Pelagic distribution of Gould's Petrel (*Pterodroma leucoptera*): linking shipboard and onshore observations with remote-tracking data

David Priddel[A], *Nicholas Carlile*[A,H], *Dean Portelli*[B], *Yuna Kim*[C], *Lisa O'Neill*[A],
Vincent Bretagnolle[D], *Lisa T. Ballance*[E], *Richard A. Phillips*[F], *Robert L. Pitman*[E]
and Matt J. Rayner[G]

[A]Office of Environment and Heritage, PO Box 1967, Hurstville, NSW 2220, Australia.

[B]Australian Wetlands, Rivers and Landscape Centre, University of New South Wales, Sydney,
  NSW 2052, Australia.

[C]Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia.

[D]Centre National de la Recherche Scientifique, Centre d'Etudes Biologiques de Chizé,
  F-79360 Beauvoir-sur-Niort, France.

[E]Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric
  Administration, 8901 La Jolla Shores Drive, La Jolla, CA, USA.

[F]British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road,
  Cambridge, CB3 0ET, UK.

[G]School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand.

[H]Corresponding author. Email: nicholas.carlile@environment.nsw.gov.au

Abstract.   This study describes and compares the pelagic distribution and migratory patterns of the two subspecies of Gould's Petrel (*Pterodroma leucoptera*), and contrasts data obtained from tracking birds at sea using geolocators with observational data (shipboard sightings, by-catch records and beachcast specimens). While breeding, tracked individuals of both subspecies (*P. l. leucoptera* and *P. l. caledonica*) foraged within the Tasman Sea and south of the Australian continent, with forays west into the Indian Ocean before laying. After breeding, both subspecies migrated to distinct non-breeding ranges within the eastern tropical Pacific Ocean. Observational data identified the general pattern of migration and foraging areas of the species, whereas data from geolocators provided details of routes and timing of migration, core foraging ranges, and marked spatial and temporal segregation between the two subspecies. However, by attaching geolocators only to established breeders, as is typical of studies of small and medium-sized seabirds, these devices failed to identify that non-breeding birds (pre-breeders and adults that are deferring breeding) may not follow the same migratory schedules or have the same at-sea distribution. We conclude that integrating data from electronic tracking with observational data substantially improves our understanding of the pelagic distribution of seabird populations.

Additional keywords: at-sea sightings, foraging distribution, geographical separation of subspecies, geolocation, GLS logger, migration, New Caledonian Petrel.

Received 25 February 2014, accepted 12 June 2014, published online 3 November 2014

Introduction

Seabirds are more threatened, and their conservation status deteriorating faster, than any other group of birds, with approximately one-third of species threatened with extinction (Croxall *et al.* 2012). Threats occur both on land, at nesting sites, and at sea where birds forage. The importance of secure nesting sites has long been recognised, leading increasingly to these areas being afforded legislative protection against degradation or over-exploitation. Many seabird nesting sites have been further protected through the eradication of alien predators, particularly rodents

(Howald *et al.* 2007; Broome 2009). The situation at sea is vastly different. Currently, <1% of the world's oceans have any form of legislative protection and there is an important and immediate need to identify and delineate a network of ecologically representative Marine Protected Areas (Ronconi *et al.* 2012). Knowledge of the movements and behaviour of seabirds is increasingly being used to identify ecologically important marine areas (e.g. Camphuysen *et al.* 2012; Le Corre *et al.* 2012; Ludynia *et al.* 2012; Montevecchi *et al.* 2012). However, for most seabirds, their movements at sea are poorly known. Large-scale banding

programs are of little utility in revealing patterns of seabird pelagic movements, owing to the difficulty of recapture on the open ocean. Until the last two decades, shipboard surveys, by-catch records from fisheries operations, recoveries of beachcast specimens and observations of seabirds from shore were the only means of identifying the pelagic distribution and movements of seabirds (Tremblay *et al.* 2009). However, such data are patchy, and collection of shipboard data is often opportunistic or prohibitively expensive, especially if vessels need to be chartered specifically for the purpose. Moreover, interpretation of sightings data can be complicated by the misidentification of morphologically similar taxa (Roberson and Bailey 1991; Onley and Schofield 2007).

In the late 1990s, the advent of geolocators (global location sensor or GLS logger) small enough to be carried year-round on a leg-band by large birds, such as albatrosses, revolutionised the study of seabird ecology by making it possible to track individuals throughout their entire period of migration (Weimerskirch and Wilson 2000; Croxall *et al.* 2005). These electronic devices record light intensity and elapsed time, and subsequent processing allows the determination of the timing of sunrise and sunset, which can then be used to calculate latitude and longitude (Phillips *et al.* 2004; Shaffer *et al.* 2005). With further miniaturisation, the development of lightweight (<1.5 g) geolocators has made it possible to study the movements of all but the smallest seabirds without any apparent adverse effects (Catry *et al.* 2009; Quillfeldt *et al.* 2012; Rayner *et al.* 2012). Although the use of such electronic devices has increased rapidly, combining the resulting data with those obtained using traditional observational methods (i.e. shipboard surveys, at-sea collections, band recoveries from fisheries by-catch and beachcast birds) has been identified as a high priority, because these may provide complementary information on the movements of seabirds, with implications for conservation (Tremblay *et al.* 2009; Croxall *et al.* 2012). Such an integrated approach also provides an opportunity to compare the quality and type of information obtained from each method.

Gould's Petrel (*Pterodroma leucoptera*) is a small (~200–250 g) gadfly petrel that breeds on several small islands off the coast of New South Wales, Australia (Priddel and Carlile 2004*a*, 2004*b*; Carlile *et al.* 2012), and on the main island of New Caledonia (de Naurois 1978; Bretagnolle and Shirihai 2010). The species is classified globally as vulnerable (BirdLife International 2012). The Australian subspecies (*P. l. leucoptera*), hereafter *leucoptera*, was considered endangered under Australian legislation when the population was found to have declined to ~300 breeding pairs in 1992 (Priddel *et al.* 1995). However, owing to a successful recovery program, the population has since increased to ~1000 pairs (Priddel and Carlile 2009). Population size of the New Caledonian subspecies (*P. l. caledonica*), hereafter *caledonica*, is poorly known but estimates of Gould's Petrel based on counts at sea in the eastern tropical Pacific Ocean (annual mean 810 000 individuals, *n* = 6 years; Ballance *et al.* 2002) indicate this subspecies must be substantially more numerous than *leucoptera*, although it is in decline owing to predation by introduced Pigs (*Sus scrofa*) and Cats (*Felis catus*) (BirdLife International 2012). Conservation action to remove alien mammalian predators from the breeding grounds of *caledonica* has recently begun.

The two subspecies of Gould's Petrel differ slightly in size (Bretagnolle and Shirihai 2010) and plumage (de Naurois 1978; Imber and Jenkins 1981), but are arguably indistinguishable when observed at sea. Beachcast specimens have been assigned to subspecies based primarily on the degree of pigmentation on the inner vane of the outer rectrix: specimens with little or no pigmentation were identified as *caledonica* (Imber and Jenkins 1981). Recent phylogenetic research has confirmed *caledonica* and *leucoptera* are genetically distinct at the subspecies level, although gene flow between them probably occurs at a low rate (Gangloff 2010).

