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Fine scale biologging of an inshore marine animal

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ABSTRACT

We compared the results of two biologging techniques used to study the foraging behaviour of a colony of small inshore predators, little penguins (*Eudyptula minor*). The first technique involved the use of satellite transmitters and diving loggers deployed on separate individuals, which has been the conventional method of tracking the movements and behaviour of this species for >10 years. The second technique combined a diving logger and a global positioning system (GPS) logger deployed on the same individual, which is similar to the biologging methods presently being developed and used for many other species. We then considered the value of each technique as a conservation tool operating at the small scale (foraging area <5000 ha and duration <1 day).

We found that the separately deployed satellite transmitters significantly underestimated the penguins' foraging area size. However, the size of the foraging area and other foraging parameters, such as total distance travelled, were influenced by the degree of GPS location sub-sampling. Furthermore, only the combined diving and GPS loggers could confidently describe the diving behaviour of the penguins in relation to the sea floor and identify that they were using small areas of conservation interest (shipping channel) inside their foraging area. Hence, the method employed to assess habitat use at fine scales can influence conservation measures that rely upon the data collected. We suggest that researchers fast-track their adoption of high resolution multi-loggers for increased data confidence when tracking animals at a fine scale, but also consider the potential effect of sampling rate on the calculation of parameters of interest.

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1. Introduction

Biologging science (use of animal-attached devices, Rutz and Hays, 2009) is commonly employed to identify animal foraging behaviour and areas of conservation significance in a wide range of species (Cooke, 2008). In the marine environment, biologging is often conducted on vertebrates that travel over extensive spatial and temporal scales such as turtles, seals, whales and seabirds (e.g. Guinet et al., 1997; Hays et al., 2006; Kirkwood et al., 2006; Robinson et al., 2007; Lagerquist et al., 2008). However, many breeding colonies and populations of marine vertebrates that are restricted to shallow environments are necessarily coastal, and often coincide with anthropogenic pressures such as run-off pollution, development, fishing, boating and dredging (for example Borboroglu and Yorio, 2007; Hines et al., 2008; Skov and Thomsen, 2008). Conservation of animals that live within such inshore areas requires accurate information about their movements and home range in order to designate appropriate protective measures, such as marine protected areas. Studies of animal movements within coastal areas

have been conducted using both Argos (Boersma et al., 2002; Thompson et al., 2003; Zbinden et al., 2007; Seney and Landry, 2008) and global positioning system (GPS) technologies (Heithaus et al., 2002; Schofield et al., 2007; Nanami and Yamada, 2008), yet few studies have compared the efficacy of these techniques to calculate animal movements at small spatial and temporal scales in the marine environment (Yasuda and Arai, 2005; Hazel, 2009).

The Argos satellite network is used to remotely identify the location of many marine vertebrates, but the raw data from this system often gives inaccurate positions (Vincent et al., 2002; Costa et al., 2010). Over large spatial and temporal scales these locations may still prove useful in identifying general movement patterns (Tougaard et al., 2008), but at the small scale position accuracy is very important (Hays et al., 2001) and a high degree of data filtering is required, removing a large number of the locations. To better understand the behaviour of a diving animal it is important to identify its vertical distribution, commonly determined through the use of diving recorders. However, diving data alone do not provide direct information on location at sea. Use of a combination of location and depth to determine the movement of diving animals is becoming more common, particularly with the recent advancements in GPS technology (e.g. Gremillet et al., 2004; Mattern et al., 2007; Schofield et al., 2007), which is able to provide a greater number of locations and accuracy than the Argos network. In some systems the Argos

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network is now being used as a means to remotely transmit data that has been collected by GPS and/or depth loggers back to the user (e.g. Fossette et al., 2008; Sims et al., 2009; Schofield et al., 2010), removing the necessity to retrieve the logging devices.

