# Pelagic distribution of Gould's Petrel *Pterodroma leucoptera*: linking shipboard and beached bird sightings with remote tracking data

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Running title: Pelagic distribution of Gould's Petrel

## Abstract

This study describes and compares the pelagic distribution and migration 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, bycatch records and beach-washed 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 prior to egg laying. After breeding, both subspecies migrated to distinct non-breeding ranges within the eastern tropical Pacific. Observational data identified the general migration pattern and foraging areas of the species, while data from geolocators provided details of migration routes and timing, 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-breeders (pre-breeders and adults that are deferring) may not follow the same migration 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.

## 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 enhanced through the eradication of alien predators, particularly rodents (Howald *et al.* 2007; Broome 2009). The situation at sea is vastly different. Currently, less than 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

54 seabird movements and behaviour is increasingly being used to identify ecologically
55 important marine areas (e.g., Camphuysen *et al.* 2012; Le Corre *et al.* 2012; Ludynia *et al.*
56 2012; Montevecchi *et al.* 2012). Yet, for most seabirds, their movements at sea are poorly
57 known. Large-scale banding programs are of limited utility in revealing patterns of seabird
58 pelagic movements, due to the difficulty of recapture on the open ocean. Until the last two
59 decades, shipboard surveys, bycatch records from fisheries operations, and recoveries of
60 beach-washed specimens were the only means of identifying the pelagic distribution and
61 movements of seabirds (Tremblay *et al.* 2009). However, such data are patchy, and collection
62 of shipboard data is often opportunistic or prohibitively expensive, especially if vessels need
63 to be chartered specifically for the purpose. Moreover, interpretation of sightings data can be
64 complicated by the misidentification of morphologically similar taxa.

65 In the late 1990s, the advent of geolocators (Global Location Sensor or GLS logger) small
66 enough to be carried year-round on a leg band by large birds, such as albatrosses,
67 revolutionised the study of seabird ecology by making it possible to track individuals
68 throughout their entire migration period (Weimerskirch and Wilson 2000; Croxall *et al.*
69 2005). These electronic devices record light intensity and time elapsed, and subsequent
70 processing allows the determination of the timing of sunrise and sunset, which can then be
71 used to calculate latitude and longitude (Phillips *et al.* 2004; Shaffer *et al.* 2005). With further
72 miniaturisation, the development of lightweight (< 1.5 g) geolocators has made it possible to
73 study the movements of all but the smallest seabirds without any apparent adverse effects
74 (Catry *et al.* 2009; Quillfeldt *et al.* 2012; Rayner *et al.* 2012). Although the use of such
75 electronic devices has increased rapidly, combining the resulting data with those obtained
76 using traditional observational methods (i.e., shipboard surveys, at-sea collections, band
77 recoveries from fisheries bycatch and beach-washed birds) has been identified as a high
78 priority, since these may provide complementary information on seabird movements, with
79 implications for conservation (Tremblay *et al.* 2009; Croxall *et al.* 2012). Such an integrated
80 approach also provides an opportunity to compare the quality and type of information
81 obtained from each method.

82 Gould's Petrel (*Pterodroma leucoptera*) is a small (~ 200–250 g) gadfly petrel that breeds on
83 several small islands off the coast of New South Wales, Australia (Priddel and Carlile 2004b;
84 Priddel and Carlile 2004a; Carlile *et al.* 2012), and on the main island of New Caledonia (de
85 Naurois 1978; Bretagnolle and Shirihai 2010). The species is classified globally as *Vulnerable*

(IUCN 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 population estimates of Gould's Petrel at sea in the eastern tropical Pacific (annual mean 810 000 individuals, $n = 6$; Ballance *et al*. 2002) indicate this subspecies must be substantially more numerous than *leucoptera*, though in decline due to predation by introduced Pigs (*Sus scrofa*) and Cats (*Felis catus*) (IUCN 2012). Conservation action to remove alien mammalian predators from the breeding grounds of *caledonica* has recently commenced.

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. Beach-washed 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 confirmed *caledonica* and *leucoptera* are genetically distinct at the subspecies level, although a low rate of gene flow probably occurs (Gangloff 2010).