The breeding biology of the two subspecies is similar, except the timing differs: *caledonica* breeds approximately 1 month later than *leucoptera*. Typically, adult *leucoptera* arrive at the breeding colony in October, lay eggs in November–December, and leave in April (Fullagar 1976). Adult *caledonica* typically arrive in November, lay eggs in December–January, and leave in May (V. Bretagnolle, pers. obs.).

In the 1950s, Gibson and Sefton (1957) surmised that Gould's Petrel migrated north after breeding, though direct evidence at that time was lacking. Imber and Jenkins (1981) surveyed seabirds in the Tasman Sea annually (1970–80) and observed Gould's Petrel only between December and April, despite similar sampling effort in other months. Additionally, beachcast specimens in New Zealand have been found only between November and June. They concluded from this evidence that the species was probably migratory. Further, they cited eight specimens collected by Rollo Beck close to the Galapagos Islands in June 1906 as evidence of a post-breeding migration to the eastern tropical Pacific Ocean (ETP), and hypothesised a migration route that, at least in part, followed the Subtropical Front at ~40°S. Analysis of records off south-eastern Australia showed a similar seasonal trend, with the greatest numbers of observations in December–April and none during June–September (Reid *et al.* 2002).

The aims of this study were to describe and compare the pelagic distribution and patterns of migration of the two subspecies of Gould's Petrel, and to contrast the data obtained from tracking birds at sea with shipboard observations and records of beachcast birds.

Methods

Observational records

Observations of Gould's Petrel away from its breeding sites were obtained from published literature, museum collection databases, other publicly available datasets and from individual observers (sources summarised in Table S1 of the Supplementary Material). The following information was extracted from each record: date, latitude, longitude, type of observation (shipboard sighting, at-sea capture, beachcast remains or stranded live bird), number of individuals sighted and source. Where published records were presented as point locations on maps, the approximate latitude and longitude were estimated. Dubious records, duplicates and those without geographical coordinates were discarded.

Methods used to obtain at-sea sightings of Gould's Petrel varied among sources, and included both opportunistic and systematic procedures. Of the observational records, 58% were derived from surveys conducted by the National Oceanic and Atmospheric Administration (NOAA, Washington, DC;

http://www.noaa.gov/), using standard strip-transect survey procedures detailed in Ballance (2006). Other systematic surveys that contributed large sets of data used similar techniques.

Geolocator tracking

Twenty-two BAS geolocators (MK14, British Antarctic Survey, Cambridge, UK) and 20 Lotek geolocators (NanoLAT2900, Lotek, Ontario, Canada) were attached to adult *leucoptera* in March 2010 when they were provisioning nestlings on Cabbage Tree Island, Australia (32°41′18″S, 152°13′28″E). All the Lotek geolocators, and all but one of the BAS geolocators, were retrieved between November 2010 and January 2011 when adults returned to their nests to breed. However, 11 BAS geolocators and eight Lotek geolocators failed to record data for more than a few weeks. Information collected from the 22 fully functional geolocators covered the non-breeding season from after chick-rearing until their return the next breeding season. Movements during breeding (late incubation to fledging) were tracked by attaching Lotek geolocators (NanoLAT2900) to 32 breeding birds between December 2011 and April 2012.

The pelagic movements of *caledonica* were tracked using BAS geolocators. These were attached to 17 adult *caledonica* incubating eggs on Grande Terre (21°20′S, 165°30′E), the main island of New Caledonia, in January 2010. Seven geolocators were retrieved in January 2011.

Both subspecies were caught by hand at the nest. Geolocators were attached with cable ties and glue to a plastic (Darvic) leg-band fitted around the tarsus of the bird. The total weight of geolocator, leg-band and attachment material was equivalent to <1.2% of adult body mass. Similar attachment methods have been used in other studies, with no detrimental effects reported (Rayner 2007; Carey 2011). The attachment of geolocators to Gould's Petrels had no discernible effect on hatching success, fledging success, fledging weight or parental weight (Kim *et al*. 2014).

BAS geolocators measured ambient light-level every 60 s and then logged the maximum value for each 10-min interval. Light data were processed using TransEdit software (Jensen Software Systems, Lammertzweg, Germany), as described by Fox (2009), to provide two locational fixes per day. Longitude was calculated from the time of local noon and midnight relative to Greenwich Mean Time, based on times of sunrise and sunset inferred from light-curve thresholds. Latitude was calculated from daylength. However, latitude cannot be computed during periods close to the equinoxes because day and night are of approximately equal length uniformly across the globe. Therefore, locations occurring within 3 weeks of the equinoxes (20 March and 23 September) were excluded. A previous study of a free-ranging seabird indicated a mean error of ~200 km for data from BAS loggers (Phillips *et al*. 2004).

Lotek geolocators functioned on a similar principle to BAS geolocators but incorporated onboard processing of the light data to compute latitude and longitude (one location per day). They also recorded sea-surface temperature when birds were resting on the water, which was combined with satellite imagery (mid-wavelength infrared), where available, to estimate latitude during the 3 weeks either side of the equinox using LATVIEWER (Lotek, Ontario, Canada). The mean error using this approach (~200 km) is similar to that of BAS geolocators (Shaffer *et al*. 2005).

Analysis of location data

We removed from the dataset any locations that involved movements of >1600 km in a single day (Guilford *et al*. 2009; Rayner *et al*. 2011), those with interruptions to light curves around sunset and sunrise, and any that were clearly outside the known or possible range of Gould's Petrel. Locations were then pooled across individuals to estimate year-round utilisation distribution (UD) kernels for each subspecies following methods detailed in Shaffer *et al*. (2009). A 1000-km buffer around each colony was used to define the extent of the breeding range (Rayner *et al*. 2008), and the 80% contour of UD kernels, calculated individually, were used to define the non-breeding range for each bird (Guilford *et al*. 2009). Dates of the first and last locations to enter and exit the breeding and non-breeding ranges were used to determine the timing of migration for each individual. Dates when individuals first entered their burrows were identified by periods of darkness recorded during the day (see Rayner *et al*. 2012). Dates and duration of migration were compared between subspecies using *t*-tests that do not assume equal variances (Welch 1947). All means are presented ± standard deviation.

Results

Observational data

A total of 2042 observational records (2375 individual birds) were collated (see Supplementary material Table S1). These comprised 1890 shipboard sightings, 31 records of birds collected (killed) at sea, and 121 records of beachcast birds, including seven live emaciated individuals. Records spanned the period 1906–2012 and were obtained from the following sources: databases (81.2%), publications (10.0%), museum records (4.9%) and individual observers (3.9%).

At-sea observations (shipboard sightings and collections) were concentrated in the Tasman Sea and in the ETP between Hawaii and the Galapagos Islands (Fig. 1). The remaining records were off the eastern and southern coasts of Australia and off New Zealand, and in the Coral Sea, the Indian Ocean to the south of Australia, and the Southern Ocean as far south as the coast of Antarctica. There was a strong seasonal trend (Fig. 1). During December–April (breeding season), records were largely confined to the Tasman Sea and Indian Ocean south of Australia (Fig. 1*a*). During May–August (the non-breeding season), most sightings were in tropical latitudes of the central and eastern Pacific Ocean, with a small number in the Tasman Sea (Fig. 1*b*). During September–November (pre-laying phase of the breeding season), sightings extended across the tropical Pacific Ocean, Tasman Sea and Indian Ocean, with some in the Southern Ocean close to Antarctica (Fig. 1*c*). Sightings south of 55°S (*n* = 19) were recorded only during September–March but typically few ships (and thus observers) are present in these cold waters outside these warmer months. Within the ETP, sightings were concentrated between 10°N and 10°S latitude, and from 90°W to 150°W longitude. Survey effort within the ETP extended further to the north, east and west of these sightings, but not to the south (Fig. 2).

