

# DISTRIBUTION, ABUNDANCE AND ASPECTS OF THE PELAGIC ECOLOGY OF BARAU'S PETREL (*Pterodroma barau*) IN THE SOUTH-WEST INDIAN OCEAN

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## ABSTRACT

Results of 3499 10 min counts and other shipboard observations made during 27 voyages between Réunion, Mauritius and the subantarctic showed pronounced seasonal variation in the distribution of Barau's Petrel. Rare south of 20°S in July - August, it appeared in numbers off Réunion by September, and remained mostly confined to tropical waters north of 25°S until November. From December to March, the range of this tropical breeding petrel expanded far south into subtropical waters, with a major foraging zone 1100-1400 km from Réunion. The southernmost record was beyond 41°S. The summer population in the SW Indian Ocean is estimated at 9000-15 000 individuals. In tropical waters, Barau's Petrels feed almost exclusively in multispecies flocks and apparently mostly on schooling fish. Topics of discussion include population trends, migration, foraging radius, and distribution in relation to breeding status and food resources.

## INTRODUCTION

A quarter of a century after its discovery (Jouanin 1964), Barau's Petrel remains a little-known Indian Ocean seabird. At Réunion, its type locality and stronghold, detailed studies and censuses have been prevented by its presumed nesting sites being all on inland mountain cliffs between 2000 and 2800 m a.s.l. (Jouanin & Gill 1967, Brooke 1978). A population of several thousand pairs has been inferred from counts of birds returning at dusk (Feare 1984). Elsewhere, only an isolated nest has been discovered on nearby Rodrigues, possibly a recent colonisation attempt as the species is not represented in subfossil deposits there (Cheke 1974, Jouanin 1987).

Barau's Petrel is a summer breeder. At Réunion, it is first seen inland in mid-September and newly fledged chicks are found between 11 and 29 April (Jouanin 1987). Assuming incubation and nestling periods intermediate between those of *P. cahow* (Wingate in Palmer 1962) and *P. phaeopygia sandwichensis* (Simons 1985), egg-laying would be between 6 and 24 November and hatching between 29 December and 16 January. From its rarity in coastal waters before late afternoon and from at-sea records south from Réunion to 27°S, Jouanin & Gill (1967) inferred that Barau's Petrel was a pelagic species feeding in subtropical waters to the south of the island. The distribution south of the Mascarenes (Réunion, Mauritius and Rodrigues) has been hardly investigated since, and only during summer months (Frost 1981, Voisin 1983). In this paper we present new data on the distribution, abundance and pelagic ecology of Barau's Petrel collected during 27 voyages between Réunion, Mauritius and the subantarctic.

## STUDY AREA

Located in the south-west Indian Ocean, the study area extends from 20°S to 43°S (c.2600 km) and from 50°E to 80°E (c.2500 km along 43°S). The southern boundary was arbitrarily chosen so as to lie slightly beyond the extreme range of Barau's Petrel, and it does not represent the limit of our voyages. A mere four islands outcrop over this oceanic region: Réunion (21°00' S 55°45' E) and Mauritius (20°15' S 57°45' E) at the northern fringe, Amsterdam (37°50' S 77°31' E) and Saint-Paul (38°43' S 77°30' E) in the south-east corner. Only Mauritius is surrounded by a shelf, and the greater part of the area consists of ocean basins 4000-6000 m deep.

Surface and near-surface hydrology is largely determined by circulation patterns within the Subtropical Anticyclonic Gyre of the southern Indian Ocean (Wyrtki 1973). Only the southernmost part of the study area, which approximately coincides with the position of the Subtropical Convergence (41-44°S, Gamberoni *et al.* 1982), lies within the Circumpolar Current. Immediately north of the convergence, a transition zone 3-5° wide consists of subtropical water interspersed with cold water eddies shed at the convergence. Subtropical South Central Surface Water (terminology of Gallagher 1966; sea-surface temperature 20-26°C in summer, 15-21°C in winter; salinity 35.0 - 35.7‰) extends over 1700 km from the boundary of the transition zone (38-41°S) north to the Tropical Convergence near 24°S (Orren 1963). Warmer and less saline South Tropical Surface Water is encountered in the northernmost part of the area. The wind regime north of 30°S (winter) and 35°S (summer) is dominated by E/SE trade winds, occasionally disrupted during summer by the passage of tropical cyclones. Winds from the westerly quarter predominate further south.

## METHODS

The study was made between 1978 and 1988 from RV *Marion-Dufresne*. Observations were made from the unenclosed bridge wings of the vessel, 13 m a.s.l., throughout daylight hours. Seabird abundance along cruise tracks was assessed by means of fixed period censuses of all birds seen during repeated 360° scans. Ten minute counts were made at half-hour intervals while in the range of Southern Ocean seabirds (south of 25°S in winter and 32°S in summer). Ship-following birds were censused separately at the end of each count.

In tropical and northern subtropical waters, where ship-following was exceptional and seabirds were markedly scarcer and clustered, censuses were continuous, all individuals or groups being recorded in chronological order of first sighting. These continuous census periods were subsequently broken down into 10 min intervals. In both situations, we recorded cruise and environmental data every 30 min or at the start of each new 10 min count (data for remaining 10 min intervals of continuous periods were interpolated). Information collected for individual birds included feeding behaviour and moult, as well as flight direction during six summer transects. We recorded overall flight direction only for birds not attracted to the ship and estimated it to the nearest 45° interval (N, NE, etc.) by means of gyrocompasses available on both bridge wings. Species composition and abundance were recorded for each seabird flock encountered.

