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Berlincourt, Maud, Angel, Lauren P. and Arnould, John P. Y. 2015, Combined use of GPS and accelerometry reveals fine scale three-dimensional foraging behaviour in the short-tailed shearwater, *PLoS one*, vol. 10, no. 10, pp. 1-16.

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Citation: Berlincourt M, Angel LP, Arnould JPY (2015) Combined Use of GPS and Accelerometry Reveals Fine Scale Three-Dimensional Foraging Behaviour in the Short-Tailed Shearwater. PLoS ONE 10(10): e0139351. doi:10.1371/journal.pone.0139351

Editor: Hans-Ulrich Peter, Institute of Ecology, GFRMANY

Received: February 13, 2015

Accepted: September 11, 2015

Published: October 6, 2015

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credited.

Data Availability Statement: All relevant data are available via Dryad (DOI: <u>10.5061/dryad.j9k60</u>).

Funding: This work was funded by ANZ Trustees Foundation - Holsworth Wildlife Research Endowment (grant RM23947) (http://www.anz.com/personal/private-bank-trustees/trustees/granting/granting-programs/small-grants/), MA Ingram Trust Application (grant RM25024) (https://www.statetrustees.com.au/uploads/content/142-MA_Ingram Trust Guidelines Application Form.pdf), and Birds Australia (grant RM23896) (http://birdlife.org.au/who-we-are/ourorganisation/awards-scholarships).

RESEARCH ARTICLE

Combined Use of GPS and Accelerometry Reveals Fine Scale Three-Dimensional Foraging Behaviour in the Short-Tailed Shearwater

Maud Berlincourt*, Lauren P. Angel, John P. Y. Arnould

School of Life and Environmental Sciences, Deakin University, Burwood, Victoria, Australia

* mberlinc@deakin.edu.au

Abstract

Determining the foraging behaviour of free-ranging marine animals is fundamental for assessing their habitat use and how they may respond to changes in the environment. However, despite recent advances in bio-logging technology, collecting information on both atsea movement patterns and activity budgets still remains difficult in small pelagic seabird species due to the constraints of instrument size. The short-tailed shearwater, the most abundant seabird species in Australia (ca 23 million individuals), is a highly pelagic procellariiform. Despite its ecological importance to the region, almost nothing is known about its at-sea behaviour, in particular, its foraging activity. Using a combination of GPS and tri-axial accelerometer data-loggers, the fine scale three-dimensional foraging behaviour of 10 breeding individuals from two colonies was investigated. Five at-sea behaviours were identified: (1) resting on water, (2) flapping flight, (3) gliding flight, (4) foraging (i.e., surface foraging and diving events), and (5) taking-off. There were substantial intra- and inter- individual variations in activity patterns, with individuals spending on average 45.8% (range: 17.1– 70.0%) of time at sea resting on water and 18.2% (range: 2.3-49.6%) foraging. Individuals made 76.4 ± 65.3 dives (range: 8–237) per foraging trip (mean duration 9.0 ± 1.9 s), with dives also recorded during night-time. With the continued miniaturisation of recording devices, the use of combined data-loggers could provide us with further insights into the foraging behaviour of small procellariiforms, helping to better understand interactions with their prey.

Introduction

Understanding and assessing the foraging behaviour of free-ranging marine animals is fundamental for determining their habitat use and responses to environmental change. However, for



Competing Interests: The authors have declared that no competing interests exist.

pelagic predators such as seabirds, it remains a constant challenge as they spend most of their time at sea, are highly mobile, and cover great distances. While at-sea distribution, species range expansion or changes in species abundance have been extensively investigated through vessel-based surveys [1–5], this method does not provide information about observed individuals' breeding status or details of their at-sea behaviour necessary for long-term monitoring or to better understand individual species and their ecology.

Since the early 1990s, the study of the foraging behaviour and movement patterns of pelagic seabirds has been made possible by the development of miniaturized electronic technologies primarily based on VHF and satellite-tracking telemetry [6-9]. Information about foraging ecology, habitat utilisation or at-sea distribution related to the heterogeneity and the patchiness of prey resources has been published on a large range of seabird species [10-13]. However, despite these major advances in biotelemetry, some challenges remain. Most of these techniques have limitations as they rely on indirect measures of foraging effort [14-18]. Furthermore, it remains difficult to collect information about at-sea movement patterns and activity budgets in small pelagic seabird species due to the constraints of instrument size [19].