A good example of a spatially restricted forager is the little penguin (*Eudyptula minor*), distributed through southern Australia and New Zealand. Little penguins are a colonial species that have one of the smallest foraging ranges among seabirds during breeding (Dann and Norman, 2006). The movement of little penguins at sea has been examined through the use of radio-transmitters, satellite transmitters (also known as platform terminal transmitters, PTT) and diving loggers (time-depth recorders, TDR) in a number of studies (e.g. Collins et al., 1999; Ropert-Coudert et al., 2003; Chiaradia et al., 2007; Hoskins et al., 2008; Fallow et al., 2009) that have examined vertical and horizontal activity ranges and diurnal patterns. However, none of these studies have combined location with diving behaviour in the same individual at the same time, due to size limitations of devices that can be used on this small species (approx. 1 kg adult body mass). This means that interpretation of penguin behaviour at sea has been limited to assumptions made from location and dive data collected separately, which has caveats as a management tool. For instance, in our initial study using satellite transmitter and diving logger data collected separately in 2006, we considered it highly likely that the penguin foraging area overlapped with a shipping channel subject to a major dredging project, but we were unable to confirm this with a high level of certainty (Preston et al., 2008).

In this study, we used a miniaturized GPS device that was small enough to be deployed together with a diving logger on little penguins. By combining the GPS with a diving logger on the same individual, we eliminated the problems of interpretation associated from separately collected location and diving data. We analysed how this high resolution multi-logger approach compared with separately deployed satellite transmitters and dive loggers. Our aim was to determine if data on animal distribution and behaviour differed significantly between the two biologging techniques when collected over small spatial (<5000 ha) and temporal (<1 day) scales. In doing so, we also sub-sampled the GPS data at a number of time intervals to examine whether different data collection rates effected calculation of foraging parameters. This study is particularly relevant as the current trend in biologging research continues toward developing higher resolution multi-logging devices. The results of this study could be particularly useful to researchers and managers working with inshore species that require biologging information on which to base conservation decisions.

2. Methods

2.1. Study site and field procedures

The St Kilda colony of little penguins numbers approximately 800 individuals and is located on the St Kilda breakwater, Melbourne, Australia, within close proximity to commercial shipping channels (37° 51' S, 144° 57' E, Fig. 1). The study site and field work is described in detail in Preston et al. (2008). Externally attached diving and location recording devices were deployed on breeding penguins during the 2007 and 2008 breeding seasons (approximately October–December). Deepening of the shipping channels occurred in the non-breeding season between the two sampling periods. Thus, there was no turbidity as a result of dredging activity during the time of our sampling, which may affect penguin foraging because they are visual predators (Cannell and Cullen, 1998).

To permit comparison between the two methods, this study considered only single foraging trips made by penguins at the chick-guard stage (first 2-weeks after hatching) when the trip duration is one day (considered typical at this stage of breeding, Chiaradia and Nisbet, 2006). We used data from 13 penguins fitted with a PTT and

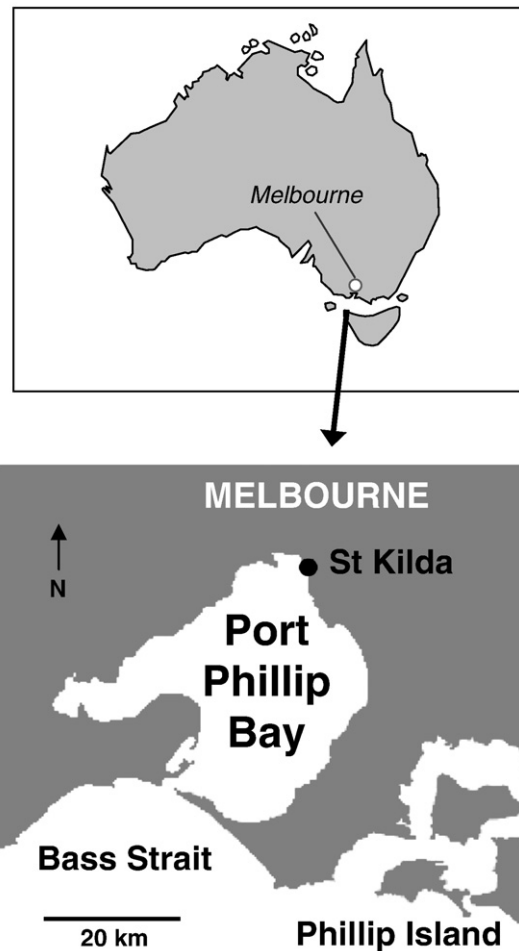


Fig. 1. Location of St Kilda penguin colony in Port Phillip bay where penguins forage.

five penguins fitted with a TDR in 2007, and 17 penguins fitted with both a GPS and TDR in 2008.

