The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*)

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Abstract.　Petrels are highly mobile seabirds that face many threats and whose conservation is frequently hampered by a lack of understanding of their biology at sea. We used a combination of data from burrow monitoring and geolocation-immersion loggers to study the intra- and inter-seasonal distribution and behaviour of the endangered Chatham Petrel (*Pterodroma axillaris*), breeding on Rangatira Island, New Zealand. Breeding extended from November to June with a pre-laying exodus of 35 days; an incubation period of 46 days, with up to five incubation shifts; and a chick-rearing period of 87 days, including a desertion period of 10 days. When breeding, Chatham Petrels foraged between the Subtropical Convergence and Subantarctic Fronts, moving 2000–3000 km to the south-east of the Chatham Islands, during the pre-laying exodus and incubation period, but restricting foraging to the south of the Chatham Islands, around the Bollons Seamount, during chick-rearing. Between April and June birds migrated east and north to core non-breeding distributions ~1000 km from the coast of Peru and Chile. Birds spent a greater proportion of time resting and nocturnally active during the non-breeding period than when breeding, when birds where active during darkness and daylight. These data contribute to the conservation management of the Chatham Petrel and to conservation initiatives to identity marine protected areas for endangered seabirds on the high seas beyond national jurisdictions.

Introduction

Efforts to protect seabirds are often confounded by a lack of even the most basic knowledge of their breeding biology and distribution at sea. Gadfly petrels (*Pterodroma* spp.) are small to medium-sized (150–600 g) seabirds, comprising approximately one-quarter of all Procellariiformes (Brooke 2004). They are among the most oceanic of all seabirds, coming to land only to breed, usually at remote island locations. Introduced species and the loss or deterioration of breeding habitat are major conservation threats common to gadfly petrels, and as a result a large proportion of species (25 of 32) are classified by the International Union for the Conservation of Nature (IUCN) as threatened (vulnerable, endangered or critically endangered) or near-threatened (Birdlife International, see http://www.birdlife.org/action/science/species/seabirds/index.html, accessed 2 April 2012).

Active conservation programs have been set up to improve breeding habitat for a limited number of threatened gadfly petrels (Carlile *et al*. 2003, 2012; Madeiros *et al*. 2012). However, understanding spatial and temporal variation in the behaviour and

distribution of gadfly petrels is essential for developing effective management programs, which require the delineation of key marine habitats and the identification and mitigation of threats at sea. Fortunately, advances in the production of small, light-weight tracking devices have provided new opportunities for such investigations of small seabirds, including terns (Egevang *et al*. 2010) and gadfly petrels (Pinet *et al*. 2011; Rayner *et al*. 2011).

The Chatham Petrel (*Pterodroma axillaris*) is one of 11 small (200 g) gadfly petrels within the subgenus *Cookilaria* (Onley and Scofield 2007). The Chatham Petrel is listed as endangered by the IUCN, and was for some years restricted to a single breeding population of ~250 breeding pairs on Rangatira Island (44°00′S, 176°32′W), in the Chatham Islands, New Zealand (Taylor 2000; IUCN 2011). Although it formerly occurred on the main Chatham Islands, both the breeding range and abundance of the Chatham Petrel declined rapidly following the introduction of exotic predators, including rodents (Pacific Rat (*Rattus exulans*), Brown Rat (*R. norvegicus*) and Black Rat (*R. rattus*)), Cat (*Felis catus*) and Weka (*Gallirallis australis*), and removal of forest breeding

habitat (Sullivan and Wilson 2001*a*), until breeding became restricted to Rangatira Island, which is free of mammalian predators. Active monitoring of the Chatham Petrel on Rangatira Island began in the early 1990s, and revealed that competition with Broad-billed Prions (*Pachyptila vittata*) was a major cause of breeding failure (Sullivan and Wilson 2001*b*). Management subsequently focused on identifying breeding burrows of Chatham Petrels and installing artificial nest-boxes with neoprene burrow flaps to discourage occupation by Broad-billed Prions (Taylor 2000). This resulted in an improvement in breeding success from 30% in the 1990s to 70–80% in the last 10 years (Taylor 2000; G. Taylor pers. comm.). Translocations of 200 Chatham Petrel chicks over 4 years from 2002 to a predator-free enclosure on nearby Pitt Island has resulted in the establishment of a new colony (17 pairs), and another translocation program is underway to re-establish the species on the main Chatham Island within the fenced Sweetwater Covenant near the Tuku Nature Reserve (H. Gummer pers. comm.).

Despite successes in the management of the Chatham Petrel, there is a lack of understanding of changes in the spatial distribution and behaviour of these birds at sea, and of how these relate to the timing of key events in the annual breeding cycle. Such information is essential not only for understanding and mitigating potential threats to the species at sea, but also for improving protection from competition and other disturbance at colonies. The current study therefore had two complementary aims. The first was to provide a detailed account of the breeding schedule of Chatham Petrel by combining unpublished historical datasets on patterns of colony attendance with data derived from birds tracked with geolocation loggers. The second was to use these same geolocation data to provide the first insights into the distribution and behaviour of the species at sea.

Methods

Study site and monitoring

Chatham Petrels breed on Rangatira Island in the Chatham Islands, New Zealand, from November to May (Gardener 1999). All known Chatham Petrel breeding burrows have been converted to artificial study burrows, through the fitting of plastic nest-chambers at the nesting site and monitored to identify nesting pairs, determine breeding success, band chicks and prevent interference by Broad-billed Prions (Taylor 2000). As part of this study, during the 2000–01 breeding season, 141 breeding burrows were intensively monitored to quantify adult attendance and behaviour. Monitoring, by opening lids to artificial burrows, included: (1) daily checks of burrows from the first week of November to establish patterns of pre-laying attendance of known breeders; (2) daily checks of burrows for several weeks from 28 December to establish dates of laying, and duration of the incubation period to the day; and (3) daily checks of burrows from mid- to late February to establish the sex of the adult in attendance at hatching, the duration of the guard and chick-rearing periods, and dates of fledging.