Until recently, equipment was unavailable to monitor the range of at-sea behaviours in small pelagic seabird species such as shearwaters. Most information available was collected through the use of GPS, geolocators, maximum depth gauges or time-depth recorders [20–26]. Studies combining the use of different devices to investigate simultaneous movement patterns and the allocation of time at sea for foraging (both at the surface and underwater) were restricted to large seabird species [27–31]. Animal-borne accelerometers have the potential to provide detailed information about behavioural modes of free-ranging animals because they allow recording behaviour directly [32]. Used in combination with GPS data-loggers, they are powerful tools to infer at-sea behaviour and activity budgets, with recent miniaturisation making them available for use on smaller species.

The short-tailed shearwater (*Puffinus tenuirostris*) is a highly pelagic small-sized procellariiform. It is the most abundant seabird species in Australia, with approximately 23 million individuals breeding annually during the austral spring/summer (September to April) [33]. A single egg is laid the last week of November and incubated for approximately 53 days (hatching occurs around the 3rd week of January). Chick-rearing starts once the egg hatches; adults provision their chick until late March or early April [34]. While short-tailed shearwaters are listed as "Least Concern" by the International Union for Conservation of Nature (IUCN), populations in south-eastern Australia have recently experienced important decreases [35]. Despite numerous studies describing the foraging ecology [36–39] and the ecological importance of the short-tailed shearwater to the south-eastern Australian region [33], little is known about its at-sea activity budget, in particular, related to its foraging behaviour [40].

During the chick-rearing period, short-tailed shearwaters use a bimodal foraging strategy involving repeated alternation between short foraging trips (1–3 days) close to the breeding colony (within 30–70 km of the colony; [36]) and longer foraging trips (9–17 days) to distant waters of the Southern Ocean (> 1000 km; [41]). Short trips allow the adults to maximise chick-provisioning rates, while performing long foraging trips allows self-replenishment of body reserves consumed during delivery of food to the chick [41]. Assuming that higher energy costs occurring during short trips are due to greater foraging intensity [42], the aims of the present study were to investigate: 1) how individuals allocate their time at sea; and 2) to describe their diving activity during these nutritionally demanding periods.



Materials and Methods

Ethics Statement

The present study was conducted following the ethical guidelines of the Deakin University Animal Ethics Committee (Approval A61-2010) and in accordance with the regulations of Department of Sustainability and Environment (Victoria, Australia, Permit 10005531).

Study sites and animal handling procedures

The study was conducted at Gabo Island Lighthouse Reserve (37°33'S, 149°54'E) and Griffith Island, Port Fairy (38°22'S, 142°13'E), two colonies located at both extremities of Bass Strait in south-eastern Australia (Fig 1). Breeding populations are estimated at more than 6,000 pairs at Gabo Island [43] and 15,000 pairs at Griffith Island [44]. Data were collected during the early chick-rearing period in February 2012. Burrows containing hatched chicks were monitored daily in order to identify adult attendance patterns. Chicks were weighed every night using a spring balance (\pm 5 g). Chicks were considered to have received a meal when their mass increased between weighing, whereas mass loss indicated no feeding event (see [41]). Both adults were considered to be performing long trips when their chicks lost weight over 5 consecutive days [37]. These burrows were targeted for GPS and accelerometer data logger deployments because the adults were likely to perform a short trip upon return. A one-way wooden trapdoor was fitted at the entrance of the burrow. Returning parents tripped a stick that closed the trapdoor when entering the burrow. Adults were left for ~30–40 minutes in the burrow to feed the chick and then captured for instrumentation.

Body mass and morphometric measurements (bill length and depth, wing length) were taken using a spring balance (\pm 5 g) and Vernier callipers (\pm 1 mm). Individuals were then instrumented with an IgotU GT–120 GPS data logger (Mobile Action Technology, Taiwan) programmed to sample location every 5 min and a tri-axial accelerometer (GCDC X6-mini, Gulf Coast Data Concepts, USA) recording acceleration at 25 Hz. A single battery was used for

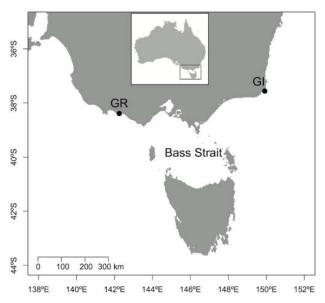


Fig 1. Location of Gabo Island (GI) and Griffith Island (GR) breeding colonies (closed circles) in the Bass Strait region, south-eastern Australia.