The PTTs used were Sirtrack KiwiSat 202 (New Zealand, 60 × 31 × 20 mm, cross-sectional area 514 mm², mass in air 43 g, 18 cm antenna spring mounted at 60°) operating on the Argos satellite network and the time-depth recorders were Cefas G5 (United Kingdom, 36 × 11 mm, cross-sectional area 95 mm², mass in air 5.8 g, set to record pressure and temperature at 1 s intervals).

The same TDR units were used in 2008, together with the mini-GPSlog by Earth & Ocean Technologies (Germany, 46.5 × 31 × 16 mm, cross-sectional area 496 mm², mass in air 29 g, acquisition time 1 to 3 s). The TDR was attached horizontally to the lower end of the GPS with waterproof tape (Tesa® 4651) to improve streamlining (GPS plus TDR mass in air, including tape, 37.7 g). Both GPS and TDR clocks were synchronised on the same computer to local time (eastern Australian daylight-savings) and were set to start approximately 1–2 h before sunrise when penguins left the colony. The GPS only recorded locations when the penguin was at the surface, but it was in continuous search mode (recording interval of 1 s) as the battery was able to last the length of the full deployment (1 day) and trials with longer search intervals were unsuccessful (A. Chiaradia and T. Preston, unpublished data).

All devices were attached using waterproof tape (Wilson et al., 1997) and a strip of adhesive compound (Mastic, Denso) to feathers along the mid-line of the lower back. Attachment and removal of all devices took <5 min and penguins were weighed to the nearest 10 g before and after deployments. Devices were retrieved for data

download when the penguins returned to the colony in the evening of the day of deployment.

2.2. Data analyses

Dive profiles were analysed using Multi-Trace Dive (Jensen Software Systems, Germany) with 1 m as the dive threshold. The following parameters were compared over the 2 years using Welch's (for unequal sample size) or randomization (for non-normality) *t*-tests: total number of dives, dive depth, dives with a bottom phase (period of dive when vertical speed first drops below and last rises above 0.25 m s^{-1}), bottom phase proportion of dive and number of dives to the intra-depth zone (based on dives within 1 m of previous dive, which is more appropriate to our data logger accuracy at these shallow depths than the 10% threshold of Tremblay and Cherel, 2000). The experimental design was randomised, with TDRs deployed on 5 individuals (2 males and 3 females) in 2007 and 17 individuals (10 males and 7 females) in 2008.

PTT data were filtered to exclude all Argos location class (LC) 0, A, B and Z positions (for which no estimate of error is provided, CLS, 2008), leaving only positions with an accuracy of between 250 and 1500 m or better (this has recently been revised up from 150 to 1000 m or better, CLS, 2008). Positions from GPS with horizontal dilution of precision >9 were filtered out of the dataset and accuracy of at least 90% of positions was within 6 m. Swimming speeds greater than the maximum of 3.3 ms^{-1} for little penguins were also filtered out of both types of data (Bethge et al., 1997). GPS data was further sub-sampled at 10 s, 1 min, 10 min, 30 min and 1 h time scales to represent various data collection regimes (Wilson et al., 1995). Each time interval was taken as a minimum period between locations, to simulate biologging interval mode where the GPS is switched off for certain periods of time to conserve battery power.

Satellite data were plotted using ArcGIS 9.1 (ESRI, Redlands, CA, U.S.A.). PTTs were deployed on 13 individuals in 2007 (5 males and 8 females) and 17 in 2008 (10 males and 7 females). Location parameters were analysed using randomised, type III, two-factor ANOVA models since the design was unbalanced and several penguins were re-sampled in consecutive years. Specifically, models were used to investigate differences in: maximum straight-line distance from the colony, total distance travelled (assuming straight line travel between successive locations), total foraging area (90% kernel density estimators, Borger et al., 2006) and amount of shipping channel occupied (expressed as a percentage of the total length of the shipping channel) between sexes and years. These variables were calculated using Hawth's Analysis Tools extension (downloaded from <http://www.spatialecology.com/index.php/3/3/09>).

