Horizontal and vertical movement behaviour of flatback turtles and spatial overlap with industrial development

Michele Thums[1,*], Jason Rossendell[2], Mick Guinea[3], Luciana C. Ferreira[1]

[1]Australian Institute of Marine Science, Indian Ocean Marine Research Centre, University of Western Australia, Crawley, Western Australia 6009, Australia
[2]Rio Tinto, Cape Lambert, Western Australia 6720, Australia
[3]Charles Darwin University, Casuarina, Darwin, Northern Territory 0909, Australia

ABSTRACT: Understanding the overlap of animal distributions and anthropogenic activity is essential for effective conservation management. Here, we analysed data from satellite transmitters deployed on 35 adult female flatback turtles nesting in the vicinity of an iron ore port to understand the spatial and temporal components of the main phases of their breeding cycle and assessed overlap with this industrial activity. During the inter-nesting phase, flatback turtles remained 14 ± 9 km from their nesting site. On their transit to foraging grounds they did not use a discrete corridor, using an area from the coast out to the 50 m contour and dispersed widely to foraging grounds (18 to 1326 km away) that had low spatial overlap among individuals. The home range of 94 % of turtles during inter-nesting, 26 % during outward transit and 3 % during foraging had overlap with the shipping channel associated with the port. Although these results suggest that risks associated with vessel collision would be increased during the nesting season and early part of the transit to foraging grounds, no such impacts were detected. Outside of these times (>80 % of the time), industrial activities in this area are likely to be low risk to flatback turtles from the main studied rookery. We also provide the first information on the diving behaviour and *in situ* water temperature data of flatback turtles during the post-nesting migration, showing that turtles forage both on the benthos and within the water column, and that some turtles forage in relatively deep and stratified water.

KEY WORDS: Distribution · Life history · Home range · Brownian Bridge kernel density · Satellite telemetry · Inter-nesting · Foraging grounds

INTRODUCTION

Description of the range of an animal is essential for any effective conservation strategy. Within an animal's range, activities are often segregated so that breeding and foraging occur in separate locations. This is especially true for migratory animals, and occurs as a result of the differing resources required during these activities (Alerstam et al. 2003). Typically, conservation efforts are focussed on breeding areas, as they are critical to the life history of any animal and also because they often tend to concentrate individuals within spatially discrete areas. Such areas are more amenable for protection (Maxwell et al. 2011, Mazaris et al. 2014, Thums et al. 2017) or commercial harvest (Hays 2004, Sadovy & Domeier 2005) and also provide easier access for research (Rodríguez et al. 2017). However, only a relatively small portion of the life span of any individual is actually spent within these breeding grounds. Much of an animal's time is spent in search of food, which may involve migration over considerable distances (Schofield et al. 2013). Thus, conservation management requires knowledge of behaviours throughout the

range, encompassing breeding, migratory and foraging phases of the target species.

Biotelemetry offers a means to track movements that identify these behaviours (Hussey et al. 2015). Marine turtles have often been the subject of studies using this approach, as these animals are at conservation risk (Jeffers & Godley 2016), with all species listed as Endangered, Critically Endangered or Vulnerable (except the flatback, which is Data Deficient) by the IUCN (IUCN 2017). Their conservation status reflects their vulnerability to anthropogenic threats such as entanglement in fishing gear, coastal development and global warming. In Australia, flatback turtles *Natator depressus* are of particular conservation concern because they are both susceptible to these threats and an endemic species with a distribution limited to northern Australia (Limpus 2007, Pendoley et al. 2014b). A key part of their range across the northwest region of Western Australia has become a concentrated hub of industrial development, with offshore gas fields and coastal processing and ship loading facilities of iron ore, petroleum and natural gas (Whittock et al. 2014). This has resulted in modification of coastal habitats due to dredging and infrastructure development and increases in vessel traffic (Whittock et al. 2017). Many key nesting sites are in close proximity to industrial operations, e.g. the Dampier Archipelago and Barrow Island (Pendoley et al. 2014a) with high overlap between core flatback turtle inter-nesting areas and petroleum title areas (Whittock et al. 2014) and activities (Whittock et al. 2016a, 2017).

Given the potential threats and limited understanding of the status of the species, there is a clear need to describe the movement patterns and identify breeding and foraging areas and migratory corridors (Pendoley et al. 2014b) across a significant part of its range. The need for this data is critical because, unlike other marine turtles, the flatback is the only species that does not have a pelagic phase; it completes its life cycle on the continental shelf (Walker & Parmenter 1990) where it is most at risk from human activities.