To draw monthly or bimonthly distribution maps, we plotted the highest 10 min tally (maximum abundance) recorded per 1° grid square traversed. Flight direction frequencies were corrected as follows to compensate for changes in sampling area caused by the relative movements of birds and ship (Gaston & Smith 1984, Gaston *et al.* 1987). For each 10 min count, we calculated the census area for different flight directions (N, NE, etc.) after transforming compass bearings into bearings relative to ship direction. The method was adapted from that detailed by Gaston & Smith (1984) for strip transects. Given the census technique used (360° scans of unlimited width), birds following a course at an angle  $r$  relative to that of the ship were counted over an area (sq km)  $A = 2 dt \sqrt{s^2 + S^2 - 2sS \cos r} (+ d^2 \pi)$ , where  $d$  = detection distance (km),  $t$  = duration of count (h),  $s$  = groundspeed of birds (km/h), and  $S$  = ship speed (km/h). The term in brackets does not apply to 10 min counts derived from continuous census periods, except for the first of each period. Average groundspeed ( $s$ ) of Barau's Petrel was estimated at 50 km/h, based on timing birds flying parallel to the ship from bow to stern. The detection distance ( $d$ ) was not measured in the field, but a maximum of 7 km was derived from the distance at which a silhouette (1/50th of life size) could be seen with the naked eye. This figure does not take into account haze, glare, waves and other limitations at sea or optical constraints of binoculars. An upper limit of 5 km is probably more realistic. Radar measurements in the Southern Ocean using land, other vessels or icebergs as references showed that species of comparable size and light/dark colour contrast (Antarctic Petrel, Black-backed Gull) could be identified in flight when up to 3 km away in clear conditions (Bartle & Stahl unpubl.). Two different corrections and subsequent density calculations were made assuming detection distances of 3 and 5 km. When visibility was noticeably reduced, detection distance was estimated for each count. The total area sampled per flight direction was obtained by adding sampling areas of counts made within the range of Barau's Petrel. Corrected flight direction frequencies were then calculated from the total numbers of birds counted per flight direction divided by the corresponding total areas sampled.

For density calculations, we used as the actual sampling area of a count the mean of the areas sampled during this count for each flight direction, weighted (to compensate for predominant zonal flight directions, Stahl & Bartle in prep.) by the flight direction frequencies with the 5° square where the count was made. Sample size was usually too small to assess the distribution of flight directions for single counts. Population estimates per 1° or 5° square were derived from mean densities, calculated by dividing the total number of birds counted by the sum of overall sampling areas per count.

## RESULTS

Altogether, 3499 10 min counts were made within the study area, distributed throughout all months except May, June and October. Monthly sampling effort is summarised in Table 1. Individual transects are referred to as SSW (Réunion or Mauritius to/from Crozet Is), SSE (Réunion to/from Kerguelen Is) and SE (Réunion or Mauritius to/from Amsterdam I.).

TABLE 1 — Summary of monthly shipboard count effort 20°S-43°S

Month	No. and direction of transects	No. 1° squares traversed	Total counts	Mean no. counts per 1° square	Range
January	2SSW-3SSE	71	970	14	1-68
February	1SSW-1SSE-1SE	70	620	9	1-38
March	3SSW-1SSE-1SE	81	829	10	1-38
April	1SE	25	141	6	1-22
July	1SSW-1SE	38	141	4	1-12
August	2SSW-1SE	31	141	5	1-12
September	2SSW	30	302	12	1-42
November	1SSW	10	33	4	1-8
December	3SSW-1SE	49	322	7	1-30

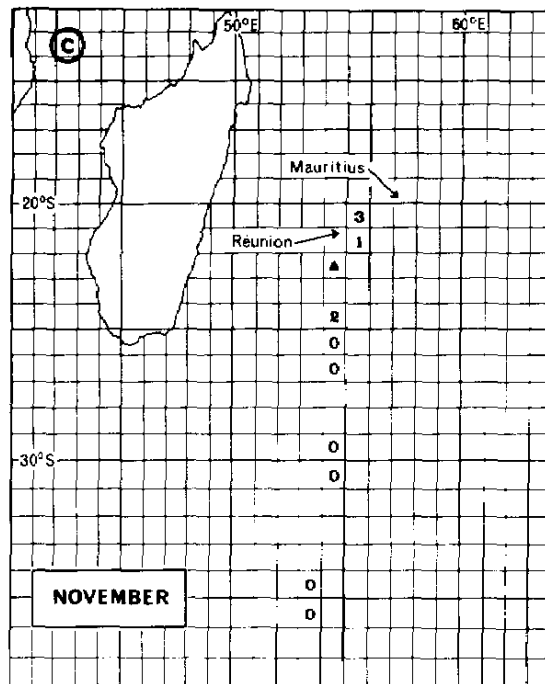
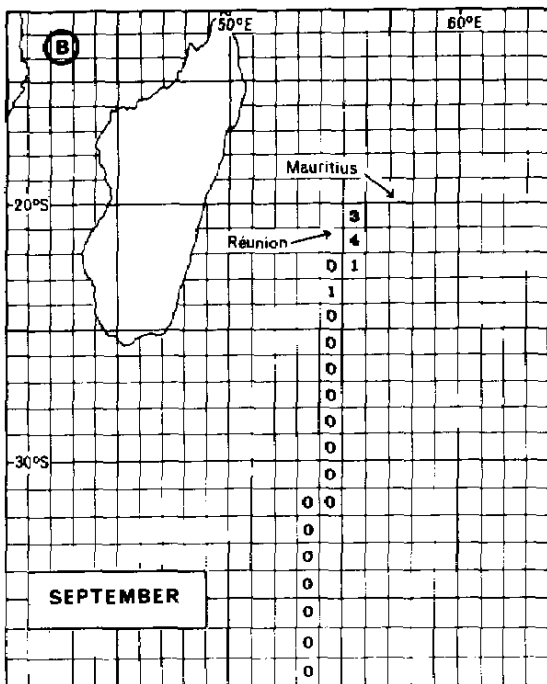
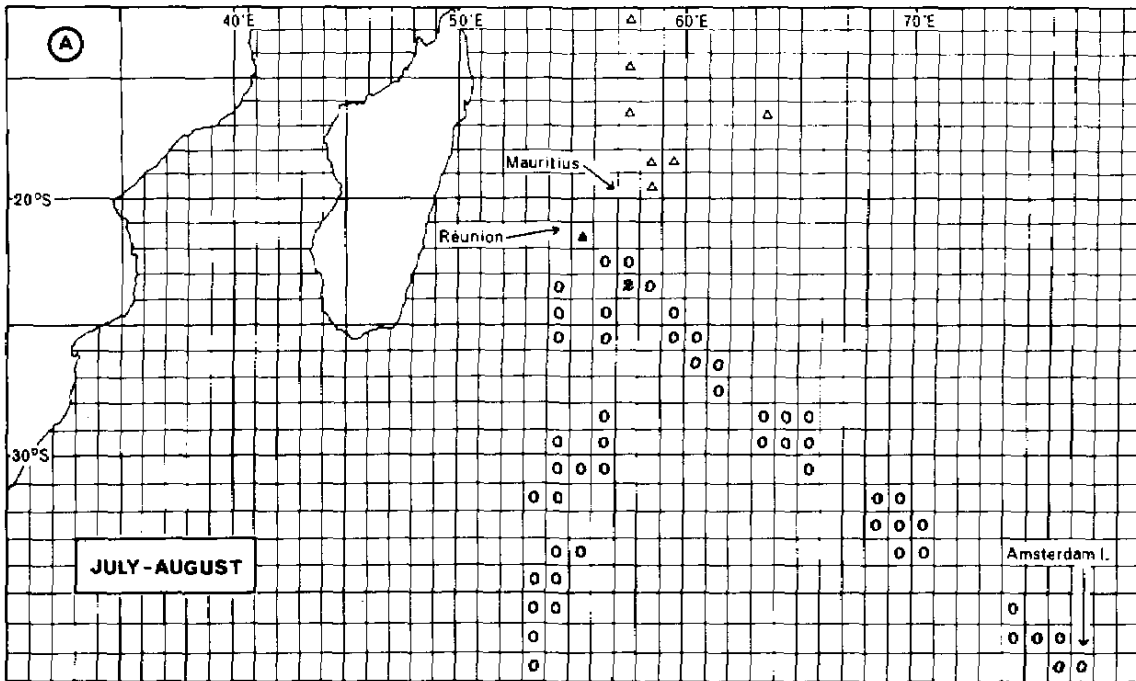
### Seasonal distribution