Combined GPS and TDR data were used to compare the diving depth with water depth and the amount of time spent at each water depth (where GPS data were available). Water depth was determined every 5 min (or as close as possible thereto) along the GPS path using bathymetry data of the foraging area plotted in 5 m contours (provided by D. Ball, Department of Primary Industries, Victoria, Australia). Intervals of 5 min were appropriate to the accuracy of our bathymetry data and the maximum speed at which little penguins can travel (Bethge et al., 1997). Calculating the proximity of dives to

the sea floor was limited by the accuracy of the bathymetry data (plotted in 5 m bins) and the shipping channel was assigned to a depth of 15.5 m (the depth it is maintained to, although it may be deeper in parts).

We examined the proportion of dives repeatedly made to the same depth (intra-depth zone dives, IDZ) at each known depth and whether those IDZ dives were benthic, as this pattern of diving often indicates (Tremblay and Cherel, 2000). Further, we determined the proportion of time spent and dives made by penguins in the shipping channel, the area of main conservation interest.

Statistical analysis was conducted using R (R Development Core Team, 2009). The statistical threshold was set at $P < 0.05$ and results are presented as mean \pm s.e.

3. Results

3.1. Comparing methods

Body mass did not differ significantly between sexes and consecutive years after deployment for both PTT or combined GPS/TDR devices ($P > 0.05$, mean weight change PTT: $20 \pm 9 \text{ g}$, GPS/TDR: $12 \pm 13 \text{ g}$).

3.2. Diving behaviour

The number of intra-depth zone dives made by individuals was significantly higher (approximately 24% on average) in 2008 than in 2007 ($t = 3.13$, randomisations = 5000, $P = 0.009$). There were no significant differences in other diving parameters measured between years (Table 1).

3.3. Penguin location

Initial filtering resulted in a mean of 11766 ± 1103 GPS locations per day compared with 8 ± 1 for the PTT. After we sub-sampled the GPS data at several time intervals and compared the results to the satellite tracking data, we found in all cases that both the number of locations and size of the foraging area significantly greater (Table 2). Maximum distance travelled from the colony did not differ between the two methods at any of the GPS sub-sampling levels and the total distance travelled was only significantly different from that calculated from the PTT data when GPS data were sub-sampled at 10 s. The amount of the shipping channel covered by the foraging area was significantly greater when calculated from the GPS compared to the PTT data, at 1, 10 and 30 min intervals (Fig. 2).

The mean size of the foraging area was greatest when calculated at the 10 min interval for GPS data, followed by the shorter time intervals of 1 min and 10 s (Fig. 3). For GPS data, estimates of the total distance travelled were quite low at the larger time intervals, increasing to distances slightly greater than that calculated by the PTT when sub-sampled at 10 min intervals (Fig. 4). The shortest sub-sampling time intervals of 1 min and 10 s gave the greatest estimate of the mean total distance travelled.

It is noted that there were no significant effects of sex, nor sex by year interactions for all location parameters (not presented).

Table 1

Mean values of diving parameters measured in 2007 and 2008 are presented in left hand columns. Results of statistical tests performed on data collected using the two methods are presented in the right hand columns (significant *P*-values in bold).

Diving parameters	2007 Mean \pm se	2008 Mean \pm se	df	<i>t</i> (<i>t</i> -test)	<i>P</i> -value
Number of dives	776.4 \pm 58.4	825.4 \pm 28.4	6.0	0.75 (Welch's)	0.479
Dive depth (m)	8.6 \pm 0.8	7.7 \pm 0.4	6.0	0.96 (Welch's)	0.375
Dives with bottom phase (%)	74.0 \pm 1.7	78.2 \pm 1.6	<i>R</i> = 5000	1.79 (Randomization)	0.051
Bottom phase as % total dive	44.6 \pm 1.8	46.1 \pm 0.9	5.9	−0.77 (Welch's)	0.475
Dives to intra-depth zone (%)	43.8 \pm 1.8	55.3 \pm 3.2	<i>R</i> = 5000	−3.13 (Randomization)	0.009

Table 2
Location parameters measured using the PTT and GPS sub-sampled at different time intervals. The difference between the PTT and GPS values are presented, significant *P*-values in bold.