Deployments of geolocators and data processing

Between 11 and 17 February 2009, 22 Chatham Petrels (9 males, 13 females) that were incubating in marked study burrows on Rangatira Island were equipped with combined geolocation-immersion loggers (hereafter called loggers; British Antarctic Survey (BAS) Mk14 model, Cambridge, UK). Loggers were deployed on birds of known breeding history and sex, the latter previously established using molecular (Fridolfsson and Ellegren 1999) and field-based methods (O'Dwyer *et al.* 2006). Loggers were attached using established protocols (Rayner *et al.* 2008), and weighed <1% of average body mass for the species. Their effect on Chatham Petrels was assessed through comparisons of breeding success (percentage of eggs laid that resulted in a fledged chick) in the 2008–09 season, and percentage of burrows containing eggs in the 2009–10 season, at burrows where adults were tracked with loggers ($n = 15$; both birds of a pair tracked in 6 of 15 burrows), and a random sample of 20 control burrows containing established breeding pairs.

Light data from the loggers were processed using the software Transedit (BAS) with sunrise and sunset transition times identified from light-curve thresholds. Latitude was calculated from length of day and night and longitude calculated from the time of local midday or midnight relative to Greenwich Mean Time. Locations (2 per day) were assumed to have a mean accuracy of 186 ± 114 km (s.d.) (Phillips *et al.* 2004). Given global daylength uniformity during the equinoxes, locations occurring within 3 weeks of the equinoxes were excluded. Moreover, points involving unlikely movements >1600 km day (Guilford *et al.* 2009) and those with logger interruptions owing to disruptions to light at and close to sunset and sunrise were removed.

Possible seasonal changes in foraging distribution were examined using kernel analysis (following Shaffer *et al.* 2009; Rayner *et al.* 2011). The non-breeding season was defined as the period between the dates of the last and first locations within a 1000-km buffer around Rangatira Island for an individual, and the breeding season as the inverse (Rayner *et al.* 2008). The migration period was defined as the dates between the first location outside the 1000-km buffer zone around the colony and the first within the core non-breeding region (based on the 80% kernel contour of each individual). Within the breeding season, breeding stages for each individual were defined, based on geolocation data and immersion (activity) or raw light data (dark periods during daytime indicate the bird was in the burrow), as follows: the pre-laying period was between first arrival in the 1000-km buffer zone and laying (females) or the start of the first incubation shift (males). Where females spent more than one day in the burrow after laying (range 1–3 days), the median date of the burrow visit was taken as the laying date; the incubation period was the time between laying and hatching, established via daily checks of the burrow during late incubation; and the chick-rearing period was the time between hatching and the departure of tracked birds on migration (last location within the 1000-km buffer). As loggers were attached during late incubation in 2009, results relate to the 2009 chick-rearing and non-breeding periods, the subsequent 2009 pre-laying period, and the 2010 incubation period. The maximum ranges of birds during pre-laying, incubation and chick-rearing were based on great circle distances between the colony and the furthest points reached by each individual.

Activity at sea

Loggers test for saltwater immersion every 3 s and log the number of positive tests within each 10-min period, with a value ranging

from 0 (dry) to 200 (immersed for entire period). Mean percentage of time spent on the water, and the number and duration of periods of extended flight, defined as two or more continuous 10-min blocks in each of which loggers recorded no more than 9-s immersion time, were calculated by month and season for daylight and darkness periods. Daylight and darkness were derived from the 10-min binned light values recorded by the logger, with values of ≥ 1 indicating the period from the start of civil twilight in the morning to the end of civil twilight in the evening (sun <6° below the horizon) (see Mackley *et al.* 2010 for full description of method).

Breeding schedule

Accurate estimates of the timing of key events during the breeding cycle were based on screening of immersion and light data from loggers, which revealed periods when tracked birds were present in their burrows for extended periods (>6 h), land-based monitoring of attendance in the 2000–01 and 2009–10 seasons, and geolocation data for birds at sea. Mean values were used if data were available for both the 2000–01 and 2009–10 seasons (Mann–Whitney *U* tests indicated there were no significant differences between years in these parameters).

Statistical analyses

Most statistical analyses were parametric tests (analysis of variance (ANOVA)), although non-parametric Mann–Whitney

U tests were used in a few instances where variables did not conform to assumptions of normality. Kernel and activity analyses were conducted using Matlab (The Mathworks Inc., Natick, MA, USA), and statistical tests were conducted using STATISTICA (Statsoft Inc, Tulsa, OK, USA). Data are shown as means $\pm$ s.d.

Results

Of the 22 Chatham Petrels equipped with loggers 18 (86%; 7 males, 11 females) were recaptured at their breeding burrows between 3 and 10 February 2010 (during late incubation) after 351 ± 3.2 days from attachment, and the loggers removed. Two loggers failed to download data, resulting in 16 datasets (for 7 males, 9 females) available for analysis. A total of 8199 locations were obtained, of which 14% were excluded as being spurious, leaving 7011 locations. There was no significant difference in breeding success in 2009 of burrows where one ($n = 9$) or both birds ($n = 6$) were fitted with a logger (one bird 100% ± 0 and both birds 83% ± 42; $F_{1, 13} = 1.56$, $P > 0.05$) nor between logger ($n = 15$) and control burrows ($n = 20$) in the same season (logger 93% ± 36, control 70% ± 47; $F_{1, 33} = 3.00$, $P > 0.05$). Moreover there was no significant difference in the percentage of burrows that contained eggs in the following (2009–10) season (logger 67% ± 49, control 75% ± 44; $F_{1, 33} = 0.28$, $P > 0.05$).