Only three Barau's Petrels were seen during winter transects, all in July and SE of Réunion between 23 and 24°S (Figure 1A). These, and occasional observations off Réunion in July (Gill *in* Jouanin 1987), are the only definite winter records south of 15°S. Temple (1976) did not specify the freshness of a dead bird found on Round Island, off Mauritius, in August. Barau's Petrel is absent N and NE of the Mascarenes in winter (Bailey 1968).

In September (Figure 1B), when colonies are first reoccupied (Jouanin 1987), the mean abundance in 1° squares adjacent to Réunion (2.5 per 10 min) was already within the range of corresponding monthly summer values (1.7 - 3.3). Only three birds were seen further away from Réunion, and none south of 24°S. All birds seen were in fresh plumage notable for the pure grey tone of the upper parts.

The distribution of Barau's Petrel showed little change in November (Figure 1C, including one previous record in Bourne 1989), but a major southward range expansion was observed in December (Figure 2A). Along the SSW transect, Barau's Petrels were then seen as far as 35°S, albeit regularly only north of 26°S, where their abundance never exceeded 1 per 10 min. The near absence of Barau's Petrel along the SE transect was surprising, with only two records of five at 24°14' S and one south of St Paul at 41°26' S 75°39' E, the southernmost observation during the study. Bourne (1989) reported a sighting at 27°S 49°E, west of the study area.

In January (Figure 2B), a marked increase in maximum numbers near Réunion reflects the appearance of feeding groups associated with other seabirds, which became a regular feature throughout summer. Further along the SSW transect, numbers remained fairly low and even, while the area of regular sightings expanded southwards from 26 to 28°S. Barau's Petrels were comparatively more abundant and ranged further south along the SSE transect, where highest numbers were encountered north of 29°S and between 32 & 33°S, with very few seen between 29 & 32°S. The pattern of distribution and abundance was intermediate on a single transect due south of Réunion. Wing moult was recorded in one individual (0.3% of the January total,  $n = 301$ ) off Réunion. Voisin (1983) saw the species off the west coast of Réunion and near 24°S. The species was also recorded between Réunion and Madagascar and off the south coast of Madagascar (Bourne 1989).



- 3 maximum per 10-minute count
- X seen outside counts
- 0 absent
- ▲/△ presence/absence (previous publications)

FIGURE 1 — South-west Indian Ocean showing the distribution of Barau's Petrel. A. July-August; B. September; C. November. Named islands are within arrowed squares