Parameters	PTT		GPS 1 h		GPS 30 min		GPS 10 min		GPS 1 min		GPS 10 s	
	Mean ± se	<i>F, P</i>	Mean ± se	<i>F, P</i>	Mean ± se	<i>F, P</i>	Mean ± se	<i>F, P</i>	Mean ± se	<i>F, P</i>	Mean ± se	<i>F, P</i>
# Locations	8.1 ± 1.2	5.042(1,26), 0.034	10.8 ± 0.5	47.275(1,26), < 0.001	19.6 ± 1.1	47.275(1,26), < 0.001	49.8 ± 3.9	76.937(1,26), < 0.001	377.1 ± 36.3	4.268(1,26), 0.049	1353.6 ± 132.2	70.742(1,26), < 0.001
Area (ha)	727.8 ± 84.5	6.531(1,26), 0.017	993.8 ± 67.3	15.295(1,26), < 0.001	1382.4 ± 127.7	15.295(1,26), < 0.001	1557.5 ± 162.5	16.194(1,26), < 0.001	1487.7 ± 157.5	14.360(1,26), < 0.001	1402.0 ± 152.9	11.949(1,26), 0.002
Max distance (km)	11.1 ± 1.8	0.001(1,26), 0.981	11.2 ± 1.1	0.212(1,26), 0.649	10.2 ± 1.1	0.138(1,26), 0.713	10.4 ± 1.1	0.138(1,26), 0.713	10.5 ± 1.0	0.100(1,26), 0.754	10.5 ± 1.0	0.100(1,26), 0.754
Total distance (km)	26.0 ± 3.0	0.218(1,26), 0.645	24.3 ± 2.3	0.627(1,26), 0.436	23.2 ± 1.9	0.522(1,26), 0.476	28.5 ± 1.9	0.522(1,26), 0.476	32.91 ± 1.8	4.107(1,26), 0.053	34.6 ± 1.8	6.319(1,26), 0.018
Shipping channel (%)	7.8 ± 2.3	1.104(1,26), 0.303	11.0 ± 2.9	4.571(1,26), 0.043	15.6 ± 3.1	4.571(1,26), 0.043	16.8 ± 3.3	5.281(1,26), 0.029	15.3 ± 3.2	70.834(1,26), < 0.001	15.3 ± 3.6	3.577(1,26), 0.069

3.4. Combined GPS and TDR: where both position and diving information are known

During periods of extensive diving, little penguins did not stay at the surface long enough for the GPS to record their location. Hence, all results presented here are from when both location and diving information are known, which accounts for 50.3% of the dives recorded during 2008.

Penguins spent an equal amount of time in areas that were 15 and 20 m deep, which constituted the major portion of the foraging area (Table 3). The amount of diving was roughly proportional to the time spent in an area. The least and greatest amount of dives were performed in regions that were 5 and 15 m deep, respectively.

Penguins showed a preference for performing dives to ≤10 m regardless of the water depth. Over 80% of time at sea was spent in areas ≥15 m, but only 35% of all dives were made to ≥11 m.

Intra-depth zone dives made to within ±1 m of the previous dive were common at the shallow depths and within the shipping channel, but less so at depths ≥20 m (Table 3). Approximately one-quarter (28%) of these IDZ dives appear to be benthic (within 5 m of the sea floor, excluding data from the 5 m and 10 m areas), with most (39%) occurring within the shipping channels.

4. Discussion

Global positioning systems are being increasingly used by biologists due to the greater number and accuracy of locations obtained compared to the commonly used Argos satellite tracking system. A lot of studies have focused on the usefulness of Argos and GPS to describe animal behaviour patterns at sea (Bradshaw et al., 2007; Jonsen et al., 2007; Tremblay et al., 2007; Pinaud, 2008), but few have examined how the calculation of marine animal home ranges differ using the two technologies at a small scale (Yasuda and Arai, 2005; Hazel, 2009). The work by Yasuda and Arai (2005) found that GPS data resulted in smaller, but more realistic, home range estimates due to the inclusion of Argos data from all location classes in their calculations and comparatively few GPS locations. Hazel (2009) on the other hand, who used approximately 50 times more GPS than Argos positions and only LC 1, 2 or 3 Argos locations, reported home ranges for green turtles were larger when calculated by Fastloc GPS. This is similar to the results obtained in our study, where GPS positions determined that little penguins used a foraging area around twice the size of that calculated from the satellite transmitters operating on the Argos system, when both datasets were stringently filtered.

