Vol. 562: 163–179, 2016
doi: 10.3354/meps11972

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 29

# Long-term and seasonal patterns of sea turtle home ranges in warm coastal foraging habitats: implications for conservation

**Takahiro Shimada[1,2,*], Rhondda Jones[3], Colin Limpus[4], Rachel Groom[5], Mark Hamann[1,2]**

[1]College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia
[2]Centre for Tropical Water and Aquatic Ecosystem Research, James Cook University, Townsville, Queensland 4811, Australia
[3]Division of Tropical Health & Medicine, James Cook University, Townsville, Queensland 4811, Australia
[4]Queensland Department of Environment and Heritage Protection, Brisbane, Queensland 4102, Australia
[5]Northern Territory Department of Land Resource Management, Flora and Fauna Division, Marine Ecosystems Group, Darwin 0828, Australia

ABSTRACT: Home range analysis is a powerful tool for identifying priority areas for conservation, but estimating the home range for many species is still challenging. In particular, highly mobile species may use different areas at different times (e.g. summer or winter), so temporally biased location data may only partially represent their home range. We investigated the temporal patterns in habitat use of green turtles *Chelonia mydas* (n = 52) and loggerhead turtles *Caretta caretta* (n = 20) at longer (>1 yr) and shorter (<1 yr) scales. The study was conducted in subtropical and tropical foraging habitats along the Queensland coast of Australia between 1991 and 2015. Each turtle was tracked by a satellite-linked tag for the effective life of the device; 3 turtles were tracked twice. Mark–recapture studies were also conducted intermittently. Single satellite-tag deployments confirmed site fidelity to a foraging habitat for up to 2.5 yr in green turtles and 2.7 yr in loggerhead turtles. Further, combining satellite telemetry and mark–recapture records indicated much longer periods of foraging residency, up to 17 yr for green turtles and 23 yr for loggerhead turtles. No tracked turtles made substantial changes in their foraging range between years. Within the long-term home range, subtropical turtles tended to shift their foraging areas seasonally. Consequently, for many turtles, the existing conservation legislation provided protection in some seasons but not others. Our results emphasise the importance of protecting areas according to the turtles' use of space, with careful consideration given to identify temporal trends in their habitat selection.

KEY WORDS: Home range · Site fidelity · Seasonal shift · Satellite telemetry · Sea turtles · *Chelonia mydas* · *Caretta caretta*



## INTRODUCTION

Conservation goals for wildlife species and their habitats can be achieved through spatial management such as activity exclusion/restriction zones and marine protected areas (Hooker & Gerber 2004, Pressey et al. 2007, Gaines et al. 2010, McCay & Jones 2011). These types of protection have been applied at both large ecological scales (e.g. the Great Barrier Reef; Fernandes et al. 2005) and smaller scales to manage threats to particular habitat zones (e.g. Macquarie Island; Environment Australia 2001) or species of conservation concern (e.g. dugong and sea turtles; McCook et al. 2010). For effective species protection, it has become increasingly clear that the spatial extent of species' habitat use and the spatial

*Corresponding author: takahiro.shimada@my.jcu.edu.au

extent of the management intervention, such as a protected area, should match (Dryden et al. 2008, Whittock et al. 2014, Cleguer et al. 2015). Designating protected areas without considering animals' use of space may not achieve the conservation goals for species and their key habitats (Rojas-Bracho et al. 2006, Schofield et al. 2013b).

Home range analysis is a powerful tool to identify priority areas for conservation, or 'hotspots' (e.g. Maxwell et al. 2011, Peckham et al. 2011). Burt (1943) defined home range as the area where an animal normally travels in search of food during a given period of its life. Thus, the term 'home range' may be used for the entire area used during the life of the animal, or for the areas used during a particular time of its life (e.g. foraging or breeding): we adopted the latter definition of home range in this study.

Reliable estimation of home ranges requires accurate location data, appropriate analytical methods and monitoring of animals for prolonged periods (Powell 2000, Laver & Kelly 2008). Since the establishment of the home range concept (Burt 1943), there have been substantial advances in the tools used to collect accurate location data (Ropert-Coudert & Wilson 2005, Rutz & Hays 2009) and to objectively quantify the home range of animals (e.g. Benhamou 2011, Cumming & Cornélis 2012). Despite these advances, estimating home range for many species is still challenging. Highly mobile species may use different habitats at different times of day, year or during different life stages, so temporally biased location data may only partially represent their habitat use. Clearly, understanding temporal variation in animal movement is essential for defining reliable home ranges (Fieberg & Börger 2012, Powell & Mitchell 2012).

Green turtles *Chelonia mydas* and loggerhead turtles *Caretta caretta* are highly mobile species of conservation concern (Seminoff 2004, Casale & Tucker 2015), making them priority targets for research and protection. Key knowledge gaps exist for their movements across space and time in foraging habitat, where they spend most of their lives (Musick & Limpus 1997, Bolten 2003, Godley et al. 2008, Hamann et al. 2010, Hays et al. 2016). Some turtles undertake seasonal movements between distant foraging habitats (tens to thousands of kilometres), but such long-distance foraging movements are typically seen in temperate waters (Morreale & Standora 2005, Hawkes et al. 2007, González Carman et al. 2012, Schofield et al. 2013a, Narazaki et al. 2015). Past research has found that seasonal foraging migrations are not common in subtropical and tropical coastal habitats, where foraging turtles generally show fidelity to more restricted geographic areas for many years (Musick & Limpus 1997, Limpus 2009, Hart & Fujisaki 2010). Yet the site fidelity observed in those studies does not preclude potential finer-scale seasonal movements by turtles foraging in warmer subtropical and tropical waters. Detection of such movements was generally beyond the technical limitation of the previous tracking methods (i.e. mark–recapture, radio/sonic telemetry, Argos satellite telemetry). Addressing this knowledge gap requires long-term, high-resolution tracking data. The newer Fastloc GPS (FGPS) tags, introduced in 2002 (Wildtrack Telemetry System), are capable of obtaining high-quality location data from marine animals with full-time global coverage (Rutz & Hays 2009, Hazen et al. 2012, Dujon et al. 2014), spanning from seasons to a few years (e.g. Shimada et al. 2016).

The primary objective of this study was to investigate the temporal variation in habitat use by green turtles and loggerhead turtles that forage along shallow coastal waters in Queensland, Australia. Both species are listed as threatened under Australian legislation (Environment Protection and Biodiversity Conservation Act 1999) due to past and current anthropogenic threats, and require comprehensive conservation efforts (Limpus 2009). We examined the temporal variation in home range size and site fidelity at longer (>1 yr) and shorter (<1 yr) scales for both species in order to find evidence for long-term site fidelity and also to investigate possible seasonal variation in habitat use.

Additionally, we wanted to explore the effects of extreme weather events on home range size and site fidelity of the turtles. During the present study (late 2010 to early 2011), the strongest La Niña events in 40 yr occurred in the South Pacific Ocean, and resulted in heavy rainfall and the tropical cyclones Tasha, Anthony, and Yasi hitting the north-eastern Australian coast. These events caused major flooding (Bureau of Meteorology 2012) and significant destruction of seagrass meadows (Devlin et al. 2012, McKenzie et al. 2012). In the months following the series of extreme weather events, sea turtle strandings along the Queensland coast were around 5 times greater than annual totals collected since 2000 (Meager & Limpus 2012). We hypothesised that sea turtles would respond to the weather events by extending their home ranges in search of food, and would consequently show lowered site fidelity compared to times without the extreme weather events. We tested this hypothesis by comparing the estimated home range size and site fidelity between months with and without influence of the extreme weather events.

## MATERIALS AND METHODS

### Field work

Data were collected from 52 green turtles and 20 loggerhead turtles in subtropical and tropical sites along north-eastern Australia (Fig. 1 and see Table S1 in the Supplement at www.int-res.com/articles/suppl/m562p163_supp.pdf). Turtles (n = 66) were captured using the rodeo method (Limpus 1978) at their foraging habitats in Moreton Bay, Sandy Strait, Port Curtis, Shoalwater Bay and Torres Strait (Fig. 1). Six loggerhead turtles were captured after successfully nesting at Mon Repos beach (Fig. 1). In all cases, turtles were taken to research bases on land or research vessels at sea to collect biological data and deploy satellite-linked tags. Study turtles were female and male adults as identified by gonad examination using laparoscopy, curved carapace length (CCL), combination of CCL and the tail length from carapace, or nesting activity (Limpus & Limpus 2003, Limpus et al. 2005). The body size (i.e. CCL) ranged from 85.6 to 121.2 cm (median = 105.7 cm) for green turtles and 85.5 to 100.7 cm (median = 94.9 cm) for loggerhead turtles (Table 1).

Each turtle was tracked at least once with a highly accurate Argos-linked FGPS tag between 2008 and 2014. Three loggerhead turtles were tracked twice: a male (T53800) that was first tracked with a platform terminal transmitter (PTT) in 1998–1999 and a second time with an FGPS tag in 2010–2012; a female (T14914) that was first tracked with a PTT in 1996–1997 and a second time with an FGPS tag in 2011–2012; and a female (T93038) that was first tracked in 2010 and second time in 2012 with FGPS tags on both occasions. No green turtle was tracked more than once. FGPS tags were set to acquire a GPS fix at intervals ranging from 15 min to 1 h. We mounted a

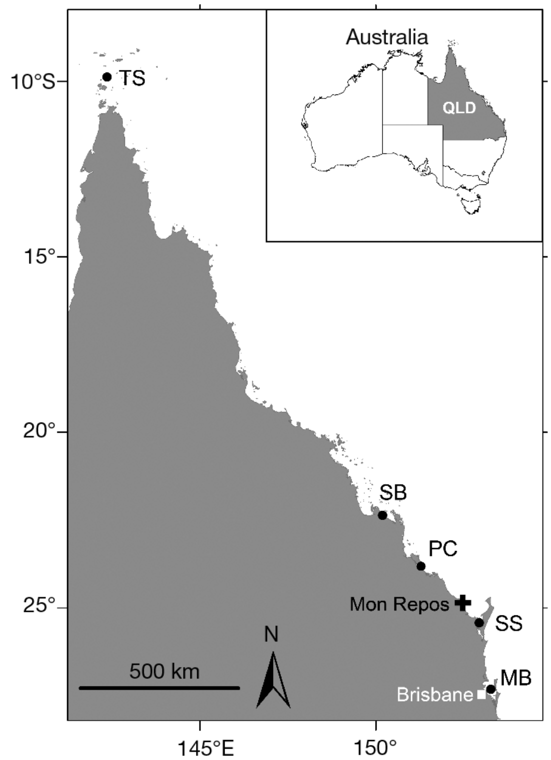


Fig. 1. Study sites in Queensland (QLD), Australia. MB: Moreton Bay, SS: Sandy Strait, PC: Port Curtis, SB: Shoalwater Bay, TS: Torres Strait