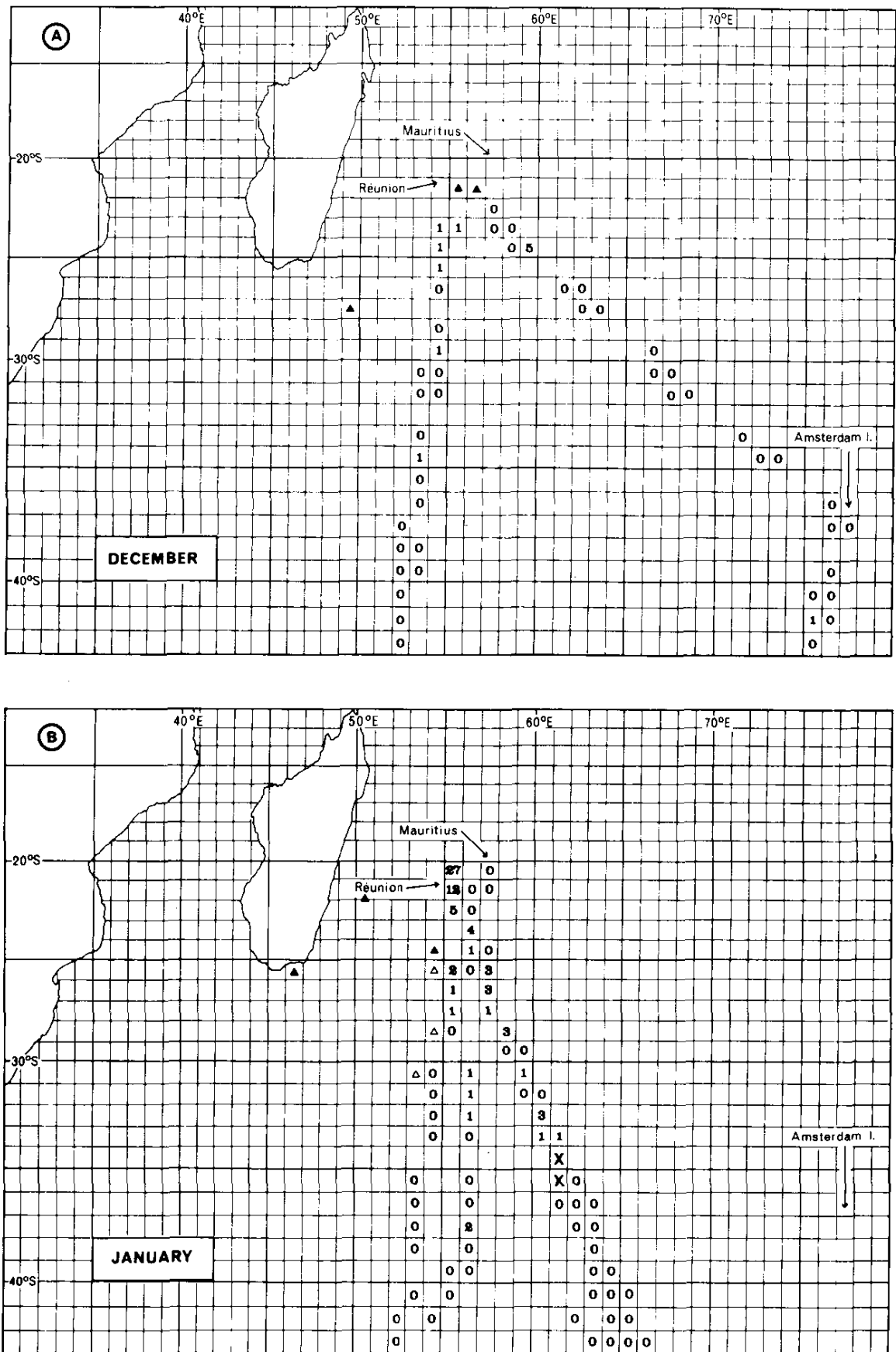


FIGURE 2 — South-west Indian Ocean showing the distribution of Barau's Petrel. A. December; B. January. Symbols as in Fig. 1.