both loggers in order to reduce total weight and packaged in heat-shrink tubing (dimension of the devices including heat-shrink tubing: 49.0 x 24.0 x 12.0 mm). Devices were attached with black waterproof tape (Tesa AG, Germany) to feathers on the dorsal midline (total weight including the waterproof casing was 19 g, < 3.5% of the total body mass). Procedures lasted < 10 min and, after the chick was weighed, individuals were returned to the nest to resume normal behaviour. After 1 to 3 days of deployment and upon completion of at least one foraging trip, birds were recaptured in their burrows after they had fed their chick and the devices removed. In addition, a total of 50 nests at Gabo Island and 106 nests at Griffith Island were marked in study plots at the time of egg-laying in November 2011 and monitored throughout the breeding season to record the chronology of laying, hatching and fledging (and their respective success). Out of these, a total of 12 individuals at both colonies were instrumented with GPS data-loggers and accelerometers. Nest of instrumented birds were monitored after deployments and their success was compared with a Chi-square test to the one of the remaining nests (control group) in the studied areas. Success was not significantly different between both groups throughout the study period (Gabo Island: $\chi^2 = 0.43$, p = 0.51 and Griffith Island: $\chi^2 = 0.39$, p = 0.53). Consequently, the data recorded by the tri-axial accelerometers were assumed to represent normal at-sea behaviour and activity levels.

Data processing and analysis

To investigate habitat use, GPS tracks were analysed with the *trip*, *adehabitatHR* and *adehabitatLT* packages [45, 46] within the R statistical environment [47]. An iterative forward/backward speed filter was used to remove locations yielding unrealistic high travel speeds [48] (speed threshold > 60 km h⁻¹ [37]). On average, the speed filtering removed 0.5% (range: 0–4.0%) of recorded locations during individual foraging trips. Analyses were performed on complete foraging trips, defined as the time between when individuals departed from, and when they returned to, the colony. For each foraging trip, (1) trip duration (h), (2) total distance travelled (km), (3) maximum distance to the colony (km), (4) average horizontal speed (km h⁻¹) and (5) average bearing (°) from the colony were calculated. In addition, wind speed (m h⁻¹) and wind direction (°) were used to characterize conditions experienced during foraging flight. Data were obtained from Buoyweather (http://www.buoyweather.com/index2.jsp) at two locations in the proximity of the breeding colonies (Gabo Island: 150°E– 38°S; Griffith Island: 143°E– 39°S) as 3 hourly readings and converted to daily means.

At-sea behaviours were characterized from body acceleration characteristics recorded along all three spatial axes with accelerometers measuring both dynamic acceleration (e.g. wing flapping) and static acceleration (e.g. gravity). Static acceleration was kept for behaviour determination, as the amplitude of the surge is influenced by gravitational acceleration, hence, relates to the angle of the bird [49]. Body acceleration data were analysed and classified into behaviour categories using the Ethographer package in Igor Pro (WaveMetrics Inc., USA). Longitudinal acceleration data (i.e. along the longitudinal axis of the body) were converted into a spectrum by continuous wavelet transformation. Each second of the spectrum was categorized into behaviour categories by unsupervised cluster analysis, using k-means methods [49]. Additionally, the pitch angle of the bird body was calculated from the three-acceleration signal (surge, heave and sway) using trigonometry [50]. Behaviours were classified based on previous studies of diving birds [27, 28, 51]. As the dive depth was not recorded directly by the accelerometer (i.e. no pressure sensor), individual dives were identified by a high surge along the x-axis and a negative pitch angle, following the methods of [49]. Misclassification of behaviours was then corrected based on pre-defined criteria (i.e. resting and gliding were distinguished based on speed of travel). Five activity types were identified and assumed to correspond to when the bird



was taking off, in flapping flight, gliding flight, resting on the surface of the water or foraging (i.e. surface foraging or diving; Fig 2).