Table 1. Summary of study turtles, tracking data obtained from Argos-linked FGPS tags and the overall home range sizes (95% utilisation distributions, UDs) estimated using the entire sequence of fixes available for each turtle. See Fig. 1 for study sites. F: female, M: male, CCL: curved carapace length. Data are presented as the median with minimum and maximum values in parentheses

| Site | Sex | N | CCL (cm) | Tracking days | No. of fixes | 95% UD (km$^2$) |
|---|---|---|---|---|---|---|
| *Chelonia mydas* | | | | | | |
| MB | F | 16 | 110.5 (101.6–119.9) | 156 (22–350) | 977 (112–2131) | 42.5 (5.6–80.4) |
| | M | 2 | 95.1 (94.0–96.1) | 119 (107–132) | 1294 (849–1740) | 82.5 (70.3–94.8) |
| SS | F | 6 | 108.3 (106.1–121.2) | 301 (179–564) | 1466 (712–2678) | 61.8 (7.7–126.5) |
| | M | 0 | – | – | – | – |
| PC | F | 10 | 105.7 (89.0–116.6) | 98 (55–241) | 324 (130–723) | 24.9 (3.6–121.7) |
| | M | 8 | 96.0 (85.6–104.3) | 165 (66–240) | 647 (417–1378) | 17.9 (9.5–61.8) |
| SB | F | 6 | 98.9 (95.5–104.5) | 334 (140–778) | 1049 (225–14295) | 7.2 (2.8–25.1) |
| | M | 0 | – | – | – | – |
| TS | F | 4 | 103.8 (98.0–118.0) | 114 (45–202) | 604 (239–854) | 46.7 (5.1–166.3) |
| | M | 0 | – | – | – | – |
| *Caretta caretta* | | | | | | |
| MB | F | 11 | 95.2 (85.5–100.1) | 230 (56–999) | 802 (362–1824) | 23.9 (10.3–47.2) |
| | M | 9 | 94.4 (87.9–100.7) | 196 (59–906) | 747 (246–1004) | 24.0 (15.0–350.6) |

satellite-linked tag on the carapace of each turtle using epoxy glue and fibreglass. Each turtle was tracked after release until transmission ceased. Mark–recapture studies were also conducted intermittently before, between and after the telemetry studies.

### Data acquisition and preparation

Argos-linked FGPS devices provided both FGPS and Argos fixes. PTTs provided Argos fixes only. For tracks obtained with Argos-linked FGPS devices (n = 72), we merged FGPS fixes (>3 GPS satellites and residual error value <30) with high-quality Argos fixes (Location Classes 3, 2, 1). For tracks obtained with PTTs (n = 3), we used only high-quality Argos fixes. Data preparation and analyses were conducted using R software (R Core Team 2016).

Prior to analysis, satellite telemetry data were thoroughly screened by water depth, spatial and temporal duplicates and the data-driven filter as described by Shimada et al. (2012, 2016) using the R package SDLfilter (Shimada 2016). The water depth at each fix was estimated using bathymetry models (Daniell 2008, Beaman 2010) and tidal data provided by the Australian Bureau of Meteorology and Queensland Department of Transport and Main Roads. The data-driven filter improves the accuracy of satellite-derived data by removing fixes with high error; estimated mean error for filtered FGPS fixes is less than 50 m (Shimada et al. 2012).

The turtles captured in their foraging habitats were relocated between 0.2 and 28.1 km away from their capture point and subsequently tracked back to the area of capture (Shimada et al. 2016). The nesting loggerhead turtles were released on the same beach where they were captured, and tracked to their foraging habitats. We excluded fixes acquired prior to turtles' arrival at their foraging habitats (see Shimada et al. 2016). Our tracking data did not suggest any breeding activities adjacent to the described foraging habitats (i.e. no consecutive FGPS fixes at a fixed interval on a beach or at sea during the breeding season), confirming that the tracks used in the subsequent analyses represent only their foraging behaviour.

### Definition of home range and site fidelity

For each turtle, we used location data obtained from Argos-linked FGPS tags to estimate utilisation distributions (UDs) in 3 ways. Overall UD was estimated using the entire sequence of fixes available; yearly UDs were estimated using subsets of fixes grouped by a duration of 12 mo since the initial fix; and monthly UDs were estimated using subsets of fixes grouped by each calendar month.

Home range was defined as the areas containing 95% of a UD. That is, for each turtle, we estimated home range at 3 different time scales; overall home range using overall UD, yearly home ranges using yearly UDs and monthly home ranges using monthly UDs. Overall home range was only used to estimate the area used by each turtle during the entire tracking period. Yearly home range was used to visually compare habitat areas across years to look for evidence of long-term site fidelity. High-quality Argos fixes and mark–recapture locations were also used for the analysis with yearly home range. Monthly home range was used to estimate the home range size for each turtle in each calendar month, and also to examine seasonal effects on home range size.

As an index for site fidelity, we calculated mean integrated squared error (MISE) between pairs of monthly UDs for each turtle. MISE measures the difference between 2 UDs as:

$$\mathrm{MISE} = \frac{1}{n}\sum_{i=1}^{n}[f_1(x_i, y_i) - f_2(x_i, y_i)]^2 \quad (1)$$

where $n$ is the number of grid points, $x$ and $y$ are the longitude and latitude at each grid point, $f_1(x_i, y_i)$ and $f_2(x_i, y_i)$ are the estimated density at the $i^{\text{th}}$ grid point of 2 UDs estimated from different months. A smaller MISE indicates more similarity between UDs.

We estimated UDs using movement-based kernel density estimators (MKDEs) based on a biased random bridge (Benhamou & Cornélis 2010, Benhamou 2011). Since the MKDE is designed for auto-correlated movement data (Benhamou & Cornélis 2010, Benhamou 2011), we did not standardise temporal intervals between successive fixes prior to UD estimation. To avoid bias in kernel-based estimates resulting from small sample sizes, monthly UDs were only estimated for months when ≥50 fixes were available (Seaman et al. 1999, Blundell et al. 2001). We treated high tide lines as a boundary for UD estimation because foraging sea turtles rarely ascend to beaches above high tide lines within our study sites. As expressed in Eq. (1), MISE values are dependent on area size and number of grid points. Therefore, size of the areas analysed and grid resolution must be kept consistent throughout any UD estimation so that MISE values are comparable. We estimated each UD with a grid resolution of 50 m over a fixed area of

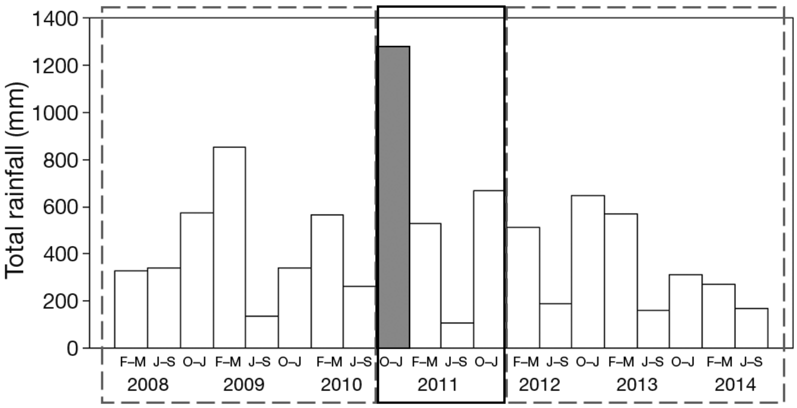


Fig. 2. Time frame in relation to the series of extreme weather events that occurred in Moreton Bay (shaded in grey). Solid line encloses the 'affected months' when the extreme weather events occurred, as well as the following 12 mo. Dotted lines enclose the 'normal months' before and after the 'affected months'. F–M: February to May; J–S: June to September; O–J: October to January. Rainfall data source: Bureau of Meteorology Station No. 40224

13 000 $km^2$, which was large enough to enclose fixes of every turtle at each study site. The R package adehabitatHR (Calenge 2006, 2015) was used to estimate the UDs and to obtain home range size for each turtle (see Table S2 in the Supplement for the parameters used).

**Factors potentially affecting home range size and site fidelity**

We examined effects of seasons and the extreme weather events on monthly home range size and site fidelity indices (i.e. MISE). We also included site and sex as covariates to account for their potential effects, given geographical variation in home range size in different study sites (e.g. Hart & Fujisaki 2010) and sexual variation in movements at a breeding site (Hays et al. 2001). However, our study only investigated the movements of non-breeding turtles in their foraging habitats.

We used changes in sea surface temperature (SST) as a surrogate variable for seasonal change since water temperature is mainly dependent on season. To test the effects of SST on monthly home range size, we estimated monthly SSTs by averaging the daily SST values for each month. To test the effect of SST on site fidelity, we calculated absolute differences in monthly SST (ΔSST) between any pairs of months for which MISE values were estimated. Daily SST was extracted from the NOAA High Resolution SST (0.25° resolution) database provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website (www.esrl.noaa.gov/psd/). Although calendar month can also represent seasonal change, we did not use both SST and calendar month as covariates in the same model because they were highly correlated, with variance inflation factors > 3 (Zuur et al. 2010).

To test the effects of the extreme weather events on monthly home range size, we associated each monthly home range with the timing of the extreme weather events. The months where extreme weather events occurred (October 2010 to January 2011) and the following 12 mo were regarded as 'affected months' (Fig. 2). We considered this time frame to be the period during which turtles may have been affected by degradation of food sources, because seagrass meadows were observed to start recovering within 12 mo following the extreme weather events (Rasheed et al. 2014), and similar rates of recovery were also observed in many species of seagrass under an experimental environment (Rasheed 2004). The months before and after the 'affected months' (before October 2010 and after January 2012) were regarded as 'normal months' (Fig. 2).

We grouped the MISE values into 2 categories to test the effect of extreme weather on site fidelity. The first group comprised MISE values between 2 'normal months'. The second group contained MISE values measured either between a 'normal month' and an 'affected month' or between 2 'affected months' (Fig. 2). The first group represents the range of shifts in habitat by turtles which occurred during the 'normal months', and the second group represents the degrees of shifts in habitat during the 'affected months' or between 'normal months' and 'affected months'.