Here, we used data from satellite transmitters deployed on 35 adult female turtles nesting in the vicinity of an iron ore processing and ship-loading facility to understand the spatial and temporal components of the main phases of their breeding cycle: the inter-nesting period, the transit to and spatial extent of the foraging grounds using state-space models and movement-based kernel density analysis. We then assessed the overlap of each of these phases with the ship-loading facility and with the existing system of marine reserves. We also analyse some of the first data on the diving behaviour in each of these phases and the physical properties of the water column while diving, thus providing further detail with which to understand flatback turtle behaviour and the drivers of their movement.

MATERIALS AND METHODS

Study sites

This study was conducted at 2 flatback turtle rookeries: Bells Beach (20.613° S, 117.152° E), approximately 38 km north-east of the town of Karratha, and Delambre Island (20.465° S, 117.075° E), approximately 18 km north of Bells Beach in northwest Western Australia (see Fig. 1). The Bells Beach site is adjacent to an iron ore port (Cape Lambert). Anually, there are thought to be around 120 nesting females in the Bells Beach rookery and over 3000 in the Delambre Island rookery, with nesting commencing around late October (J. Rossendell et al. unpubl. data).

Telemetry

Satellite-linked transmitters were attached to 35 nesting female flatback turtles over 3 nesting seasons (2010/2011 to 2012/2013) on Bells Beach (30 turtles) and Delambre Island (5 turtles) (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m602 p237_supp.pdf); 3 transmitters were deployed in season 2010/2011, 10 in 2011/2012 and 22 in 2012/2013. The transmitters were deployed between mid-late November and early January (Table S1). Sixteen of the transmitters were Kiwisat 101 and 9 were Fastloc F4G291A, both manufactured by Sirtrack (Havelock North) and 10 were conductivity-temperature-depth-satellite relay data loggers (CTD-SRDL) manufactured by SMRU (Table S1).

Turtles were caught as they were returning to the ocean after nesting, and were placed on a 0.5 m high rectangular container over which a turtle harness was draped. The design of the harness was based on that of Sperling & Guinea (2004), and was composed of a molded polypropylene base-plate, straps made from 22 mm wide seatbelt webbing with Velcro ends and a centralised corrodible plastron ring with raised nodules to reduce the potential for snagging. Satellite tags were fixed to the base-plate using a fast-curing marine adhesive/sealant (Sikaflex®-291) coated with antifouling paint. The transmitter was positioned over the top of the second central scute, and harness lines were threaded through the tag

base plate, tightened, then fixed into place by the Velcro strips and 2.5 mm diameter steel staples crimped over the harness lines and tightened with pliers. The staples break down over time, helping to allow the Velcro to separate, but the main mechanism allowing the harness to come free of the turtle over time is the central corrodible plastron ring.

Flipper tags (Titanium Stockbrands) were attached to the front flippers of each turtle and the curved carapace length (CCL) and curved carapace width (CCW) were measured using a flexible measuring tape to the nearest cm.

All transmitters relayed position information via the ARGOS satellite network (www.argos-system.org). In 2010, the transmitters were programmed to transmit positions continuously for the first 90 d and then for 4 h every 12 h when the saltwater switch was dry. The CTD-SRDL tags transmitted positions on a cycle of 10 h on and 2 h off, with the off times (11:00 to 12:00 and 23:00 to 24:00 h) corresponding to the times when satellite coverage over the study area is relatively low. For the Fastloc tags, position acquisition was attempted every 1 h for the GPS and 6 h d^{-1} for ARGOS when the saltwater switch was dry. The CTD-SRDL tags also reported vertical profiles of conductivity, temperature and pressure. They sampled pressure every 4 s during a dive (when wet and below 2 m for 8 s); 5 main inflection points are selected for transmission via a broken stick algorithm (Boehme et al. 2009), from which dive duration and post-dive surface interval can be determined. This is because the limited ARGOS bandwidth does not allow all data points to be transmitted (Boehme et al. 2009). Information from the wet–dry sensor was also collected to form dive and haulout records; a haulout begins when dry for 10 min and ends when wet for 40 s. The deepest CTD profile in each 6 h period was sent and during each profile, the CTD sensor was sampled every 1 s; each profile contained a maximum of 19 cut points. Water temperature at the surface was also reported by Kiwisat 101 tags, measured on the transmitter board inside the tag. The value registered by the sensor was then manually converted to temperature in °C according to a conversion table provided by Sirtrack (Havelock North).