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

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 (1970–1980) 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 Beck close to the Galapagos Islands in June 1906 as evidence of a post-breeding migration to the eastern tropical Pacific (ETP), and hypothesised a migration

route that, at least in part, followed the Subtropical Front at around 40°S. Analysis of records off south-eastern Australia showed a similar seasonal trend, with the greatest numbers of observations recorded 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 migration patterns of the two subspecies of Gould's Petrel, and to contrast the data obtained from tracking birds at sea with shipboard observations and beach-washed birds.

## Methods

### *Observational records*

Observations of Gould's Petrel away from its breeding sites were obtained from published and unpublished literature, museum collection databases, other publicly-available datasets and from individual observers. The following information was extracted from each record: date, latitude, longitude, type (shipboard sighting, at-sea capture, beach-washed remains or stranded 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 geographic coordinates were discarded.

Methods used to obtain at-sea sightings of Gould's Petrel varied among sources, and included both opportunistic and systematic procedures. Fifty-eight percent of all observational records were derived from surveys conducted by the National Oceanic and Atmospheric Administration (NOAA), USA, using standard strip transect survey procedures detailed in Ballance (2006). Other systematic surveys that contributed large datasets used similar techniques.

### *Geolocators*

Twenty-two BAS geolocators (MK14, British Antarctic Survey, UK) and 20 Lotek geolocators (NanoLAT2900, Lotek, 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 Lotek, 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 8 Lotek geolocators failed to record more than a few weeks of data.

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, Lotek, Canada) 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.* in press).

BAS geolocators measured ambient light level every 60 sec and then logged the maximum value for each 10 min interval. Light data were processed using TransEdit software (Jensen Software Systems) 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 sunrise and sunset times inferred from light curve thresholds. Latitude was calculated from day length. 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 c. 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, Canada).

177 The mean error using this approach (c. 200 km) is broadly similar to that of BAS geolocators
178 (Shaffer *et al.* 2005).

179 *Analysis of location data*

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

194 **Results**

195 *Observational data*

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

202 At-sea observations (shipboard sightings and collections) were concentrated in the Tasman
203 Sea and in the ETP between Hawaii and the Galapagos Islands (Figure 1). The remaining
204 records were off the eastern and southern coasts of Australia and off New Zealand, and in the
205 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 (Figure 1). During December–April (breeding season), records were largely confined to the Tasman Sea and Indian Ocean south of Australia (Figure 1A). During May–August (non-breeding season), most sightings were in tropical latitudes of the central and eastern Pacific Ocean, with a small number in the Tasman Sea (Figure 1B). 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 (Figure 1C). Sightings south of latitude 55°S ($n$ = 19) were recorded only during September–March, but typically few ships (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 (Figure 2).

INSERT FIGURE 1 HEREABOUTS

INSERT FIGURE 2 HEREABOUTS

Records of beach-washed 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 birds were collected from the west coast of the North Island in November–June. Overall, 41 beach-washed 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; Australian Antarctic Database), 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).

*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 (Figure 3A), 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 04 April ± 6 days and travelled eastward then north/northwest 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 9,355 ± 1584 km. Birds remained in their non-breeding ranges for 141.3 ± 17.6 days (Table 2), departing 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 colony on 12 October ± 6 days (Table 1).

INSERT FIGURE 3 HEREABOUTS

INSERT TABLE 1 HEREABOUTS

INSERT TABLE 2 HEREABOUTS

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 (Figure 3A) was in the Tasman Sea along the east 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 (Figure 3B), predominantly west and southwest of the Galapagos Islands (0°S–20°S, 90–140°W). Birds departed 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), departing 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 (Figure 3B).

*Breeding phenology*

The mean date of departure from the breeding range was 10 days earlier for *caledonica;* however, the range in dates of *caledonica* encompassed 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 25 days for *leucoptera*); differences between subspecies in the variance of other departure and arrival dates were 5 days or less (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 two months in the Tasman Sea and in waters to the south of Australia before arriving at the non-breeding ranges at about 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 ranges 24 days earlier than *caledonica* (Table 1). Both subspecies spent a similar amount of time in the non-breeding range (approximately 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 migration pattern 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 during non-breeding.

### *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; therefore it is 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 reducing the level of intra-specific 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 approximately one month before laying, and within a few days visited the burrow. 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) beach-washed 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

323 and chick provisioning, and are thus restricted to foraging within a certain distance from the
324 breeding colony.