However, the dataset was unbalanced in terms of weather, species, sex and sites. Only female green turtles in Moreton Bay, male green turtles in Port Curtis and loggerhead turtles of both sexes in Moreton Bay were tracked during the 'affected months'. Female green turtles were tracked at 5 sites but male green turtles were tracked only in Moreton Bay and Port Curtis. Both female and male loggerhead turtles were tracked only in Moreton Bay (Table 1).

We therefore used 5 different data subsets to investigate different questions about monthly home range size and site fidelity. The effects of weather were examined for female green turtles in Moreton Bay (Subset 1) and male green turtles in Port Curtis (Subset 2). The effect of site was only examined for female green turtles, which were tracked at 5 different sites

(Subset 3). We also examined the effects of sex for green turtles tracked in Moreton Bay and Port Curtis (Subset 4). Finally, the last data subset only used loggerhead turtles in Moreton Bay to examine the effects of sex and weather (Subset 5). The effect of SST was tested in all data subsets. We also tested the effect of sample size (i.e. number of fixes) on monthly home range size in all data subsets.

Finally, seasonal habitat shifts were examined in detail. We first extracted a data subset for which the first month of paired monthly UDs was in summer (i.e. December to February) so that shifts in habitats could be examined for a particular season. For example, if a pair of monthly UDs was estimated first in December 2010 (summer) and second in June 2011 (winter), the MISE value of the pair represents the difference in habitat area between summer and winter. We chose this data subset because, for both green and loggerhead turtles, temporal range (i.e. number of months apart between paired monthly UDs) was wider in this category than in the data subsets for which the first month of paired monthly UDs was in autumn, winter or spring.

### Statistical methods

We used generalised additive mixed models (GAMMs) to investigate factors that affected monthly home range sizes and site fidelity indices. Five different data subsets were used to test the effects of weather, site, sex, monthly SST or ΔSST and sample size. We tested for interaction effects between site and monthly SST or ΔSST when the data subset included turtles from multiple study sites. Since multiple UDs were estimated for each turtle (i.e. monthly UDs), we treated each turtle as a random effect to allow for within-turtle correlations. We verified that there was no issue with collinearity among covariates: variance inflation factors were all $<3$ (Zuur et al. 2010). We also used GAMMs to examine seasonal shifts in habitat by modelling MISE as a function of the number of months since summer. For clarity, fixed components of each model are specified in the Results. Fixed variables that were allowed to have a nonlinear effect are indicated as '$f$(variable)'. The GAMMs used an identity link with a Gaussian distribution error structure (Wood 2011). The optimal amount of smoothing was determined with the cross-validation process (Wood 2006). Wald tests were performed to examine the effect of each explanatory variable tested in the GAMMs. We used the R package mgcv to fit GAMMs and to perform the Wald tests (Wood 2016).

## RESULTS

### General properties of tracking data, home range and site fidelity

Tracking durations with Argos-linked FGPS tags ranged from 22 to 778 d (median = 158 d) for 52 green turtles, and from 56 to 999 d (median = 221 d) for 20 loggerhead turtles (Table 1). The estimated overall home range size of green turtles was highly variable, ranging from 2.8 to 166.3 km$^2$ with a median of 31.3 km$^2$ (Table 1). The variation in overall home range size was also large in loggerhead turtles, ranging from 10.3 to 350.6 km$^2$ with a median of 24.0 km$^2$ (Table 1).

Tracking duration in months, measured between the first and last month for which monthly home range was estimated, ranged from 1 to 26 mo (median = 5 mo) for green turtles and 2 to 30 mo (median = 4 mo) for loggerhead turtles. It is important to note that monthly home range was not estimated for every month during each tracking period due to a lack of fixes in some months (i.e. $n < 50$). Consequently, monthly home range was estimated for up to 26 different months (median = 4 mo) for each green turtle and up to 10 different months (median = 4 mo) for each loggerhead turtle. Monthly home range size ranged from 0.7 to 174.3 km$^2$ (median = 12.5 km$^2$) for green turtles, and from 1.7 to 424.7 km$^2$ (median = 15.8 km$^2$) for loggerhead turtles (Table 2). Variation in monthly home range size within each individual ranged from $<0.1$ to 152.7 km$^2$ (median = 3.9 km$^2$) for green turtles and from $<0.1$ to 400.2 km$^2$ (median = 8.9 km$^2$) for loggerhead turtles.

Monthly SST ranged from 18.2 to 30.4°C (median = 23.4°C) at 5 study sites when green turtles were tracked, and from 19.2 to 27.3°C (median = 23.0°C) in Moreton Bay when loggerhead turtles were tracked (Table 2). Using data associated with green turtles, we modelled ΔSST as a function of study sites in a generalised linear model (GLM) using log link with Gamma distribution. The likelihood ratio test, performed using the R package lmtest (Zeileis & Hothorn 2002), indicated a significant effect of study sites on ΔSST ($\chi^2 = 45.16$, df = 2, $p < 0.0001$). ΔSST was significantly smaller in Port Curtis and Torres Strait than in other sites (Fig. 3).

In total, 11 turtles were tracked for >1 yr: 5 female green turtles, 5 female loggerhead turtles and 1 male loggerhead turtle. In particular, >2 yr of tracking were achieved using a single satellite-tag deployment on 3 turtles: a female green turtle in Shoalwater Bay for 2.1 yr (Fig. 4a), a female loggerhead turtle in

Table 2. Summary statistics associated with monthly utilisation distributions (UDs) of the study turtles. See Fig. 1 for study sites. F: female, M: male, SST: sea surface temperature. Data are presented as the median with minimum and maximum values in parentheses. Monthly 95 % UD area for a turtle was estimated only for a month when ≥50 location fixes were acquired

| Site | Sex | No. fixes mo$^{-1}$ | 95 % UD (km$^2$ mo$^{-1}$) | SST (°C mo$^{-1}$) | ΔSST (°C between months) |
|---|---|---|---|---|---|
| *Chelonia mydas* | | | | | |
| MB | F | 101 (2–471) | 24.8 (1.8–97.7) | 23.6 (19.3–27.1) | 2.5 (0.2–6.5) |
| | M | 283 (43–462) | 39.2 (16.6–98.8) | 21.1 (19.7–22.6) | 1.4 (0.6–2.9) |
| SS | F | 122 (1–333) | 19.6 (0.7–127.2) | 22.4 (18.2–27.4) | 3.1 (<0.1–9.2) |
| | M | – | – | – | – |
| PC | F | 51 (1–294) | 10.3 (2.5–67.2) | 23.4 (19.6–27.0) | 1.2 (0.1–3.8) |
| | M | 105 (6–412) | 12.7 (3.5–50.3) | 21.8 (19.6–27.6) | 2.2 (0.1–7.2) |
| SB | F | 176 (1–700) | 4.9 (1.1–23.0) | 23.2 (19.9–28.0) | 2.7 (<0.1–8.2) |
| | M | – | – | – | – |
| TS | F | 79 (5–289) | 5.5 (3.5–174.3) | 28.2 (25.6–30.4) | 1.4 (0.5–4.5) |
| | M | – | – | – | – |
| *Caretta caretta* | | | | | |
| MB | F | 35 (1–490) | 11.8 (1.7–45.8) | 24.6 (19.2–27.3) | 1.8 (0.1–6.8) |
| | M | 37 (1–428) | 24.5 (4.8–424.7) | 21.8 (20.2–26.4) | 2.2 (<0.1–6.2) |

Moreton Bay for 2.7 yr (Fig. 4e) and a male loggerhead turtle in Moreton Bay for 2.5 yr (Fig. 4i). Each of the 11 turtles used overlapping home ranges repeatedly over multiple years (Fig. 4). Yearly home ranges of only 9 turtles are presented in Fig. 4 because second-year home ranges could not be estimated for 2 of the female green turtles due to an insufficient number of location fixes (i.e. <5 fixes) during the second year of tracking.

Further, over 3 yr of foraging residency was inferred for 5 green turtles (up to 17 yr) and for 12 loggerhead turtles (up to 23 yr) using the combination of satellite telemetry (up to 2 deployments per turtle) and intermittent mark–recapture records (Fig. 4, Table S1). Neither the satellite telemetry data nor mark–recapture records indicated shifts in foraging habitat by each turtle across years.

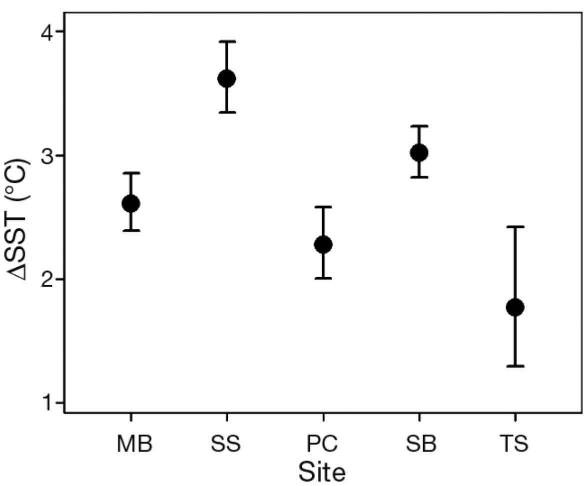


Fig. 3. Absolute difference in sea surface temperature (ΔSST) between any pairs of utilisation distributions (UDs) estimated for green turtles *Chelonia mydas* at 5 different study sites (see Fig. 1). Dots are generalised linear model fits with error bars denoting 95 % confidence intervals

## Monthly home range size

We asked 4 different questions related to monthly home range size using 5 subsets of the tracking data.

(1) We tested the effect of the extreme weather events on monthly home range size of female green turtles in Moreton Bay (Subset 1) and male green turtles in Port Curtis (Subset 2) in separate models. The model is:

$$\text{Monthly home range size} \sim \text{Weather} + f(\text{SST}) + \text{Sample size}$$

Neither weather, SST nor sample size was associated with variation in the monthly home range size (Table 3: Subset 1, 2). Based on these results, subsequent analyses used green turtle data regardless of association with the extreme weather events.