Trip parameters were compared between breeding colonies using non-parametric tests (Kruskal-Wallis or Wilcoxon tests) as all dependent variables differed from normal distribution. To investigate the response of at-sea behaviours to foraging trip parameters and wind conditions experienced at sea, linear mixed effects (LME) models were used with the arcsine-transformed proportions of time spent at sea (i.e. proportion of time resting or foraging) as response variables and foraging trip parameters (i.e. trip duration, total distance travelled and maximum distance to the colony) or wind parameters as explanatory variables (nlme package [52]). Additionally, to investigate the response of foraging trip parameters to wind conditions, LME models were used with the log-transformed foraging trip parameters as response variables and wind parameters as explanatory variables. In both cases, breeding site was held as fixed factors and bird ID was held as random factor. Only individuals performing a 1-day foraging trip were included in the models. All analyses were conducted within the R statistical environment [47]. Unless stated otherwise, data are presented as Mean \pm SD and significance level was set at $\alpha = 0.05$.

Results

Some individuals could not be recaptured upon first return to the colony, either due to the friable nature of the nesting habitat preventing access to the studied burrows or because some individuals succeeded in burrowing out after they had fed the chick and avoided recapture. As a consequence, few data loggers could be recovered. Other individuals were recaptured after several short foraging trips and by this stage some data loggers were still on the birds while others had fallen off. Consequently, only 6 individuals equipped with data loggers at Gabo Island and 5 at Griffith Island were retrieved. Furthermore, due to data logger failure, data could not be downloaded for all the loggers retrieved. Complete short foraging trips were obtained from 10 individuals (see Table 1 for details) with multiple trips recorded for 2 individuals at Griffith Island (2 and 3 trips, respectively), providing a total number of 13 trips for analysis (See S1 Appendix). The average trip duration was similar for both colonies, 16.1 ± 1.3 h for individuals at Gabo Island and 19.7 ± 9.6 h for birds at Griffith Island (Wilcoxon rank sum test, W = 17, p = 0.62). All individuals completed a one-day trip with the exception of one bird at Griffith Island, which was away from the colony for 2 days. Although not significantly different, birds at Griffith Island travelled substantially longer distances (316.1 ± 163.3 km) than bird at Gabo Island (195.6 \pm 70.5 km) (W = 8, p = 0.07). Furthermore, the maximum distance from the colony was greater for birds at Griffith Island (86.9 ± 29.9 km) compared to individuals from Gabo Island (38.8 \pm 6.1 km) (W = 1, p = 0.002).

The proportion of time spent at sea in each activity varied greatly between individuals, regardless of the breeding colony (Fig 3). Resting on water was the predominant behaviour category in all individuals ($45.8 \pm 15.3\%$ of time at sea, range: 17.1–70%). Flapping flight ($20.4 \pm 7.8\%$, range: 10.4–33.5%) and foraging (including both surface foraging and diving; $18.2 \pm 15.5\%$, range: 2.3–49.6%) contributed the second and third highest proportion of the atsea activity budget. Intra-individual variations were also observed for the two birds tracked during sequential 1-day foraging trips at Griffith Island (Fig 3; individuals 7 and 9). For individual 7, the proportion of time spent resting on water was 28.9% and 42.6% for the respective days of tracking, and 63.1%, 57.9% and 47.7%, for individual 9, with corresponding proportion of time spent foraging of 20.5% and 7% for individual 7, and 4.8%, 2.3% and 23.1% for individual 9. For the bird (individual 10) that performed a 2-day foraging trip at Griffith Island, the proportion of time spent resting on water was similar whether night-time period was included



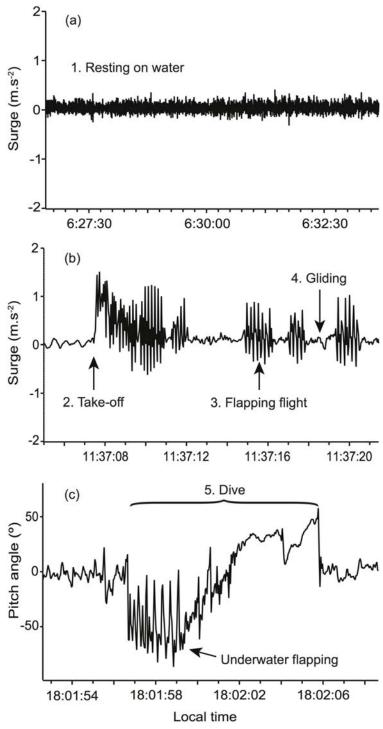


Fig 2. Acceleration (surge) and pitch angle profiles during the different behaviours identified. Panels represent behaviour (a) while resting at the surface of the water, (b) taking-off, flapping and gliding, and (c) while diving (underwater flapping is indicated by the arrow).