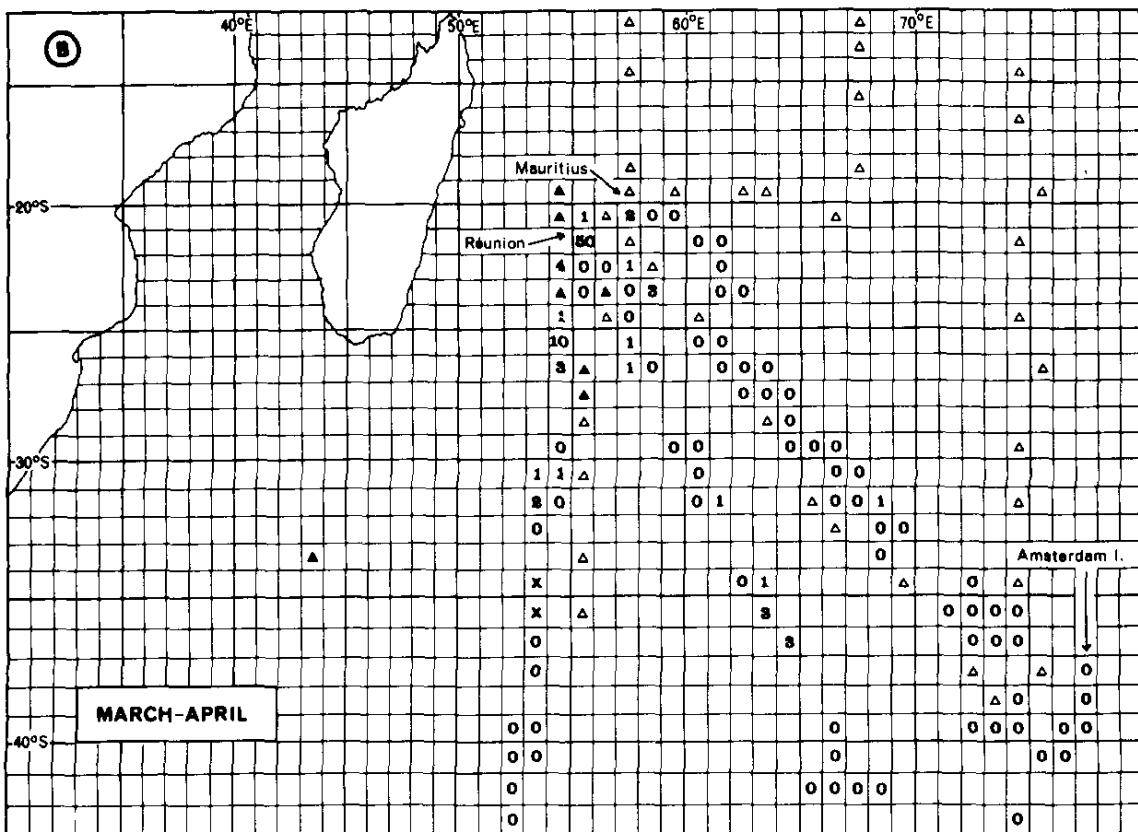
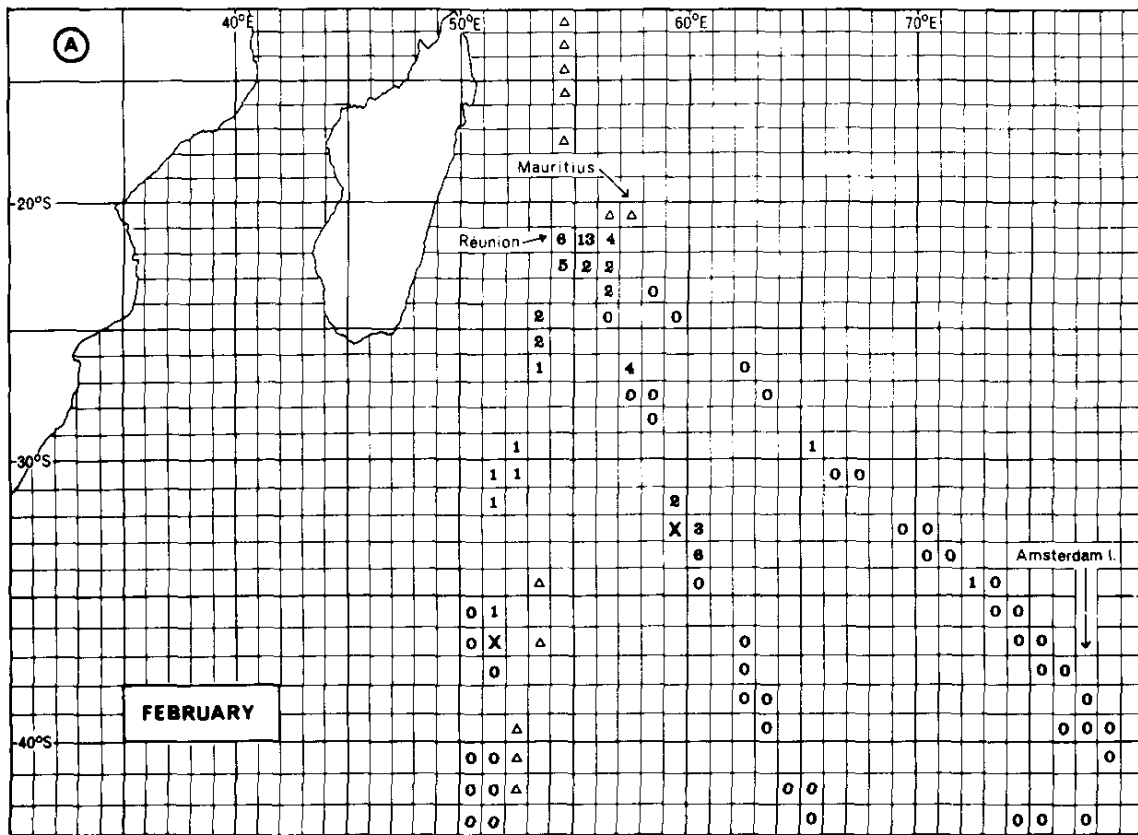


FIGURE 3 — South-west Indian Ocean showing the distribution of Barau's Petrel. A. February; B. March-April. Symbols as in Fig. 1

In February (Figure 3A), SSW transects slightly further west than usual crossed an area where single Barau's Petrels were seen at regular intervals south to 37°S. Distribution was more uneven along the SSE transect, with abundance maxima between 26 & 27°S and 32 & 34°S respectively and none seen elsewhere south of 24°S. The species was again very rare along the SE transect, and the only bird in wing moult (0.6%,  $n = 169$ ) was seen off Réunion. Gill (1967) and Voisin (1983) did not record the species north of Réunion or south of 34°S, respectively.

In March (Figure 3B), the range of Barau's Petrel still extended to near 37°S on the SSW and SSE transects. Along the SSW transect, up to ten per 10 min were counted between 25 and 26°S, the highest abundance observed beyond the immediate vicinity of Réunion. As in previous months, the SSE transect showed a peak near the southern range limit (35-37°S) and few records further north. Along the SE transect only a single bird was seen south of 24°S, but several were seen off Mauritius, including two heading at dusk towards Morne Brabant, a mountainous outcrop on the south-west coast. The species is not reported breeding on Mauritius and has been recorded there only twice before: the bird found dead on offshore Round Island and one seen heading inland in February 1974 (Cheke *in* Jouanin 1987). No Barau's Petrels were seen along the single SE transect in April. Previous March-April sightings have been made at Walter's Shoal (33°09' S 45°58' E) south of Madagascar (Frost 1981) and between Réunion and 28°S (Gill 1967), but none north of 20°S (Bailey 1968) or south along 75°E (Gill 1967). At this time of year all birds seen were in worn plumage with a distinctly brown tinge on the upper parts.

### Population estimates

During summer (January-March), when Barau's Petrel is most widespread and numerous south of Réunion, an estimated 2673-4588 birds were present within all 176 of the 1° squares traversed (minimum and maximum derived by using a 5 km and a 3 km detection radius respectively). These figures are necessarily underestimates because of incomplete coverage of the species' range, but they provide a reliable baseline, being calculated from actual densities per 1° square rather than extrapolated densities per 5° square. A more complete estimate based on mean density per 5° square amounts to 7977-13 847 birds for the 18 squares traversed between 20°S and 40°S. These include most of the summer range of Barau's Petrel west of 80°E, except for the area between Réunion, Madagascar and Walter's Shoal (Frost 1981, Bourne 1989). Assuming that the range extends westwards to squares 25-30°S and 30-35°S, at 45-50°E, and that densities there are similar to those in the adjacent squares to the east, the rounded population estimate for the SW Indian Ocean in summer amounts to 9000-15 000 birds.