(2) We examined the geographical effects on monthly home range size of female green turtles tracked at 5 different study sites (Subset 3). The model is:

$$\text{Monthly home range size} \sim \text{Site} + f(\text{SST}){:}\text{Site} + \text{Sample size}$$

The sample size did not have a perceptible effect on the monthly home range size of the female green turtles. Site did affect monthly home range size

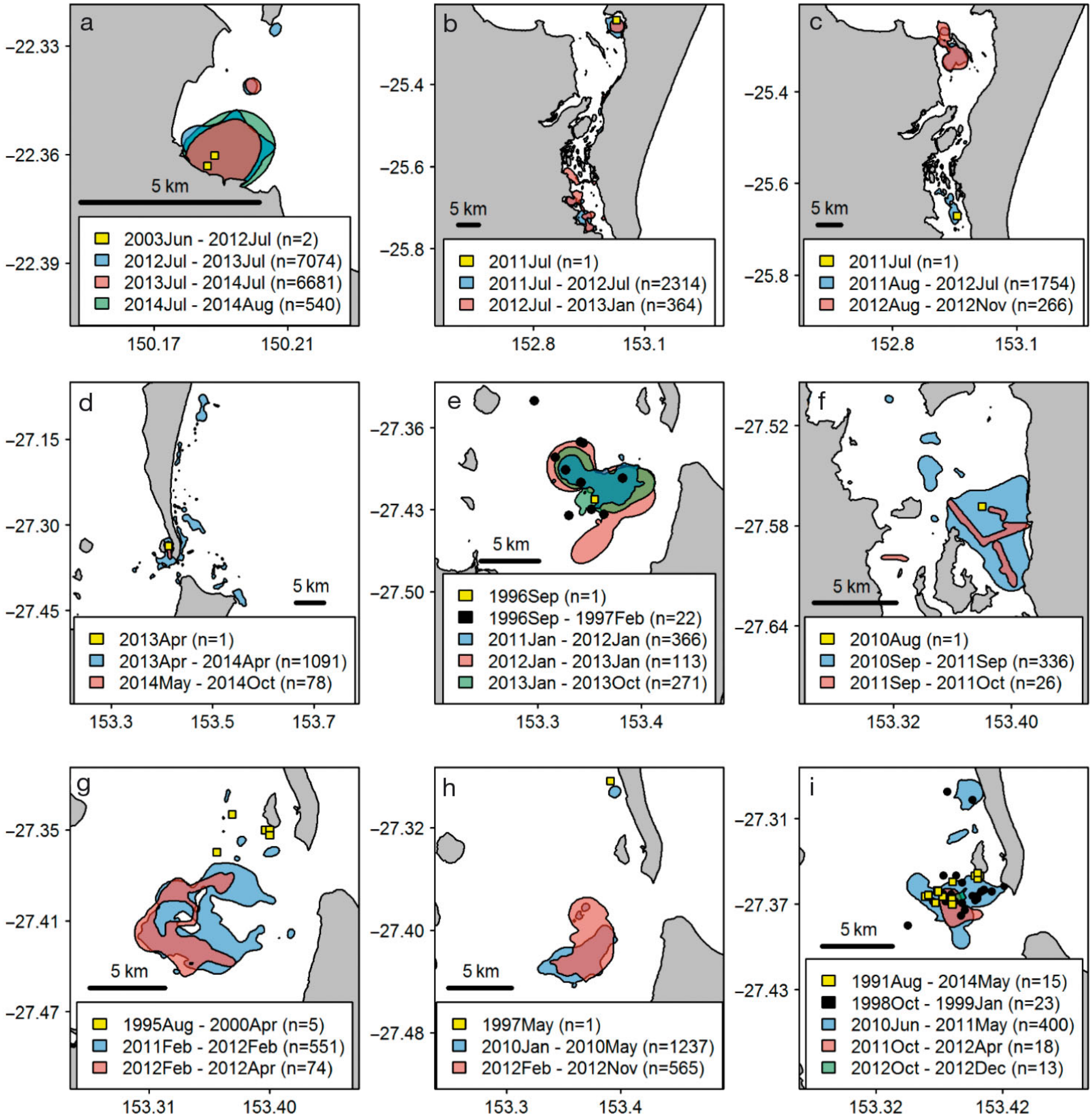


Fig. 4. Yearly home ranges (coloured polygons), high-quality Argos fixes (black dots) and capture locations (yellow squares) for green turtles *Chelonia mydas* and loggerhead turtles *Caretta caretta* which were tracked for more than 1 yr. Sample size (number of locations) is presented in brackets within the legend. Female green turtles: (a) K55740 in Shoalwater Bay, (b) QA23117 in Sandy Strait and (c) QA23188 in Sandy Strait; female loggerhead turtles in Moreton Bay: (d) QA13932, (e) T14914, (f) T23158, (g) T29282 and (h) T93038; and a male loggerhead turtle (i) T53800 in Moreton Bay

(Table 3: Subset 3). Female green turtles in Shoalwater Bay had significantly smaller monthly home ranges than those at other sites (Fig. 5). SST was only associated with the monthly home range size of the turtles in Sandy Strait (Table 3: Subset 3): the turtles used larger areas in warmer water, indicating a seasonal change in home range size (Fig. 6b). At the other study sites, home range size was consistent throughout the range of SST recorded during our tracking study (Fig. 6a,c,d,e). Thus, only turtles in Sandy Strait

Table 3. Factors affecting monthly home range size (mHR) of green turtles *Chelonia mydas* and loggerhead turtles *Caretta caretta*. See Fig. 1 for study sites. F: female, M: male, SST: sea surface temperature. All data subsets include location fixes acquired during 'affected months' and 'normal months' (weather; see Fig. 2). Individual turtles were treated as random effects. $f$(SST) indicates that SST was allowed to have a nonlinear effect in the generalised additive mixed models. The effective degrees of freedom are provided for SST to indicate the amount of smoothing used. N is the number of fixes used for mHR estimation (i.e. sample size)

| Data subsets: Species | Site | Sex | Fixed effects | df | $F$ | p |
|---|---|---|---|---|---|---|
| **Subset 1** | | | | | | |
| *Chelonia mydas* | MB | F | Weather | 1 | 0.31 | 0.578 |
| | | | $f$(SST) | 1 | 1.53 | 0.22 |
| | | | N | 1 | 0.01 | 0.937 |
| **Subset 2** | | | | | | |
| *Chelonia mydas* | PC | M | Weather | 1 | 0.15 | 0.698 |
| | | | $f$(SST) | 1 | 3.27 | 0.08 |
| | | | N | 1 | 3.44 | 0.073 |
| **Subset 3** | | | | | | |
| *Chelonia mydas* | All | F | Site | 4 | 5.62 | <0.001 |
| | | | $f$(SST):MB | 1 | 1.82 | 0.178 |
| | | | $f$(SST):SS | 2.36 | 11.03 | <0.001 |
| | | | $f$(SST):PC | 1 | 1.12 | 0.291 |
| | | | $f$(SST):SB | 1 | 0.02 | 0.876 |
| | | | $f$(SST):TS | 1 | 0 | 0.998 |
| | | | N | 1 | 0.11 | 0.745 |
| **Subset 4** | | | | | | |
| *Chelonia mydas* | MB, PC | F, M | Sex | 1 | 0.83 | 0.365 |
| | | | Site | 1 | 8.07 | 0.005 |
| | | | $f$(SST):MB | 1 | 3.36 | 0.069 |
| | | | $f$(SST):PC | 1 | 0.01 | 0.92 |
| | | | N | 1 | 0.04 | 0.837 |
| **Subset 5** | | | | | | |
| *Caretta caretta* | MB | F, M | Weather | 1 | 0.46 | 0.5 |
| | | | Sex | 1 | 1.88 | 0.174 |
| | | | $f$(SST) | 1 | 0.57 | 0.093 |
| | | | N | 1 | 2.9 | 0.454 |

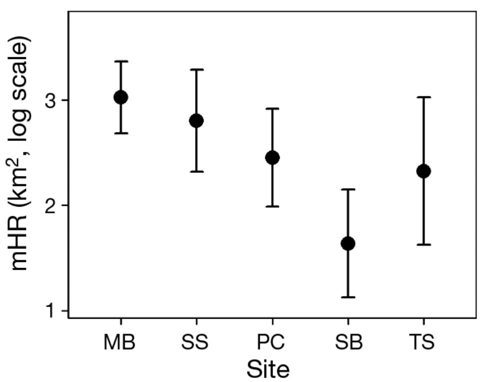


Fig. 5. Geographical differences in monthly home range size (mHR) of adult female green turtles *Chelonia mydas* in northeastern Australia. See Fig. 1 for study sites. Dots are generalised additive mixed model fits with error bars denoting 95% confidence intervals

were used to model the monthly home range size as a function of calendar month using GAMM. The model is:

$$\text{Monthly home range size} \sim f(\text{Calendar month})$$

Month of year had a significant effect on the monthly home range size of the turtles in Sandy Strait ($F = 6.94$, edf = 2.95, $p < 0.001$), i.e. smaller during winter and larger during summer (Fig. 7).

(3) The sexual differences in monthly home range size of green turtles were tested for turtles in Moreton Bay and Port Curtis (Subset 4). The model is:

$$\text{Monthly home range size} \sim \text{Sex} + \text{Site} + f(\text{SST})\text{:Site} + \text{Sample size}$$

Neither sex nor sample size had an effect on the monthly home range size (Table 3: Subset 4). Site had a significant effect, but SST was not associated with the monthly home ranges of the turtles in Moreton Bay and Port Curtis.

(4) Lastly we tested the effects of the extreme weather events, sex and SST on monthly home range size of loggerhead turtles in Moreton Bay (Subset 5). The model is:

$$\text{Monthly home range size} \sim \text{Weather} + \text{Sex} + f(\text{SST}) + \text{Sample size}$$

Neither weather, sex, SST nor sample size had significant effects on monthly home range size of the loggerhead turtles (Table 3: Subset 5).

## Site fidelity

We also investigated 4 different questions related to site fidelity using 5 subsets of tracking data. The following analyses did not include the sample size (i.e. number of fixes) as a covariate since monthly home range size was not affected by sample size (Table 3).

