, Stage 5
2. Dorsal, Stage 6
3. Dorsal, Stage 7
4. Ventral, Stage 7
5. Adult head, Stages 5, 6 or 7

most 5–7 years old, females slightly earlier than males (Pickering 1989). At S. Georgia, interval between first return and first breeding 2–8 years, median value in females, 4 years ($n=51$), in males, 5 years ($n=45$); establishment of pair-bond over one to three seasons, most (75%; 28 pairs) over two seasons (Pickering 1989). Age at first breeding: Iles Crozet, females 11.2 years (2.0; 7–16; 64), males 12.1 years (9–16; 24) (Weimerskirch & Jouventin 1987); S. Georgia minimum 7 years, av. females 10.6 years, males 11.0 years (Croxall 1982). Pair-bonds of breeders re-established during pre-laying period. During first season ashore, pre-breeders present at colonies early Feb.–early Mar. (median values); after five seasons, arrival synchronized with that of breeders; departure late Mar. (Pickering 1989). Nesting, incubation and chick-rearing by both sexes although share of male slightly higher. Chicks independent after fledging.

BREEDING DISPERSION **NESTING.** Colonial when breeding. Nest density: Ile de la Possession, Iles Crozet, 35–101 nests/km² (Weimerskirch & Jouventin 1987); S. Georgia, 40–106 nests/ha in most favourable areas (Tickell 1968); Antipodes I., 26 nests/10 000 m² (Warham & Bell 1979). Distance between nests, three to hundreds of metres; at Iles Kerguelen, very dispersed, minimum distance 50 m (Milon & Jouanin 1953). **TERRITORIES.** Limited to area close round nest; 1 m² to radius of 2 m (Tickell 1968; Voisin 1969).

Territorial only when breeding.

ROOSTING Solitary when roosting on land (Voisin 1969). Unknown at sea.

SOCIAL BEHAVIOUR Descriptions by Matthews (1929) and Murphy, partly re-interpreted by Richdale (1950) and by van Zinderen Bakker (1971); functions of courtship displays not analysed. Displays conspicuous, diurnal and easy to observe at close range. Royal Albatross *D. epomophora* has most complex sexual behaviour of all albatrosses; agonistic and sexual displays of Wandering similar to Royal, except that Head-shaking not described for Wandering and Bill-vibrating not described for Royal. Individual distance usually not less than 2–3 m, except round food or between individuals of mated pairs.

AGONISTIC BEHAVIOUR **THREAT.** Displays as Royal Albatross: **Snapping**, which becomes **Clapping** with increased aggression. When threatened, unguarded chick sits back in nest, neck stretched up, facing intruder; as threat increases, bill snapped repeatedly with gobbling noise and, ultimately, vomiting of oil or stomach contents. **APPEASEMENT.** No appeasement or submissive displays described.

SEXUAL BEHAVIOUR **COURTSHIP.** Displays similar to those of Royal Albatross and include **Aerial Activity**, **Sky-call**, **Yapping** (=Bowling; Matthews 1929), **Gawky Look**, **Billing**, **Scapular Action**, **Wing-stretching** and **Mutual Preening**. Also occasional **AERIAL DISPLAY**: in flight, wings stiffened, downturned, while head swung from side to side (Warham & Bell 1979). **Ecstatic Ritual.** Apparently differs from displays of Royal Albatross by performing **Bill-vibrating** and **Whine**. **Bill-vibrating** (=Braying; van Zinderen Bakker 1971): standing bird first bends neck forwards, bill held below horizontal, mandibles slightly apart and begins to vibrate mandibles rapidly against each other while bill slowly raised to vertical; clapping ended with single snap as bill reaches highest position; performed by both sexes; reported to follow **Billing** and precede **Wing-stretching**. **Whine.** Not described as being accompanied by **Head-shaking** as in Royal Albatross. Head thrown back so that bill points vertically, bird emitting powerful expiratory braying whistle followed by inhaled sigh; usually performed in conjunction with **Wing-stretching**; climax of **Ecstatic Ritual**. **Whine** usually followed by **Display Meeting** (van Zinderen Bakker 1971): bird places bill in breast feathers while producing loud bill-clapping sound. **Parties**, as in Royal Albatross. **GREETING** Apparently similar to mutual **Gawky Looks** performed by birds of opposite sex when meeting (van Zinderen Bakker 1971). At nest, **Yapping** observed at nest-relief during incubation (Murphy). Once pair formed, displays become less complex with much time spent **Yapping** and **Mutual Preening** (van Zinderen Bakker 1971). **COPULATION**, occurs 1–26 days before laying (Tomkins 1983).

RELATIONS WITHIN FAMILY GROUP Nest-building, incubation and chick-raising by both parents, with male taking slightly greater share.

VOICE Not well known; no detailed study. Described by Matthews (1929), Murphy and van Zinderen Bakker (1971). Noisy at colonies during pre-laying period (re-establishment of pair-bond by breeders), incubation and chick-guarding period (parties of pre-breeders establishing pair-bond). Sexual differences reported only for Croak where, in duets, croaks of males lower than those of females (Warham & Fitzsimons 1987). No individual differences or geographical variation re-

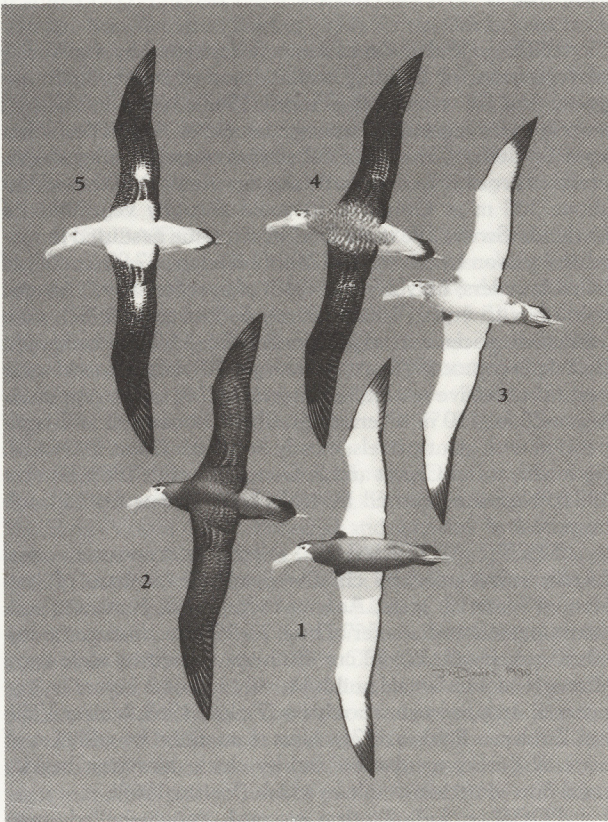
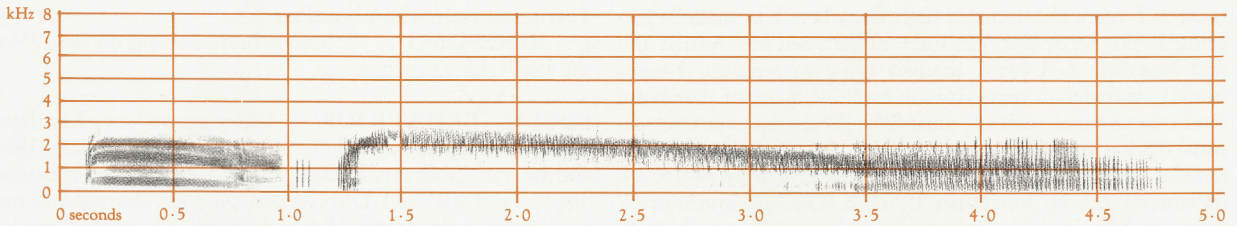


Plate 14

Wandering Albatross *Diomedea exulans*

1. Juvenile, ventral, Stage 1
2. Juvenile, dorsal, Stage 1
3. Ventral, Stage 3
4. Dorsal, Stage 3
5. Dorsal, Stage 4



A J. Kendrick; Auckland Is, NZ, Feb. 1965; P26, P100

ported. Calls similar to those of Royal Albatross, but Croak (= Yapping) apparently harsher and less musical. Numerous non-vocal sounds made by vibrating, snapping or clapping mandibles together.

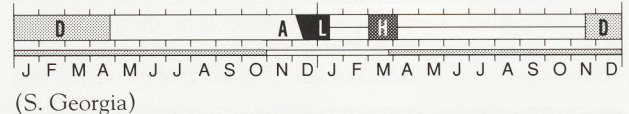
ADULT Croak (Warham & Fitzsimons 1987): harsh groaning sound uttered repeatedly during Yapping display, often in duet. **Whine**: powerful expiratory braying whistle or shriek (van Zinderen Bakker 1971) (sonagram A; with preceding inhalation), emitted at climax of Ecstatic Ritual. Also **Deep Gurgling**, audible at close range, emitted during Sky-call (van Zinderen Bakker 1971), and a guttural vocal sound uttered with each bill-clap during agonistic Clapping. **NON-VOCAL SOUNDS**: **Bill-snaps**: mandibles snapped together during agonistic Snapping; by adults and chicks. **Bill-clapping**: loud rapid clapping given a few times during agonistic Clapping; also given during Display Preening. **Bill-clicks** caused by clashing of bills of pair during Billing. **Rattling**: peculiar rattling sound with slight musical ring (Matthews 1929), also described as rubbery burring, rising from low to high note with increasing rapidity of vibration, filled lungs acting as sound-box, whole terminated by single snap; given during Bill-vibration display.