### Marine habitat

In winter and early spring (July-November) Barau's Petrel is absent from all but the warmest part (Figures 1A-C) of the study area (SST 22.7 - 24.0°C). Salinity at the locations of July records was 35.14‰ (no salinometer was available on board during spring transects). Such values are diagnostic of South Tropical Surface Water (Gallagher 1966), a homogenous layer



extending to an average depth of 100 m around Réunion (Gamberoni *et al.* 1984). At this time of the year, Barau's Petrel also frequents hotter and less salty waters closer to the equator (SST 26.3-26.5°C, salinity 34.34 - 34.42‰; Dunlop *et al.* 1988a).

In late spring and summer, records were spread over temperature and salinity ranges of (14.2) 18.0 - 28.6°C (December - March) and 35.08 - 35.65‰ (January - March), both markedly broader than those figured by Pocklington (1979). The isolated value of 14.2°C corresponds to the December sighting south of St Paul, the only one made over the transition zone north of the Subtropical Convergence. Remaining observations were associated with either South Tropical Surface Water, South Central Surface Water, or waters with intermediate characteristics presumably generated by mixing between these water masses (Figure 4B). Over South Central Surface Water, few were seen south of the 21°C isotherm (except in December), and the southern limit of range did not correspond to any recognised hydrological boundary. The same applies to its northern limit of range (Gill 1967) in tropical waters.

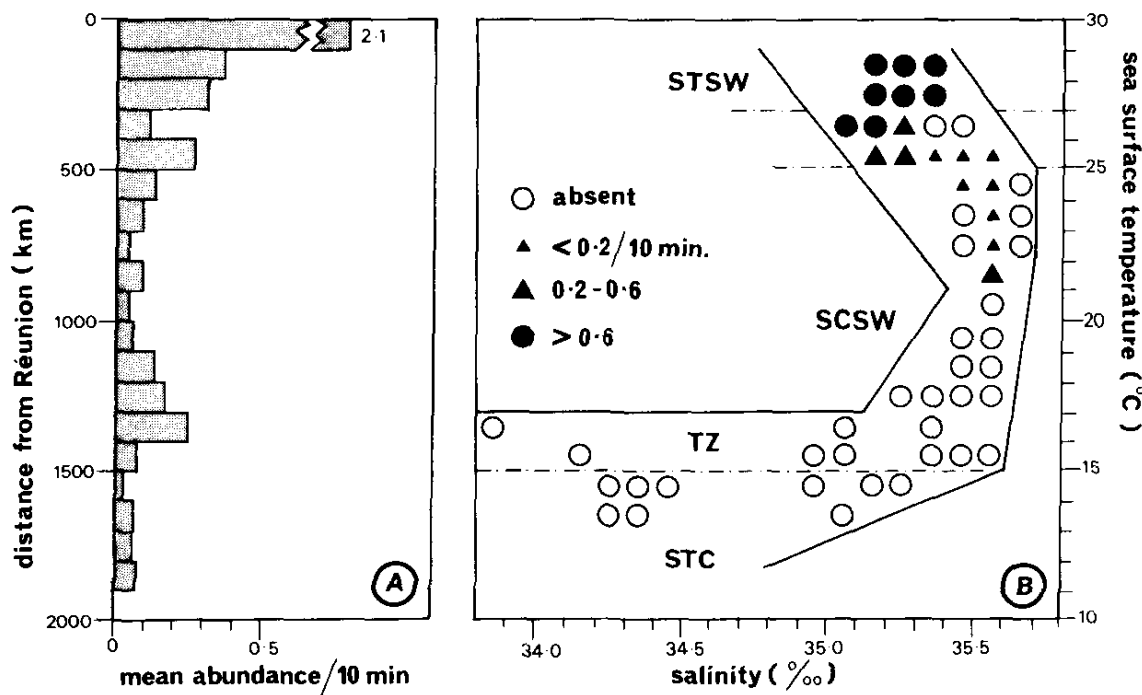


FIGURE 4 — Distribution of Barau's Petrel in relation to distance from Réunion (A) and to sea-surface temperature and salinity (B) during summer months. STSW: South Tropical Surface Water. SCSW: South Central Surface Water. TZ: Transition Zone. STC: Subtropical Convergence

During summer, highest densities were encountered in three distinct habitats, which appear to be the major feeding areas in the region covered (Figure 4A,B). The first consists of tropical and mixed tropical/subtropical waters within 300 km of Réunion. At all times of day, Barau's Petrels were regularly seen feeding between 13 and 130 km off the south and south-west coast of Réunion, an indication that high densities in this area were not simply reflecting the concentration of transiting birds at the periphery of a breeding locality. The second lies between 400 and 500 km south of Réunion (25-26°S), an area often marked by a salinity or thermohaline front, or by

a localised vein of warmer and less saline water. Plumes of decaying phytoplankton were seen in the same area during some transects. The third is in subtropical waters (SST 21-22°C, salinity 35.5-35.6‰) between 1100 and 1400 km SSE of Réunion. All three areas consist of oceanic waters, including that in the vicinity of Réunion where Barau's Petrel was not seen feeding in waters less than 1000 m deep.

### Foraging and feeding

Nearly a quarter (24.5%, n = 721) of all Barau's Petrels seen and nearly all (98.0%, n = 150) of those seen feeding were part of multispecies seabird flocks. They joined such flocks only from January to March, and only over the foraging areas off the south and southwest coast of Réunion and between 25 and 26°S. The average size of flocks attended by Barau's Petrel was 49 birds (range 2 - 305, n = 22). Barau's Petrels were most often associated with Audubon's Shearwaters and, to a lesser degree, with Wedge-tailed Shearwaters, Common Noddies, and Sooty Terns (Table 2). Of the 22 flocks seen, two were associated with schooling fish visibly escaping predators and two others were circling over floating objects (driftwood, fishing buoys). When attending such flocks, Barau's Petrel fed by surface-seizing, dipping and surface-plunging (*sensu* Ashmole 1971), and fishes c. 10 cm long were the main prey taken.