(5) We first examined the effect of the extreme weather events on site fidelity for female green turtles in Moreton Bay (Subset 1) and male green turtles in Port Curtis (Subset 2). The model is:

$$\text{MISE} \sim \text{Weather} + f(\Delta\text{SST})$$

The extreme weather events did not have an effect at those 2 study sites (Table 4: Subsets 1, 2). ΔSST

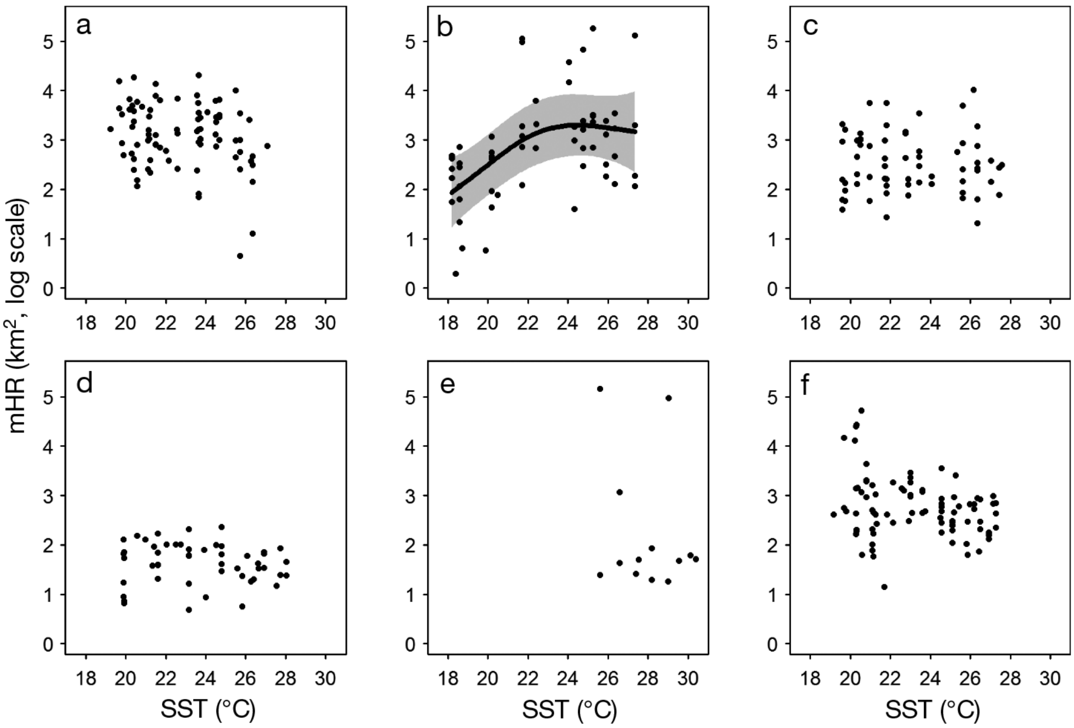


Fig. 6. Effects of sea surface temperature (SST) on monthly home range size (mHR) of adult green turtle *Chelonia mydas* (a) females and males in Moreton Bay, (b) females in Sandy Strait, (c) females and males in Port Curtis, (d) females in Shoalwater Bay and (e) females in Torres Strait; and of adult loggerhead turtles *Caretta caretta* (f) females and males in Moreton Bay. Dots are monthly home range sizes (log scale) for each observation, corrected for individual turtle variation. Generalised additive mixed model fit (solid line) and 95% confidence interval (grey band) are presented for the Sandy Strait data for which the relationship is significant (see Table 3: Subset 3)

was only associated with site fidelity for female green turtles in Moreton Bay (Table 4: Subset 1) but not for male green turtles in Port Curtis (Table 4: Subset 2). Based on these results, the following analyses used green turtle data regardless of the association with the extreme weather events.

(6) We tested the effect of study site on site fidelity for female green turtles (Subset 3). The model is:

$$\text{MISE} \sim \text{Site} + f(\Delta\text{SST})\text{:Site}$$

Study site had no effects on site fidelity, but ΔSST had significant effects on site fidelity for female green turtles in Moreton Bay, Sandy Strait and Shoalwater Bay: the effects were not significant in Port Curtis and Torres Strait (Table 4: Subset 3).

(7) We tested for sex-based differences in site fidelity for green turtles tracked in Moreton Bay and Port Curtis (Subset 4). The model is:

$$\text{MISE} \sim \text{Sex} + \text{Site} + f(\Delta\text{SST})\text{:Site}$$

Neither sex nor study site had an effect on site fidelity (Table 4: Subset 4). ΔSST was significantly related to site fidelity in green turtles in Moreton Bay

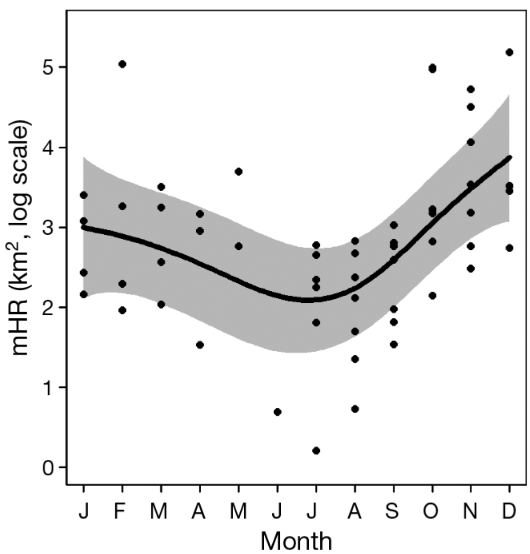


Fig. 7. Estimated home range size (mHR) of adult female green turtles *Chelonia mydas* in Sandy Strait in each month of year. Solid line is a generalised additive mixed model fit with the grey band denoting a 95% confidence interval. Dots are monthly home range sizes (log scale) for each observation, corrected for individual turtle variation

Table 4. Environmental and biological factors affecting site fidelity (indexed by the mean integrated squared error, MISE) of green turtles *Chelonia mydas* and loggerhead turtles *Caretta caretta*. See Fig. 1 for study sites. F: female, M: male, SST: sea surface temperature. All data subsets include location fixes acquired during 'affected months' and 'normal months' (weather; see Fig. 2). $f(\Delta SST)$ indicates that ΔSST was allowed to have a nonlinear effect in the generalised additive mixed models. The effective degrees of freedom are provided for SST to indicate the amount of smoothing used

| Data subsets: Species | Site | Sex | Fixed effects | df | *F* | p |
|---|---|---|---|---|---|---|
| **Subset 1** | | | | | | |
| *Chelonia mydas* | MB | F | Weather | 1 | 1.77 | 0.185 |
| | | | $f(\Delta SST)$ | 1 | 4.33 | 0.038 |
| **Subset 2** | | | | | | |
| *Chelonia mydas* | PC | M | Weather | 1 | 0.89 | 0.349 |
| | | | $f(\Delta SST)$ | 1 | 0.36 | 0.55 |
| **Subset 3** | | | | | | |
| *Chelonia mydas* | All | F | MSite | 4 | 0.42 | 0.797 |
| | | | $f(\Delta SST)$:MB | 1 | 6.46 | 0.011 |
| | | | $f(\Delta SST)$:SS | 1 | 37.04 | <0.001 |
| | | | $f(\Delta SST)$:PC | 1 | 0.08 | 0.78 |
| | | | $f(\Delta SST)$:SB | 1 | 111.5 | <0.001 |
| | | | $f(\Delta SST)$:TS | 1 | 1 | 0.318 |
| **Subset 4** | | | | | | |
| *Chelonia mydas* | MB, PC | F, M | Sex | 1 | 0.26 | 0.61 |
| | | | Site | 1 | 0.02 | 0.904 |
| | | | $f(\Delta SST)$:MB | 1 | 5.83 | 0.016 |
| | | | $f(\Delta SST)$:PC | 1 | 0.89 | 0.346 |
| **Subset 5** | | | | | | |
| *Caretta caretta* | MB | F, M | Weather | 1 | 1.05 | 0.306 |
| | | | Sex | 1 | 0.92 | 0.337 |
| | | | $f(\Delta SST)$ | 1 | 24.45 | <0.001 |

but the effect was not significant in Port Curtis (Table 4: Subset 4).

(8) Lastly we examined the effects of the extreme weather events, sex and ΔSST on site fidelity of loggerhead turtles in Moreton Bay (Subset 5). The model is:

$$\text{MISE} \sim \text{Weather} + \text{Sex} + f(\text{SST})$$

As seen in green turtles, ΔSST had a significant effect, but neither weather nor sex was associated with site fidelity for loggerhead turtles (Table 4: Subset 5).

There were linear relationships between MISE (log scale) and ΔSST for turtles in Moreton Bay, Sandy Strait and Shoalwater Bay (Fig. 8a,b,d,f), demonstrating differential habitat use associated with different SST values. Since SST is strongly affected by seasons, we investigated in detail how the shifts in habitat were related to seasons. More specifically, for each turtle, we examined temporal shifts in monthly UDs relative to summer months. The model is:

$$\text{MISE} \sim f(\text{Number of months since summer})$$

For this analysis, we pooled the data for each species regardless of weather, site and sex, as those parameters did not have perceptible effects on MISE values (Table 4). However, we did not include data for green turtles in Port Curtis and Torres Strait due to their lack of relationship between MISE and ΔSST (Table 4: Subsets 2, 3 and 4).

A total of 167 pairs of monthly UDs were in the category of 'shifts since summer months' for green turtles. The maximum time difference between each pair of monthly UDs was 20 mo. Green turtles shifted their habitats between the summer months and the following winter months during the first year of tracking, but in the summer of the second year of tracking, they shifted back to the habitats which they had used during the previous summer months (Fig. 9a). As the time moved away from the summer months in the second year, the green turtles again shifted away from the summer habitat (Fig. 9a).

For loggerhead turtles, a total of 34 pairs of monthly UDs were in the category of 'shifts since summer months'. The maximum time difference between each pair of monthly UDs was 29 mo. Similar to green turtles, loggerhead turtles showed a seasonal shift in habitat between the summer months and the following winter months in the first and third year of tracking (Fig. 9b).

Plots of summer and winter home range polygons (Fig. 10) are consistent with the seasonal patterns that were identified by the analyses with MISE. Both species remained in shallow coastal areas throughout a year, but a summer–winter habitat shift was evident for turtles at our 3 sub-tropical sites: Moreton Bay, Sandy Strait and Shoalwater Bay (Fig. 10). There was no apparent movement that resembles an escape from cold water during winter, such as migration to waters at lower latitudes or to deeper off-shore waters where temperature would be higher.