325 After breeding, both subspecies migrated to the tropical Pacific. The distribution of at-sea
326 observations of Gould's Petrel within the ETP appears to be generally coincident with the
327 eastward-flowing North Equatorial Countercurrent, though clearly many individuals were also
328 associated with the westward-flowing South Equatorial Current (Fiedler and Talley 2006).
329 There appears to be an absence of birds in the general region of the Equatorial Front,
330 supporting distribution patterns for piscivorous seabirds that have been proposed for this area
331 in general (Ballance *et al.* 2006). Data obtained by geolocators provided insight into the at-sea
332 sightings by revealing subspecies-specific associations with different currents. The foraging
333 range of *caledonica* was concentrated in equatorial waters of the eastern Pacific (90–140°W),
334 predominately at latitudes south of the equator, in waters influenced by the westward flowing
335 South Equatorial Current. Ribic and Ainley (1997) also documented an association between
336 Gould's Petrel and the South Equatorial Current, particularly during El Niño–Southern
337 Oscillation events. In contrast, the foraging range of *leucoptera* was concentrated in the
338 central Pacific (140–170°W), several thousand kilometres west of that of *caledonica*, and
339 north of the equator in waters primarily influenced by the North Equatorial Current. Thus, the
340 association of this species with both currents evident in the sightings data may be explained
341 by subspecies-specific associations that represent distinct preferences for different currents,
342 apparent in the geolocator data.

343 Migration schedules of the two subspecies were asynchronous: *leucoptera* arrived at the
344 breeding and non-breeding areas approximately three weeks before *caledonica*. Consistent
345 with their migration timetables, breeding of the two subspecies was also asynchronous
346 (Figure 4): *caledonica* first visited the burrow about three weeks later than *leucoptera*. The
347 high variation among *caledonica* in the time of their departure from the breeding grounds was
348 indicative of a high incidence of nesting failure, with many adults leaving long before chicks
349 normally fledge. Deploying geolocators on *caledonica* earlier in the breeding cycle (when
350 incubating eggs or brooding young chicks) compared to *leucoptera* (when feeding well-grown
351 chicks) may have contributed to us recording a greater failure rate for *caledonica*, although
352 higher rates of predation in New Caledonia (see below) are also likely to have played a role.

353 INSERT FIGURE 4 HEREABOUTS

When migrating across the South Pacific, both subspecies travelled about 20,000 km or more in a counter-clockwise direction, moving eastward at high southern latitudes (approximately 45–55ºS) 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 beach-washed 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 prior to 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/back and white underside (Shirihai 2007). Furthermore, there are numerous records spanning many

years (*n* = 18, 1982–2001), so misidentification would have had to involve numerous 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. Alternatively, the difference could be a response to interannual variation in prey distribution and abundance.

Sightings of birds in the eastern tropical Pacific 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 eastern tropical Pacific 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 path 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 eastern tropical Pacific 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 Figure 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, while both breeding and non-breeding. There is no evidence that this species congregates in groups to forage on locally abundant prey, suggesting that their prey is diffuse 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 about 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 migration schedules and patterns. This may explain much of the variation associated with observational data since non-breeders can account for a substantial proportion of the Gould's Petrel population (Priddel *et al.* 1995), thereby explaining much of the variation associated with observational data. It is unclear to what extent Gould's Petrels utilise 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 to 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 because of their high nest-site fidelity. 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.

Through combining tracking data acquired over a single year with historical observations collected over a century, this study revealed the at-sea distribution and migration patterns of Gould's Petrel in unprecedented detail. Sightings identified only the general migration pattern and foraging areas of the species, while 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 problematic due to the difficulties associated with retrieving devices from individuals that are not obliged 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 and deferring birds were generally only available through shipboard observations, and although a number of 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.

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**Figure legends**

**Figure 1.** Locations of observations of Gould's Petrel (*n* = 2042) during (A) December–April, (B) May–August and (C) September– November.

**Figure 2.** Locations of shipboard sightings of Gould's Petrel in the eastern Pacific (*n* = 1180) during surveys undertaken by NOAA. Black lines indicate the track lines of survey vessels. Surveys were undertaken August-November in the eastern tropical Pacific (1988–1990, 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).