TABLE 2 — Composition of seabird flocks attended by Barau's Petrel (n = 22)

	Barau's Petrel ( <i>Pterodroma barau</i> )	Audubon's Shearwater ( <i>Puffinus herminieri</i> )	Sooty Tern ( <i>Sterna fuscata</i> )	Wedge-tailed Shearwater ( <i>Puffinus pacificus</i> )	Common Noddy ( <i>Anous stolidus</i> )	Bridled Tern ( <i>Sterna anaethetus</i> )	White-tailed Tropicbird ( <i>Phaethon lepturus</i> )	Pomarine Skua ( <i>Stercorarius pomarinus</i> )
Percentage occurrence	100.0	86.4	40.9	36.4	27.3	4.5	4.5	4.5
Mean no. birds per flock	8.1	6.5	21.9	8.6	2.5	1.0	0.1	0.1
Maximum abundance per flock	50	40	150	100	41	21	1	1

The foraging behaviour in southern subtropical waters was strikingly different. There, Barau's Petrel was essentially a solitary bird reminiscent of *P. mollis* and *P. macroptera*, the range of which slightly overlaps that of *P. barau*. As with those species, Barau's Petrel was rarely seen feeding here and, in such cases, only surface-seizing was recorded, suggesting latitudinal dietary differences as well.

## DISCUSSION

Apart from the nest found on Rodrigues and the distinct possibility that a few pairs breed on Mauritius, Barau's Petrel is confined to Réunion, where Feare (1984) conjectured the population to number thousands of pairs. This order of magnitude is supported by our estimate of 9000-15 000 birds in the south-west Indian ocean during summer. Given that most birds seen in the study area were commuters from Réunion colonies (see below), and assuming that half of them were breeders (based on a proportion of 48% found in colonies of *P. phaeopygia sandwichensis*, Simons 1985), this figure suggests that some 2200-3800 pairs were breeding on Réunion between 1978 and 1988.

Cheke claims (1987, p.31) that the population has expanded since the species was discovered in 1963, "to judge by increasing numbers seen around the coast [of Réunion] and sightings on neighbouring islands". Cheke was presumably referring to his own observations on Rodrigues (one nest) and Mauritius (one sighting) and to counts made off the south-west coast of Réunion in 1964 ("in numbers", Jouanin & Gill 1967), in 1974 (up to several hundred, Cheke in Jouanin 1987) and in 1977-78 (up to 1000+, Jadin & Billiet 1979). The inference of an upward trend from these imprecise observations seems questionable. A more accurate baseline for 1964 is provided by the results of pelagic counts made along 55°E in early March (Gill 1967). These fall within the range of results obtained in the same area and period in 1981 and 1986 (Table 3), and suggest that numbers have remained stable since 1964.

TABLE 3 — Average number of Barau's Petrels seen per 10 min during transects along 55°E in 1964 (Gill 1967), 1981 and 1986 (this study). Asterisks indicate lack of samples

	20-21°S	21-22°S	22-23°S	23-24°S	24-25°S	25-26°S	26-27°S
3-6 Mar. 1964	0.89	*	*	0.50	0.33	*	0.08
4-5 Mar. 1981	0.67	4.52	1.24	*	0.11	0.69	0.31
14-16 Feb. 1986	*	2.80	1.50	*	0.45	0.55	0.10

As similar *Pterodroma* species are very vulnerable to introduced predators (Harris 1970), existing colonies have presumably remained largely inaccessible to the cats and rats on Réunion since the 17th century (Cheke 1987). The extremely rugged topography of the presumed nesting sites (Brooke 1978) has undoubtedly secured the relative abundance of Barau's Petrel. On the other hand, present high numbers come as no surprise in view of the pelagic ecology of the species. It has been shown (Diamond 1978) that, given safe breeding grounds, the population size of a tropical seabird species primarily reflects the extent of its feeding area, and that the major strategies boosting population size are migration during the non-breeding season and, to a lesser degree, extension of the foraging radius when breeding.

Barau's Petrel is clearly a migratory species. Our results show that most leave the waters around and south of Réunion between April and June (most

probably in May, as chicks fledge in April and the species appears in its winter quarters in early June), with an apparently well synchronised return in September. Until recently, probable sightings west of the Seychelles in June (Gill 1967) and between the Seychelles and the Chagos archipelago in June-July (Bourne 1971) pointed to the western part of the tropical South Indian Ocean as a wintering area. New records have considerably extended the winter distribution both northwards and eastwards, with sightings in the southern Arabian Sea (van den Berg *et al.* 1991), between the Maldives and Sumatra (van Marle & Voous 1988, van den Berg *et al.* 1991), and in the Cocos-Keeling Is region (Chapman & Cheshire 1987). Small numbers seen near the Mascarenes in June-July (Pocklington *et al.* 1972, Jouanin 1987, this study) indicate that a few remain, but the Réunion area is deserted by August. In this respect, it is noteworthy that, whereas June-July observations (Barau's Petrel has yet to be tracked down in May) are spread across the Indian Ocean, August sightings are all east of 90°E (Fig. 5), which may indicate an eastward movement in mid-winter, unless it simply reflects biased coverage.