Records of beachcast birds were from Australia (*n* = 68) and New Zealand (*n* = 36). Australian recoveries were from Tasmania and the coasts of southern and south-eastern mainland Australia in all months except July (61% of 56 live or recently dead birds were recorded in January–March). All but one of the New Zealand
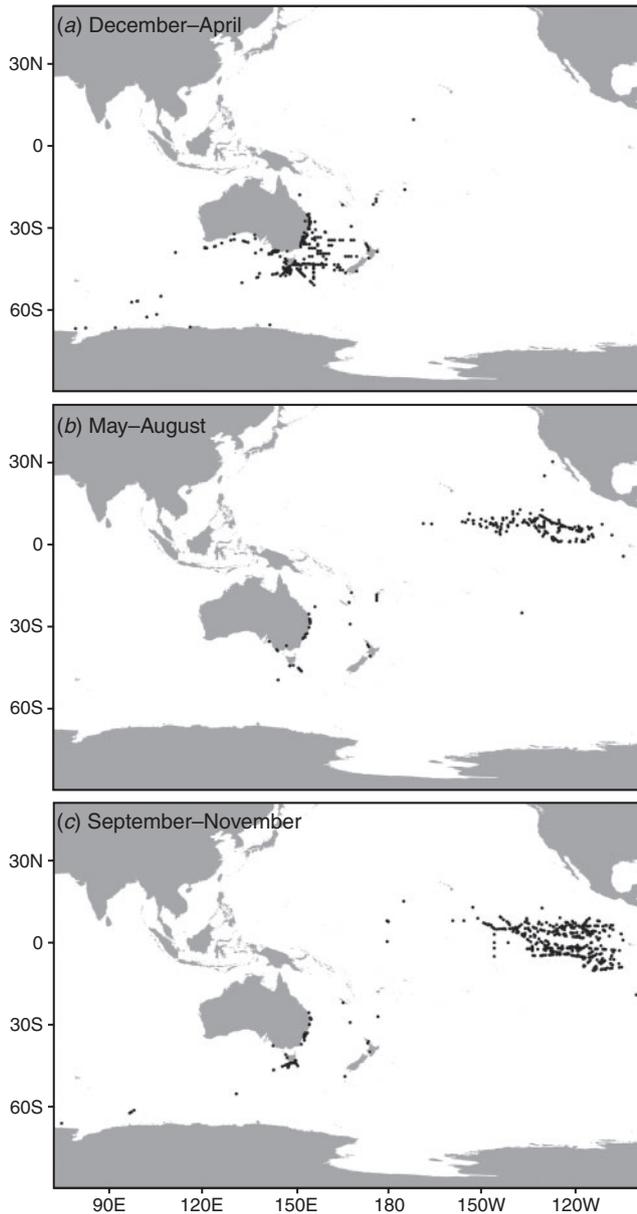
Fig. 1. Locations of observations of Gould's Petrel (*n* = 2042) during (*a*) December–April; (*b*) May–August; and (*c*) September–November.

birds were collected from the western coast of the North Island in November–June. Overall, 41 beachcast birds had been identified to subspecies: 79% from Australia (*n* = 24) were *leucoptera*, whereas 94% from New Zealand (*n* = 17) were *caledonica*. Of specimens collected at sea, 10 from the Tasman Sea and one from near Tonga were identified as *caledonica*. Further, Spear *et al.* (1995) described eight birds (of 70) collected in the ETP as '*leucoptera*-type' based on the same criterion.

Within the Tasman Sea and Indian Ocean, Gould's Petrels were uncommon and usually encountered singly (mean group size = 1.7 ± 1.2, *n* = 258 sightings; Australian Antarctic Data Centre, https://data.aad.gov.au/), and only rarely in groups of six or more birds. Within the ETP, Gould's Petrel was one of the

most common petrels observed, but again was frequently encountered singly (mean group size = 1.2 ± 1.1, *n* = 1284; NOAA database, L. T. Ballance, unpubl. data).

Tracking data: P. l. leucoptera

The 22 functional geolocators retrieved from *leucoptera* recorded data for a mean period of 252 ± 11 days (239–275 days) and provided a total of 4277 filtered locations. All *leucoptera* that carried geolocators during the breeding season successfully reared chicks to fledging.

Locations of the 22 individuals tracked after breeding were concentrated in equatorial waters of the central Pacific Ocean (Fig. 3*a*), predominantly south of Hawaii (20°N–20°S, 140–170°W) and between Hawaii and Japan (20°N–40°N, 160–170°E). Individual birds began the post-breeding migration on 4 April ± 6 days and travelled eastward then north to north-west to reach their non-breeding range on 24 April ± 10 days (Table 1), after 22.6 ± 8.1 days (Table 2). The average maximum distance from the breeding site was 9355 ± 1584 km. Birds remained in their non-breeding ranges for 141.3 ± 17.6 days (Table 2), leaving on 14 September ± 19 days (Table 1) to undertake a return migration westward to eastern Melanesia then southward into the Tasman Sea. Birds completed this return migration in 27.0 ± 16.3 days (Table 2), arriving at waters around the breeding colony on 12 October ± 6 days (Table 1).

Birds first visited their burrow on 18 October ± 6 days (Table 1). In November, shortly before laying, birds foraged in the Tasman Sea and waters to the south of Australia, with one individual going west into the Indian Ocean, as far as 100°E. During the incubation and provisioning period, the core foraging area (Fig. 3*a*) was in the Tasman Sea along the eastern coast of mainland Australia and around Tasmania.

Tracking data: P. l. caledonica

The seven functional geolocators retrieved from *caledonica* recorded data for a period of 347 ± 3 days (342–349 days) and provided a total of 1872 filtered locations. Locations of the seven individuals tracked after breeding were concentrated in equatorial waters of the eastern Pacific Ocean (Fig. 3*b*), predominantly west and south-west of the Galapagos Islands (0°S–20°S, 90–140°W). Birds left their breeding range on 25 March ± 30 days and travelled eastward, passing the north of New Zealand before bearing north to reach their non-breeding range on 18 May ± 13 days (Table 1) after 54.6 ± 24.5 days (Table 2). The average maximum distance from the breeding site was 10 083 ± 1279 km. The birds remained in their non-breeding ranges for 135.9 ± 31.1 days (Table 2), leaving on 4 October ± 24 days (Table 1) to undertake a return migration westward to Melanesia then southward into the Tasman Sea. Birds completed this migration in 30.7 ± 19.3 days (Table 2), arriving at their breeding range on 4 November ± 7 days (Table 1).