YOUNG Newly hatched chick emits soft *chirping* when hungry; older chick, gobbling cry when begging for food (Matthews 1929).

BREEDING Detailed studies at S. Georgia (Tickell 1968) and Iles Crozet (Voisin 1969; Mougouin 1970; Fressanges du Bost & Segonzac 1976). Information supplied by J.-C. Stahl. Colonial breeder on vegetated exposed flats on gentle slopes on subantarctic islands and S. Georgia.

SEASON ARRIVAL AT COLONIES: S. Georgia, first arrival 9 Nov., mean date: males 29 Nov. \pm 2 days, females 10 Dec. \pm 9 days; Iles Crozet, first arrival 19 Nov. (14–23 Nov.; for 7 years), males arrive first; peak of arrival late Nov.–early Dec. (Mougouin 1970); Iles Kerguelen, 17 Nov.–5 Jan. (Paulian 1953); Marion I., first arrival 22 Nov. (van Zinderen Bakker 1971); Auckland Is, first arrival 10 Dec. (Bailey & Sorensen 1962). **PRE-LAYING PERIOD**: Iles Crozet, 26 days (15–44); S. Georgia, 26.6 days (8–45; 8). At S. Georgia, male present 73.6% of days, female 7.4%. Pre-laying exodus noted at Marion, but period undetermined (van Zinderen Bakker 1971). At S. Georgia, females return 0–4 days before laying after absence of 5–18 days. Copulations 1–26 days before laying; fertilization probably 1–5 days before laying (Tomkins 1983). **DEPARTURE FROM COLONIES**: **Fledgelings**: S. Georgia, mean date 10 Dec. (17 Nov.–18 Jan.; 63). Iles Crozet, first departure 25 Nov. (20–30 Nov.), last 19 Jan. (9 Jan.–2 Feb.) over seven seasons; average date 14 Dec. Marion I., most mid-Dec. to mid-Jan. (van Zinderen Bakker 1971). Iles Kerguelen, first departure 21 Nov. (Paulian 1953). Campbell I., late Dec.–mid-Feb. (Bailey & Sorensen 1962). Auckland Is, 22 Jan.–5 Feb.+ (Bailey & Sorensen

1962). Antipodes Is, end Jan.–12 Mar.+ (Warham & Bell 1979). **Pre-breeders**: Mar.–Apr. in most localities. At S. Georgia, pre-breeders at colonies early Feb.–early Mar. during first season ashore; arrival date progressively earlier during following seasons, synchronized with that of breeders by sixth season; stay ashore progressively longer, median 3 days first season; median 34 days (males), 24 days (females) during sixth season; median departure date, sixth season ashore, 20 Mar. (Pickering 1989).



SITE Selection of nest-site restricted by availability of vegetation for building material and of nearby open exposed site for taking-off (Tickell 1968). Nests established among short vegetation (among tussocks at Antipodes; Warham & Bell 1979) on coastal plains, swampy valley floors, crests of broad ridges or gentle slopes; usually 0–300 m asl but above 300 m at Gough I. to avoid shrubby vegetation of lowlands (Swales 1965). At Iles Crozet, same nest used in successive season by 23.3% (n=176) of breeders, 37.9% (n=66) of failed breeders; only 2.5% (n=810) of breeders have changed colony in 15 years (Weimerskirch & Jouventin 1987), with average displacements of 3.2 km (0.6; 0.6–14.0; Fressanges du Bost & Segonzac 1976). At S. Georgia, 20% of pairs used same nest in successive season; nest moved by 7 m on average (maximum 23 m; 150 m if remating). Slight association and competition with giant-petrels, mostly Southern Giant-Petrels *M. giganteus*, at Iles Crozet and S. Georgia (Voisin 1968; Hunter 1984). Nest-site selected by male, who arrives first on colonies.

NEST, MATERIALS Nest, a truncated cone, usually surrounded by circular patch almost bare of vegetation. Material: grass, *Acaena* twigs, moss, roots and soil. **MEASUREMENTS**: diameter of base 70–100 cm; diameter at top 40–50 cm; height 20–50 cm. Building started by male soon after arrival, but female builds actively 1–2 days before laying; material dropped over shoulders (Tickell 1968; Voisin 1969; van Zinderen Bakker 1971). Nest maintained by addition of material during incubation and by chick; new nest besides natal one sometimes built by chick (Voisin 1969).

EGGS Sub-elliptical to oval; rough-shelled, mat; white with diffuse ring of red-brown dots round broad end (Tickell 1968).

MEASUREMENTS.

Gough I. 127.0 (117–130.8; 87) x 77.0 (71.6–82.3) (Verrill 1895)
 Marion I. 133.4 (123.5–142.5; 47) x 81.0 (75.5 x 85.5; 47) (Rand 1954)

Iles Crozet	133.2 (130.7-136.0; 3) x 80.9 (80.4-81.4)
Iles Kerguelen	136.2 (122.4-140.0; 6) x 80.1 (76.4 x 83.4)
Macquarie I.	129.1 (5.9; 121.3-139.0; 16) x 81.5 (2.8; 78.1-87.2) (Tomkins 1984b).
Antipodes Is	125.1 (5.1) x 78.1 (2.7) (Warham & Bell 1979)
Auckland Is	126.9 (120.8-134.4; 12) x 77.3 (73.0-81.7) (Robertson 1975).

WEIGHTS.

Marion I.	484 (437-551; 9) (Rand 1954)
Macquarie I.	476.7 (46.9; 415-520; 4) (Tomkins 1984b)
S. Georgia	Median, 448.5

CLUTCH-SIZE One; one record of two abnormally small eggs (Tickell 1968). At Iles Crozet, no successful breeders lay in next season after success; 89% lay again in second season. Of failed breeders, 84% lay again in next season after failure and 10% not until second season (Jouventin & Weimerskirch 1988). At S. Georgia, 73% of birds that fail lay again next season but, if loss occurs after June, do not do so till second season (Tickell 1968). Development of gonads blocked throughout period of rearing chick (Hector *et al.* 1986).

LAYING S. Georgia, 24 Dec. (6 days; 10 Dec.-17 Jan.; 3 years, 260 eggs), no significant difference between years (Tickell 1968). Iles Crozet, starts 20 Dec. (17-24 Dec.), ends 19 Jan. (7-25 Jan.) for seven years. Iles Kerguelen, 10 Dec.-15 Jan. (Paulian 1953; Thomas 1983). Marion I., 22 Dec.-12 Jan., peak 1-6 Jan. (van Zinderen Bakker 1971). Antipodes Is, start mid-Jan. (Warham & Bell 1979). Auckland Is 42% of eggs laid by 22 Jan. (Bailey & Sorensen 1962). Campbell I., starts 13 Feb. (Bailey & Sorensen 1962). Most eggs (70%; n=20) laid during daytime (Tickell 1968). In successive seasons only 4.2 days difference in laying dates (9.0; 0-20; 50), irrespective of change of mate; seems to indicate genetic control of laying date (Tickell 1968).

INCUBATION By both sexes in alternate shifts. At Iles Crozet, average of 7.4 shifts (4-10); shortest shift, first by female, 2.4 days; longest, third by female 13.8 days; share of male, 52.4%. At S. Georgia, 9.7 shifts (1.8; 5-14); shortest shift, first by female, 3-6 days; longest, fourth by male, 11.5 days; share of male 57.7%. **INCUBATION PERIOD.** Gough I., c. 68 days (Swales 1965); Marion I., 78.6 days (75-81; 12) (van Zinderen Bakker 1971); Iles Crozet 79 (77-83); S. Georgia, 78.4 (1.1; 75-82; 163).

NESTLING Semi-altricial, nidicolous. Hatching lasts 3.2 days (1-5) (Tickell 1968). Down entirely white at hatching (Voisin 1969). Brooded and guarded by both parents. **BROOD-STAGE:** Marion I. 29 days (24-33; 5) (La Grange 1962); Iles Crozet 31 days (24-43; 11); brooding shifts, male 4.0 days, female 4.2 days; S. Georgia 32 days (21-43; 74), c. 11 brooding shifts of 2.6 days (1-10; 735). At Iles Crozet, guard-stage of up to 6 days (Voisin 1969). Chicks fed by both parents: at S. Georgia, 53% (n=118) of feeding by male. Not fed first 24 h, only small amounts of food given for next 3 days. Feeding usually lasts 10-30 min, but parent may stay for up to 2 days (Voisin 1969). Meal consists of 5-7 regurgitations; chick inserts mandibles across those of parent. Most (94%) of feeding during daytime, 61% during morning hours (n=166) (Tickell 1968). **NESTLING PERIOD.** At Iles Crozet, 271 days (258-288; 31); S. Georgia 277.7 (16.7; 263-303; 35).