Table 1. Short foraging trip parameters in short-tailed shearwaters rearing chicks at two breeding colonies. Individuals 7 and 9 were tracked during sequential 1-day foraging trips (2 and 3, respectively) and individual 10 performed a 2-day foraging trip.

Colony	Bird ID	Body mass at deployment (g)	Trip duration (h)	Total distance travelled (km)	Maximum distance (km)	Average horizontal speed (kmſh ⁻¹)	Average bearing (°)
Gabo Island	1	565	16.3	207.9	37.2	12.4	239.1
	2	555	15.1	118.7	38.1	6.4	24.0
	3	610	15.6	140.9	31.3	9.4	211.9
	4	565	16.5	257.9	36.3	15.3	210.9
	5	590	18.4	295.9	49.5	17.1	13.6
	6	565	15.0	152.3	40.7	9.0	21.1
	Mean ± SD	575 ± 20.7	16.1 ± 1.3	195.6 ± 70.5	38.8 ± 6.1	11.6 ± 4.1	120.1 ± 110.7
Griffith Island	7a	625	16.0	319.1	130.3	22.3	107.6
	7b	-	15.8	264.5	47.3	17.3	206.2
	8	595	17.2	306.7	68.1	19.9	267.4
	9a	565	16.0	195.7	81.1	12.4	110.5
	9b	-	15.8	181.7	71.4	11.1	118.3
	9c	-	15.4	277.9	87.1	18.7	169.3
	10	595	41.5	667.2	122.9	14.6	125.6
	Mean ± SD	595 ± 24.5	19.7 ± 9.6	316.1 ± 163.3	86.9 ± 29.9	16.6 ± 4.1	157.9 ± 60.3

or excluded from analyses (47.6% and 47.5%, respectively). However, the proportion of time spent in flapping flight was lower, and foraging time correspondingly higher, when the night-time period was excluded (Fig 3). This indicates that birds spent more time at night foraging than flying.

Most individuals started their outward foraging trip travelling along the coast and/or following the prevalent wind direction (Figs $\underline{4}$ and $\underline{5}$). No commuting between the breeding colonies and foraging grounds was observed with most individuals starting to surface feed or dive in areas very close to the breeding site. At Gabo Island, individuals performed their first dive on average 1.5 ± 2.3 km from the colony (range: 0.01-5.4 km) (Fig 4), 11.3 ± 9.4 % of the total dives occurred within the first 10 km around the breeding colony (range: 2.7-25.0%), and $46.5 \pm 36.5\%$ of the dives events occurred further than 30 km from the colony (range: 0-93.7%). Individuals began to surface-forage within 0.2 ± 0.4 km (range: 0.002-1.0 km) of the colony and $15.1 \pm 14.1\%$ of the surface foraging events occurred within 10 km of the colony (range: 3.9–40.6%). At Griffith Island, individuals first dived within 11.7 \pm 18.9 km of the breeding colony (range: 0.01-48.4 km) (Fig 5) and only $4.8 \pm 4.9\%$ of the total dives were performed within 10 km of the colony (range: 0-13.5%), while $83.1 \pm 26.4\%$ occurred further than 30 km from the colony (range: 24.4-100%). In contrast, individuals surface-foraged for the first time within 0.7 ± 1.2 km of the colony (range: 0.01 ± 2.7 km) but most of the surface foraging activity occurred further than 30 km away from the colony. Individuals were recorded to perform 76.4 ± 65.3 dives per short foraging trip (range: 8–237), with an average dive duration of 9.0 ± 1.9 s (range: 6.0-11.6 s). While individual 10, which conducted a 2-day trip, spent a considerable proportion of time (6.7%) surface foraging at night, few dives were recorded at this time.