However, inter-annual variations in home ranges may be accounted for by changes in environmental conditions in some cases (Schofield et al., 2010). Little penguin distribution is known to be affected by prey availability (Weavers, 1992; Collins et al., 1999), and at a small scale has been linked with sea-surface temperature (Hoskins et al., 2008) and the presence of thermoclines (Ropert-Coudert et al., 2009). Large amounts of rainfall in the catchment (which could potentially cause stratification in the otherwise well mixed shallow bay) did not occur during the period of our study in either year (rainfall data accessed at <http://www.bom.gov.au> 16/3/2010) and a slightly higher (approximately 1–2 °C) sea-surface temperature (SST) in the north of Port Phillip during 2007 (data accessed <http://www.earthsci.unimelb.edu.au/~awatkins/temps.html> accessed 16/3/2010) did not result in a greater foraging area that year, as would be predicted based on typical prey responses to SST (Hobday, 1992; Mickelson et al., 1992). Therefore, considering that maximum distances travelled from the colony did not differ between the 2 years and the overall pattern of distribution looked very similar, the differences between foraging area size can be attributed to the different methods used and the significantly different number of locations obtained. The number of locations is also responsible for differences between GPS time intervals in calculating

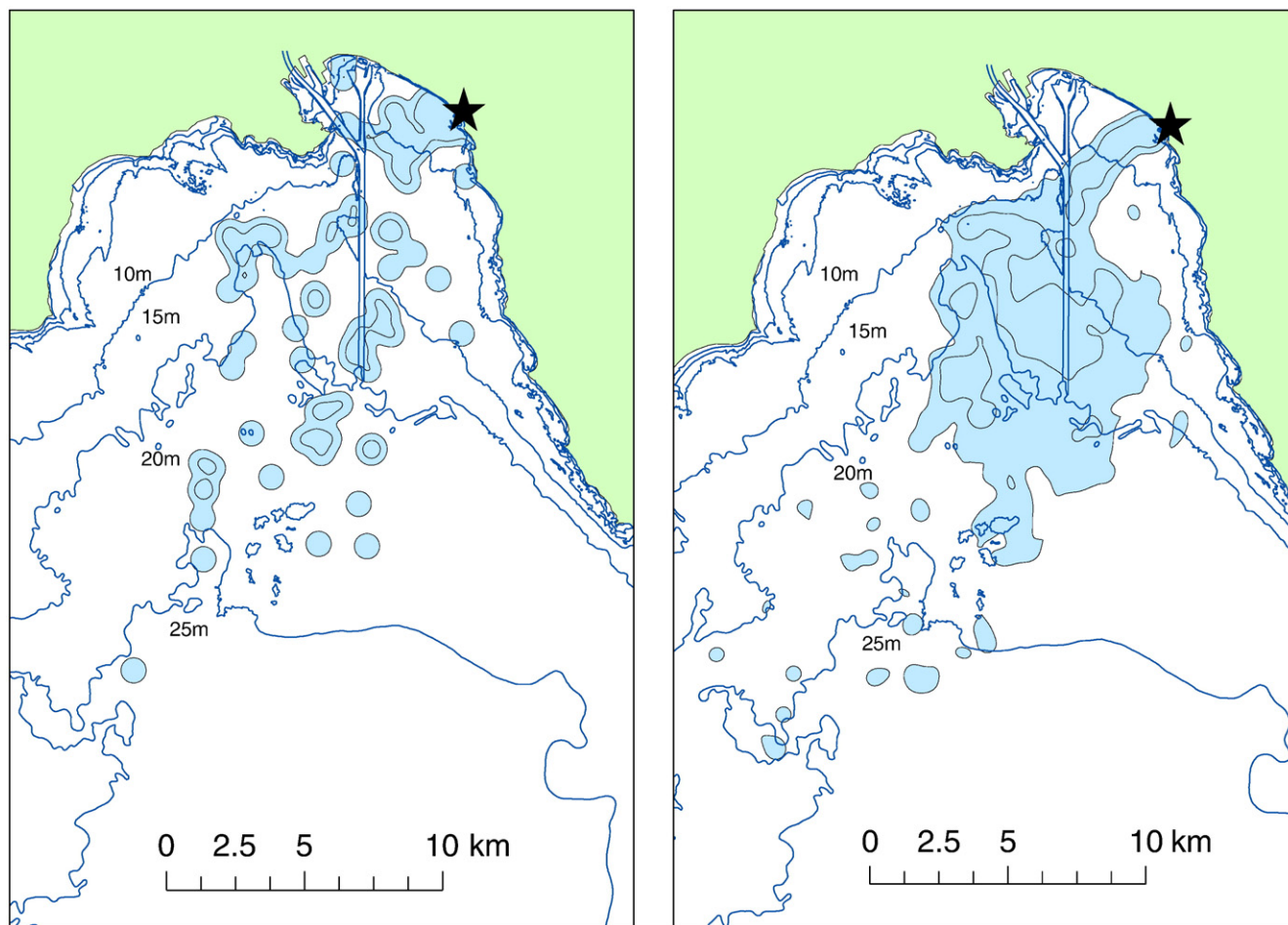


Fig. 2. Penguin foraging areas calculated by 90% fixed kernel density estimators based on PTT data (left) and GPS data sub-sampled at 10 min intervals (right). Location of penguin colony is indicated with star and bathymetry (including that of the shipping channel) is in dark blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

total distance travelled (Ryan et al., 2004), foraging area size and amount of shipping channels contained within the foraging area.

A distinct advantage of the combined GPS and TDR over the separately deployed PTT and TDR was that it provided simultaneous information on the penguin's three-dimensional space usage, which