GROWTH At Iles Crozet, weight at hatching c. 400 g, maximum weight 13 100 g (137% ad. weight) after c. 210 days, weight at fledging 9980 g (104% ad. weight; 12 chicks in two seasons) (Mougin 1970). At S. Georgia, weight at hatching 352 g (303-410; 6); max. weight 11 700 g (135% ad. weight),

after 221-230 days, weight at fledging 8930 g (103% ad. weight). Culmen and wing almost full grown at fledging (Tickell 1968; Voisin 1969).

FLEDGING TO MATURITY Independent at fledging. Age at first return to colonies: Iles Crozet av. 7.8 years (4-14; 87); S. Georgia, 3-11 years, most 5-7 years, males at slightly older age than females (Pickering 1989). Age at first breeding: Iles Crozet, females 11.2 years (2.0; 7-16; 64), males 12.1 years (9-16; 24) (Weimerskirch & Jouventin 1987); mean age of first breeding has decreased from 13 to 10.5 years since 1975 following population decrease; minimum age of first breeding has remained unchanged (Jouventin & Weimerskirch 1985); S. Georgia, minimum 7 years, average females 10.6 years, males 11.0 years (Croxall 1982). Males physiologically mature at 5 years old; females at 4-7 years; gonadal maturation blocked by high progesterone levels, thus female condition decisive in determining when a pair first attempts to breed (Hector *et al.* 1986).

SUCCESS At Iles Crozet, hatching 66.9% (10.3; 54.2-79.3; 166 eggs, three seasons), fledging 89.4% (5.0; 84.2-96.9; 188 chicks, five seasons), total success 64% (13; 25-77; 15 seasons) (Weimerskirch & Jouventin 1987); 0.37 chicks produced per year per female (Weimerskirch *et al.* 1987). At **Marion I.**, hatching 50-59% (44 eggs, two seasons), fledging 38.5% (13 chicks, one season), total success 22.7% (22 eggs, one season) (van Zinderen Bakker 1971). **Macquarie I.**, hatching 61.4% (25.9; 14-89; 57 eggs, five seasons), fledging 85.7% (39.7; 0-100; 35 chicks, five seasons), total success, 52.6% (26.7; 0-78; 57 eggs, five seasons) (Tomkins 1985a). At **S. Georgia**, hatching 72.2% (385 eggs, one season), fledging 81.3% (278 chicks, one season), total success 64.8% (6.5; 1185-1523 eggs, ten seasons) (Croxall *et al.* 1988a). **ANNUAL SURVIVAL:** Iles Crozet: age 0-5 years, 71.5%; 5-11 years, 91.8%; over 11 years, 92.2% (males 93.8%, females 89.9%) (Weimerskirch & Jouventin 1987). **S. Georgia:** adult average 96% (Croxall 1982), males 94.6%, females 96.9% (Tickell 1968); **Macquarie I.:** males 85.4%, females 73.2% (Tomkins 1985a). **CONTROLLING FACTORS:** egg loss mainly in first 10 days of incubation, mostly from trampling by incubating birds, delayed return of partner, infertility (van Zinderen Bakker 1971; Fressanges du Bost & Segonzac 1976). Loss of chicks c. 50% in first 10 days; mainly by starvation, predation by skuas, giant-petrels, rarely by rats at Ile de la Possession, Iles Crozet, bad weather (Fressanges du Bost & Segonzac 1976). Recent population decline at Iles Crozet mainly because fewer adults have survived; 90.5% during period of rapid decline 1968-76 (6.2%/year), 94.4% during more gradual decline 1977-86 (2.5%/year); survival of adults apparently affected during breeding cycle, as breeding success strongly correlated with adult survival; lower survival of females attributed to their more northern foraging area where more exposed to long-line fishing operations (Weimerskirch & Jouventin 1987). At Macquarie I., decline attributed to reduced survival of adults and possibly immatures; adult survival dropped from 94.6% in 1965-68 (Carrick & Ingham 1970) to 78.7% in 1974-78 (Tomkins 1985b), while breeding success remained similar (Tomkins 1985b).

PLUMAGES Except for juveniles and downy young, no two Wandering Albatrosses look alike. Starting with mostly dark plumage, birds become whiter over a long period. Rate of whitening not known precisely, nor whether whitening is continuous, interrupted or briefly reversed. Degree of whiteness of breeding adults varies individually, geographically and sexually (Tickell 1968; Tomkins 1984b). Not known whether

whitening halts at a given age, or whether rate of whitening geographically and sexually varies. The descriptions below are given under stages suggested by Harrison (1979, 1985, 1987) for guidance in the field; Stage 1 is darkest and probably youngest; Stage 7, palest and probably oldest. These are not distinct plumages defined by different generations of feathers, and many intermediates occur. The 'Gibson Code' (GC), a more detailed classification for use in the hand, was developed by Gibson (1967) and is also given below. His scheme has been modified and expanded by Jouventin *et al.* (1989).

D. e. chionoptera.

ADULT **Stage 7.** Probably only old males. At S. Georgia, 43% of breeding males, and no breeding females, showed this condition (Tickell 1968). Recorded on a non-breeding male at least 16 years old (Tomkins 1984b); age of attainment unknown but probably after age of first breeding, which has been given as c. 10 years (Tickell 1968) and 9–13 years (extremes 7–17) (Hector *et al.* 1986; Pickering 1989). **HEAD AND NECK** (GC=6), white; hindneck feathers have trace of light-grey (85) vermiculation at tips; only visible at close range; can be lost with wear and may be totally absent. Varying pink (-) to orange-pink (c5) stain at the edges of feathers just behind ears; often absent or restricted to one side of head; when most extensive, stain extends round back of neck, forming narrow to broad connecting band. Large stains sometimes partially or completely brown (-). At S. Georgia, stain tends to be larger when feeding young than when incubating or brooding. Stain often wet, although underlying skin usually dry (Tickell 1968); often lost shortly after death or after feathers are plucked (e.g. Gibson & Sefton 1959), but feathers from Antipodes I. showed pink stain 8 years after plucking (Warham & Bell 1979), and stains retained in some skins (Murphy). It apparently occurs in all Stages except downy young and perhaps juveniles, both at breeding grounds and at sea. **UPPERPARTS** (GC=6), white. Feathers of mantle and back can have trace of light-grey (85) vermiculation at tips. **TAIL** (GC=4, occasionally 3), white; feathers have cream (54) shafts. **UPPERWING** (GC=5), looks mostly white, with mottled transition to broad dark tip and narrow dark trailing-edge. At, and inside, elbow, all coverts white. Other upper wing-coverts and secondaries white with inconspicuous dark-grey (83) vermiculations; outer quarter of median coverts and lower lesser coverts, alula and all greater coverts have large grey-black (c82) spots at tip of outer web causing a rather mottled transition to dark trailing-edge. In alula, primary coverts, outermost secondary coverts and most secondaries, grey-black (c82) spot, large, extending halfway down outer web, and encroaching onto tip of inner web; in these feathers, only grey-black areas are usually exposed. Innermost secondaries and inner secondary coverts have smaller grey-black (82) spots at tip of outer web. Visible parts of primaries, grey-black (c82) with cream (c54) shafts that grade to dark brown (c23) tips; all primaries have concealed white bases to inner web. In palest birds, this narrows to sharply defined, concealed white wedge that almost meets tip of inner web. Grey-black (82) areas of remiges fade to black-brown (c119) with wear. **UNDERPARTS**, white. **UNDERWING**. Remiges as above; only grey-black (c82) areas are exposed when wing spread; reflect grey (84) in some direct light. Under wing-coverts, white.

DOWNY YOUNG Protophyle, white on head and neck, tinged grey (-) on body; described as pure white and silky (Murphy), and as dirty white (Watson 1975). Mesophyle, long and woolly; grey (Murphy) or brownish grey (Matthews 1951), fading to grey-white in older birds.

STAGE 1 All juveniles and probably no other ages, have this plumage; unknown when lost. **HEAD AND NECK** (GC=1). Chin to mid-throat, forehead and face, white. Rest, dark brown (121); all feathers have concealed white bases, narrowest on crown and nape; those of nape have fine white tips. **UPPERPARTS** (GC=1), dark brown (121); feathers of mantle and upper back, and shorter scapulars, have narrow open pennaceous brown (119B) tips, perhaps becoming larger with wear. **TAIL** (GC=1), black-brown (c19). **UPPERWING** (GC=1). Coverts, black-brown (119); marginals have narrow white fringes. Remiges look grey-black (82) when fresh, become black-brown (119) with wear. Shafts, cream (54), grading to brown (23) tips; in flight, pale primary shafts contrast strongly with rest of dark upperwing. **UNDERPARTS**, dark greyish-brown (c121); feathers have white bases, smaller on upper breast, occasionally exposed in centre of lower breast and belly but concealed elsewhere. Axillaries, white; uppermost sometimes have dark greyish-brown (c121) upper web. **UNDERWING**. Most coverts, white; on leading-edge between carpal joint and p10 have grey-black (82) outer web. Marginal coverts and lesser subhumeral at base of wing, sometimes dark greyish-brown (c121), giving appearance of dark pre-axillary notch. Remiges, grey-black (82), reflecting grey (84) in some direct light.