Birds first visited their burrow on 6 November ± 8 days (Table 1). In November, shortly before laying eggs, six of the seven birds foraged in the Indian Ocean to the south and south-west of Australia, as far west as 100°E. The remaining bird travelled no further west than Tasmania (145°E). All birds then contracted their range to a core foraging area in the central Tasman Sea for the duration of the breeding season (Fig. 3*b*).
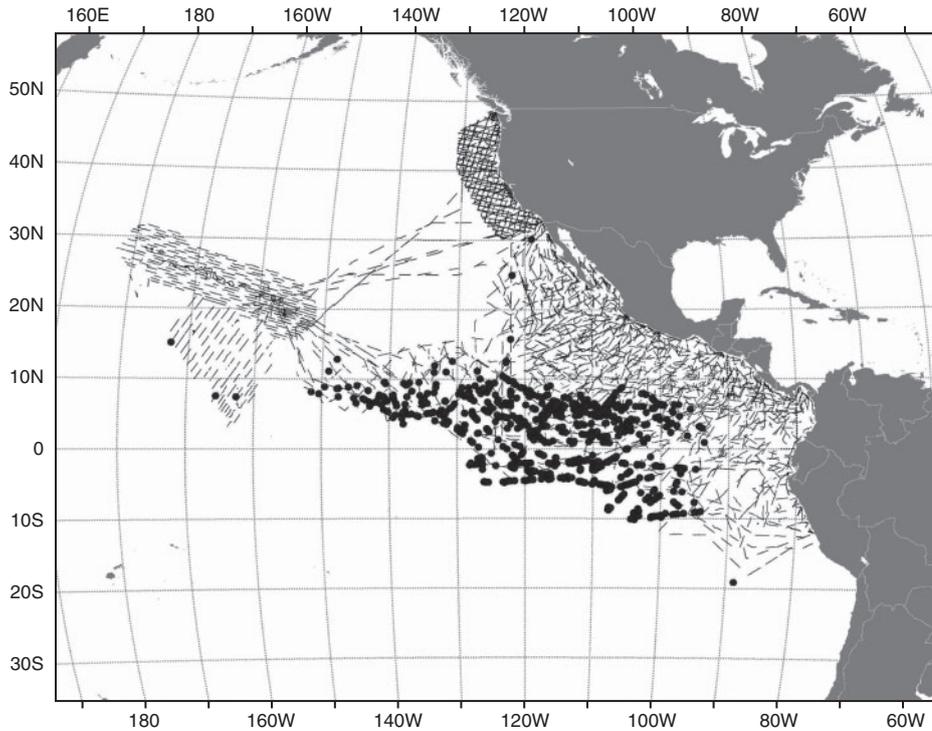
Fig. 2. Locations of shipboard sightings of Gould's Petrel in the eastern Pacific Ocean (*n* = 1180) during surveys undertaken by the National Oceanic and Atmospheric Administration (NOAA). Grey broken lines indicate the track-lines of survey vessels. Surveys were undertaken August–November in the eastern tropical Pacific (1988–90, 1998–2000, 2003, 2006), central Pacific (2002, 2005, 2010), and California Current (2001, 2005, 2008). A single observer seated in the flying bridge and using handheld binoculars counted all seabirds within a 300-m strip-transect on one side of the ship travelling at 18.5 km h⁻¹ (10 knots).

Breeding phenology

The mean date of departure from the breeding range was 10 days earlier for *caledonica*. However, the range in dates of *caledonica* encompass those of *leucoptera* and this difference was not significant (*P* = 0.413). The variance in the date of departure from the breeding range was particularly high for *caledonica* (65 days) compared to *leucoptera* (25 days); differences between subspecies in the variance of other dates of departure or arrival were ≤5 days (Table 1). The high variability in departure date for *caledonica* is because two tagged individuals left the colony early (February cf. April), presumably after failing in their breeding attempt. These failed breeders spent the next 2 months in the Tasman Sea and in waters to the south of Australia before arriving at the non-breeding range at approximately the same time as successful breeders. Consequently, the duration between leaving the breeding range and arriving at the non-breeding range (termed here as the duration of post-breeding migration) was longer and more variable for *caledonica* than for *leucoptera* (Table 2).

On average, *leucoptera* arrived at their non-breeding range 24 days earlier than did *caledonica* (Table 1). Both subspecies spent a similar amount of time in the non-breeding range (~140 days; Table 2), with *leucoptera* departing 19 days earlier than *caledonica* (although this difference was not significant; *P* = 0.091; Table 1). The duration of the return migration was similar for each subspecies (Table 2), with *leucoptera* arriving at

the breeding range 23 days earlier than *caledonica*, and first visiting the nest burrow 19 days earlier (Table 1).

Discussion

This study provides the first clear insight into the pelagic distribution and pattern of migration of Gould's Petrel, during both the breeding and non-breeding seasons. The integration of sightings at sea with data from remote tracking has demonstrated that this threatened seabird has a seasonal reliance on two discrete oceanic regions: the Tasman Sea and waters to the south of Australia during breeding, and the tropical Pacific Ocean during the non-breeding period.

Spatial and temporal separation of subspecies

Tracking revealed both subspecies of Gould's Petrel are trans-Pacific migrants. Although the at-sea distributions of the two subspecies overlap, there is a high degree of spatial and temporal separation evident in the kernel analysis of all tracks for each subspecies. Examination of the tracks for each individual corroborated these results. It is therefore unlikely that the observed separation between subspecies is a an artefact of the disparity in sample size between subspecies (22 *leucoptera* and seven *caledonica*). As suggested for other procellarids, the spatiotemporal separation between subspecies may facilitate a reduction in the
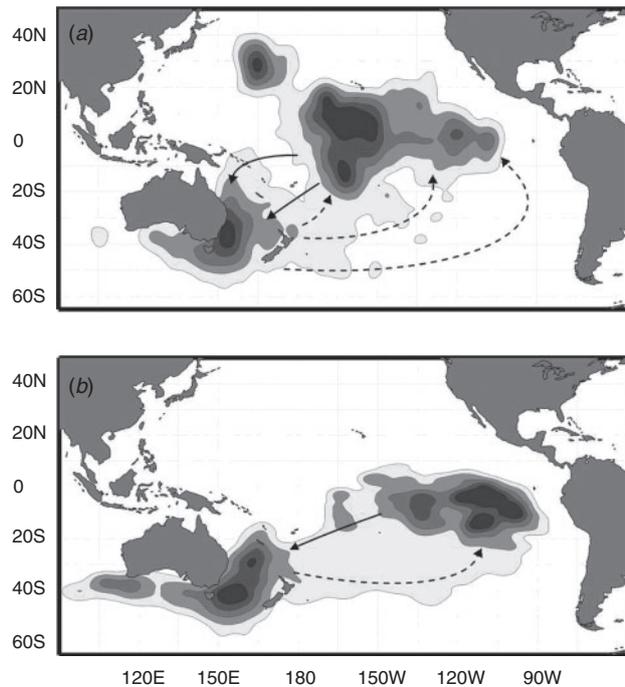
Fig. 3. Kernel density distributions for (*a*) *P. l. leucoptera* tracked with geolocators March 2010 – February 2011; and (*b*) *P. l. caledonica* tracked January 2010 – January 2011. Shaded polygons represent the 20, 40, 60, 80 and 95% density contours. The approximate post-breeding (dashed lines) and pre-breeding migration (solid lines) paths are shown. Breeding and non-breeding ranges were defined as those areas enclosed by the 80% contour lines.

level of intraspecific competition for resources (Pitman and Jehl 1998; Croxall *et al.* 2005; Phillips *et al.* 2005).