is essential in conservation applications for animals with limited foraging ranges. GPS data were also capable of describing penguin behaviour within the small, defined area of the shipping channel in much greater detail than the satellite transmitter. This is due both to

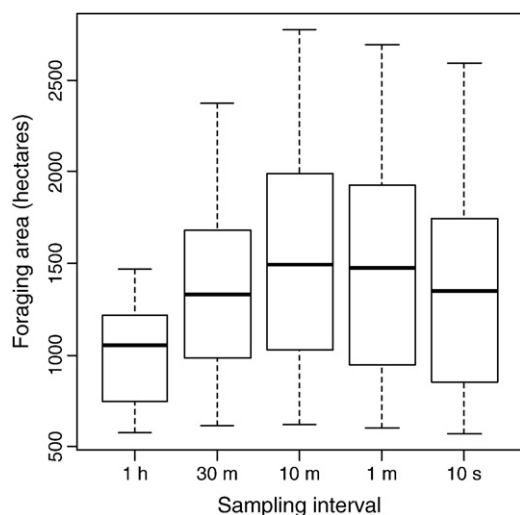


Fig. 3. Foraging area calculated from GPS data sub-sampled at various time intervals.

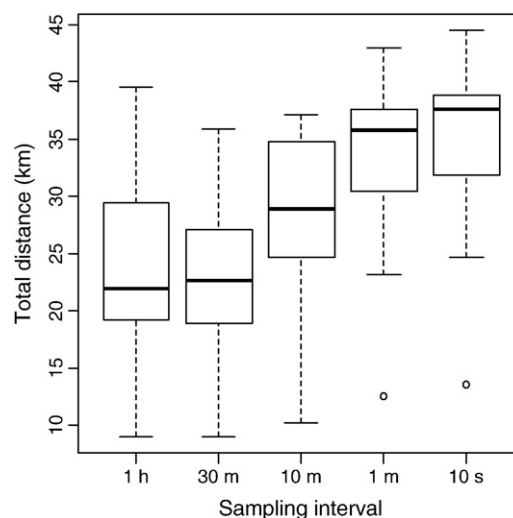


Fig. 4. Total daily distance swum by penguins calculated from GPS data sub-sampled at various time intervals.

Table 3
Foraging zone and diving behaviour by water depth, where known from GPS locations (filtered by 10 min intervals).

Sea depth (m)	Mean dive depth (m)	% Foraging zone	% Time spent	% Dives made	% Dives IDZ
5	2.45 ± 0.21	3.8	6.2	0.9	50
10	5.32 ± 0.10	16.3	13.0	14.7	69.9
15	8.48 ± 0.07	28.0	32.6	37.3	48.7
20	9.95 ± 0.12	44.5	32.6	29.8	31.6
25	10.54 ± 0.40	4.3	4.2	4.4	23.5
Shipping channel	7.73 ± 0.15	3.0	11.4	13.0	62.3

the number and accuracy (within 6 m) of those locations collected by the GPS. Even with the best location accuracy of the PTT on the Argos network (to within 250 m), the data are of limited value when determining use of small habitat areas in the penguin's activity range such as the shipping channel (that is approximately 200 m wide). Further, given that errors are often greater than that reported by the service provider (see Hazel, 2009 for review), the use of the PTT data at this scale for conservation purposes is open to criticism that may undermine the results presented. Prior to the use of GPS, we speculated that penguins were making benthic dives in the channel and pursuing prey from below (Preston et al., 2008). Deepening of the channel occurred before our device deployments in 2008, so we cannot be certain as to whether the increased depth has altered penguin behaviour in this area. However, our results show that a large amount of diving made in the channels is benthic and the penguins spend a disproportionately high amount of time there compared to the size it occupies within the foraging range, so the shipping channel appears to be an important foraging area for this colony.