STAGE 2 Does not occur on breeding birds at S. Georgia (Tickell 1968). At Macquarie I., not yet found on breeding birds, but recorded in 4-, 6- and 14-year-old females (Tomkins 1984b). Age of attainment, unknown; probably at 1–2 years because brought about by wear and replacement of juvenile plumage. **HEAD AND NECK** (GC=1–2). Pattern at first similar to Stage 1, but lower neck and hindneck later develop white mottling, causing brown appearance that does not contrast with white face so strongly as in Stage 1. Feathers of crown and nape remain dark brown (121), giving dark-capped appearance to older birds. In the one skin examined, change in appearance was caused by wear, dark tips of feathers of neck having worn away to expose some white bases. **UPPERPARTS** (GC=1), beginning to obtain some white mottling, partly because wear exposes some white bases of feathers, especially on rump, and then because white feathers with heavy grey (84) or brown-grey (grey 121) vermiculations at tip appear to do so last on rump. **TAIL**, as Stage 1. **UPPERWING** (GC=2). Traces of white mottling appear in centre, most commonly at elbow; in the skin examined, caused by slightly exposed white bases to median and secondary coverts. Belly begins to whiten before upperwing. No white tips to feathers, *contra* Harrison (1985). **UNDERPARTS**, mostly off-white to white; younger birds often have dark-brown (121) under tail-coverts, flanks and band across upper breast, formed by remnant juvenile feathers. Dark tips of juvenile feathers on rest of underparts wear faster, last traces of tips causing off-white tinge. Emergent feathers, white; those on flanks and upper breast have dark-brown (c121) or grey (84) vermiculations near tip. **UNDERWING**, as Stage 1.

STAGE 3 At S. Georgia, not recorded on breeding males, on about 9% of breeding females; also recorded on two 5-year-old and four 6-year-old pre-breeding females (Tickell 1968). At Macquarie I., recorded on 8-year-old non-breeding male (not recorded in breeding birds), a 14-year-old female non-breeder and a female breeder at least 13 years old (Tomkins 1984b). **HEAD AND NECK** (GC=2–3), mostly white, with dark-brown (121) cap on hindcrown and nape; feathers of crown, hindmost ear-coverts, and lower neck have dark-brown (119A) vermiculations at tip. **UPPERPARTS** (GC=3–4),

white, heavily vermiculated dark brown (121) to grey (84) at tips of feathers; vermiculations tend to be fewest on mantle, rump and upper tail-coverts. TAIL (GC=2). Feathers, black-brown (c19) with white bases, largest on inner webs for about half length. When closed, tail looks white with broad dark sides and tip. UPPERWING (GC=2). Distinct but small white patch at elbow formed by white bases to secondary and median coverts. Elsewhere, white bases to secondary and lesser coverts are smaller. UNDERPARTS, white; upper breast and flanks vermiculated dark brown (c121) at tips of feathers; very slight vermiculations at tips of feathers on thighs and under tail-coverts. UNDERWING, as Stage 1.

STAGE 4 At S. Georgia, recorded on about 8% of breeding males, and 69% of breeding females. Three 5-year-old pre-breeding males were in this condition (Tickell 1968); at Macquarie I., found in 15- and 16-year-old breeding males, and on two 14-year-old non-breeding males; recorded in five of 13 females, including a 16-year-old non-breeder and four breeding birds (Tomkins 1984b). HEAD AND NECK (GC=3-4), generally whiter than Stage 3; dark-capped appearance lost, although feathers of crown and nape tend to have larger dark vermiculation at tips than rest of head and neck. UPPERPARTS (GC=4), white, with dark-brown (121) to grey (84) vermiculations at tips of feathers, smaller than in Stage 3. TAIL (GC=2-3), usually looks white, with dark sides and tip narrower than at Stage 3. Some feathers in centre can be wholly white, and outer feathers may have more white at base, especially on inner web. Order in which white feathers appear varies, and tail can have streaked appearance by alternating white and dark feathers. UPPERWING (GC=3). Distinct white streak, broadest at elbow, extending about halfway to carpal joint, and halfway to body; formed by white bases to secondary and median coverts, largest on inner webs. Inner marginal coverts have smaller white bases, giving appearance of slight white mottling on inner leading edge. UNDERPARTS, white, with dark vermiculations at tips of feathers of upper breast and flanks. UNDERWING, as Stage 1, but no dark pre-axillary notch.

STAGE 5 At S. Georgia, occurs on about 15% of breeding males, and 20% of breeding females (Tickell 1968). At Macquarie I., recorded on five of 17 males, including one 19-year-old, and in a bird at least 2 years old; not recorded in 13 females (Tomkins 1984b). HEAD AND NECK (GC=5-6), white, with narrow dark vermiculations on tips of feathers of neck. UPPERPARTS (GC=5), white; dark vermiculation at tips of feathers, indistinct; can be lost with wear. TAIL (GC=3), mostly white; outer feathers have grey-black (82) to black-brown (c19) markings on outer webs. UPPERWING (GC=4-5) White elbow-patch larger than in Stage 4, forming broad white wedge, widest at junction with body, which runs down centre of wing, petering out near carpal joint. Broad dark line separates white wedge from narrow whitish leading-edge; rest of wing, grey-black (82), becoming black-brown (c19) with wear. White wedge formed by white humeral coverts, white secondary and median coverts at elbow, and by white inner webs and large white bases to outer webs of secondary coverts, median coverts and lower rows of lesser coverts. Except at elbow, white areas usually vermiculated grey (c84) at tips. Grey-black (c82) spot at tips of these coverts is larger in outermost feathers and in those closer to leading-edge; near carpal joint, and in upper rows of lesser coverts, these dark spots are the only exposed parts of the feathers, forming dark leading-edge to white wedge. Marginal coverts, white, with varying narrow grey-black (c82) tips, forming pale leading-

edge. UNDERPARTS, white. UNDERWING, as Stage 4.

STAGE 6 At S. Georgia, occurs on about 23% of breeding males and less than 3% of breeding females (Tickell 1968). Recorded in 37% of Macquarie I. males, including two birds at least 21 years old; not recorded in Macquarie I. females (Tomkins 1984b). HEAD AND NECK, UPPERPARTS, UNDERPARTS, as Stage 7. TAIL (GC=3, occasionally 4), white; usually some outer tail-feathers have grey-black (c82) markings near tip of outer web that give appearance of dark sides to tail. UPPERWING (GC=5). Dark spots at tips of outer webs of lesser coverts smaller than in Stage 5; almost absent in some, so white wedge looks continuous with white leading-edge. White area does not extend beyond carpal joint. UNDERWING, as Stage 4.

BARE PARTS Except where stated, based on photographs in Lindsey (1986), NZRD, and unpublished (D.W. Eades).

D.e. chionoptera and *D.e. exulans*.

ADULT Plumage Stages 2-7. Iris, black-brown (119) to dark brown (22). Eye-ring white, sometimes with pale-blue (-) or pale-green (-) tinge. Pink (108D), scarlet (Falla 1937) and lacquer red (Murphy) also reported; these colours probably associated with bill-flush described below, but they have also been attributed to blood infusion following injury or death (Falla 1937). In 15 photographs examined, on birds at Macquarie I. in Jan. or Feb., on others in Aust. waters in winter, and some at breeding grounds without dates: bill, mostly light pink (pale 7) to light orange-pink (light 5), sometimes with deeper pink (7-108D) culminicorn, nares and base of ramicorn. Ungues usually cream (92), occasionally pink-white, sometimes with green-blue (65) to light grey (85) base to maxillary unguis. These photographs assumed not to be of adults in early breeding season, when Murphy described bill as yellow-buff and Matthews (1951) described bills as grading from pink at base to yellow at tip. Tomkins (1983) regarded whitish-bone as normal colour at Macquarie I. between late Nov. and early Mar.; noted that bill of many breeding birds rapidly became pink or deep purple when handled, returning to original colour after an hour or two. This bill-flush may have been more common after laying; 19 non-breeders and three fledgelings did not flush. Photographed birds described above assumed to show various stages of flush. Flushing of bill at Macquarie I. may occur for only short period; for, at S. Georgia, bill is salmon-pink (Murphy) or rose-pink (Matthews 1951) in winter when large chicks are being fed, and at Antipodes I. some adults have bright pink bills throughout incubation and nestling periods. Flushing not given by non-breeders in Antipodes I. (Warham & Bell 1979; Tomkins 1983). Flushing appears to be caused by increased flow of blood below ramphotheca; perhaps breeding condition, stress and heat shedding may bring it on (Warham & Bell 1979; Tomkins 1983). Pink colour is lost shortly after death. Light brown (-) lower tomtia have been seen on a bird from Antipodes I. (C.J.R. Robertson), an inconspicuous marking that has not been looked for in other populations. Tarsus and toes vary from pale horn (92) or pale brownish-grey (c85), at least sometimes with pinkish (-) spot at heel, to pink-white or pink (3). In dark footed birds, front of tarsus and tops of toes often paler. Webs, pale brown-grey (c85) or pale blue-grey (88) to pink (-). Pink coloration of feet apparently associated with flush (Murphy; Tomkins 1983; Warham & Bell 1979). Soles, grey (84) to pinkish (-). Claws, pale horn (92) to pink-white or white.