As in other small *Pterodroma* species (e.g. Rayner *et al.* 2012), both subspecies of Gould's Petrel returned to waters around the breeding colony ~1 month before laying, and visited the burrow within a few days. During the breeding season (including the pre-laying, incubation and chick-rearing periods) the core foraging areas of *leucoptera* were close to Australia, whereas those of *caledonica* were midway between Australia and New Zealand. The more-easterly distribution of *caledonica* is consistent with observations; almost all (94%, *n* = 17) beachcast specimens in New Zealand as well as the only bird collected in the eastern Tasman Sea have been identified as this subspecies. Given that both taxa probably occupy the same pelagic foraging niche, this difference in distribution may be linked to the central-place constraints associated with breeding (Orians and Pearson 1979). Like all breeding seabirds, Gould's Petrels must return to their nest at regular intervals for incubation and chick-provisioning and are thus restricted to foraging within a finite distance of the breeding colony.

After breeding, both subspecies migrated to the tropical Pacific Ocean. The distribution of at-sea observations of Gould's Petrel within the ETP appears to be generally coincident with the eastward-flowing North Equatorial Countercurrent, though clearly many individuals were also associated with the westward-flowing South Equatorial Current (Fiedler and Talley 2006). There appears to be an absence of birds in the general region of the Equatorial Front, supporting distributional patterns for piscivorous seabirds that have been proposed for this area in general (Ballance *et al.* 2006). Data obtained by geolocators provided insight into the at-sea sightings by revealing subspecies-specific

Table 1. Timing of stages of migration for the two subspecies of Gould's Petrel as revealed by geolocators
All dates are 2010. Means presented ± standard deviation in days

		P. l. leucoptera	*P. l. caledonica*	*t*	*P*
Post-breeding migration					
Departure	Mean date	4 Apr ± 5.7 days	25 Mar ± 29.7 days	0.88	0.413
	Earliest – latest dates	26 Mar–20 Apr	18 Feb–24 Apr		
	Range (days)	25	65		
	n	22	7		
Arrival	Mean date	24 Apr ± 9.8 days	18 May ± 13.0 days	4.57	0.002
	Earliest – latest dates	7 Apr–12 May	4 May–13 Jun		
	Range (days)	35	40		
	n	22	7		
Pre-breeding migration					
Departure	Mean date	14 Sep ± 18.7 days	4 Oct ± 23.5 days	1.85	0.091
	Earliest – latest dates	15 Aug–16 Oct	31st Aug–28 Oct		
	Range (days)	62	58		
	n	11	7		
Arrival	Mean date	12 Oct ± 5.5 days	4 Nov ± 7.1 days	7.50	<0.001
	Earliest – latest dates	5 Oct–26 Oct	25 Oct–16 Nov		
	Range (days)	21	22		
	n	13	7		
First visit to burrow	Mean date	18 Oct ± 5.6 days	6 Nov ± 7.7 days	5.56	<0.001
	Earliest – latest dates	11 Oct–26 Oct	25 Oct–18 Nov		
	Range (days)	15	24		
	n	8	7		

Table 2.   Duration of migration and of time spent in the non-breeding range for the two subspecies of Gould's Petrel as revealed by geolocators

Means presented ± standard deviation, in days

		P. l. leucoptera	*P. l. caledonica*	*t*	*P*
Post-breeding migration	Mean	22.6 ± 8.1	54.6 ± 24.5	3.36	0.012
	Range	12–40	24–88		
	n	14	7		
Non-breeding range	Mean	141.3 ± 17.6	135.9 ± 31.1	0.42	0.686
	Range	113–161	78–174		
	n	9	7		
Pre-breeding migration	Mean	27.0 ± 16.3	30.7 ± 19.3	0.40	0.697
	Range	10–55	16–63		
	n	10			
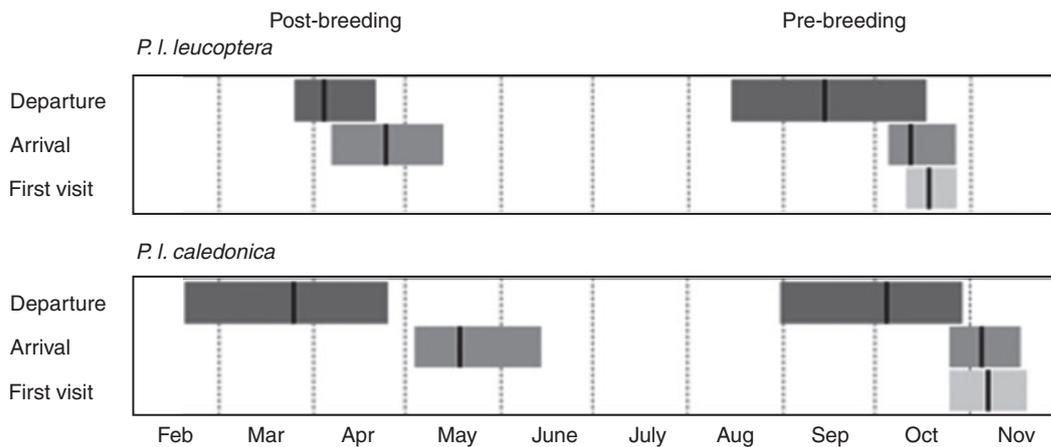
Fig. 4.   Migration schedule of the two subspecies of Gould's Petrel as revealed by geolocation data. Post-breeding migration begins on departure from the breeding range and concludes on arrival at the non-breeding range. Pre-breeding migration is the return journey. The date of the first visit to the nesting burrow is also shown. Vertical lines indicate means; shaded areas show the range.

associations with different currents. The foraging range of *caledonica* was concentrated in equatorial waters of the eastern Pacific (90–140°W), predominately at latitudes south of the Equator, in waters influenced by the westward flowing South Equatorial Current. Ribic and Ainley (1997) also documented an association between Gould's Petrel and the South Equatorial Current, particularly during El Niño–Southern Oscillation events. In contrast, the foraging range of *leucoptera* was concentrated in the central Pacific Ocean (140–170°W), several thousand kilometres west of that of *caledonica*, and north of the Equator in waters primarily influenced by the North Equatorial Current. Thus, the association of this species with both currents evident in the sightings data may be explained by subspecies-specific associations that represent distinct preferences for different currents, apparent in the geolocator data.

The migratory schedules of the two subspecies were asynchronous: *leucoptera* arrived at the breeding and non-breeding areas ~3 weeks before *caledonica*. Consistent with their migration timetables, breeding of the two subspecies was also asynchronous (Fig. 4): *caledonica* first visited the burrow

~3 weeks later than *leucoptera*. The high variation among *caledonica* in the time of their departure from the breeding grounds was indicative of a high incidence of nesting failure, with many adults leaving long before chicks normally fledge. Deploying geolocators on *caledonica* earlier in the breeding cycle (when incubating eggs or brooding young chicks) compared to *leucoptera* (when feeding well-grown chicks) may have contributed to us recording a greater failure rate for *caledonica*, although higher rates of predation in New Caledonia (see below) are also likely to have played a role.