This study compared two different methods of describing foraging behaviour using externally attached devices of three different sizes, which can potentially affect the behaviour of little penguins (Ropert-Coudert et al., 2007). The larger cross-sectional area and drag created by the external antenna of the satellite transmitter may have had a greater affect on the foraging behaviour of the penguins than the combined GPS and diving loggers, but the change in penguin body mass after deployment with these devices was not significantly different. This suggests that the significant differences between years for the size of the foraging area are a result of the higher number of locations collected by the GPS, which would affect calculation of kernel density estimators, rather than an effect of the different devices used in this study. Additionally, we found no significant differences in the number of dives or bottom phase proportion of the dive, parameters that are likely to change as a result of device size (Ropert-Coudert et al., 2007), thus it is unlikely that there was an effect on the diving behaviour between the methods used.

Most diving parameters measured were similar in both years, but the interpretation of 2007 diving behaviour was limited as geographic location was unknown. In studies of fish, horizontal movements are often interpreted from barometric pressure or light determined from diving recorders (Le Port et al., 2008; Hobson et al., 2009). Likewise, with penguins the shape of dives or intra-depth zone dives may give an indication of which part of the water column penguins are utilizing (Tremblay and Chérel, 2000; Hoskins et al., 2008). Penguins in this study made most of their dives with long bottom phases indicative of demersal diving (Ropert-Coudert et al., 2006) and commonly made dives to the intra-depth zone, which may be indicative of benthic diving when repeatedly made within a diving bout (Tremblay and Chérel, 2000). However, when diving profiles were combined with penguin location, we found that most of the dives were performed to mid-water in areas 15–20 m. About a quarter of intra-depth zone dives were made to within 5 m of the sea floor (the accuracy of our bathymetric data) and thus, the majority of the flat bottomed demersal dives were actually performed mid-water column. Visual examination of the diving bouts in areas of known depth suggests

that the penguins employ some diving strategies near to the sea floor, but more dives are made to the mid-water column than previously thought (Preston et al., 2008).

Use of highly accurate combined location and diving data provided better estimates of the area used by foraging animals, and were also capable of identifying behaviour within small areas of interest, such as the shipping channel, which was not possible with separately collected data or location data with the accuracy of the Argos network. However, the calculation of parameters varied depending on the time interval GPS data at which was sub-sampled. Compared with 1 h and 30 min GPS intervals the PTT provided a greater estimate of total distance travelled, which may due to relative error associated with PTT that may artificially increase the distance between actual concurrent locations. The higher total foraging distances calculated by 10 s and 1 min GPS sub-sampling are more representative of actual foraging length, as they are approximately 70% of the total length calculated from all 1 s GPS data, which takes into account the influence of measurement error (Ryan et al., 2004). Overall, we found that the data collected at short-medium time intervals provided us with the greatest estimates for each of the foraging parameters and was also suitable for describing diving behaviour in relation to the sea floor.

Further improvements to our data collection method could be made by using GPS units with longer battery life to provide more sampling time. Improving miniaturized Fastloc® or TrackTag® GPS units to be used on diving animals would provide quicker acquisition of positions for diving animals during periods of extensive diving (Rutz and Hays, 2009). The results of our study justify the continued advancement and use of biologging technologies, including the miniaturization of devices that is required for many small animals (Burger and Shaffer, 2008), such as little penguins. Of particular benefit from these technological developments will be animals that forage over small temporal and spatial scales, or within coastal areas that are subject to a high level of anthropogenic disturbance.

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Glossary

- Biologging:** the science of attaching remote logging or tracking devices to animals, to record information on their movements, behaviour and environment
- GPS:** global positioning system
- TDR:** time-depth recorder, a biologging device to record animal dives
- PTT:** platform terminal transmitter, satellite tracking biologging device
- Argos:** a global satellite network