The seasonal shifts in habitat resulted in variation of protection given to turtles in eastern Moreton Bay, where regulation protects sea turtles from boat strikes (i.e. 'Go Slow Zones'). For example, a female green turtle mostly used habitat within the Go Slow Zones during winter but extended its habitat outside of the protected zones during summer (Fig. 10a). In

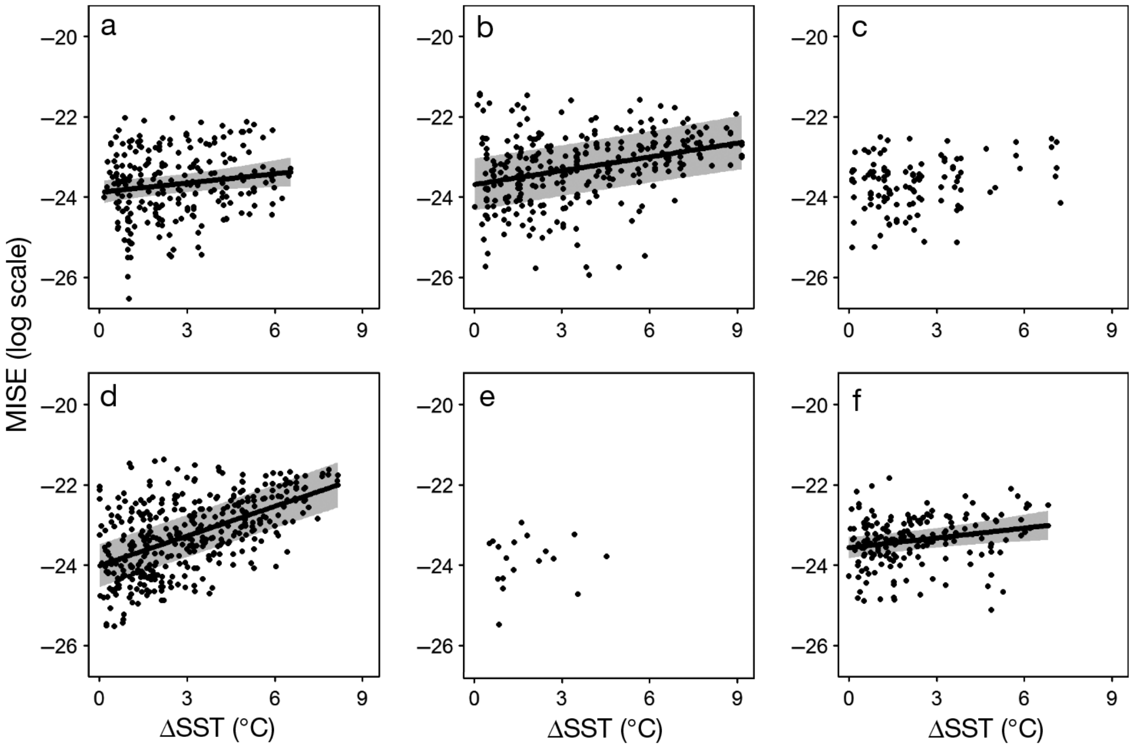


Fig. 8. Effects of sea surface temperature (SST) on site fidelity for adult green turtle *Chelonia mydas* (a) females and males in Moreton Bay, (b) females in Sandy Strait, (c) females and males in Port Curtis, (d) females in Shoalwater Bay and (e) females in Torres Strait; and for adult loggerhead turtle *Caretta caretta* (f) females and males in Moreton Bay. Mean integrated squared error (MISE) values (indices of site fidelity) represent the differences between each combination of utilisation distributions (UDs; a smaller MISE value indicates similar home ranges). ΔSST is the absolute difference in SST between each combination of UDs. Dots are MISE values (log scale) for each observation, corrected for individual turtle variation. Generalised additive mixed model fits (solid line) and 95% confidence intervals (grey band) are presented for data for which the relationship is significant (see Table 4)

the case of a male loggerhead turtle, the summer habitat was mostly inside the Go Slow Zones, but its winter habitat spread extensively over non-protected areas (Fig. 10d).

## DISCUSSION

We demonstrated that spatio-temporal home range analysis can reveal important movement patterns of threatened sea turtles. Our results represent the first evidence of seasonal variation in habitat use by adult green and loggerhead turtles in subtropical coastal foraging habitat in the southern hemisphere. We also provided further evidence of long-term fidelity to a foraging habitat and geographical variation in home range size for those populations.

Using satellite-derived location data, site fidelity for more than 1 yr was clearly demonstrated by green and loggerhead turtles in various foraging areas along the Queensland coast of Australia. Further, from the combination of satellite telemetry and mark–recapture records we inferred extended foraging residency, up to 17 yr by green turtles and up to 23 yr by loggerhead turtles. These are among the longest periods of fidelity to particular foraging habitats reported in sea turtles. Limpus & Limpus (2003) recorded loggerhead females maintaining foraging residency on a single small coral reef for up to 23 yr, following their recruitment from oceanic pelagic dispersal to benthic foraging on these reefs and continuing across multiple foraging periods between successive adult breeding migrations. Having long-term site fidelity may increase sea turtles' biological and reproductive fitness by ensuring reliable access to good foraging and resting areas. It may also reduce the impacts of predation by knowing where predators are most likely found and where they can be evaded.

Within each long-term habitat, our study turtles were observed to seasonally shift their main habitat at our 3 subtropical sites (Moreton Bay, Sandy Strait

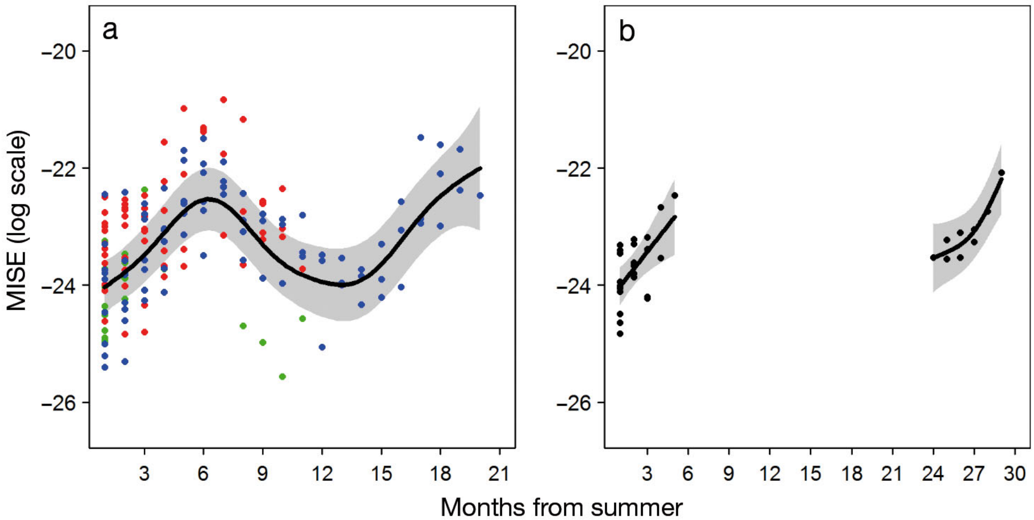


Fig. 9. Chronological shift in foraging habitat from summer months (a) by adult green turtles *Chelonia mydas* in Moreton Bay (green), Sandy Strait (red) and Shoalwater Bay (blue); and (b) by adult loggerhead turtles *Caretta caretta* in Moreton Bay (black). Mean integrated squared error (MISE) values (indices of site fidelity) represent the differences between each combination of utilisation distributions (UDs; a smaller MISE value indicates similar home ranges). Solid lines are generalised additive mixed model fits with grey bands denoting 95% confidence intervals. Dots are MISE values (log scale) for each observation, corrected for individual turtle variation

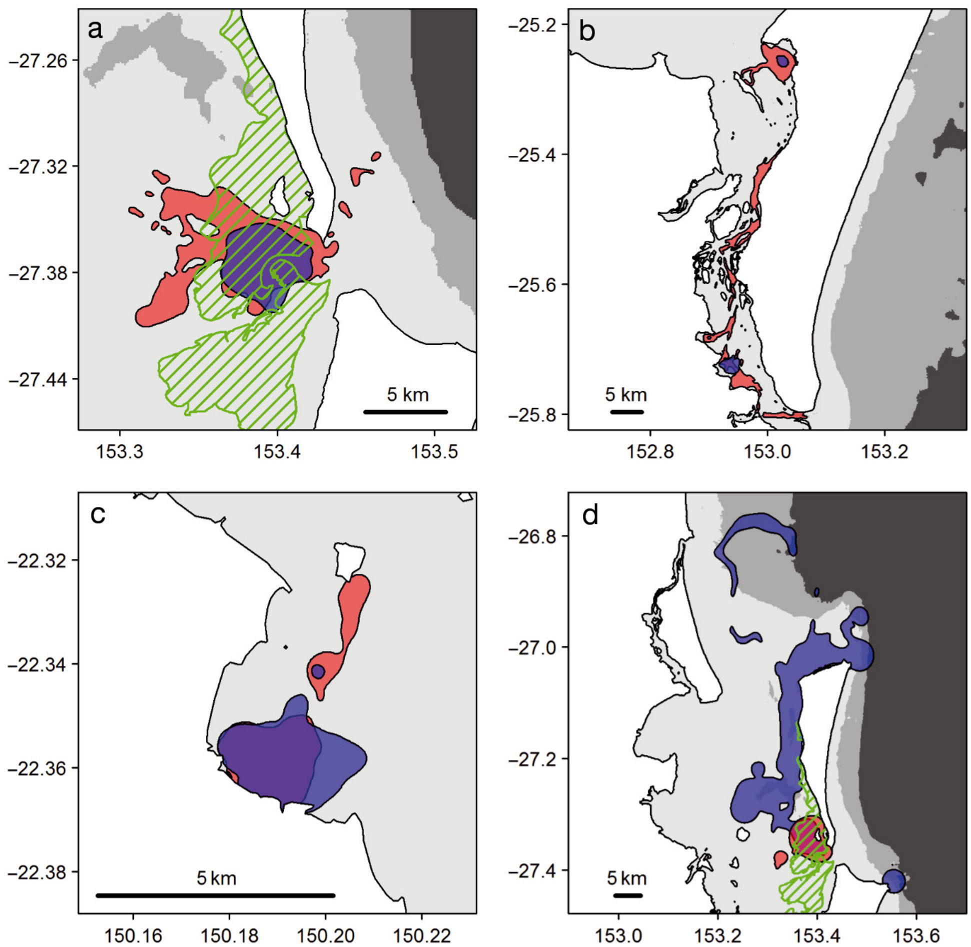


Fig. 10. Summer (red polygons) and winter (blue polygons) home range of a female green turtle *Chelonia mydas* in (a) Moreton Bay, (b) Sandy Strait and (c) Shoalwater Bay; and of a male loggerhead turtle *Caretta caretta* in (d) Moreton Bay. Water depth zones at mean sea level are shown by grey gradient: >0–25 m (light grey), >25–50 m (grey) and >50 m (dark grey). Green hatched polygons denote the 'Go Slow Zones' for turtles and dugongs in Moreton Bay

and Shoalwater Bay). The seasonal shifts made by green turtles in Sandy Strait were due to habitat expansion during the summer months and contraction during the winter. Yet, for the turtles in Moreton Bay and Shoalwater Bay, the shifts in habitat were not necessarily related to changes in home range size; rather, these shifts indicated changes in localised fidelity resulting from shifts to overlapping habitat of similar area during different seasons (Figs. 6a,d & 8a,d). Similarly, a seasonal shift in habitat commonly occurs in sea turtles living in temperate waters, where turtles move according to changes in water temperature, resulting in tens to thousands of kilometres of foraging migration (e.g. *Chelonia mydas*: Godley et al. 2002, González Carman et al. 2016; *Caretta caretta*: Morreale & Standora 2005, Schofield et al. 2013a, Narazaki et al. 2015; *Lepidochelys kempii*: Morreale & Standora 2005). Although the seasonal movements seen in our study turtles are not as extreme as those detected in temperate waters, the behaviour could be related to local-scale variation of water temperature as seen in female loggerhead turtles during inter-nesting periods (Schofield et al. 2009), and does not preclude potential thermoregulatory effects. Testing this hypothesis requires concurrent data of turtle movements and water temperature at high resolution (e.g. hourly SST at 50 m grid resolution to match the expected temporal and spatial resolutions of FGPS data).