DOWNY YOUNG In protopile: iris, dark grey (Rand 1954); bill, pinkish white with cream tip, at least sometimes with green-blue (65) base to maxillary unguis; feet, brown (Murphy) or bluish grey with white claws (Rand 1954). Feet later become whitish or flesh with darker webs (Murphy); large chicks have iris and bill colour similar to juvenile.

JUVENILE Similar to adults, but much pink flushing of bill, eye-ring and legs not reported. However, several juveniles photographed at breeding grounds or at sea had mostly pink-horn to light-pink (pale 7) bill contrasting with pale horn (c92) unguis.

MOULTS Based on skins of 34 birds, including nine breeding adults from Auckland and Antipodes Is, five juveniles and 20 birds at plumage Stages 2-7 from Vic. and NZ waters, mostly beachcast (MV; NMNZ).

ADULT Stages 3-7. Remiges replaced in staffelmauser, interrupted, at least by breeding birds, during breeding season. Non-moulting birds have a jumble of primaries of different ages, at least three generations of feathers being recognizable in primaries of some. Fifteen wings from 12 skins, including ten beachcasts, have been examined with active primary moult; mean number of growing primaries = 2.0 (15; 1-4; 1.0). As with primary wear, often asymmetry in number of growing primaries in each wing, the most extreme case being two beachcast *D.e. exulans* with three growing primaries in left wing, one in right. Of nine wings examined with more than one growing primary, all had 2-3 adjacent primaries in growth, and only two had two active moult-centres. In most of these, waves of moult were moving outwards, but in two birds, both with moult formula $O^3 1^2 2^1 N^1 O^3$, waves of moult may have been moving inwards. Sequence of moult of secondaries, unknown; usually occurs at same time as primaries; may be up to four moult-centres in secondaries of one wing (D. W. Eades photograph). Tail-moult generally occurs at same time as primary moult; waves begin centrifugally from two points, usually t2 and t5. Body-moult has only been checked on five non-juveniles, all of which had heavy body-moult; two were adults with chicks, collected from Antipodes Is. in late Nov.; others collected at sea or beachcast between May and Aug.

Adults moulting near nest at Marion I. in late Mar. (Rand 1954). Of nine adults collected on breeding grounds at Auckland or Antipodes Is between late Nov. and Feb., only one had a growing primary; may have been accidental moult. These birds had between 0 and 8 old primaries; even in those with no old primaries, subtle differences in wear of different primaries contrasted with uniform wear of juvenile wing. Of 20 birds beachcast or collected at sea between Apr. and Nov., 11 had, and nine had not, active primary moult; perhaps, as claimed, moult occurs in years when breeding does not take place. Active moult of remiges recorded in *D.e. chionopectera* in Feb. (Brooke 1981).

POST-JUVENILE Unknown when primary moult begins; beachcast in Wellington on 10 June still had fresh primaries, but had begun moult in head, neck, back and under wing-coverts.

MEASUREMENTS *D.e. exulans*: (1) Auckland Is, freshly dead adults (NMNZ). (2) Auckland Is, adult skins (NMNZ). (3) Auckland Is, live birds; methods unknown (Robertson 1975). (4) Antipodes I., freshly dead adults (NMNZ). (5) Antipodes I., adult skins (NMNZ). (6) Antipodes I., live adults; WING = flattened chord; other methods as here

(Warham & Bell 1979).

	MALES	FEMALES
WING	(1) 635, 642, 660	636
	(3) 649 (630-665; 5)	642 (625-657; 11)
	(4) 645, 640	626 (16.0; 602-636; 4)
	(6) 655 (17.0; 8)	626 (5.0; 6)
8TH P	(2) 342, 355, 354	
	(5) 347	339 (10.9; 326-352; 4)
TAIL	(1) 203, 204	203
	(4) 205, 193	192.0 (7.48; 182-200; 4)
	(6) 203 (2.85; 8)	199 (6.11; 6)
BILL	(1) 152, 151, 155	143.5
	(3) 152.1 (150-154; 5)	142.8 (138-147; 11)
	(4) 152, 148.5	141.5 (5.2; 135.5-148.1; 4)
	(6) 148.1 (2.32; 8)	138.0 (4.55; 6)
BILL D	(6) 41.4 (1.53; 8)	37.0 (1.74; 6)
TARSUS	(1) 120, 117.1, 118.5	
	(4) 119, 122	112.6 (4.46; 110-119.2; 4)
	(6) 116.6 (3.24; 8)	108.7 (2.87; 6)
TOE	(1) 169, 164.2, 169	158.5
	(4) 168, 169	162.3 (4.67; 159-169.2; 4)
	(6) 176.6 (2.34; 8)	167.0 (7.00; 6)

Unsexed birds (7) Auckland Is, live birds; methods unknown (Robertson & Jenkins 1985).

WING	(7) 647 (185-205; 12)
BILL	(7) 147.6 (140.4-156.7; 12)
TARSUS	(7) 114 (108.8-119.5; 12)
TOE	(7) 161.3 (154.0-176.5; 12)

D.e. chionopectera: (1) Macquarie I., live birds at Stages 3-7; measurements for breeders and non-breeders, which do not differ significantly in this sample, combined. Bill length from junction of skin and culmen to most distant point of curve of maxillary unguis; bill depth at shallowest point; other methods as here (Tomkins 1984b). (2) Indian Ocean, skins, including specimens from Marion I. and Iles Kerguelen and Crozet, and adjacent waters; methods probably as here (Murphy). (3) S. Georgia, adults; methods unknown (Tickell 1968).

	MALES	FEMALES
WING	(1) 671 (16.7; 635-701; 17)	635 (14.0; 618-657; 10) **
	(2) 640 (625-679; 10)	-
	(3) 679 (14.4; 655-710; 21)	657 (13.7; 630-680; 22) **
TAIL	(1) 220 (9.0; 201-228; 17)	204 (8.0; 193-215; 10) **
	(2) 197 (190-205; 10)	-
	(3) 227 (7.40; 215-246; 21)	215 (6.23; 20.6-22.7; 23) **
BILL	(1) 165.8 (5.98; 158-181; 17)	158.3 (2.95; 156-166; 10) **
	(2) 171 (162-177; 10)	-
BILL D	(3) 169.1 (4.03; 163-180; 21)	163.8 (3.62; 155-171; 23) **
	(1) 37.0 (1.39; 34.8-40.4; 17)	33.5 (1.73; 31.1-36.7; 10) **
	(3) 40.1 (1.66; 37.2-44.6; 21)	35.8 (1.92; 32.0-40.0; 22) **
TARSUS	(1) 126.7 (2.02; 123-132; 17)	120.6 (1.78; 117-123; 10) **
	(2) 123.2 (118-128; 10)	-
	(3) 118.0 (4.61; 110-127; 21)	35.8 (1.92; 32.0-40.0; 22) **
TOE	(1) 164.8 (5.12; 148-172; 17)	159.8 (5.22; 151-169; 10) *
	(2) 171.7 (167-176; 10)	-
	(3) 184.4 (6.93; 172-193; 21)	174.7 (4.73; 165-181; 22) **

Unsexed birds: (4) Iles Crozet; methods unknown (Voisin 1969).

WING	(4)	678 (4.0; 640-788; 40)
BILL	(4)	154.7 (0.9; 141-165; 40)

WEIGHTS All in kg. (1) S. Georgia, adults (Tickell 1968). (2) Macquarie I., Stages 3-7, breeders and non-breeders. (3) Antipodes I., breeders and non-breeders, 19, 23 Feb. (Warham & Bell 1979).

	MALES	FEMALES	
(1)	9.768 (0.875; 8.193-11.907; 20)	7.686 (0.559; 6.719-8.703; 22)	**
(2)	8.0, 8.6, 8.6	6.8, 6.4, 7.5	
(3)	7.35 (0.75; 8)	5.67 (0.94; 6)	**

Unsexed birds: (4) Marion I.; combined data for unsexed adults and incubating females (Brown & Adams 1984). (5) Iles Crozet (Voisin 1969). (6) Auckland Is (Robertson & Jenkins 1985).