When migrating across the South Pacific, both subspecies travelled ~20 000 km or more in a counter-clockwise direction, moving eastward at high southern latitudes (~45–55°S) and returning at lower equatorial latitudes. These tracks overlap with part of the migration routes of several other seabirds that migrate across the South Pacific, including the Sooty Shearwater (*Puffinus griseus*; Shaffer *et al*. 2006), Cook's Petrel (*Pterodroma cookii*; Rayner *et al*. 2011) and Westland Petrel (*Procellaria westlandica*; Landers *et al*. 2011). These species presumably take advantage of the prevailing winds to conserve energy, similar to

trans-equatorial migrants in the Atlantic Ocean (Felicísimo *et al.* 2008; Egevang *et al.* 2010).

Combining tracking and observational data

Until this study, our understanding of the pelagic distribution of Gould's Petrel was based on the interpretation of observations at sea and beachcast specimens recorded during the past century. These data were collected using a range of survey methodologies and exhibited a high level of spatial and temporal variation in observer effort, which rendered them unsuitable for examining past changes in the at-sea distribution of Gould's Petrel. Identifying such changes requires longitudinal tracking studies or systematic surveys spanning the entire distribution. Nonetheless, observational records elucidated the main features of the at-sea distribution of Gould's Petrel (albeit both subspecies combined) revealed by tracking. There are, however, some substantial differences in the findings obtained using the two techniques.

Shipboard observations during breeding (*leucoptera*: October–March; *caledonica*: November–April) showed a concentration of foraging in the Tasman Sea, with some sightings in the waters south of the Australian continent as far south as the Antarctic Shelf (mainly November–December) and beyond the western extremity of the continent. Tracking over the same period revealed a similar pattern of movements, except that birds with geolocators did not travel to Antarctic waters. Tracking did, however, identify that foraging to the west of Australia involved breeding adults before egg-laying and, *contra* Surman *et al.* (1997), these birds are more likely to be *caledonica* than *leucoptera*. The lack of tracking records in Antarctic waters is at odds with shipboard observations. Possible misidentification of sightings in the Southern Ocean is unlikely as Gould's Petrel is readily distinguishable from other small- or medium-sized gadfly petrels found there by the diagnostic blackish-brown hood (head to upper mantle and breast sides) contrasting with the grey lower mantle and back and white underbody (Shirihai 2007). Furthermore, there are many records spanning many years ($n = 18$, 1982–2001), so misidentification would have had to involve numerous reliable observers, which seems unlikely. We suspect that birds at polar latitudes during the breeding season are either non-breeders (immature birds or mature birds taking a sabbatical from breeding) or breeding birds that failed early, which are foraging in highly productive waters unencumbered by the need to return regularly to a breeding site. The deployment of geolocators only on breeding birds would then explain why no tracked bird was recorded foraging this far south at this time of year. Alternatively, the difference could be a response to inter-annual variation in prey distribution and abundance.

Sightings of birds in the ETP between late July and late November, along with identification of some individuals to subspecies level, correctly suggest that *caledonica* migrate across the Pacific after breeding. However, whether *leucoptera* also migrate to the ETP is not clear from the at-sea observations, as no specimens confirmed as this subspecies have been recorded far from the breeding grounds in eastern Australia. Two imprecise records involving nine individuals (see Results) are the only observational evidence to suggest that *leucoptera* ventures into the tropical Pacific. Thus, observational data failed to differentiate the migration route and foraging grounds of *leucoptera*. The two

subspecies are indistinguishable at sea and their distributions overlap, hindering our understanding of their pelagic distributions based on sightings alone.

The distribution of Gould's Petrel in the ETP based on sightings data does not correspond well with the tracking data. This is because the geographical extent of the shipboard surveys did not extend any further south or west than the cluster of sightings shown in Fig. 2 and most sightings were at the southern limits of the survey area. Despite such limitations, at-sea sightings can provide information about foraging behaviour that is not attainable with geolocators. For example, observations of group-size at sea indicate that Gould's Petrels are solitary foragers, during both breeding and non-breeding periods. There is no evidence that this species congregates in groups to forage on locally abundant prey, suggesting that their prey is diffusely distributed across broad expanses of ocean. Other *Pterodroma* species (e.g. Barau's Petrel (*Pterodroma baraui*)) and indeed other tropical seabirds (e.g. Wedge-tailed Shearwater (*Puffinus pacificus*)) similarly seem to have large non-breeding ranges and presumably also target diffusely distributed prey during the non-breeding season (Catry *et al.* 2009; Pinet *et al.* 2011).

All tracked individuals migrated and, apart from the early departure of presumed failed breeders, the timing was largely synchronous within each subspecies. Failed breeders, as evidenced by the tracks of a few *caledonica*, do undergo post-breeding migration, but their movements are less direct than their successful counterparts. Consequently, although they leave the breeding range earlier than successful breeders, they arrive at the non-breeding range at approximately the same time. Sightings of individuals in the Tasman Sea in all months except June suggest migration timing may be staggered in birds of differing status. Birds that migrate late or not at all, we suggest, are likely to be non-breeders that are not tied to the colony, and so do not need to follow rigid migratory schedules and patterns. This may explain much of the variation associated with observational data, because non-breeders can account for a substantial proportion of the Gould's Petrel population (Priddel *et al.* 1995). It is not clear to what extent Gould's Petrels use the Tasman Sea and Southern Ocean when not breeding because survey effort is considerably lower in these waters during the austral winter (e.g. only 8% of 257 Australian Antarctic Division voyages 1977–2005 were undertaken between May and August).

Unlike satellite-linked devices, geolocators need to be retrieved before data can be accessed, so they are typically attached only to breeding birds that are likely to be recaptured owing to their high fidelity to nest-sites. By targeting only established breeders, the use of geolocators failed to identify that some Gould's Petrels forage in Antarctic waters or do not follow the standard migration timetable. Such discrepancies are presumably attributable to non-breeders. The survival rate of immature individuals is a key component of the demography of long-lived species like seabirds, and an important aspect of their life history that should not be overlooked. Consequently, studies of the pelagic distribution of seabirds should, where possible, involve all stages of the life cycle.

By combining tracking data acquired over a single year with historical observations collected over a century, this study revealed the at-sea distribution and patterns of migration of Gould's Petrel in unprecedented detail. Sightings identified only

the general migration pattern and foraging areas of the species, whereas data from geolocators provided substantially more information by clarifying migration routes and timing, delineating core foraging areas, and revealing marked spatial and temporal segregation between the two subspecies. Geolocator deployments, however, might not reveal the full spatial or temporal variance associated with the distribution of a species at sea unless immatures and deferring breeders (and perhaps failed breeders) are also sampled. However, deploying geolocators on birds in these status groups is likely to be problematic owing to the difficulties associated with retrieving devices from individuals that do not have to return to a particular nesting site and, particularly in the case of fledglings, also tend to show lower survival. Data on the pelagic distribution of immature birds and birds deferring breeding were generally only available through shipboard observations, and although several recent tracking studies have targeted these life-history stages, they are mainly limited to large, surface-nesting species (Phillips *et al.* 2005; Alderman *et al.* 2010; Votier *et al.* 2011; Péron and Grémillet 2013; Riotte-Lambert and Weimerskirch 2013; Gutowsky *et al.* 2014). We conclude, therefore, that integrating data from electronic tracking with shipboard observations substantially improves our knowledge of the pelagic distribution of seabird populations at all life-history stages, particularly in those species that lack distinct juvenile plumage.