Breeding schedule

The breeding schedule of Chatham Petrels is summarised in Fig. 1 and Table 1. The first visit of breeding birds to their burrows,
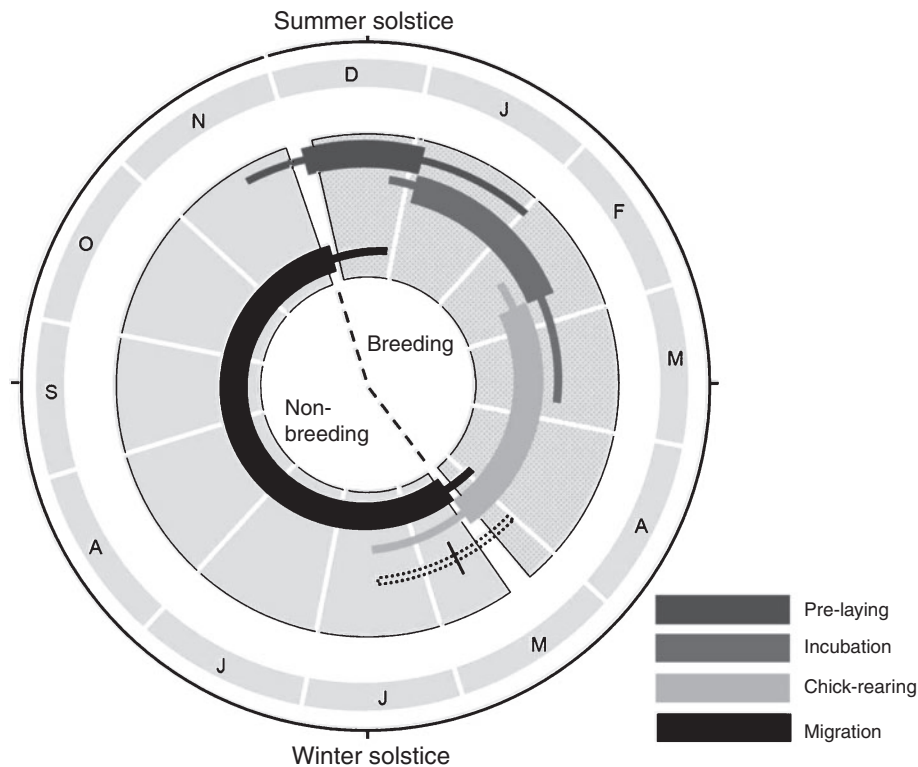

Fig. 1. The annual cycle of Chatham Petrels breeding on Rangatira Island derived from monitoring nesting burrows and data from geolocation-immersion loggers (see Methods and Table 1). Thick bars define peak activity, with the thin bars indicating the range. The black line with double dotted bar shows the mean date and range of fledging of chicks.

Table 1. Summary of the breeding cycle of Chatham Petrels from intensive monitoring of burrows and data from geolocation-immersion loggers

Figures are means; variation ± s.d.; dates in parentheses are ranges; numbers in parentheses are first visits

Burrow first visited	4 December (17 November–27 December) ($n = 246$)[A]
Duration of pre-laying exodus	34.6 ± 4.0 days ($n = 12$)[B]
Date of laying	5 January (27 December–2 February) ($n = 42$)[A]
Length of incubation shifts	15.6 ± 2.2 days ($n = 7$)[B]
Duration of incubation period	46.5 ± 1.6 days ($n = 83$)[C]
Date of hatching	25 February (10 February–25 March) ($n = 61$)[C]
Duration of guard stage	1.8 ± 0.9 days ($n = 82$)[C]
Duration of chick-rearing period	86.8 ± 4.4 days ($n = 82$)[C]
Date of fledging	21 May (1 May–>15 June) ($n = 83$)[C]
Date of departure for post-breeding migration	11 May (29 April–17 June) ($n = 13$)[B]
Duration of post-breeding migration	20.1 ± 5.0 days ($n = 16$)[B]
Date of arrival in non-breeding core (80%)	28 May (15 May–7 July) ($n = 16$)[B]
Days spent in non-breeding core	162.8 ± 10.0 days ($n = 16$)[B]
Date of departure for pre-breeding migration	11 November (19 October–6 December) ($n = 16$)[B]
Duration of pre-breeding migration	22.8 ± 5.4 days ($n = 16$)[B]