The small-scale seasonal movements we found could also be driven by spatial shifts of the turtles' food sources. Seagrass is the main diet for green turtles whilst loggerhead turtles mostly feed on benthic invertebrates at our study sites (Garnett et al. 1985, Limpus et al. 2001, 2005, Arthur et al. 2008b). Green turtles may have simply followed any shifts in the spatial distribution and abundance of seagrass, which is known to be affected by various environmental and geographical factors (Rasheed & Unsworth 2011). Loggerhead turtles in Moreton Bay forage on benthic invertebrates, which are often found in seagrass meadows (Limpus et al. 2001). It may be expected that the home range of loggerhead turtles changed in concert with seasonal distributions of seagrass and associated invertebrate prey species. Temporal blooms of gelatinous plankton at our study sites (Arthur et al. 2008a) could also have contributed to the observed shifts in habitat, as some loggerhead and green turtles are known to consume planktonic invertebrates at our study sites (Limpus et al. 2001, Arthur et al. 2007).

Comparison of home range (for areas or fidelity) can be challenging when data from varying tracking durations and seasons are used. For example, a seasonal shift in habitat was not detected in turtles from Port Curtis although the climate there is similar to our other subtropical sites (Moreton Bay, Sandy Strait and Shoalwater Bay). That is likely because the turtles in Port Curtis were not tracked across periods with major seasonal changes (e.g. summer to winter), and consequently changes in SST across the tracking periods were significantly smaller in Port Curtis than other subtropical sites (Fig. 3). The same explanation may apply for failure to detect seasonal shifts in habitat by turtles in Torres Strait. However, since Torres Strait is nearer to the equator (approximately 9–10° S), it is also likely that seasonal effects were trivial in Torres Strait. Clearly, long-term tracking data are essential for robust home range studies, as aforementioned hypotheses could be verified through satellite telemetry data across periods including both summer and winter. Other studies using different species or simulations have also documented the issue with tracking duration when estimating home range size (Swihart & Slade 1997, Börger et al. 2006). Therefore, we emphasise that tracking duration and season should always be accounted for when comparing multiple home ranges or data across studies to avoid misleading statistical inferences. This precaution would be highly relevant to most studies using satellite telemetry because the transmission can unexpectedly cease for many reasons (Hays et al. 2007), resulting in shortened tracking durations.

Geographical variations in home range size were evident in the present study and others (Hart & Fujisaki 2010, Schofield et al. 2010, Gredzens et al. 2014). Home range size may be determined by distribution and abundance of food sources, and therefore is highly dependent on the unique environmental and biological factors present at each site. While climate may be another determinant for home range size, we did not find any evidence that latitude affected the home range size in subtropical and tropical habitats (Fig. 5). Nevertheless, this is potentially an important indication for research and management to be examined at local scales.

We did not find any evidence that the extreme weather events affected home range size or site fidelity of sea turtles at 2 of our study sites (eastern Moreton Bay and eastern Port Curtis), despite an increase of stranded turtles along the Queensland coast during 2011 (Meager & Limpus 2012). Similarly, the same extreme weather events did not appear to affect habitat use by herbivorous dugongs *Dugong dugon* in Moreton Bay (Sobtzick et al. 2012). Although the extreme weather events resulted in a release of large amounts of sediments into the bay, the flood plumes did not spread onto the seagrass meadows of our study area in eastern Moreton Bay (Yu et al. 2014). This is largely because a portion of the strong eastern Australian Current streams into the bay, pushing the turbid water away from eastern Moreton Bay (Milford & Church 1977, Yu et al. 2014). Unlike eastern Moreton Bay, the flood plumes reached our turtle tracking site in Port Curtis. However, we speculate that much of the flood plume may have migrated quickly by currents through the adjacent passage linking to the outside of the bay. Testing this hypothesis requires high-resolution current data and satellite imagery. Nonetheless, these potential geographical advantages underline the high conservation value of eastern Moreton Bay and eastern Port Curtis as foraging habitats for many wildlife species including sea turtles and dugongs.

Long-term fidelity to a foraging habitat is a strong behavioural feature of many sea turtle species (e.g. *Chelonia mydas*: Chaloupka et al. 2004, Shimada et al. 2014, this study; *Caretta caretta*: Limpus & Limpus 2001, 2003, Thomson et al. 2012, this study; *Eretmochelys imbricata*: Limpus 1992), which may persist for decades even after human-induced displacement (Shimada et al. 2016). Ideally, the home range of sea turtles should be estimated using year-round tracking data, as highlighted by the seasonal movements within the long-term foraging habitats. These characteristics of sea turtle behaviour warrant careful consideration by conservation managers when planning or revising designated conservation areas such as marine protected areas or restricted area zones (e.g. Go Slow Zones, Fig. 10a,d) to protect threatened species or their foraging habitat from increasing human activities. Given that food resources and other environmental variables are expected to vary among seasons, this guidance could be applicable to research and conservation of various species in marine and terrestrial habitats globally.

*Acknowledgements*. This research was funded by the National Environmental Research Program (NERP), Department of Environment and Heritage Protection of the Queensland government (EHP), James Cook University (JCU), Healthy Waterways, Gladstone Port Corporation Limited, GHD Australia and the Gas Industry Social and Environmental Research Alliance, comprised of CSIRO, Australia Pacific LNG and QGC. T.S. was supported by a NERP scholarship and an Ito Foundation for International Education Exchange Scholarship. We acknowledge the support of J. Limpus, D. Limpus, M. Savige, staff of Queensland Parks and Wildlife Service, staff of Torres Strait Regional Authority, Mabuiag Community, R. Pillans, G. Fry and R. Babcock of CSIRO Oceans and Atmosphere, and numerous volunteers. We also thank K. Riskas and R. Spinks for proofreading. This research was conducted following all applicable guidelines for the care and use of animals as outlined in the ethics permits SA212/11/395 of EHP and, A1229 and A1683 of JCU.

## LITERATURE CITED

Arthur KE, O'Neil JM, Limpus CJ, Abernathy K, Marshall G (2007) Using animal-borne imaging to assess green turtle (*Chelonia mydas*) foraging ecology in Moreton Bay, Australia. Mar Technol Soc J 41:9–13

Arthur K, Limpus C, Balazs G, Capper A and others (2008a) The exposure of green turtles (*Chelonia mydas*) to tumour promoting compounds produced by the cyanobacterium *Lyngbya majuscula* and their potential role in the aetiology of fibropapillomatosis. Harmful Algae 7:114–125

Arthur KE, Boyle MC, Limpus CJ (2008b) Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. Mar Ecol Prog Ser 362:303–311

Beaman R (2010) Project 3DGBR: a high-resolution depth model for the Great Barrier Reef and Coral Sea. Marine and Tropical Sciences Research Facility (MTSRF) Project 2.5i.1a Final Report. James Cook University, Cairns

Benhamou S (2011) Dynamic approach to space and habitat use based on biased random bridges. PLOS ONE 6: e14592

Benhamou S, Cornélis D (2010) Incorporating movement behavior and barriers to improve kernel home range space use estimates. J Wildl Manag 74:1353–1360

Blundell GM, Maier JAK, Debevec EM (2001) Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecol Monogr 71:469–489

Bolten AB (2003) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Vol II. CRC Press, Boca Raton, FL, p 243–257

Börger L, Franconi N, De Michele G, Gantz A and others (2006) Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol 75: 1393–1405

Bureau of Meteorology (2012) Record-breaking La Niña events. An analysis of the La Niña life cycle and the impacts and significance of the 2010–11 and 2011–12 La Niña events in Australia. Bureau of Meteorology, Melbourne

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Calenge C (2015) adehabitatHR: home range estimation. R package v. 0.4.14. Available at http://CRAN.R-project.org/package=adehabitatHR (accessed 19 September 2015)

Casale P, Tucker AD (2015) *Caretta caretta*. The IUCN Red List of Threatened Species 2015: e.T3897A83157651. https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T3897A83157651.en (accessed 19 July 2016)

Chaloupka M, Limpus C, Miller J (2004) Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. Coral Reefs 23:325–335

Cleguer C, Grech A, Garrigue C, Marsh H (2015) Spatial mismatch between marine protected areas and dugongs in New Caledonia. Biol Conserv 184:154–162

Cumming GS, Cornélis D (2012) Quantitative comparison and selection of home range metrics for telemetry data. Divers Distrib 18:1057–1065

Daniell JJ (2008) Development of a bathymetric grid for the Gulf of Papua and adjacent areas: a note describing its development. J Geophys Res 113:F01S15

Devlin MJ, McKinna LW, Álvarez-Romero JG, Petus C, Abott B, Harkness P, Brodie J (2012) Mapping the pollutants in surface riverine flood plume waters in the Great Barrier Reef, Australia. Mar Pollut Bull 65:224–235

Dryden J, Grech A, Moloney J, Hamann M (2008) Rezoning of the Great Barrier Reef World Heritage Area: Does it afford greater protection for marine turtles? Wildl Res 35: 477–485

Dujon AM, Lindstrom RT, Hays GC (2014) The accuracy of Fastloc-GPS locations and implications for animal tracking. Methods Ecol Evol 5:1162–1169

Environment Australia (2001) Macquarie Island marine park management plan. Marine and Water Division, Canberra