During the study period, the daily wind strength observed ranged from $21.6-47.9 \text{ km.h}^{-1}$. The proportion of time spent foraging was positively correlated to average wind speed ($F_{1,10} = 9.9, p = 0.01$) (Fig 6a) while the proportion of time spent resting was negatively correlated to the total distance travelled ($F_{1,10} = 21.7, p < 0.001$) (Fig 6b). Finally, while the proportion of time spent in flapping flight was not correlated to horizontal travel speed ($F_{1,10} = 2.8, p = 0.12$),



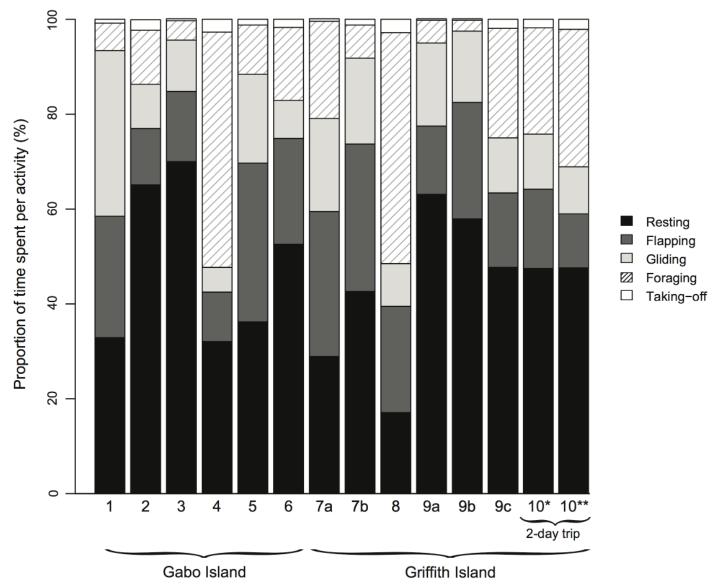


Fig 3. At-sea activity budget of breeding short-tailed shearwaters during short foraging trips. Proportion of time spent resting, flapping, gliding, foraging (diving and surface foraging) and taking-off during a short foraging trip. Individuals 7 and 9 were tracked during sequential 1-day foraging trips (2 and 3, respectively) and individual 10 performed a 2-day foraging trip (*activity calculated over entire trip, **activity calculated with night-time excluded).

the total distance travelled per foraging trip was positively correlated to horizontal travel speed $(F_{1,10} = 253.3, p < 0.001)$ (Fig 6c).

Discussion

Previous studies have suggested that short-tailed shearwaters rely mainly on surface feeding and diving techniques to forage (i.e. seizing prey at the surface or pursuit diving from the surface) [40, 41, 53], as has been documented in other shearwater species using information obtained from at-sea observations [21], capillary tubes measuring maximum diving depths [20], or diving patterns recorded by time-depth data-loggers [22, 24]. However, for the first



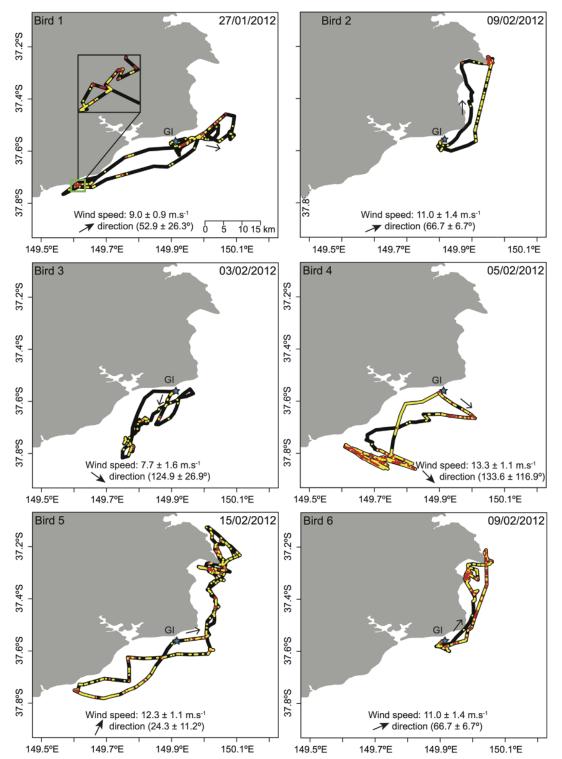


Fig 4. Foraging trips and related at-sea behaviour of 6 short-tailed shearwaters tracked with GPS and tri-axial accelerometers at Gabo Island. For clarity, only location of surface foraging (yellow dots) and diving events (red dots) are shown on the figure and the black line represents either resting on the water, flapping flight or gliding flight. Arrows along the tracks indicate the movement direction and the star indicates the location of the breeding colony. Wind speed and direction (mean ± SD) are indicated for each foraging trip.