Movement behaviour

The Bayesian state-space switching model developed by Jonsen et al. (2003, 2005) was fitted to the ARGOS locations received for each individual turtle to account for position error and to provide behavioural state estimation. Briefly, the position error is modelled with the observation equation, assuming t-distributed error with associated variance and degrees of freedom, and behavioural state (transient or resident) is inferred from the autocorrelation to the previous displacement and turn angle. The resident state has low autocorrelation to the previous displacement and high turn angles, and the transient state has high autocorrelation to the previous displacement and low or near-zero turning angles (directed movement) (see Jonsen et al. 2005 for more details). Resident state is commonly associated with foraging (Kareiva & Odell 1987) and also resting or breeding (Bailey et al. 2008, 2009). This approach is useful as it provides a statistically rigorous approach for the determination of hidden behavioural states underlying animals' tracks (Jonsen et al. 2013) (see Costa et al. 2012 for a useful review).

GPS positions were only available for a small number of animals (26%), and to maintain consistency in the analysis, we used only the ARGOS data in the state-space model. The observation error for each ARGOS estimate was as per the reported (by Argos) error associated with each ARGOS location class (Z, B, A, 0, 1, 2, 3). The first 3 classes have no accuracy information assigned by Argos and the remaining classes have reported accuracy of >1500, 500–1500, 250–500 and <250 m, respectively. However, accuracy had been measured on marine mammals at 10.3 and 6.2 km for class B and A and 4.2, 1.2, 1.0 and 0.49 km, respectively, for the remaining classes (Costa et al. 2010).

The state-space switching models were fit via Markov chain Monte Carlo (MCMC) implemented in JAGS 3.2.0 (Plummer 2003) called from R (R Development Core Team 2016) using the R package 'bsam' (Jonsen et al. 2013, 2017). We ran 2 MCMC chains of length 120 000, of which the initial 80 000 were discarded, and every 40th of the remaining samples were retained. We used a 6 h time step for all turtles, giving 4 location estimates d^{-1}. This was selected taking into consideration the mean number of locations received per day for all turtles (5.2 ± 2.6) (Table S1). All models were checked for convergence using the methods outlined by Jonsen et al. (2013).

We took the 2 movement states statistically inferred from the raw Argos locations (see Fig. S1a,e) by the state-space model (resident and transient) (Fig. S1b,f) and further divided resident state into 2 distinct behaviours (inter-nesting and foraging) and transient state into 2 other behaviours (outward transit and other transit) (Fig. S1c–h). Inter-nesting behaviour was identified as the period of time between the start of the deployment and the switch to transient behav-

iour, and foraging was all other resident state not classified as inter-nesting (Fig. S1b−h). Outward transit was identified as the time between inter-nesting behaviour and the first occurrence of foraging behaviour (Fig. S1b−h). Other transit was all transit behaviour not classified as outward transit (Fig. S1b−h). For some turtles, a switch in movement behaviour was not detected by the model, so it was not possible to identify the different behavioural modes.

We overlayed the state-space modeled position estimates onto the Geosciences Australia, Australian bathymetry and topography grid (250 m) (Whiteway 2009) and extracted the underlying bathymetry for each point.

Utilisation distribution

To assess the area used by the turtles, we calculated the 50 and 95% utilisation distributions for each individual using the Brownian Bridge Kernel method implemented in the function 'kernelbb' of the R package 'adehabitatHR' (Calenge 2011). This method takes into account not only the animal's position, but also the path travelled by the animal between suc-cessive positions (Calenge 2011). Two smoothing parameters needed to be set; sig1, which controls the width of the 'bridge' connecting successive positions, and sig2, which is related to the imprecision of the positions. Values of sig1 were chosen using the function 'liker' that implements the maximum likelihood approach developed by Horne et al. (2007), and sig2 was set at 1910 m which was the median ARGOS location error across all position classes combined (Costa et al. 2010). We also calculated the 50 and 95% utilisation distributions for each turtle during each behavioural mode (inter-nesting period, outward transit and foraging) and overlaid these, and the number of turtles in each 3 km grid cell was counted. This was done to identify the areas of highest use and to calculate the total 50 and 95% utilisation distribution for all turtles combined for inter-nesting, outward transit and foraging. We then calculated the overlap between the total utilisation distribution during each behaviour mode with the combined total area of the Cape Lambert shipping channel and area associated with a new wharf.