Fernandes L, Day J, Lewis A, Slegers S and others (2005) Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. Conserv Biol 19:1733–1744

Fieberg J, Börger L (2012) Could you please phrase 'home range' as a question? J Mammal 93:890–902

Gaines SD, Lester SE, Grorud-Colvert K, Costello C, Pollnac R (2010) Evolving science of marine reserves: new developments and emerging research frontiers. Proc Natl Acad Sci USA 107:18251–18255

Garnett ST, Price IR, Scott FJ (1985) The diet of the green turtle, *Chelonia mydas* (L.), in Torres Strait. Wildl Res 12: 103–112

Godley BJ, Richardson S, Broderick AC, Coyne MS, Glen F, Hays GC (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. Ecography 25:352–362

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? Endang Species Res 4:3–22

González Carman V, Falabella V, Maxwell S, Albareda D, Campagna C, Mianzan H (2012) Revisiting the ontogenetic shift paradigm: the case of juvenile green turtles in the SW Atlantic. J Exp Mar Biol Ecol 429:64–72

González Carman V, Bruno I, Maxwell S, Álvarez K, Albareda D, Acha EM, Campagna C (2016) Habitat use, site fidelity and conservation opportunities for juvenile loggerhead sea turtles in the Río de la Plata, Argentina. Mar Biol 163:1–13

Gredzens C, Marsh H, Fuentes MMPB, Limpus CJ, Shimada T, Hamann M (2014) Satellite tracking of sympatric marine megafauna can inform the biological basis for species co-management. PLOS ONE 9:e98944

Hamann M, Godfrey MH, Seminoff JA, Arthur K and others (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. Endang Species Res 11:245–269

Hart KM, Fujisaki I (2010) Satellite tracking reveals habitat use by juvenile green sea turtles *Chelonia mydas* in the Everglades, Florida, USA. Endang Species Res 11: 221–232

Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007) Only some like it hot — quantifying the environmental niche of the loggerhead sea turtle. Divers Distrib 13:447–457

Hays GC, Broderick AC, Glen F, Godley BJ, Nichols WJ (2001) The movements and submergence behaviour of male green turtles at Ascension Island. Mar Biol 139: 395–400

Hays GC, Bradshaw CJA, James MC, Lovell P, Sims DW (2007) Why do Argos satellite tags deployed on marine animals stop transmitting? J Exp Mar Biol Ecol 349:52–60

Hays GC, Ferreira LC, Sequeira AMM, Meekan MG and others (2016) Key questions in marine megafauna movement ecology. Trends Ecol Evol 31:463–475

Hazen EL, Maxwell SM, Bailey H, Bograd SJ and others (2012) Ontogeny in marine tagging and tracking science: technologies and data gaps. Mar Ecol Prog Ser 457: 221–240

Hooker SK, Gerber LR (2004) Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. Bioscience 54:27–39

Laver PN, Kelly MJ (2008) A critical review of home range studies. J Wildl Manag 72:290–298

Limpus CJ (1978) The reef. In: Lavery HJ (ed) Exploration north: Australia's wildlife from desert to reef. Richmond Hill Press, Richmond, p 187–222

Limpus CJ (1992) The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground. Wildl Res 19: 489–506

Limpus CJ (2009) A biological review of Australian marine turtle species. Queensland Environmental Protection Agency, Brisbane

Limpus CJ, Limpus DJ (2001) The loggerhead turtle, *Caretta caretta*, in Queensland: breeding migrations and fidelity to a warm temperate feeding area. Chelonian Conserv Biol 4:142–153

Limpus CJ, Limpus DJ (2003) Biology of the loggerhead turtle in western south Pacific Ocean foraging areas. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution, Washington, DC, p 93–113

Limpus CJ, de Villiers DL, de Villiers MA, Limpus DJ, Read MA (2001) The loggerhead turtle, *Caretta caretta* in Queensland: feeding ecology in warm temperate waters. Mem Queensl Mus 46:631–645

Limpus CJ, Limpus DJ, Arthur KE, Parmenter CJ (2005) Monitoring green turtle population dynamics in Shoalwater Bay: 2000–2004. Research publication no. 83. Great Barrier Reef Marine Park Authority, Townsville

Maxwell SM, Breed GA, Nickel BA, Makanga-Bahouna J and others (2011) Using satellite tracking to optimize protection of long-lived marine species: olive ridley sea turtle conservation in central Africa. PLOS ONE 6:e19905

McCay BJ, Jones PJS (2011) Marine protected areas and the governance of marine ecosystems and fisheries. Conserv Biol 25:1130–1133

McCook LJ, Ayling T, Cappo M, Choat JH and others (2010) Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. Proc Natl Acad Sci USA 107: 18278–18285

McKenzie LJ, Collier C, Waycott M (2012) Reef rescue marine monitoring program — inshore seagrass. Annual report for the sampling period 1st July 2010 – 31st May 2011. Fisheries Queensland, Cairns

Meager JJ, Limpus CJ (2012) Marine wildlife stranding and mortality data base annual report 2011. III. Marine turtle. Department of Environment and Heritage Protection, Brisbane

Milford SN, Church JA (1977) Simplified circulation and mixing models of Moreton Bay, Queensland. Mar Freshw Res 28:23–34

Morreale SJ, Standora EA (2005) Western north Atlantic waters: crucial developmental habitat for Kemp's ridley and loggerhead sea turtles. Chelonian Conserv Biol 4: 872–882

Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol I. CRC Press, Boca Raton, FL, p 137–163

Narazaki T, Sato K, Miyazaki N (2015) Summer migration to temperate foraging habitats and active winter diving of juvenile loggerhead turtles *Caretta caretta* in the western north Pacific. Mar Biol 162:1251–1263

Peckham SH, Maldonado-Diaz D, Tremblay Y, Ochoa R and others (2011) Demographic implications of alternative foraging strategies in juvenile loggerhead turtles *Caretta caretta* of the North Pacific Ocean. Mar Ecol Prog Ser 425:269–280

Powell RA (2000) Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology. Columbia University Press, New York, NY, p 65–110

Powell RA, Mitchell MS (2012) What is a home range? J Mammal 93:948–958

Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA (2007) Conservation planning in a changing world. Trends Ecol Evol 22:583–592

R Core Team (2016) R: a language and environment for statistical computing (v. 3.3.1). https://www.r-project.org (accessed 3 July 2016)

Rasheed MA (2004) Recovery and succession in a multi-species tropical seagrass meadow following experimental disturbance: the role of sexual and asexual reproduction. J Exp Mar Biol Ecol 310:13–45

Rasheed MA, Unsworth RKF (2011) Long-term climate-associated dynamics of a tropical seagrass meadow: implications for the future. Mar Ecol Prog Ser 422:93–103

Rasheed MA, McKenna SA, Carter AB, Coles RG (2014) Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia. Mar Pollut Bull 83: 491–499

Rojas-Bracho L, Reeves RR, Jaramillo-Legorreta A (2006) Conservation of the vaquita *Phocoena sinus.* Mammal Rev 36:179–216

Ropert-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote sensing. Front Ecol Environ 3:437–444

Rutz C, Hays GC (2009) New frontiers in biologging science. Biol Lett 5:289–292

Schofield G, Bishop CM, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC (2009) Microhabitat selection by sea turtles in a dynamic thermal marine environment. J Anim Ecol 78:14–21

Schofield G, Hobson VJ, Fossette S, Lilley MKS, Katselidis KA, Hays GC (2010) Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. Divers Distrib 16:840–853

Schofield G, Dimadi A, Fossette S, Katselidis KA and others (2013a) Satellite tracking large numbers of individuals to infer population level dispersal and core areas for the protection of an endangered species. Divers Distrib 19: 834–844

Schofield G, Scott R, Dimadi A, Fossette S and others (2013b) Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. Biol Conserv 161:101–109

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. J Wildl Manag 63: 739–747

Seminoff JA (2004) *Chelonia mydas.* The IUCN Red List of Threatened Species 2004: e.T4615A11037468. https://doi.org/10.2305/IUCN.UK.2004.RLTS.T4615A11037468.en (accessed 19 July 2016)

Shimada T (2016) SDLfilter: filtering satellite-derived locations. R package v. 0.2.0. https://github.com/TakahiroShimada/SDLfilter (accessed 17 April 2016)

Shimada T, Jones R, Limpus C, Hamann M (2012) Improving data retention and home range estimates by data-driven screening. Mar Ecol Prog Ser 457:171–180

Shimada T, Aoki S, Kameda K, Hazel J, Reich K, Kamezaki N (2014) Site fidelity, ontogenetic shift and diet composition of green turtles *Chelonia mydas* in Japan inferred from stable isotope analysis. Endang Species Res 25: 151–164

Shimada T, Limpus C, Jones R, Hazel J, Groom R, Hamann M (2016) Sea turtles return home after intentional displacement from coastal foraging areas. Mar Biol 163:1–14

Sobtzick S, Hagihara R, Grech A, Marsh H (2012) Aerial survey of the urban coast of Queensland to evaluate the response of the dugong population to the widespread effects of the extreme weather events of the summer of 2010-11. Final Report to the Australian Marine Mammal Centre and the National Environmental Research Program. Reef and Rainforest Research Centre Limited, Cairns, www.nerptropical.edu.au/publication/project-12-technical-report-aerial-survey-urban-coast-queensland-evaluate-response

Swihart RK, Slade NA (1997) On testing for independence of animal movements. J Agric Biol Environ Stat 2:48–63

Thomson JA, Heithaus MR, Burkholder DA, Vaudo JJ, Wirsing AJ, Dill LM (2012) Site specialists, diet generalists? Isotopic variation, site fidelity, and foraging by loggerhead turtles in Shark Bay, Western Australia. Mar Ecol Prog Ser 453:213–226

Whittock PA, Pendoley KL, Hamann M (2014) Inter-nesting distribution of flatback turtles *Natator depressus* and industrial development in Western Australia. Endang Species Res 26:25–38

Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc B Stat Method 73: 3–36

Wood SN (2016) mgcv: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation. R package v.1.8-12. http://CRAN.R-project.org/package=mgcv (accessed 15 July 2016)

Yu Y, Zhang H, Lemckert C (2014) Numerical analysis on the Brisbane River plume in Moreton Bay due to Queensland floods 2010-2011. Environ Fluid Mech 14:1–24

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. R News 2:7–10

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

*Editorial responsibility: Graeme Hays, Burwood, Victoria, Australia*

*Submitted: February 22, 2016; Accepted: November 6, 2016*
*Proofs received from author(s): December 14, 2016*