Acknowledgements

References

Alderman, R., Gales, R., Hobday, A., and Candy, S. (2010). Post-fledging survival and dispersal of Shy Albatross from three breeding colonies in Tasmania. *Marine Ecology Progress Series* **405**, 271–285. doi:10.3354/meps08590

Ballance, L. T. (2006). Seabird survey instruction manual: Star 2006 *Stenella* abundance research – eastern tropical Pacific – July 2006. Southwest Fisheries Science Center, National Oceanic and Atmospheric Administration, National Maritime Fisheries Service, La Jolla, CA.

Ballance, L. T., Pitman, R. L., Spear, L. B., and Fiedler, P. C. (2002). Investigations into temporal patterns in distribution, abundance and habitat relationships within seabird communities of the eastern tropical Pacific. Administrative Report LJ-02–17. Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, La Jolla, CA.

Ballance, L. T., Pitman, R. L., and Fiedler, P. C. (2006). Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Progress in Oceanography* **69**, 360–390. doi:10.1016/j.pocean.2006.03.013

BirdLife International. (2012). *Pterodroma leucoptera*. The IUCN Red List of Threatened Species. Version 2014.2. Available at www.iucnredlist.org [Verified 22/06/2012].

Bretagnolle, V., and Shirihai, H. (2010). A new taxon of Collared Petrel *Pterodroma brevipes* from the Banks Islands, Vanuatu. *Bulletin of the British Ornithologists' Club* **130**, 286–300.

Broome, K. (2009). Beyond Kapiti – a decade of invasive rodent eradications from New Zealand islands. *Biodiversity* **10**, 14–24. doi:10.1080/14888386.2009.9712840

Camphuysen, K., Shamoun-Baranes, J., Bouten, W., and Garthe, S. (2012). Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biological Conservation* **156**, 22–29. doi:10.1016/j.biocon.2011.12.024

Carey, M. J. (2011). Leg-mounted data-loggers do not affect the reproductive performance of Short-tailed Shearwaters (*Puffinus tenuirostris*). *Wildlife Research* **38**, 740–746. doi:10.1071/WR11024

Carlile, N., Priddel, D., and Callaghan, S. (2012). Seabird islands No. 18/1: Broughton Island, New South Wales. *Corella* **36**, 97–100.

Catry, T., Ramos, J. A., Le Corre, M., and Phillips, R. A. (2009). Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the Wedge-tailed Shearwater in the western Indian Ocean. *Marine Ecology Progress Series* **391**, 231–242. doi:10.3354/meps07717

Croxall, J. P., Silk, J. R., Phillips, R. A., Afanasyev, V., and Briggs, D. R. (2005). Global circumnavigations: tracking year-round ranges of non-breeding albatrosses. *Science* **307**, 249–250. doi:10.1126/science.1106042

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., and Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International* **22**, 1–34. doi:10.1017/S0959270912000020

de Naurois, R. (1978). Procellariidae reproductions en Nouvelle-Caledonie pendant l'ete austral. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. Série D, Sciences Naturelles* **287**, 269–271.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W., and Silk, J. R. D. (2010). Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 2078–2081. doi:10.1073/pnas.0909493107

Felicísimo, Á. M., Muñoz, J., and González-Solis, J. (2008). Ocean surface winds drive dynamics of transoceanic aerial movements. *PLoS ONE* **3**, e2928. doi:10.1371/journal.pone.0002928

Fiedler, P. C., and Talley, L. D. (2006). Hydrography of the eastern tropical Pacific: a review. *Progress in Oceanography* **69**, 143–180. doi:10.1016/j.pocean.2006.03.008

Fox, J. W. (2009). 'Geolocator Manual v7 (09/09).' (British Antarctic Survey, Natural Environment Research Council: Cambridge, UK.)

Fullagar, P. J. (1976). Seabird islands No. 35: Cabbage Tree Island, New South Wales. *Australian Bird Bander* **14**, 94–97.

Gangloff, B. (2010). Systematics and phylogeography in gadfly petrels (Aves : Procellariiformes) and implications for conservation. Ph.D. Thesis, University of Poitiers, Poitiers, France.

Gibson, J. D., and Sefton, A. R. (1957). The Gould Petrel – Australian records. *Emu* **57**, 49–52. doi:10.1071/MU957049

Guilford, T., Meade, J., Willis, J., Phillips, R. A., Boyle, D., Roberts, S., Collett, M., Freeman, R., and Perrins, C. M. (2009). Migration and stopover in a small pelagic seabird, the Manx Shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society of London – B. Biological Sciences* **276**, 1215–1223. doi:10.1098/rspb.2008.1577

Gutowsky, S. E., Tremblay, Y., Kappes, M. A., Flint, E. N., Klavitter, J., Laniawe, L., Costa, D. P., Naughton, M. B., Romano, M. D., and Shaffer, S. A. (2014). Divergent post-breeding distribution and habitat associations of fledgling and adult Black-footed Albatrosses *Phoebastria nigripes* in the North Pacific. *Ibis* **156**, 60–72. doi:10.1111/ibi.12119

Howald, G., Donlan, C. J., Galvan, J. P., Russell, J. C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A., and Tershy, B. (2007). Invasive rodent eradication on islands. *Conservation Biology* **21**, 1258–1268. doi:10.1111/j.1523-1739.2007.00755.x

Imber, M. J., and Jenkins, J. A. F. (1981). The New Caledonian Petrel. *Notornis* **28**, 149–160.

Kim, Y., Priddel, D., Carlile, N., Merrick, J., and Harcourt, R. (2014). Do tracking tags impede breeding performance in the threatened Gould's Petrel *Pterodroma leucoptera? Marine Ornithology* **42**, 63–68.

Landers, T. J., Rayner, M. J., Phillips, R. A., and Hauber, M. E. (2011). Dynamics of seasonal movements by a trans-pacific migrant, the Westland Petrel. *Condor* **113**, 71–79. doi:10.1525/cond.2011.100064

Le Corre, M., Jaeger, A., Pinet, P., Kappes, M. A., Weimerskirch, H., Catry, T., Ramos, J. A., Russell, J. C., Shah, N., and Jaquemet, S. (2012). Tracking seabirds to identify potential Marine Protected Areas in the tropical western Indian Ocean. *Biological Conservation* **156**, 83–93. doi:10.1016/j.biocon.2011.11.015

Ludynia, K., Kemper, J., and Roux, J.-P. (2012). The Namibian Islands' Marine Protected Area: using seabird tracking data to define boundaries and assess their adequacy. *Biological Conservation* **156**, 136–145. doi:10.1016/j.biocon.2011.11.014

Montevecchi, W. A., Hedd, A., McFarlane Tranquilla, L., Fifield, D. A., Burke, C. M., Regular, P. M., Davoren, G. K., Garthe, S., Robertson, G. J., and Phillips, R. A. (2012). Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. *Biological Conservation* **156**, 62–71. doi:10.1016/j.biocon.2011.12.001

Onley, D. and Schofield, P. (2007). 'Albatrosses, Petrels and Shearwaters of the World.' (Princeton University Press: Princeton, NJ.