(4)	8.02 (0.96; 9)
(5)	9.58 (0.2; 6.80-11.5; 40)
(6)	5.96 (5.0-7.1; 10)

During incubation shifts at S. Georgia, males lose c. 85 g/day, and females c. 80 g/day, amounting on average to 17% of body weight per shift; weights at beginning of shifts, estimated from individuals weighed three times during shifts, in males 10.5 (0.80; 9.49-11.94; 10), in females 9.00 (0.91; 8.18-9.83; 9). No evidence for general decline of weight during incubation period (Croxall & Ricketts 1983). Little other information on temporal variation; feeding birds off NSW in winter 8.3 (5.9-11.3; 108; Gibson 1967), but sex and origin of birds unknown. NZ beachcasts, ages combined, believed to be *D.e. exulans* on basis of length of bill: males 6.16 (1.261; 3.560-8.520; 14), females 4.87 (1.31; 3.33-8.02; 7); these include emaciated birds of 3.33 (female), 3.56 (male), males with no fat of 7.76, 5.74, and 5.95, and a fat juvenile female weighing 5.03.

STRUCTURE Wing, very long and narrow. Eleven primaries; p11 minute. In five Auckland Is birds, p10 longest, p9 14-26 shorter, p8 41-69, p7 81-117, p6 136-180, p5 189-243, p4 241-301, p3 293-336, p2 340-369, p1 368-398. In six Antipodes Is birds, p10 longest, p9 7-20 shorter, p8 35-53, p7 80-103, p6 127-150, p5 175-207, p4 237-268, p3 287-321, p2 329-360, p1 357-386; wings possibly less pointed than at Auckland Is, but few data. About 38 secondaries, including seven tertials; 12 humerals, about same length as secondaries. Tail, short and rounded; 12 feathers. Bill, long and heavy, least deep in centre; maxillary unguis, hooked and mandibular unguis slightly decurved. No sulcus; plates of bill sharply defined. Nostril tubes, short with straight sides; nares point obliquely forwards and slightly upwards (differing from *D. epomophora* in which sides of nostril tubes bulge outwards and nares face slightly inwards). Tarsus slightly laterally compressed; scales hexagonal, 2-4 mm in diameter. Feet webbed, webs cancellate. Middle toe longest, outer 96-97%, inner 83-88%; no hind toe.

GEOGRAPHICAL VARIATION Mostly in size and plumage whiteness attained; juvenile plumages similar in all populations. Slight evidence for geographical variation in

flushing of bill is discussed in Bare Parts. *D.e. chionopectera*, described in Plumages, breeds S. Georgia, Prince Edward, Crozet, Kerguelen and Macquarie Is. N. populations, presently combined as one subspecies *D.e. exulans*, breed at Tristan da Cunha, Auckland, Antipodes and Campbell Is (Peters). All smaller than *chionopectera*, notably in length of bill. Plumages are similar to those of *chionopectera*, but the snowy plumage, Stages 6 and 7, is seldom, perhaps never, attained; breeding apparently begins in darker plumages. Antipodes I. birds have been said to be darker than in other populations (Falla 1937; Warham & Bell 1979) but adequate data have yet to be published. Ten birds collected or photographed from Antipodes I. (six breeding birds from NMNZ, two pairs of unknown status in Warham & Bell 1979 and NZRD) had cumulative Gibson scores ranging from 5-11 (plumage Stages 3-5); in nine collected or photographed at Auckland Is (NMNZ; Lindsey [1986]; J.A. Bartle), cumulative Gibson scores 10-17 (plumage Stages 3-5). No comparable data available for extralimital populations at Tristan da Cunha and Gough I., which used to be classed as separate subspecies on basis of small size; published measurements in Murphy, Hagen (1952) and Elliott (1957) are too few to support any conclusion. Birds from Ile Amsterdam, once combined with *D.e. exulans* (Peters), are now classified as separate species *D. amsterdamensis* (Roux *et al.* 1983; Jouventin & Roux 1983; Jouventin *et al.* 1989). Their plumages are similar to younger stages of *D.exulans*, most birds breeding at plumage Stage 2; measurements published in Jouventin *et al.* (1989) seem similar to those of *D.e. exulans*. The major difference is in bill colour: *D. amsterdamensis* have conspicuous dark-brown lower tomia, similar to those of *D. epomophora*, and unguis are dark brownish-green, darker than rest of bill.

DIR

REFERENCES

- Ainley, D.G., *et al.* 1984. AOU *orn. Monogr.* 32.
 Bailey, A.M., & J.H. Sorensen. 1962. *Proc. Denver Mus. nat. Hist.* 10.
 Barton, D. 1979. *Emu* 79: 31-5.
 Barton, D. 1980. *A'sian Seabird Grp Newsl.* 14: 9-13.
 Bennett, A.G. 1948. *Ibis* 90: 143-5.
 Bierman, W.H., & K.H. Voous. 1950. *Ardea* 37 (Extra no.): 1-123.
 Blaber, S.J.M. 1986. *Emu* 86: 239-44.
 Bourne, W.R.P. 1966. *Sea Swallow* 18: 9-36.
 Bourne, W.R.P., & W.F. Curtis. 1985. *Sea Swallow* 34: 18-28.
 Brooke, R.K. 1981. *Cormorant* 9: 13-18.
 Brown, C.R., & N.J. Adams. 1984. *Condor* 86: 182-6.
 Carrick, R., & S.E. Ingham. 1970. Pp 505-525. In: Holdgate 1970.
 Clark, G.S. 1987. *Cormorant* 14: 20-30.
 Clarke, M.R., *et al.* 1981. *Br. Antarct. Surv. Bull.* 54: 1-8.
 Cooper, J. 1988. *S. Afr. J. Antarct. Res.* 18: 21-22.
 Croxall, J.P. 1982. *Com. natn. fr. Rech. Antarct.* 51: 479-88.
 Croxall, J.P. (Ed.) 1987. *Seabirds: Feeding Ecology and Role in Marine Ecosystems*.
 Croxall, J.P., & P.A. Prince. 1980. *Biol. J. Linn. Soc.* 14: 103-31.
 Croxall, J.P., & P.A. Prince. 1987. Pp. 347-68. In: Croxall 1987.
 Croxall, J.P., & C. Ricketts. 1983. *Ibis* 125: 33-9.
 Croxall, J.P., *et al.* 1984. *ICBP Tech. Publ.* 2: 637-66.
 Croxall, J.P., *et al.* 1988a. Pp. 261-85. In Sahrhage 1988.
 Croxall, J.P., *et al.* 1988b. *Polar Biol.* 9: 9-16.
 Darby, M.M. 1970. *Notornis* 17: 28-55.
 Dell, R.K. 1960. *Rec. Dom. Mus.* 3: 293-305.
 Derenne, P., *et al.* 1972. *Oiseau Revue fr. Orn.* 42 (Spec. no.): 111-129.
 Dixon, C.C. 1933. *Trans. R. Canad. Inst.* 19: 117-39.
 Eakin, R.R., *et al.* 1986. *Antarct. Res. Ser.* 44: 69-86.