[A]Combined 2000–01 burrow monitoring and 2009–10 logger data.
[B]2009–10 logger data only.
[C]2000–01 burrow monitoring data only.
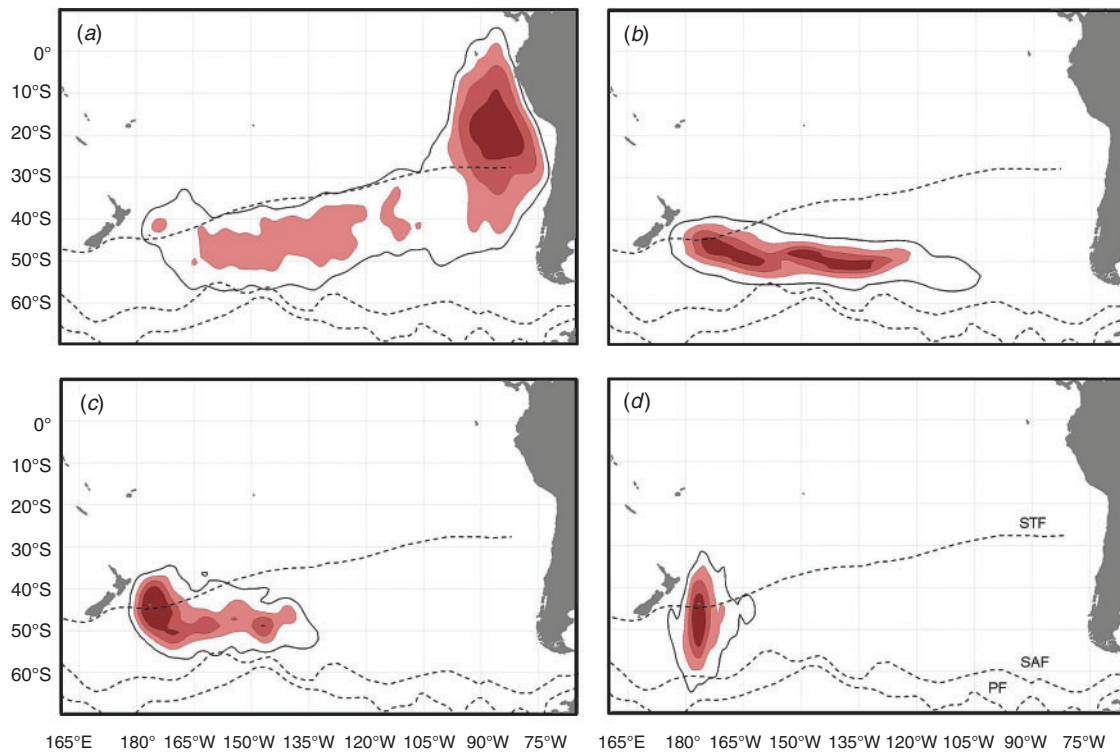
Fig. 2. Kernel density distributions for Chatham Petrels tracked with geolocator-immersion loggers during: (*a*). the non-breeding period (May–October 2009); (*b*) pre-laying exodus (November 2009–January 2010); (*c*) incubation period (January–February 2010) and (*d*) chick rearing period (February–May 2009). Coloured polygons represent the 25, 50 and 75% density contours, and the outer black line represents the 95% density contour. Approximate locations of the Subtropical Front (STF), Subantarctic Front (SAF) and Polar Front (PF) adapted from Harris and Orsi (2006) are shown as dotted lines.

which lasts for 1–6 days between late November and early December, is for preparation of the nest and mating. This tended to be earlier in tracked males (28 November ± 6.7 days, $n = 7$) than females (8 December ± 12 days, $n = 8$), although the difference was not statistically significant ($F_{1,13} = 3.00$, $P > 0.05$). For

four of five pairs where both partners were tracked with loggers, males arrived first and the female joined the male within 1–4 days. For one pair the male returned to sea after 4 days in the burrow, returning 1 day later on the same night as the female made her first visit. Pairs remained together in their burrow (presumably

mating) for 1–3 days. The pre-laying exodus was significantly longer for tracked males (37.5 ± 2.9 days) than females (31.6 ± 2.4 days) ($F_{1,\ 10}$ = 14.01, $P < 0.01$). Eggs were laid between late December and early February (Table 1). Females returned first from the pre-laying exodus in three of five tracked pairs; in one pair the male preceded the female by one night, and in another pair both partners arrived on the same night. Tracked females spent between 1 h and 4 days in the burrow during laying. Following laying, in two pairs the female left the burrow on the night before the arrival of the male for his first incubation shift, leaving the egg unattended for 1 day. The incubation period was 46.5 ± 1.6 days (Table 1) with three main (long) incubation spells identified: males conducted two shifts (first and third), females one long shift (second), with a mean length of the long shifts of 15.6 ± 2.2 days (n = 2 females, 5 males). In 75% of burrows (31 of 44) in 2000–01, females conducted an additional short shift (fourth) of 6.2 ± 2.5 days before hatching (i.e. overall sequence

of shifts male, female, male, female, hatching) or, in the remaining 25% (13 of 44 burrows), females were relieved after 8.3 ± 1.5 days by males who subsequently conducted a fifth short shift of 2.6 ± 1.4 days before hatching (i.e. male, female, male, female, male, hatching). Chicks hatched between mid-February and late March, were brooded for 1.8 ± 0.9 days, and fledged between early May and June after 86.8 ± 4.4 days (Table 1).