Orians, G. H., and Pearson, N. E. (1979). On the theory of central place foraging. In 'Analysis of Ecological Systems'. (Eds D. J. Horn, R. D. Mitchell and G. R. Stairs.) pp. 154–177. (Ohio State University Press: Columbus, OH.)

Péron, C., and Grémillet, D. (2013). Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird. *PLoS ONE* **8**, e72713. doi:10.1371/journal.pone.0072713

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V., and Briggs, D. R. (2004). Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* **266**, 265–272. doi:10.3354/meps266265

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V., and Bennett, V. J. (2005). Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology* **86**, 2386–2396. doi:10.1890/04-1885

Pinet, P., Jaquemet, S., Pinaud, D., Weimerskirch, H., Phillips, R. A., and Le Corre, M. (2011). Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's Petrel *Pterodroma baraui*. *Marine Ecology Progress Series* **423**, 291–302. doi:10.3354/meps08971

Pitman, R. L., and Jehl, J. R. J. (1998). Geographic variation and reassessment of species limits in the 'masked' boobies of the eastern Pacific Ocean. *Wilson Bulletin* **110**, 155–170.

Priddel, D., and Carlile, N. (2004a). Seabird islands No. 22/1: Boondelbah Island, New South Wales. *Corella* **28**, 104–106.

Priddel, D., and Carlile, N. (2004b). Seabird islands No. 35/1: Cabbage Tree Island, New South Wales. *Corella* **28**, 107–109.

Priddel, D., and Carlile, N. (2009). Key elements in achieving a successful recovery programme: a discussion illustrated by the Gould's Petrel case study. *Ecological Management & Restoration* **10**, S97–S102. doi:10.1111/j.1442-8903.2009.00460.x

Priddel, D., Carlile, N., Davey, C., and Fullagar, P. J. (1995). The status of Gould's Petrel, *Pterodroma leucoptera leucoptera*, on Cabbage Tree Island, New South Wales. *Wildlife Research* **22**, 601–610. doi:10.1071/WR9950601

Quillfeldt, P., McGill, R. R., Furness, R., Möstl, E., Ludynia, K., and Masello, J. (2012). Impact of miniature geolocation loggers on a small petrel, the Thin-billed Prion *Pachyptila belcheri*. *Marine Biology* **159**, 1809–1816. doi:10.1007/s00227-012-1971-0

Rayner, M. J. (2007). Effects of dummy global location sensors on foraging behaviour of Cook's Petrel (*Pterodroma cookii*). *Wilson Journal of Ornithology* **119**, 107–109. doi:10.1676/06-057.1

Rayner, M. J., Hauber, M. E., Clout, M. N., Seldon, D. S., Van Dijken, S., Bury, S., and Phillips, R. A. (2008). Foraging ecology of the Cook's Petrel *Pterodroma cookii* during the austral breeding season: a comparison of its two populations. *Marine Ecology Progress Series* **370**, 271–284. doi:10.3354/meps07660

Rayner, M. J., Hauber, M. E., Steeves, T. E., Lawrence, H. A., Thompson, D. R., Sagar, P. M., Bury, S. J., Landers, T. J., Phillips, R. A., Ranjard, L., and Shaffer, S. A. (2011). Contemporary and historical separation of transequatorial migration between two genetically-distinct seabird populations. *Nature Communications* **2**, 332. doi:10.1038/ncomms1330

Rayner, M. J., Taylor, G. A., Gummer, H. D., Phillips, R. A., Sagar, P. M., Shaffer, S. A., and Thompson, D. R. (2012). The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*). *Emu* **112**, 107–116. doi:10.1071/MU11066

Reid, T. A., Hindell, M. A., Eades, D. W., and Newman, M. (2002). 'Seabird Atlas of South-eastern Australian Waters.' Birds Australia Monograph 4. (Birds Australia: Melbourne.)

Ribic, C. A., and Ainley, D. G. (1997). The relationships of seabird assemblages to physical habitat features in Pacific equatorial waters during spring 1984–1991. *ICES Journal of Marine Science* **54**, 593–599. doi:10.1006/jmsc.1997.0244

Riotte-Lambert, L., and Weimerskirch, H. (2013). Do naive juvenile seabirds forage differently from adults? *Proceedings of the Royal Society of London – B. Biological Sciences* **280**, 20131434. doi:10.1098/rspb.2013.1434

Roberson, D., and Bailey, S. F. (1991). Cookilaria Petrels in the eastern Pacific Ocean: identification and distribution. *American Birds* **45**, 1067–1081.

Ronconi, R. A., Lascelles, B. G., Langham, G. M., Reid, J. B., and Oro, D. (2012). The role of seabirds in Marine Protected Area identification, delineation, and monitoring: introduction and synthesis. *Biological Conservation* **156**, 1–4. doi:10.1016/j.biocon.2012.02.016

Shaffer, S. A., Tremblay, Y., Awkerman, J. A., Henry, R. W., Teo, S. L. H., Anderson, D. J., Croll, D. A., Block, B. A., and Costa, D. P. (2005). Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* **147**, 833–843. doi:10.1007/s00227-005-1631-8

Shaffer, S. A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D. R., Sagar, P. M., Moller, H., Taylor, G. A., Foley, D. G., Block, B. A., and Costa, D. P. (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 12799–12802. doi:10.1073/pnas.0603715103

Shaffer, S. A., Weimerskirch, H., Scott, D., Pinaud, D., Thompson, D. R., Sagar, P. M., Moller, H., Taylor, G. A., Foley, D. G., Tremblay, Y., and Costa, D. P. (2009). Spatiotemporal habitat use by breeding Sooty Shearwaters *Puffinus griseus*. *Marine Ecology Progress Series* **391**, 209–220. doi:10.3354/meps07932

Shirihai, H. (2007). 'A Complete Guide to Antarctic Wildlife: The Birds and Marine Mammals of the Antarctic Continent and the Southern Ocean.' 2nd edn. (A. &C. Black: London.)

Spear, L. B., Ainley, D. G., Nur, N., and Howell, S. N. G. (1995). Population size and factors affecting at-sea distribution of four endangered procellariids in the tropical Pacific. *Condor* **97**, 613–638. doi:10.2307/1369172

Surman, C. A., Cheshire, N. G., and Wooller, R. D. (1997). Gould's Petrel *Pterodroma leucoptera* off south-western Australia. *Marine Ornithology* **25**, 70–71.

Tremblay, Y., Bertrand, S., Henry, R. W., Kappes, M. A., Costa, D. P., and Shaffer, S. A. (2009). Analytical approaches to investigating seabird-environment interactions: a review. *Marine Ecology Progress Series* **391**, 153–163. doi:10.3354/meps08146

Votier, S. C., Grecian, W. J., Patrick, S., and Newton, J. (2011). Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology* **158**, 355–362. doi:10.1007/s00227-010-1563-9

Weimerskirch, H., and Wilson, R. P. (2000). Oceanic respite for Wandering Albatrosses. *Nature* **406**, 955–956. doi:10.1038/35023068

Welch, B. L. (1947). The generalization of 'Student's' problem when several different population variances are involved. *Biometrika* **34**, 28–35.