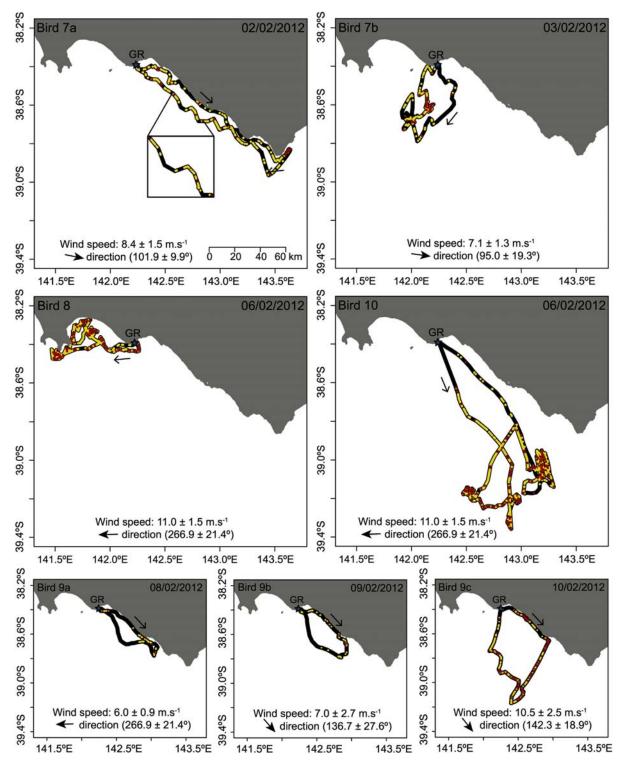


Fig 5. Foraging trips and related at-sea behaviour of 4 short-tailed shearwaters tracked with GPS and tri-axial accelerometers at Griffith Island. For clarity, only location of surface foraging (yellow dots) and diving events (red dots) are shown on the figure and the black line represents either resting on the water, flapping flight or gliding flight. Arrows along the tracks indicate the movement direction and the star indicates the location of the breeding colonies. Wind speed and direction (mean ± SD) are indicated for each foraging trip.



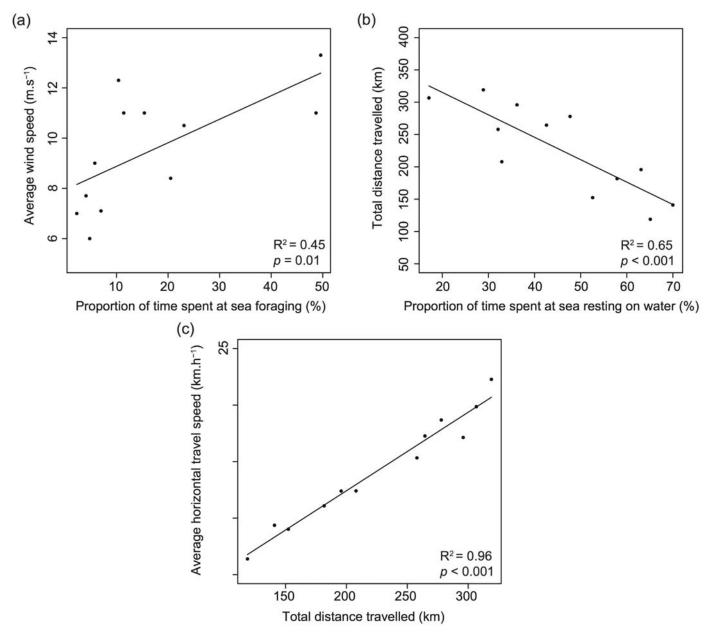


Fig 6. Relationships between foraging parameters, at-sea activity and wind patterns during 1-day short foraging trips in short-tailed shearwaters (n = 12). (a) Relationship between the proportion of time spent at sea foraging and the average wind speed. (b) Relationship between the proportion of time spent at sea resting on water and the total distance travelled. (c) Relationship between the total distance travelled per foraging trip and the average horizontal travel speed.

time fine-scale information on the at-sea behaviour of short-tailed shearwaters performing short foraging trips is described in the current study. The results of the present study have revealed high levels of inter-individual variation in at-sea behaviour patterns and spatial distribution of foraging activity at both colonies sampled.

While the maximum range differed between the two colonies, most likely reflecting differences in local prey distribution and weather patterns (see below), individuals from both sites