**Figure 3.** Kernel density distributions for (A) *P. l. leucoptera* and (B) *P. l. caledonica* tracked with geolocators from March 2010 – February 2011 and January 2010 – January 2011, respectively. 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.

**Figure 4.** Migration schedule of the two subspecies of Gould's Petrel, as revealed by geolocators. 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.

**Table 1. Timing of migration events for the two subspecies of Gould's Petrel, as revealed by geolocators.**

Dates presented as day/month; all dates from 2010. Means presented with ± standard deviation in days.

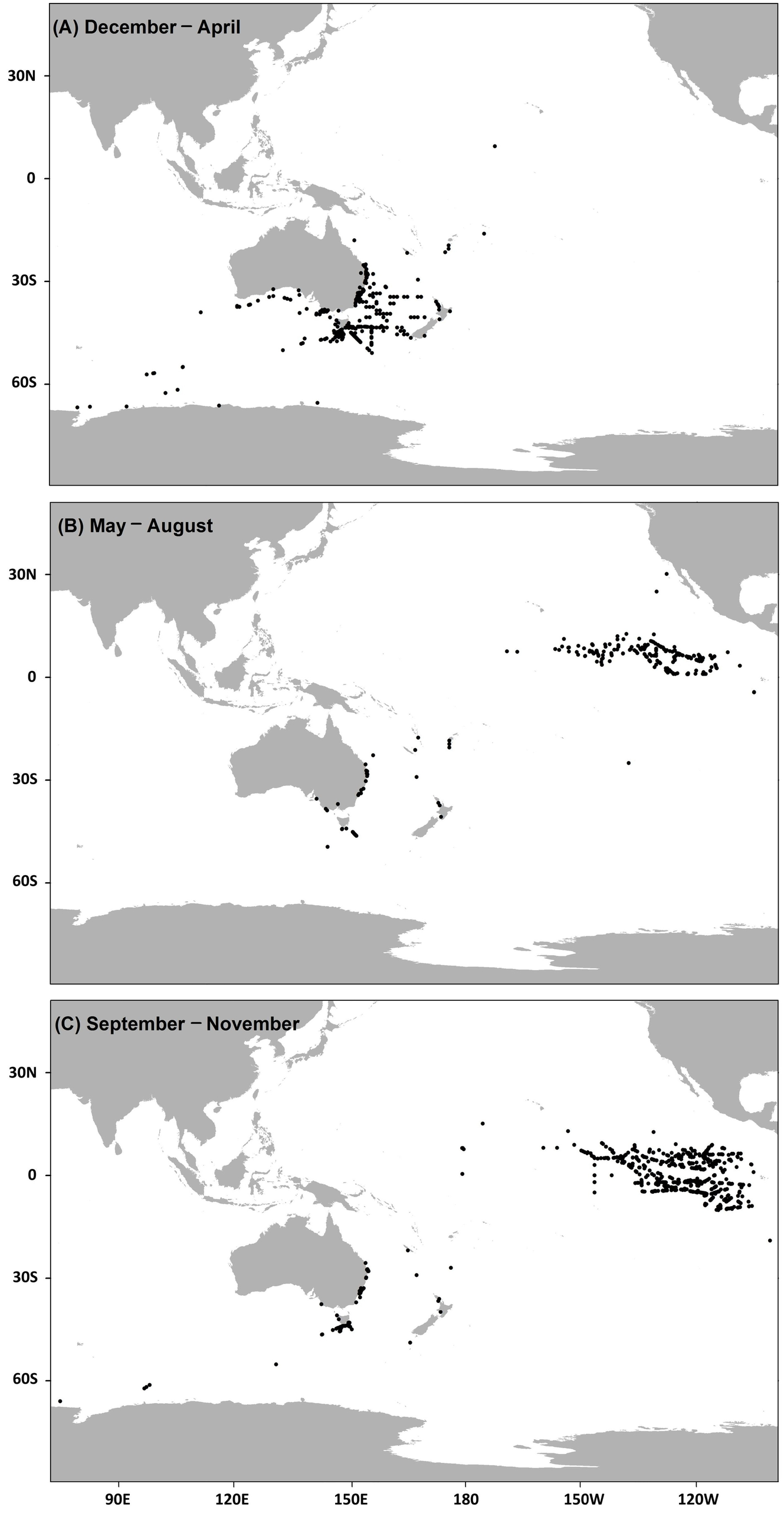
| | | *P. l. leucoptera* | *P. l. caledonica* | *t* | *P* |
|---|---|---|---|---|---|
| Post-breeding migration | | | | | |
| Departure | mean | 4th April ± 5.7 days | 25th March ± 29.7 days | 0.88 | 0.413 |
| | earliest – latest | 26th March – 20th April | 18th February – 24th April | | |
| | range (days) | 25 | 65 | | |
| | *n* | 22 | 7 | | |
| Arrival | mean | 24th April ± 9.8 days | 18th May ± 13.0 days | 4.57 | 0.002 |
| | earliest – latest | 7th April – 12th May | 4th May – 13th June | | |
| | range (days) | 35 | 40 | | |
| | *n* | 22 | 7 | | |
| Pre-breeding migration | | | | | |
| Departure | mean | 14th September ± 18.7 days | 4th October ± 23.5 days | 1.85 | 0.091 |
| | earliest – latest | 15th August – 16th October | 31st August – 28th October | | |
| | range (days) | 62 | 58 | | |
| | *n* | 11 | 7 | | |
| Arrival | mean | 12th October ± 5.5 days | 4th November ± 7.1 days | 7.50 | <0.001 |
| | earliest – latest | 5th October – 26th October | 25th October – 16th November | | |
| | range (days) | 21 | 22 | | |
| | *n* | 13 | 7 | | |