Distribution at sea

Seasonal changes in the at-sea distribution of Chatham Petrel tracked with loggers are shown on Fig. 2. During the pre-laying and incubation periods in the 2009–10 season, birds foraged far from the colony over deep waters of the temperate South Pacific Ocean between the Subtropical Front and Subantarctic Front (~50°S; Fig. 3a). In contrast, during chick-rearing, birds foraged
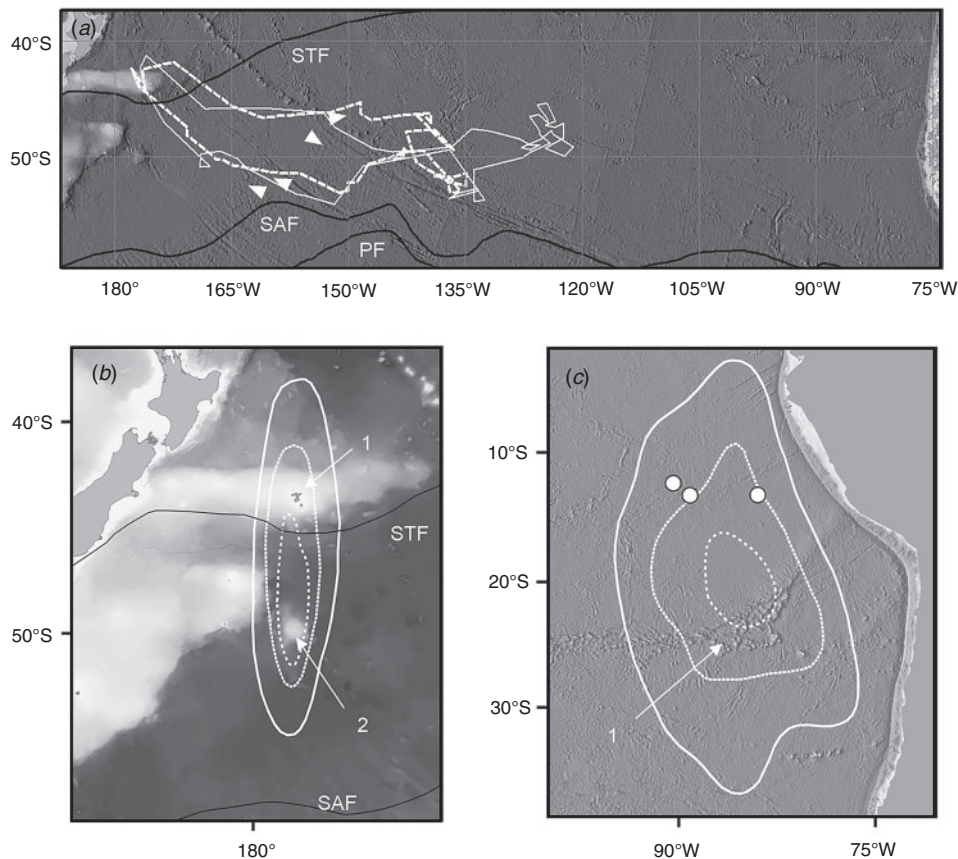

Fig. 3. (*a*) Pre-laying movements by two paired Chatham Petrels. The female (dashed white line) first visited the burrow 4–7 December 2009, returning 7–10 January 2010 to lay her egg after a 31 day pre-laying exodus. The male (solid white line) first visited the burrow on 5 December 2009, departing the same night, and returning 11 January 2010, after 38 days, for his first shift of incubation. (*b*) Kernel density distribution of 16 Chatham Petrels tracked with geolocators during the chick-rearing period, February–June 2009. Contours represent the 10% (more widely spaced dashed white line), 25% (more closely spaced dashed white line) and 50% (solid white line) density contours. Numbers mark the locations of: (1) the Chatham Islands and (2) the Bollons Seamount. (*c*) Kernel density distribution of 16 Chatham Petrels tracked with geolocators during the non-breeding season, May–November 2009. Contours represent the 10% (more widely spaced dashed white line), 25% (more closely spaced dashed white line) and 50% (solid white line) density contours. The Nazca Ridge is shown by the 1 and the solid circles show the locations of the three at-sea sightings of Chatham Petrels made by Force *et al.* (2009).

over deep waters south of the Chatham Rise, mainly around the Bollons Seamount, east of the New Zealand Subantarctic Plateau (Fig. 3*b*). Maximum range was significantly greater during the pre-laying period (3081 ± 1182 km) than incubation (2095 ± 1029 km; $F_{1,23} = 4.90$, $P < 0.05$) and chick-rearing (1354 ± 300 km; $F_{2,35} = 11.57$, $P < 0.001$). The maximum foraging range of males was significantly greater than that of females during the pre-laying period (males 3753 ± 992 km, females 2297 ± 895 km; $F_{1,10} = 6.22$, $P < 0.05$), but not during the incubation period (males 1875 ± 1229 km, females 2316 ± 839 km; $F_{1,10} = 0.53$, $P > 0.05$) or chick-rearing (males 1334 ± 409 km, females 1372 ± 201 km; $F_{1,11} = 0.05$, $P > 0.05$).

In 2009, tracked birds left on post-breeding migration between late April and June, with a mean departure date from New Zealand waters (11 May) that was 10 days earlier than the mean fledging date for chicks (21 May) (Fig. 4*b*, Table 1). There was no significant difference in the mean departure dates of males (7 May $\pm$ 6.7 days) and females (11 May $\pm$ 15.5 days; $Z = -0.69$, $P > 0.05$). Both sexes migrated east, following a great circle route at ~50°S, and then north to reach core non-breeding grounds centred north of the Nazca Ridge off South America (~20°S, 84°W) in 20.1 ± 5.0 days (Figs 1*a*, 3*c*). Pre-breeding migration

began between late October and early December (Table 1), and the mean date was not significantly different between the sexes (males 6 November $\pm$ 10.6 days, females 13 November $\pm$ 15.4 days; $P > 0.05$). The return to Rangitira Island followed a more northwards route on average (~40°N) than the post-breeding migration, and was of a very similar mean duration (22.8 ± 5.4 days; Fig. 4).