Elliott, H.F.I. 1957. *Ibis* 99: 545-86.
 Enticott, J.W. 1986. *S. Afr. J. Antarct. Res.* 16: 25-8.
 Falla, R.A. 1937. *Rep. B.A.N.Z. Antarct. Res. Exped. 1929-31, Ser. B, II.*
 Fleming, C.A. 1950. *Emu* 49: 169-88.
 Fraser, M.W., et al. 1988. *Cormorant* 16: 7-33.
 Fressanges du Bost, D. & M. Segonzac. 1976. *Com. natn. fr. Rech. Antarct.* 40: 53-60.
 Gain, L. 1914. *Doc. Scient. Deux. Exped. Antarct. fr.* 1-200.
 Gartshore, N.A., et al. 1988. *S. Afr. J. Antarct. Res.* 18: 23-9.
 Gibson, J.D. 1967. *Notornis* 17: 47-57.
 Gibson, J.D., & A.R. Sefton. 1955. *Emu* 55: 44-8.
 Gibson, J.D., & A.R. Sefton. 1959. *Emu* 59: 73-82.
 Gill, F.B. 1967. *Proc. US Natn. Mus.* 123 (3605).
 Griffiths, A.M. 1982. *Cormorant* 10: 9-14.
 Grindley, J.R. 1981. *Proc. Symp. Birds Sea Shore*: 169-88.
 Hagen, Y. 1952. *Res. Norw. Scient. Exped. Tristan da Cunha 1937-38*, 20.
 Hansen, L. 1978. *Dansk Drn. Foren. Tidssker* 72: 179-88.
 Harper, P.C. 1987. *Notornis* 34: 169-92.
 Harper, P.C., et al. 1985. *BIOMASS Handbook* 24.
 Harrison, P. 1979. *Cormorant* 6: 13-20.
 Harrison, P. 1985. *Seabirds: An Identification Guide.*
 Harrison, P. 1987. *Seabirds of the World: A Photographic Guide.*
 Harrison, P.P.O. 1962. *Sea Birds of the South Pacific.*
 Hector, J.A.L., et al. 1986. *Ibis* 128: 9-22.
 Hicks, G.R.F. 1973. *Notornis* 20: 231-50.
 Holdgate, M.W. (Ed.). 1970. *Antarctic Ecology*. 1.
 Holgersen, H. 1957. *Scient. Res. Brategg Exped. 1947-48*, 4.
 Hunter, S. 1984. *J. Zool., Lond.* 203: 441-60.
 Imber, M.J., & A. Berruti. 1981. *Proc. Symp. Birds Sea Shore*: 43-61.
 Imber, M.J., & R. Russ. 1975. *Notornis* 22: 27-36.
 Jehl, J.R. 1973. *Auk* 90: 114-35.
 Jenkins, J.A.F. 1979. *Notornis* 26: 331-48.
 Jenkins, J.A.F. 1980. *Notornis* 27: 205-34.
 Jenkins, J.A.F. 1986. *A'sian Seabird Grp Newsl.* 25: 1-70.
 Johnstone, G.W. 1980. *Bird Obs.* 586: 85-7.
 Johnstone, G.W. 1982. *Dept of Natn. Develop. Energy, Div. Natn. Mapping, Tech. Rep.* 31: 33-37.
 Johnstone, G.W., & K.R. Kerry. 1976. *Proc. Int. orn. Congr. XVI*: 725-38.
 Jouventin, P., & J-P. Roux. 1983. *RAOU Newsl.* 58: 1-2.
 Jouventin, P., & H. Weimerskirch. 1985. *Proc. Int. Conf. Seabird Grp II*: 6-7.
 Jouventin, P., & H. Weimerskirch. 1988. *Proc. Int. orn. Congr. XIX*: 857-65.
 Jouventin, P., & H. Weimerskirch. 1990. *Nature* 343: 746-8.
 Jouventin, P., et al. 1982. *Com. natn. fr. Rech. Antarct.* 51: 427-36.
 Jouventin, P., et al. 1984. *ICBP Tech. Publ.* 2: 603-25.
 Jouventin, P., et al. 1989. *Ibis* 131: 171-82.
 La Grange, J.J. 1962. *J. S. Afr. Biol. Soc.* 3: 27-84.
 Lambert, K. 1971. *Beitn. Vogelkd., Leipz.* 17: 1-32.
 Lindsey, T.R. 1986. *The Seabirds of Australia.*
 Linkowski, T.B., & J.M. Rembiszewski. 1978. *Pol. Arch. Hydrobiol.* 25: 717-27.
 Matthews, L.H. 1929. *Discovery Rep.* 1: 561-92.
 Matthews, L.H. 1951. *Wandering Albatross.*
 McQuaid, C.D., & L.H. Ricketts. 1984. *Cormorant* 12: 14-28.
 Meeth, P., & K. Meeth. 1986. *A'sian Seabird Grp Newsl.* 23: 15-35.
 Milledge, D. 1977. *Corella* 1: 1-12.
 Milon, P., & J. Jouanin. 1953. *Oiseau Revue fr. Orn.* 23: 4-52.
 Mougin, J-L. 1970. *Oiseau Revue fr. Orn.* 40 (Spec. no.): 15-36.
 Mougin, J-L. 1977. *C.r. hebd. Seanc. Acad. Sci., Paris*, 284, D: 2277-80.
 Murphy, R.C. 1938. *Condor* 40: 126.
 Norris, A.Y. 1967. *Emu* 67: 33-55.
 Orlando, C. 1958. *Riv. Ital. Orn.* 28: 101-13.
 Ozawa, K. 1967. *Antarct. Rec.* 29: 1-36.
 Paulian, P. 1953. *Mem. Inst. Scient. Madagascar, Ser. A*, 8: 111-231.

Paxton, R.O. 1968. *Auk* 85: 502-504.
 Pickering, S.P.C. 1989. *Ibis* 131: 183-195.
 Powlesland, R.G. 1985. *Notornis* 32: 23-41.
 Pratt, H.D., et al. 1987. *The Birds of Hawaii and the Tropical Pacific.*
 Prince, P.A., & R.A. Morgan. 1987. Pp. 135-71. In: Croxall 1987.
 Rand, R.W. 1954. *Ibis* 96: 171-206.
 Rand, R.W. 1963. *Ostrich* 34: 121-8.
 Richdale, L.E. 1950. *Biol. Monogr.* 3.
 Robertson, C.J.R. 1972a. *Notornis* 19: 91.
 Robertson, C.J.R. 1972b. *Notornis* 19: 61-73.
 Robertson, C.J.R. 1973. *Notornis* 20: 59-70.
 Robertson, C.J.R. 1975. Pp. 143-51. In: Yaldwyn 1975.
 Robertson, C.J.R. 1980. Pp. 106-16. In: *Prelim. Rep. Campbell I. Exped. 1975-76. Dept Lands Surv., Wellington.*
 Robertson, C.J.R., & B.D. Bell. 1984. *ICBP Tech. Publ.* 2: 573-86.
 Robertson, C.J.R., & J. Jenkins. 1985. In: *Prelim. Rep. Exped. Auckland Is Nature Reserve 1973-84.*
 Rodhouse, P.G., et al. 1987. *Mar. Biol.* 96: 1-10.
 Rounsevell, D.E., & N.P. Brothers. 1984. *ICBP Tech. Publ.* 2: 587-92.
 Roux, J-P., et al. 1983. *Oiseau Revue fr. Orn.* 53: 1-11.
 Sahrhage, D. (Ed.). 1988. *Antarctic Ocean and Resources Variability.*
 Secker, H.L. 1969. *Emu* 69: 155-60.
 Siple, P.A. & A.A. Lindsey. 1937. *Auk* 54: 147-159.

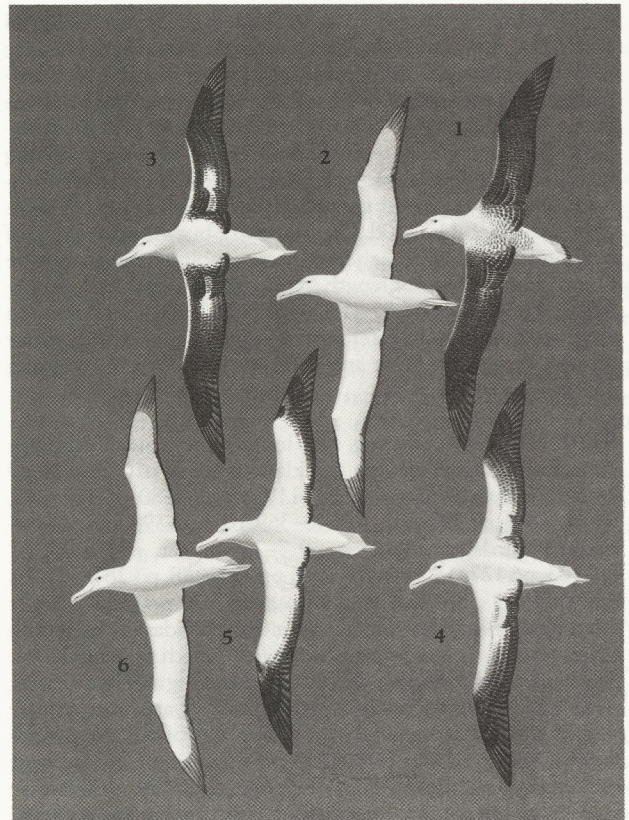


Plate 15

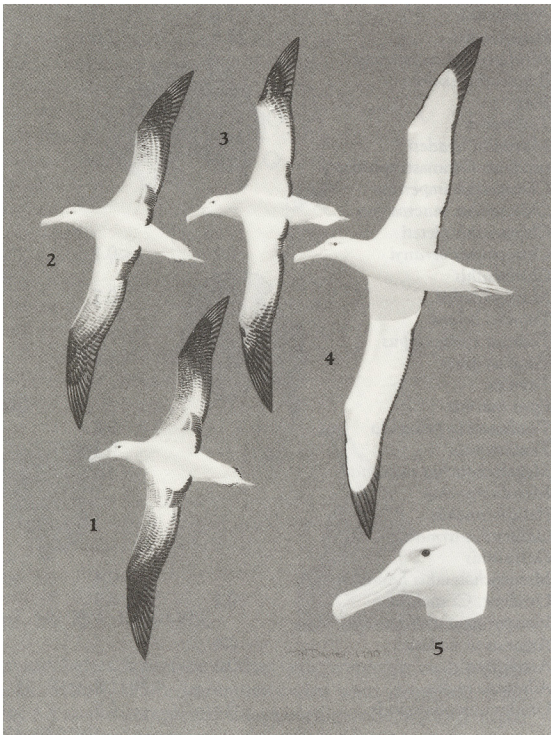
Royal Albatross *Diomedea epomophora epomophora*

1. Juvenile, dorsal, Stage 1
2. Juvenile, ventral, Stage 1
3. Dorsal, Stage 2
4. Dorsal, Stage 3
5. Adult, dorsal, Stage 5
6. Adult, ventral, Stage 5