To assess whether the sample size used to calculate the total 95% utilisation distribution was sufficient to characterise the total area of use by flatback turtles from Bells Beach, we calculated the cumulative utilisation distribution after the addition of each additional turtle (from 1 to the total). We did 100 iterations of this, randomly selecting the turtle IDs to be included in the sample at each iteration and then plotted the cumulative mean and SD of these 100 iterations to determine when an asymptote was reached.

In situ oceanography and dive behaviour

For the 10 CTD-SRDL tags deployed, diving data reported for each dive included 5 main dive inflection points, dive start and end time, maximum depth, dive duration and post-dive surface duration. We calculated the mean of each of these statistics as well as the percentage of the water depth reached on each dive. In some cases the maximum dive depth recorded was greater than the maximum bathymetry, and in these cases we assumed the bathymetry was
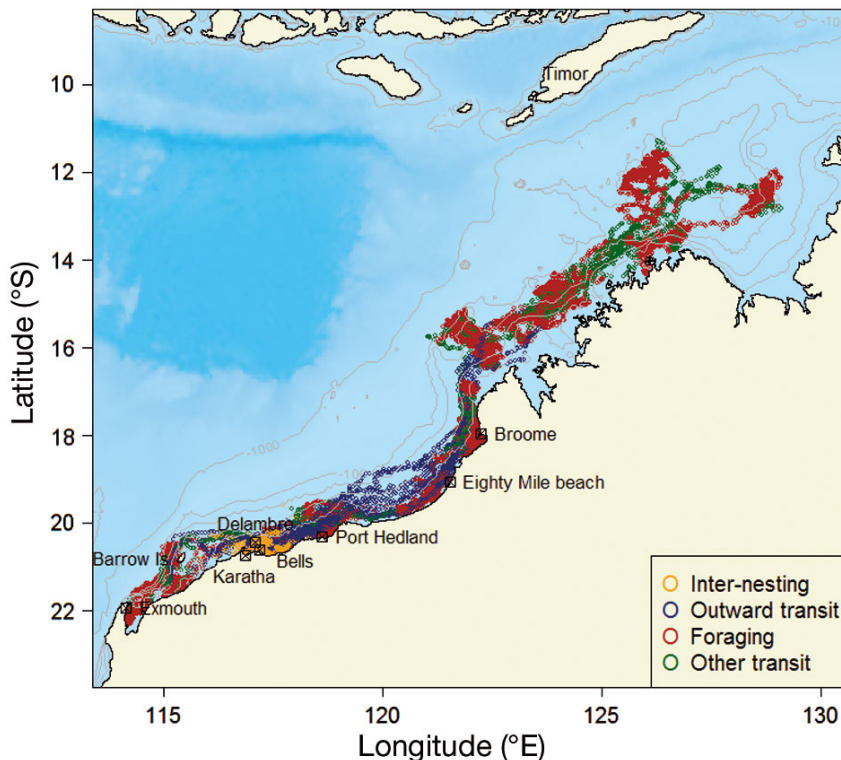

Fig. 1. State-space model position estimates of all flatback sea turtles. Tracks are coloured by behavioural mode: yellow: inter-nesting; blue: outward transit; red: foraging; green: other transit. The 25, 50, 75, 100 and 1000 m depth contours are shown in grey

equivalent to the maximum dive depth. This occurs because some turtle positions were close to shore, and bathymetry is recorded at lowest astronomical tide, i.e. it does not take into consideration tidal range, which is high in this region (up to 10 m). We also calculated descent and ascent rate, time spent at maximum depth and the TAD index (Fedak et al. 2001). The TAD index varies between 0 and 1 and is used to provide an indication of the 2-dimensional shape of dives (as obtained from plotting depth by time), with values near 0.5 and below corresponding to more V-shaped dives and values near 1.0 indicating more U-shaped dives (McMahon et al. 2007). As well as sending records of individual dive events, the SRDL also calculates summary statistics of those events over a specified time period (usually 3, 4 or 6 hours). These statistics are based on all the data recorded by the SRDL and so are not prone to distortion by variations in the efficiency of transmission via ARGOS. Where there were discrepancies between the dive statistics calculated from the individual dive records and the summaries, boxplots were made to assist in determining the most robust value.