Activity at sea

The flight activity of Chatham Petrels changed significantly between seasons (Fig. 5) with birds spending more time on the water and exhibiting less frequent and shorter bouts of flight during the non-breeding period than during the pre-laying, incubation and chick-rearing periods (pre-laying $F_{3,51} = 70.04$, $P < 0.001$; incubation $F_{3,51} = 36.54$, $P < 0.001$; chick-rearing $F_{3,51} = 83.78$, $P < 0.001$; Fig. 5, Table 2). Incubating birds spent more time on the water and exhibited shorter bouts of flight than those rearing chicks ($F_{1,25} = 12.3$, $P < 0.01$; $F_{1,25} = 33.4$, $P < 0.01$
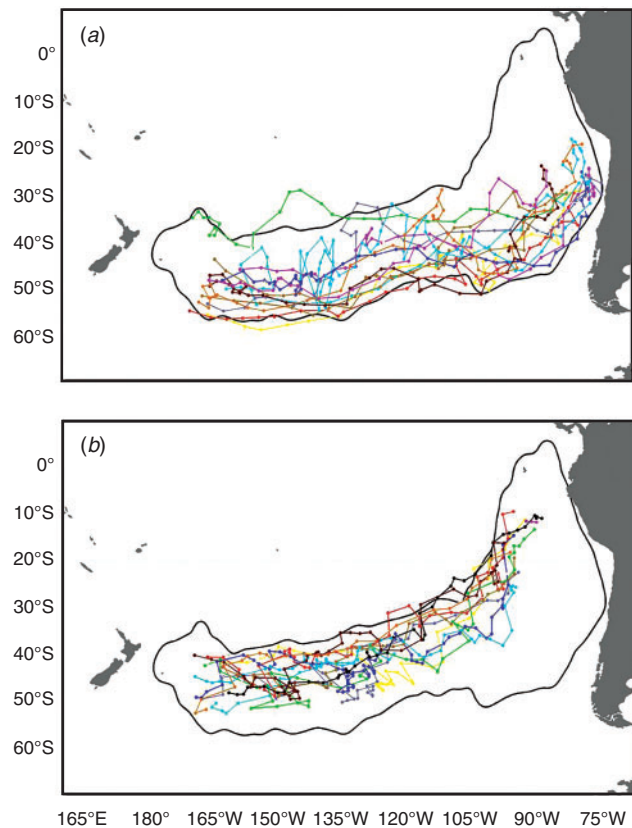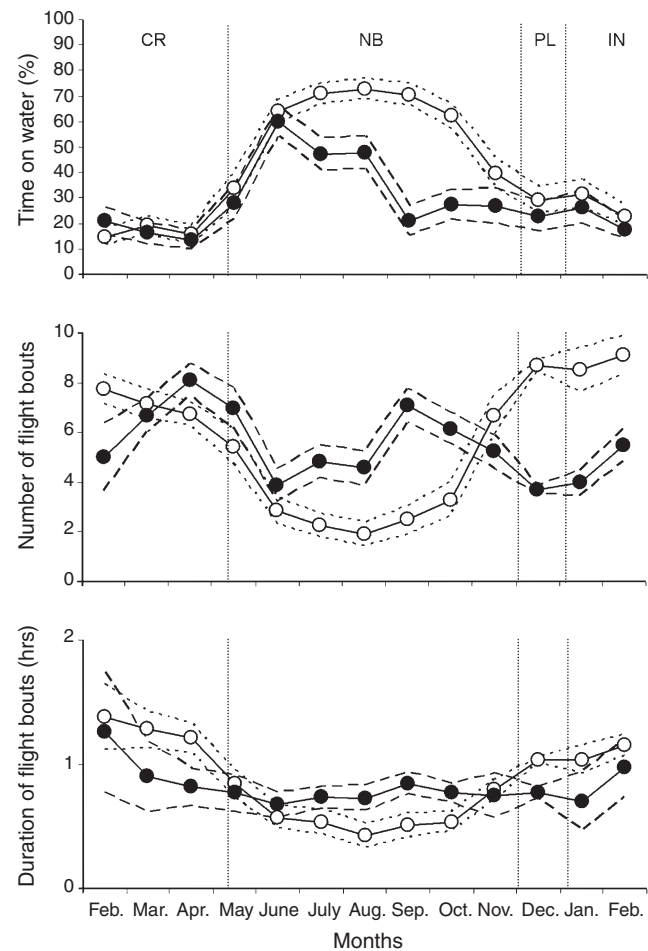

Fig. 4. Migration routes of 16 Chatham Petrels tracked with geolocation-immersion loggers from Rangatira Island, New Zealand. Colours represent the same bird during (*a*) post-breeding and (*b*) pre-breeding migration. The black perimeter line represents the 95% kernel distribution of all tracking data during the non-breeding period.

Fig. 5. Mean monthly activity during daylight (clear circles) and darkness (filled circles); for 16 Chatham Petrel tracked with geolocator-immersion loggers during the chick-rearing (CR), non-breeding (NB), pre-laying (PL) and incubation (IN) periods. Standard deviation of daylight activity shown by dotted lines, and darkness activity by dashed lines.

Table 2. Seasonal at-sea activity of Chatham Petrels tracked with geolocation-immersion loggers

	Proportion of day (24 h) spent on water (%)	Number of flight bouts per 24 h	Mean duration of flight bouts per 24 h (min)	Time spent on water during	
				Daylight (%)	Darkness (%)
Non-breeding	68.1 ± 13.8	3.9 ± 1.4	38.1 ± 7.5	78.8 ± 4.8	57.3 ± 11.2
Pre-laying	35.2 ± 14.1	6.2 ± 3.0	52.2 ± 13.7	35.8 ± 11.6	34.6 ± 16.7
Incubation	31.2 ± 11.9	6.6 ± 2.4	50.8 ± 14.1	31.1 ± 9.5	33.3 ± 14.2
Chick-rearing	19.6 ± 8.7	7.0 ± 0.7	67.0 ± 13.9	15.7 ± 5.4	23.6 ± 9.8

respectively) though the average number of flight bouts did not differ significantly ($F_{1, 25} = 0.7$, $P > 0.05$) (Table 2).