| | | | | | |
|---|---|---|---|---|---|
| First burrow visit | mean | 18th October ± 5.6 days | 6th November ± 7.7 days | 5.56 | <0.001 |
| | earliest – latest | 11th October – 26th October | 25th October – 18th November | | |
| | 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 with ± standard deviation in days.

| | | *P. l. leucoptera* | *P. l. caledonica* | *t* | *P* |
|---|---|---|---|---|---|
| Post-breeding migration | Mean (days) | 22.6 ± 8.1 | 54.6 ± 24.5 | 3.36 | 0.012 |
| | Range (days) | 12 – 40 | 24 – 88 | | |
| | *n* | 14 | 7 | | |
| Non-breeding range | Mean (days) | 141.3 ± 17.6 | 135.9 ± 31.1 | 0.42 | 0.686 |
| | Range (days) | 113 – 161 | 78 – 174 | | |
| | *n* | 9 | 7 | | |
| Pre-breeding migration | Mean (days) | 27.0 ± 16.3 | 30.7 ± 19.3 | 0.40 | 0.697 |
| | Range (days) | 10 – 55 | 16 – 63 | | |
| | *n* | 10 | | | |


(A) December – April
(B) May – August
(C) September – November
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180
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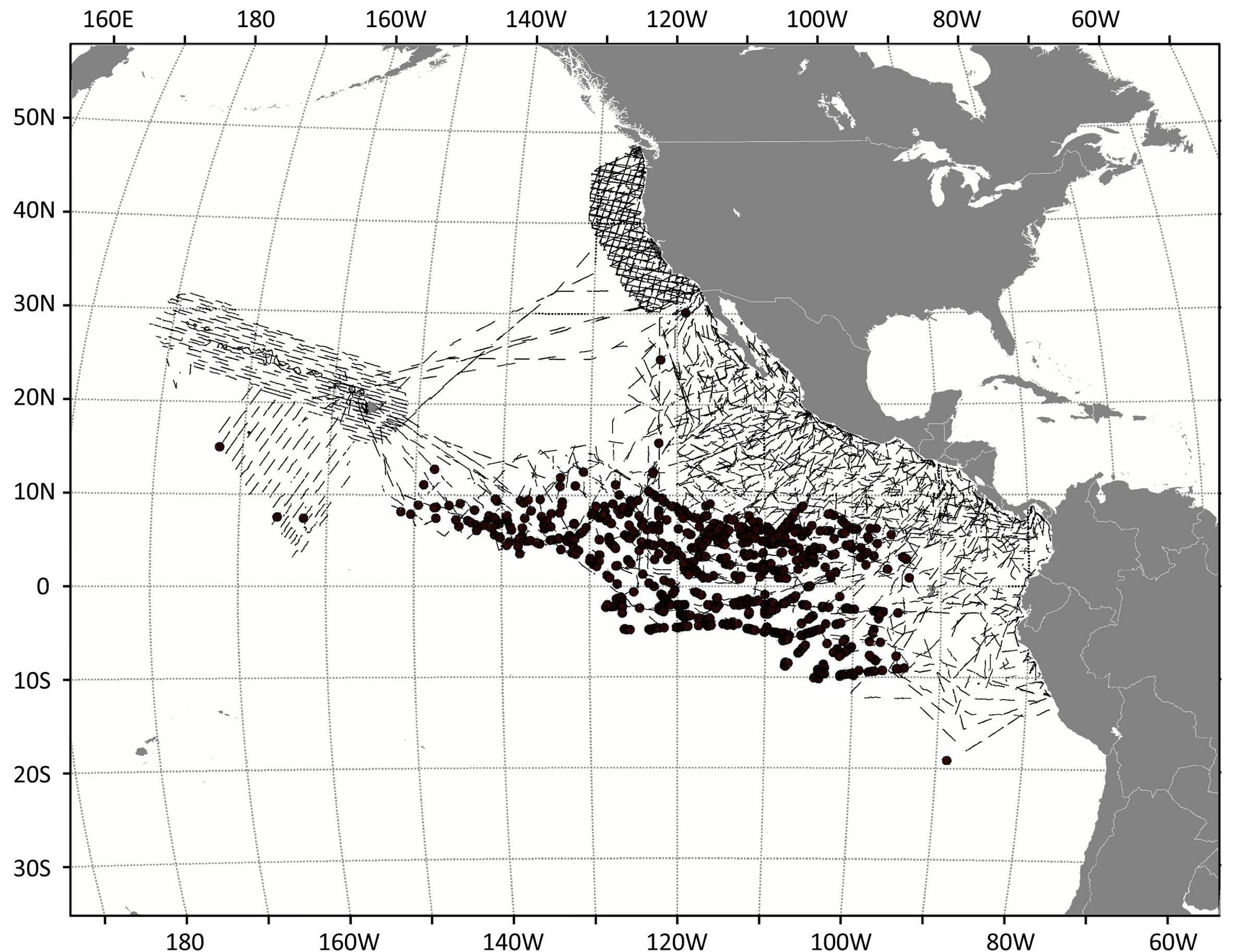
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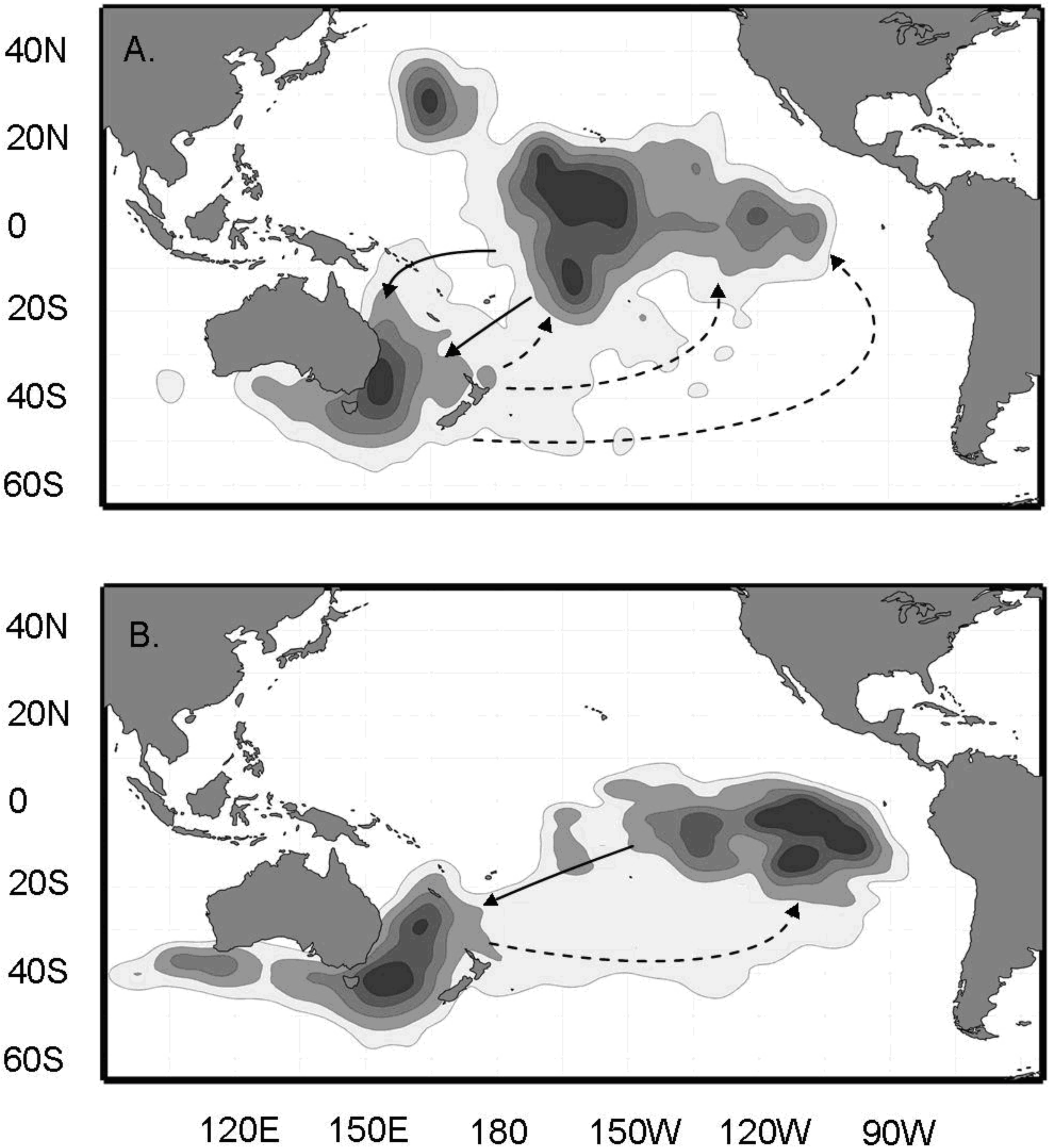
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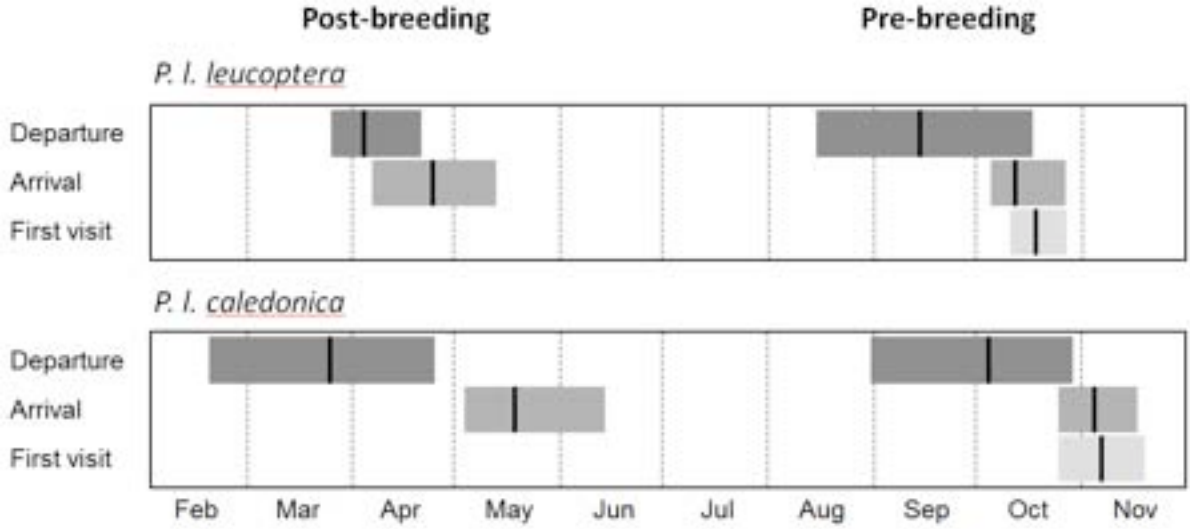
Post-breeding
Pre-breeding
P. l. leucoptera
Departure
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P. l. caledonica
Departure
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Feb
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