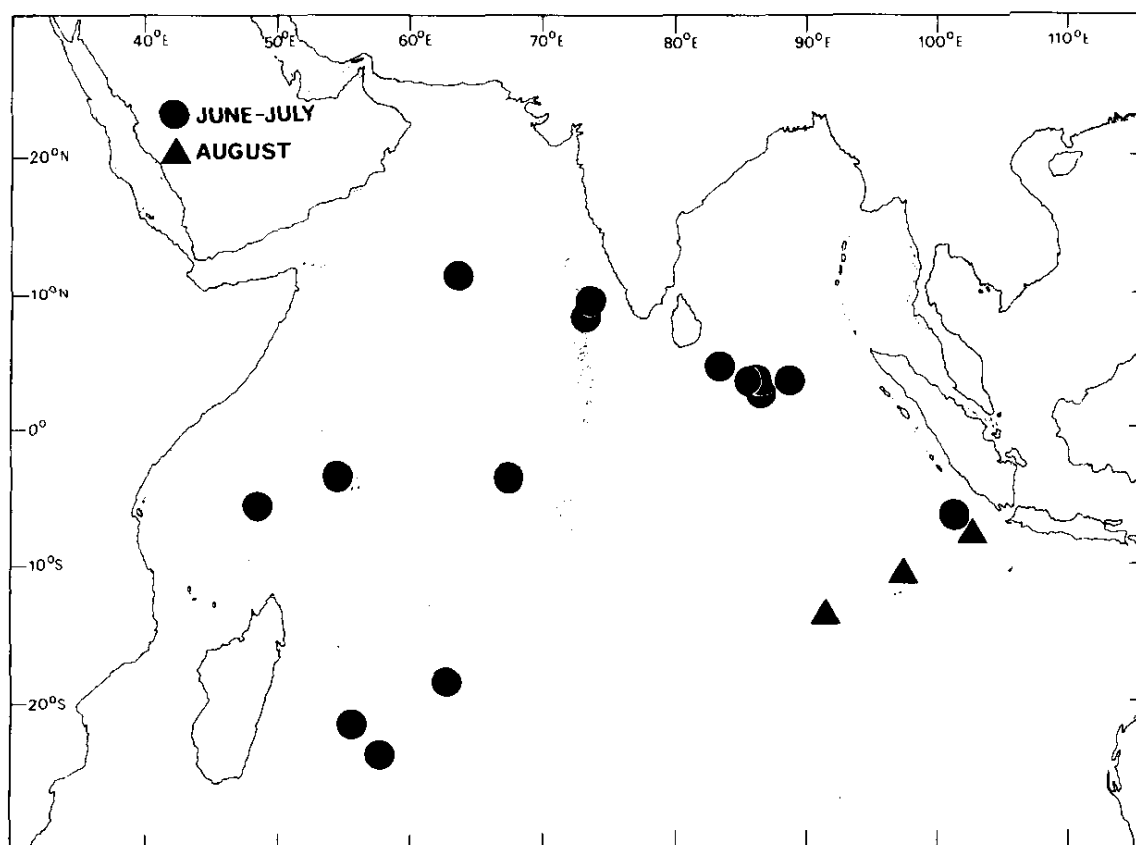


FIGURE 5 — Location and month of definite and probable at-sea records of Barau's Petrel during the non-breeding season

As for the foraging radius of breeders, Barau's Petrels were seen as far as 1850 km south of Réunion during summer, and there is evidence that even the southernmost birds may have been breeders. Firstly, a marked predominance of north-south movements between Réunion and 30°S (Stahl & Bartle, in prep.) suggests that many, if not most, birds seen there and

further south were commuters from Réunion colonies. Secondly, the near absence of birds in wing moult during the breeding season when, in other *Pterodroma*, immatures and failed breeders renew their flight feathers (Warham 1967, Robertson 1985) indicates that a significant proportion of non-breeders was distributed outside the study area. These non-breeders spend spring and summer in the tropical and subtropical SE Indian Ocean respectively, as suggested by sightings of Barau's Petrels near Christmas I. in October (Dunlop *et al.* 1988b) and between Amsterdam I., western Australia and Victoria in February - March (Carter *et al.* 1989). The Victorian bird seen in February was freshly moulted, with grey upperparts and light edgings to the feathers (Carter *et al.* 1989), at a time when the upperparts of breeders around Réunion are brown. It thus must have been immature. Geographical segregation between breeders and non-breeders is both widespread and almost certainly a further mechanism boosting population size in seabirds. Segregation has been documented for *P. ultima* and *P. solandri* (Bailey *et al.* 1989, Bartle *et al.* in press), *P. mollis* (Bartle & Stahl unpubl.) and *Lugensa brevirostris* (Harris 1982).

In the Indian Ocean, Barau's Petrel is the only *Pterodroma* known to exploit resources of tropical and subtropical waters in alternate seasons. Both *P. mollis* and *P. macroptera* rarely venture north of 23°S (Watson *et al.* 1971, Jouventin *et al.* 1982, Bartle & Stahl unpubl.), whereas *P. arminjoniana* remains confined to tropical waters throughout the year (Bartle & Stahl unpubl.). In this respect, and in view of its size, Barau's Petrel occupies a niche most like that of *P. externa* in the South Pacific, of *P. phaeopygia sandwichensis* in the North Pacific (Bartle *et al.* in press) and of *P. hasitata* in the North Atlantic (Haney 1987). These species also show the same preference for feeding in multispecies flocks (King 1970, Pitman 1982, Haney 1987).

Such a migration pattern seems to have evolved primarily as a response to out of phase fluctuations of resource availability in tropical and subtropical waters. In the South Indian Ocean (9-32°S), the distribution of subsurface micronekton biomass shows a marked contrast between summer, when highest values are found south of 20°S, and winter, when the area of maximum biomass is located north of 12°S (Legand 1969), a pattern in broad correspondence with seasonal shifts of the range of Barau's Petrel. Furthermore, dates of fledging and departure of adults from subtropical waters are closely synchronised with the rapid transition, in mid-April to mid-May, from the summer to the winter pattern of micronekton distribution.

However, the biomass differential in favour of tropical waters north of 12°S essentially persists until November, suggesting that the return to Réunion waters in September is determined by the need to breed rather than food supply. October observations of non-breeders still at 10°S in the eastern Indian Ocean (Dunlop *et al.* 1988b) support this idea. Limited southward extension and low abundance in the study area until December (except near Réunion) suggest that birds visiting Réunion at this time are mostly foraging over the richer waters to the north of the island.

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