Flight activity differed significantly between daylight and darkness within seasons (Fig. 5, Table 2). During the non-breeding season, birds spent less time on the water ($F_{1,30} = 50.32$, $P < 0.001$) with more frequent ($Z = 4.67$, $P < 0.001$) and longer bouts of flight ($Z = -4.521$, $P < 0.001$) during darkness than during daylight. However, birds were more active during daylight during the breeding season (Fig. 5, Table 2), with incubating birds exhibiting significantly more frequent ($F_{1, 26} = 97.4$, $P < 0.001$) and longer flight bouts ($F_{1, 26} = 23.6$, $P < 0.001$) during daylight, although they spent the same amount of time on the water during darkness and daylight ($F_{1, 26} = 0.3$, $P > 0.05$). During chick-rearing, birds exhibited longer bouts of flight during daylight ($Z = -1.97$, $P < 0.05$), but neither the amount of time spent on the water nor the number of flight bouts was significantly different between darkness and daylight ($P > 0.05$).

Discussion

The results of this study provide detailed information on the breeding schedule, and the first tracking data on the at-sea distribution of the Chatham Petrel. Understanding the seasonal behaviour and movements of migratory species is imperative for informed conservation management (Robinson *et al*. 2010) and this study shows how such data can be obtained for small pelagic seabirds by combining intensive studies in colonies and remote tracking studies. Long-term management of the Chatham Petrel, including daily observations and the swapping of eggs between burrows, has resulted in increased breeding success. Similarly, there was no indication that the intensive monitoring used in the present study had a deleterious effect on natural behaviour. Moreover, the recapture rate of birds fitted with loggers in our study (86%) was higher than in most studies cited by Carey *et al*. (2009) (range 31–100%), and similar to that of the closely related Cook's Petrel (*P. cookii*) (89%) (Rayner *et al*. 2011). We are thus confident the behaviour of birds in this study is representative of the species.

The breeding behaviour of Chatham Petrels seems consistent with current understanding of the breeding biology of *Pterodroma* petrels, including broadly synchronous arrival of males and females, long incubation shifts, a prolonged chick-rearing period, and pre-fledging abandonment of chicks by adults (Warham 1996; Brooke 2004). Tracking of breeding pairs of Chatham Petrels revealed synchronisation in the timing of arrival at burrows after migration and that birds spent only a short time together (1–3 days) before the pre-laying exodus. The duration of the incubation and chick-rearing periods in Chatham Petrels

(46 and 87 days) are similar to those of other small *Cookilaria* petrels (160–200 g), including the Black-winged Petrel (*P. nigripennis*) (45 and 85 days; Hutton and Priddel 2002), Bonin Petrel (*P. hypoleuca*) (49 and 82 days; Pettit *et al*. 1982), Cook's Petrel (47 and 87 days; Imber *et al*. 2003) and Pycroft's Petrel (*P. pycrofti*) (45 and 80 days; Marchant and Higgins 1990) but not the larger Mottled Petrel (*P. inexpectata*) (315 g, 50 and 95–105 days; Warham *et al*. 1977). The length of the main incubation shifts identified (15.6 days) is longer than in the species discussed above (10–14 days) but this statistic does not incorporate the shorter fourth and fifth shifts conducted by both males and females near hatching and, given the limited sample size from tracked individuals from which it was calculated ($n = 7$), should be interpreted with caution.

The frequency with which chicks are fed in Chatham Petrels declines during the chick-rearing period, culminating in an abandonment of ~10 days before chicks fledge (Gardener 1999; present study). The period of abandonment is similar to that of Cook's Petrel (minimum 9–11 nights; Imber *et al*. 2003), but longer than that of Pycroft's Petrel (~7 nights; Gangloff and Wilson 2004). Similarity in the duration of chick abandonment in Chatham and Cook's Petrels may reflect their similar body size (~190 g), and thus rates of chick development, in comparison with Pycroft's Petrel (~150 g; Marchant and Higgins 1990). Moreover, time constraints of migratory behaviour may play a role in patterns of abandonment with Chatham and Cook's Petrels making extensive trans-Pacific and trans-equatorial migrations (Rayner *et al*. 2011; this study) compared with Pycroft's Petrel, which from recent tracking data, migrates shorter distances to equatorial waters of the mid-Pacific Ocean (M. Rayner, unpubl. data).

During breeding, Chatham Petrels occupy pelagic foraging habitats primarily south and east of the Chatham Islands, between the Subtropical and Subantarctic Fronts. Limited shipboard observations from previous years confirm the importance of this region, with previous records of birds between the Chatham and Bounty Islands (47°45′S, 179°01′E), in 1970 (West 1994), 2000 and 2007 (Force *et al*. 2009). Shifts in the distribution of seabirds during the stages of breeding reflect varying energetic demands associated with changing reproductive duties and constraints of central-place foraging, and potentially also changing foraging opportunities as a result of seasonal shifts in oceanic productivity (Phillips *et al*. 2005a; Weimerskirch 2007; González-Solís *et al*. 2007a; Péron *et al*. 2010; Rayner *et al*. 2010). In the Chatham Petrel, reduction in the maximum range between the pre-laying and incubation periods, and the greater maximum range of males than females during pre-laying, likely reflect the time available at sea rather than changes in habitat selection, as birds tended to remain in similar oceanic regions. However, use of a region close

to, and south of, the Chatham Islands during chick-rearing probably results from the increased energetic requirements of provisioning chicks (shorter foraging trips to feed the chick, potentially at the cost of adult condition) (Weimerskirch 1998; Rayner *et al.* 2010), and enhanced oceanic primary productivity that occurs at higher latitudes during the late southern hemisphere summer (Shaffer *et al.* 2006). That the centre of the foraging distribution during chick-rearing was over the Bollons Seamount suggests that this feature may play a role in promoting local productivity or concentrating prey that are exploited by foraging birds. Further study of the ecology, oceanography and the use of the area by Chatham Petrels is required given its obvious importance for the species.