Potential nesting emergences

For the 10 CTD-SRDL tags, potential nesting emergences were determined from the haulout events reported by the wet/dry sensor, with only those haulout events >45 min and within 2 km of the nesting beach considered. Whilst flatback turtles might be able to nest in a shorter amount of time, we selected 45 min to ensure false crawls were more likely to be excluded. Unfortunately, ARGOS location class was not reported with each of the haulout events; thus, we were not able to restrict these data further to only the highest quality location classes.

Statistical analysis

We used linear mixed effects models (with a Gaussian distribution) and an information-theoretic approach to test for an effect of behavioural mode (inter-nesting, outward transit and foraging) on each dive statistic by comparing the Akaike′s information criterion weights (*w*AIC) of the slope model (dive statistic ~ behavioural mode + turtle ID as random effect) to the intercept only, or null model (dive statistic ~ 1 + turtle ID as random effect), where the *w*AIC varies from 0 (no support) to 1 (complete support). We used the 'corAR1′ function to account for tempo-

ral autocorrelation of the response, and for some models, the variance had to be weighted according to behavioural mode using the 'varIdent′ function and data had to be square-root transformed. We calculated both the marginal (fixed components only) and conditional (fixed and random components) R-squared in order to assess goodness of fit. Salinity recorded by the tags was also examined using a similar approach but without the need for transformation. Due to the strong seasonal effects on water temperature, it was modelled with explanatory variables day-of-year and maximum diving depth using generalised additive models, where the null model included day-of-year. We were not able to model the interaction with behavioural mode as we did not have the same temporal range across each of the behavioural modes. As above, we also included the 'corAR1′ correlation structure and turtle ID was coded as a random effect. We also used generalised additive mixed effects models to test for the effect of year on daily temperature at the surface recorded by Kiwisat tags during foraging and inter-nesting. The effect of year on temperature was not tested for outward transit because we had only 1 yr of data from multiple Kiwisat tags for that behavioural mode. Similar to above, we compared the slope model to the null model (which included day-of-year). We used the 'corAR1′ function to account for autocorrelation, and turtle ID was used as a random effect. All data were modelled with a Gaussian distribution. All means presented are grand means followed by the standard deviation unless otherwise stated.

RESULTS

The number of days for which transmitters provided data ranged from 14 to 790 d with a mean of 333.7 ± 227.6 d (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m602p237_supp.pdf). Data from 3 of the turtles (IDs 122410, 122416 and 122419) were only of very short duration (14, 15 and 19 d, respectively) and were not included when calculating summary spatial statistics. There was a very low proportion (16%) of higher quality location estimates (location class 0, 1, 2 and 3) with the majority of the estimates (84%) assigned to location class A and B (Table S1). There were 5.2 ± 2.6 raw locations recorded per day for each individual (Table S1).

After transmitter attachment, the turtles spent an average of 28.3 ± 17.4 d in inter-nesting mode prior to switching to transient movement, with the switch

Table 1. Utilisation distribution (in km^2) calculated for flatback sea turtles using the Brownian Bridge Kernel method using state-space model position estimates for each behaviour mode (inter-nesting, outward transit, foraging), and for the full track (all behavioural modes combined). Top rows: median and range for the analysis undertaken on individual turtles; bottom rows: total area of the 50 and 95% utilisation distribution (UD) in km^2 calculated from all turtles combined for each behavioural mode and the full track

	Inter-nesting	Outward transit	Foraging	Full track
Median (range)				
50	131 (23–771)	847 (93–3850)	165 (54–1496)	295 (64–4260)
95	888 (83–4308)	4086 (840–9994)	1642 (431–6674)	4704.1 (115–33810)
Total				
50	1474.1	18366.2	10461.1	7829.1
95	9280.3	72808.7	71961.1	75060.3

occurring between 22 November and 5 February, and a median (based on day-of-year) leaving date of 8 January for all seasons combined. During the inter-nesting phase, flatback turtles remained at an average distance of 14.2 ± 8.8 km from their nesting site in water depths of 8.1 ± 2.7 m. The median 50% kernel utilisation distribution for the inter-nesting period for individual turtles was 131 km^2 (range = 23 to 771 km^2) (Table 1). The total, combined area of the 50 and 95% utilisation distributions during nesting encompassed 1474 and 9280 km^2, respectively (Fig. 2A,B, Table 1). The main area of individual home range overlap occurred between Bells Beach and Nickol Bay, and turtles utilising Nickol Bay were predominantly those that were tagged at Delambre Island.