- Stahl, J.-C. 1987. TAAF. MR. *Rapports des Campagnes à la mer*. 84-01: 175-90.
- Sudbury, A.W., et al. 1985. *Emu* 85: 195-7.
- Summerhayes, C.P. 1969. *NZ J. mar. freshwat. Res.* 3: 560-70.
- Summerhayes, C.P., et al. 1974. *Ostrich* 45: 83-109.
- Swales, M.K. 1965. *Ibis* 107: 17-42.
- Sziji, L.J. 1967. *Auk* 84: 366-78.
- Thomas, T. 1983. *Oiseau Revue fr. Orn.* 53: 133-41.
- Thurston, M.H. 1982. *Br. Antarct. Surv. Bull.* 55: 77-103.
- Tickell, W.L.N. 1968. *Antarct. Res. Ser.* 12: 1-55.
- Tickell, W.L.N., & J.D. Gibson. 1968. *Emu* 68: 6-20.
- Tickell, W.L.N., & R.W. Woods. 1972. *Br. Antarct. Surv. Bull.* 31: 63-84.
- Tomkins, R.J. 1983. *Notornis* 30: 244-6.
- Tomkins, R.J. 1984a. *Tas. Nat.* 79: 24-32.
- Tomkins, R.J. 1984b. *Emu* 84: 29-32.
- Tomkins, R.J. 1985a. *ANARE Res. Notes* 29: 1-20.
- Tomkins, R.J. 1985b. *Emu* 85: 40-2.
- van Oordt, G.J., & J.P. Kruijt. 1954. *Ardea* 42: 245-80.
- van Zinderen Bakker, E.M. Jr. 1971. Pp. 273-82 In: van Zinderen Bakker et al. 1971.
- van Zinderen Bakker, E.M. et al. (Ed.) 1971. *Marion and Prince Edward Islands*.
- Verrill, G.E. 1895. *Conn. Acad. Arts Sci. Trans.* 9: 430-78.
- Voisin, J.F. 1968. *Oiseau Revue fr. Orn.* 38 (Spec. no.): 96-122.
- Voisin, J.F. 1969. *Oiseau Revue fr. Orn.* 39 (Spec. no.): 83-106.
- Voisin, J.F. 1981. *Cormorant* 9: 136.
- Voisin, J.F. 1984. *S. Afr. J. Antarct. Res.* 14: 11-17.
- Warham, J., & B.D. Bell. 1979. *Notornis* 26: 121-69.
- Warham, J., & C.H. Fitzsimons. 1987. *NZ J. Zool.* 14: 65-79.
- Watkins, B.P. 1987. *S. Afr. J. Antarct. Res.* 17: 155-62.
- Watson, G.E. 1975. *Birds of the Antarctic and Sub-Antarctic*.
- Weimerskirch, H., & P. Jouventin. 1987. *Oikos* 49: 315-22.
- Weimerskirch, H., et al. 1985. *Emu* 85: 22-34.
- Weimerskirch, H., et al. 1986. *Ibis* 128: 195-213.
- Weimerskirch, H., et al. 1987. *J. Anim. Ecol.* 56: 1043-55.
- Weimerskirch, H., et al. 1988. *Condor* 90: 214-19.
- Weimerskirch, H., et al. 1989. *Emu* 89: 15-29.
- Wilkins, G.H. 1923. *Ibis* 65: 474-511.
- Woods, R.W. 1975. *The Birds of the Falkland Islands*.
- Yaldwyn, J.C. (Ed.) 1975. *Prelim. Results Auckland Is Exped. 1972-73*. Dept. Lands Surv., Wellington.
- Zink, R.M. 1981. *Gerfaut* 71: 59-74.



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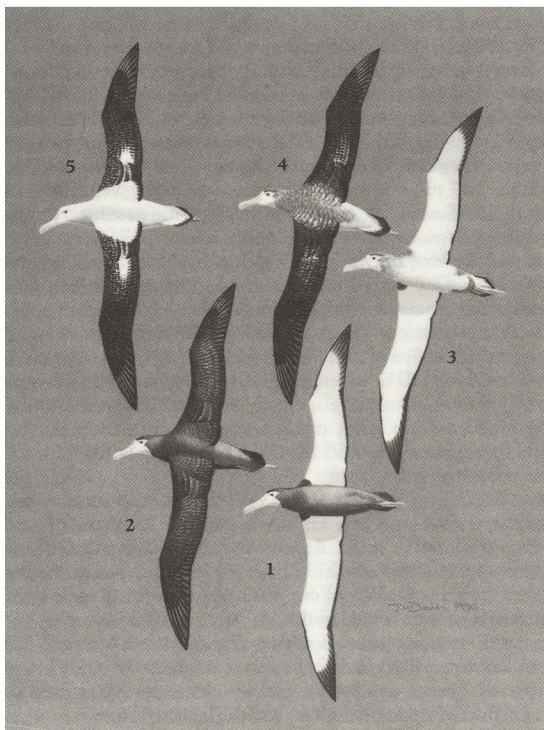
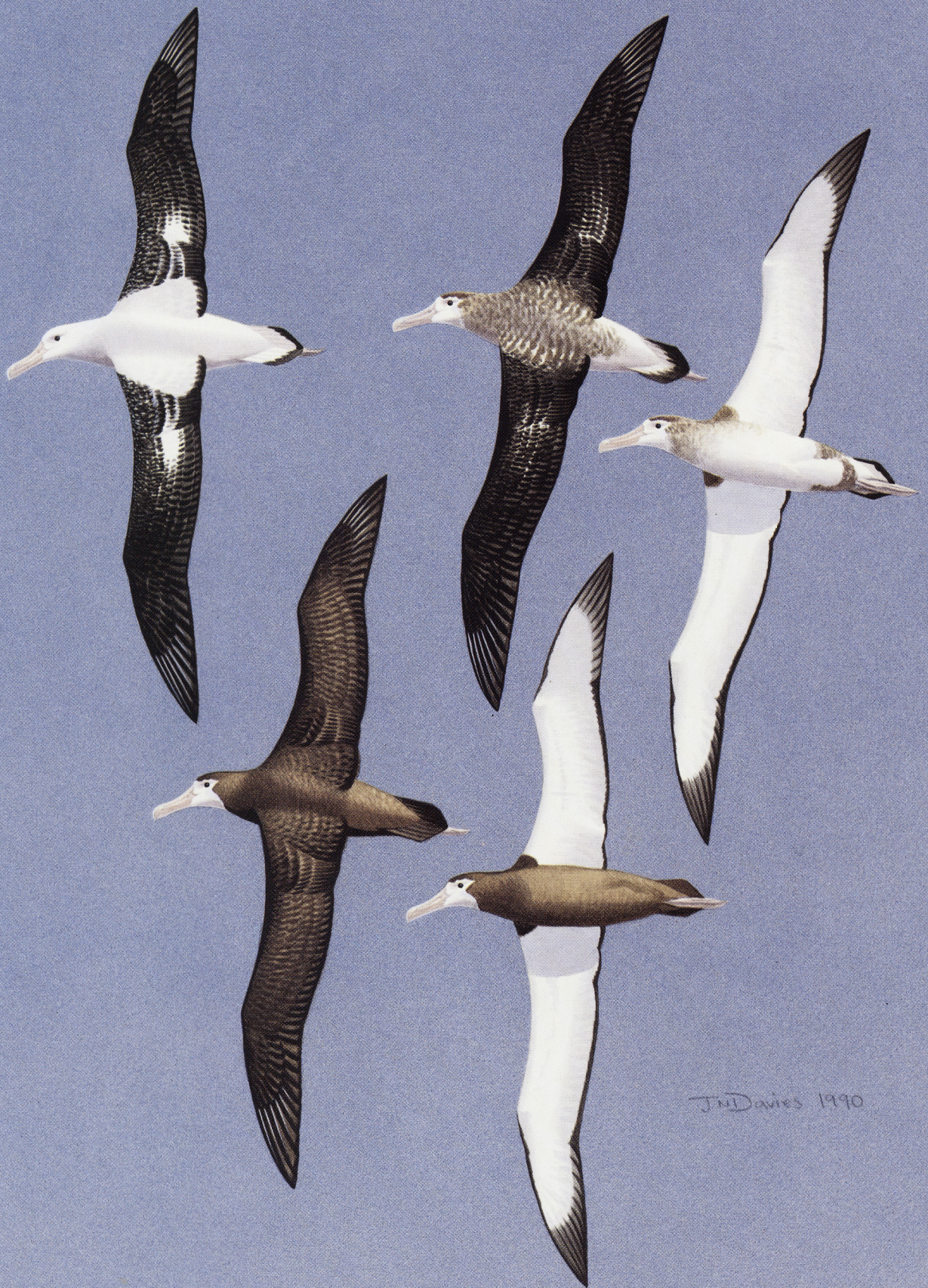


Volume 1 (Part A), Plate 13

Wandering Albatross *Diomedea exulans*

1. Dorsal, Stage 5
2. Dorsal, Stage 6
3. Dorsal, Stage 7
4. Ventral, Stage 7
5. Adult head, Stages 5, 6 or 7

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Volume 1 (Part A), Plate 14

Wandering Albatross *Diomedea exulans*

1. Juvenile, ventral, Stage 1
2. Juvenile, dorsal, Stage 1
3. Ventral, Stage 3
4. Dorsal, Stage 3
5. Dorsal, Stage 4

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