Preceding this study, the non-breeding distribution of the Chatham Petrel was poorly known beyond three opportunistic shipboard observations in the eastern Pacific Ocean, one in 1999 and two in 2006 (Force *et al.* 2009). Here we confirm the migration of the species to the outer edge of the Humboldt Current system adjacent to Peru and Chile (~20°S). The post-breeding easterly migration routes of Chatham Petrel were similar, in direction and latitude (~45–55°S), to those of Westland Petrel (*Procellaria westlandica*) (Landers *et al.* 2011) and Sooty Shearwater (*Puffinus griseus*) (Shaffer *et al.* 2006) from New Zealand, and both the post- and pre-breeding routes were similar to those taken by Cook's Petrel from Codfish Island, New Zealand (Rayner *et al.* 2011). Such similarities across species presumably reflect the exploitation of the predominant wind direction at particular latitudes, a process known to facilitate rapid migration in migrant seabirds in the Atlantic Ocean (Felicísimo *et al.* 2008; González-Solís *et al.* 2009).

Temperate and polar seabirds commonly migrate to productive oceanic or neritic regions during the non-breeding period (Shaffer *et al.* 2006; González-Solís *et al.* 2007*b*; Guilford *et al.* 2009; Rayner *et al.* 2011). The Humboldt Current is one of the most productive oceanic habitats in the world (Chavez *et al.* 2008), and consequently is visited by several seabirds from New Zealand during their non-breeding season, including Cook's Petrel (Rayner *et al.* 2011), Westland Petrel (Landers *et al.* 2011), Black Petrel (*Procellaria parkinsoni*) (Spear *et al.* 2005) and Buller's Albatross (*Thalassarche bulleri*) (Stahl and Sagar 2000). While wintering in the Humboldt Current, Chatham Petrels occupied pelagic foraging habitats beyond the continental shelf (~1000 km from South America) with the core of their distribution centred on and north of the Nazca Ridge, possibly indicating exploitation by birds of elevated productivity known to occur in this region (Chavez *et al.* 2008). That the three shipboard observations for the species by Force *et al.* (2009) fall within the core of the distribution of tracked birds, suggests this is the traditional wintering area, particularly given the clear evidence for regional non-breeding site fidelity among years in other Procellariiformes (Phillips *et al.* 2005*b*, 2007; Rayner *et al.* 2011). Interestingly, comparison of tracking data for Chatham Petrels with those of Cook's Petrel that breed on Codfish Island and also winter off South America (Rayner *et al.* 2011) suggests distinct habitat segregation: Cook's Petrels occupy a distribution much closer to the South American coast (~15°S) over both shelf and pelagic waters, whereas Chatham Petrels are distributed entirely over pelagic waters (~20°S). However, as the two datasets were collected in different years (Cook's Petrel 2008–09, Cha-

tham Petrel 2009–10), a climate-induced shift in distribution cannot be ruled out entirely.

At-sea immersion data demonstrate the marked change in behaviour of Chatham Petrels between the breeding and non-breeding periods. Tracked birds spent a much greater proportion of time resting on the sea surface when off South America than off the Chatham Islands. In contrast, they exhibited more and shorter bouts of flight (i.e. more landings and take-offs) during chick-rearing. This pattern is similar to that of larger Procellariiformes (Mackley *et al.* 2010, 2011; Péron *et al.* 2010) and reflects the high energetic demands of central-place foraging during breeding (Rayner *et al.* 2010). However, diel behaviour during the non-breeding period was markedly different from that of large albatrosses, which are usually more active during daylight (Mackley *et al.* 2010; Péron *et al.* 2010), but similar to that of other petrels (Mackley *et al.* 2011). The greater night-time activity of Chatham Petrel supports the hypothesis that, for the non-breeding period at least, the species exploits nocturnally available prey, as suggested by studies of other gadfly petrels (Brooke and Prince 1991; Imber 1996; Rayner *et al.* 2008).

Intensive conservation management of the Chatham Petrel at its breeding site has resulted in improved breeding success, and recent translocations have established additional populations within the Chatham Islands to better safeguard the species 'on land' (Gummer *et al.*, in prep). However, our data reveal the vast region exploited by this species between New Zealand and South America, and thus the difficulty in protecting it at sea. Nevertheless, there are recent conservation initiatives to identity marine protected areas for seabirds that are outside national jurisdictions (http://www.birdlife.org/action/science/species/seabirds/index.html), to which datasets such as ours contribute. Unlike many larger Procellariiformes, the Chatham Petrel is not directly affected by mortality associated with fisheries. However, the susceptibility of the species to changes in climate and oceanography is not known and warrants immediate study given the small size of the population. In particular, understanding how shifts in the Southern Oscillation Index (between La Niña and El Niño conditions) affect breeding and non-breeding distribution, and breeding success, could provide an indication of the potential effect of human-induced climate change in the long-term.

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