In total, 17 haulout events met the criteria of being >45 min and within 2 km of the nesting beach. Removing the haulouts that were associated with deployment left 10 records; 2 of these records were determined to be false crawls due to subsequent haulout events within the next 24 h. The approximate distance to the nesting beach of these location estimates was 1.65 ± 1.19 km and the mean duration 71.06 ± 12.62 min. These haulout events suggest that only 6 turtles could have re-nested—all only once except for turtle 123161 which nested 3 times (Table S2). These data suggest that the re-nesting interval for these 6 turtles was 16.43 ± 4.10 d.

Turtles spent 22.8 ± 14.9 d in outward transit, in average depths of 22.0 ± 14.5 m, before switching to foraging behaviour. Turtles did not use a discrete, common pathway for the outward transit to foraging grounds (Figs. 1 & 2C). The highest area of overlap was between Bells Beach and Port Hedland, with tracks fanning out thereafter. The median 50% kernel utilisation distribution for outward transit for individual turtles was 847 km^2 (range = 93 to 3850 km^2)

(Table 1). The total combined areas of the 50 and 95% kernel utilisation distributions comprised approximately 18366 and 72809 km^2, respectively, and delineated a wide migratory corridor along the northwest continental shelf that extends from shallow coastal waters to a depth of 50 m (Table 1, Fig. 2C).

When in foraging mode, the turtles were in water depths of 26.1 ± 25.1 m and 25.6 ± 36.6 km from shore. However, 18% of foraging locations were far from shore (105 ± 38 km) and in relatively deep (71.8 ± 8.5 m) water (Fig. 1 & 2E,F). There was a large range in the distance of foraging grounds from the nesting grounds: 18.2 to 1325.8 km (median = 412.6 km). The median 50% kernel utilisation distribution for foraging mode for individual turtles was 165 km^2 (range = 54 to 1496 km^2) (Table 1). As with outward transit, the turtles did not use a common foraging ground, with little overlap of the 50 and 95% utilisation distributions (Fig. 2E,F). The main areas of home range overlap occurred in the area around Barrow Island, Eighty Mile Beach, Lynher Bank and near Adele Island, although only a maximum of 3 turtles had overlapping foraging areas. The total, combined areas of the 50 and 95% kernel utilisation distributions on the foraging grounds were 10461 and 71961 km^2, respectively (Table 1, Figs. 2E,F & S5).

The median proportion of time that the turtles spent in each mode was 75% for foraging, 12% inter-nesting, 8% outward transit and 5% other transit (between foraging sites). However, these proportions are relative to the length of time the turtles were tracked, and time spent in inter-nesting mode is likely an under-estimate, as we do not know the length of time each turtle was on the nesting grounds prior to deployment of the tag. Three (9%) satellite-tracked flatback turtles from Bells Beach, appeared to re-migrate; 111631, 111633 and 103235, after 352, 690 and 354 days, spending 10, 50 and 13 days in the vicinity of Bells Beach, respectively. During this period the former 2 turtles' locations were clustered at, or very near, Bells Beach; however, the latter turtle did not have clustered locations and was 16 km from Bells Beach at this time, suggesting it did not nest. The timing spent in the vicinity during re-migration would suggest that only turtle 111633 nested. Using 1 complete round trip from this turtle (from the start of the first foraging trip to the start of
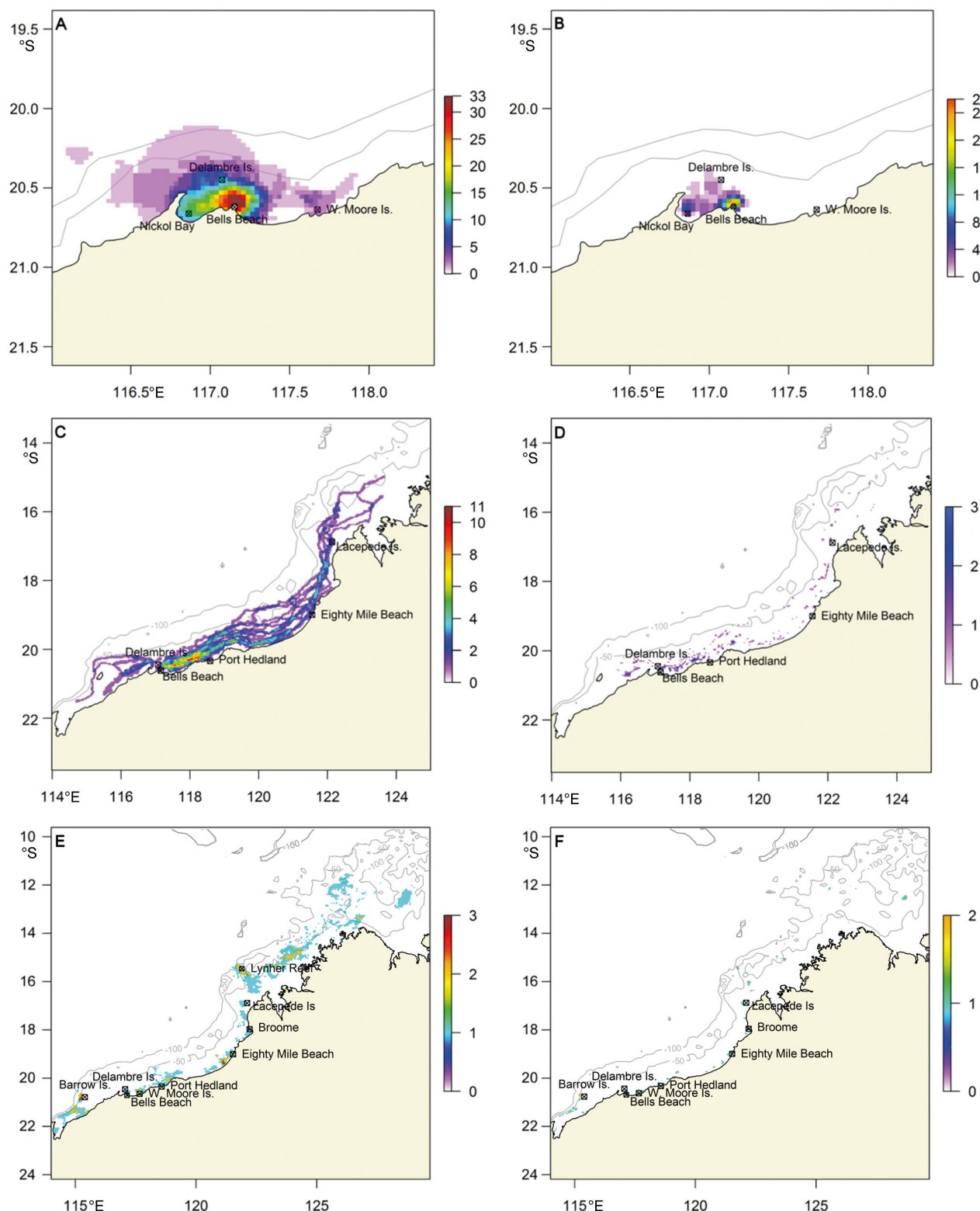
Fig. 2. Utilisation extent of all flatback sea turtles calculated as the maximum number of individual turtle Brownian Bridge utilisation distributions (UDs) in each 3 km grid cell during (A,B) nesting season, (C,D) outward transit, (E,F) foraging mode. Depth contours—10 m and 25 m in (A,B) and 50 m and 100 m in (B–F)—are shown in grey. 95% UDs are shown in (A), (C) and (E), and 50% UDs are shown in (B), (D) and (F). See Fig. S5 in the Supplement at www.int-res.com/articles/suppl/m602p237_supp.pdf for finer scale resolution of (E) and (F)

the second foraging trip) (Figs. S2 & S3), 87% of the time was spent foraging (considering only the first foraging trip), 3.5% migrating to and from foraging grounds (after the first foraging trip), 6.5% nesting (at the second, complete nesting season) and 3% in other transit (Figs. S2 & S3). All 3 turtles returned to the previously used foraging grounds. Only one other turtle (111632) had a record nearing 2 yr, but it did not re-migrate and was 751 km from Bells Beach at the end of the data record (727 d at large), suggest-

ing it was unlikely to return for nesting at the 2 yr interval. A further 31% of the turtles had tracks longer than 1 yr but less than 2 yr (567 ± 98 d) but did not re-migrate.

The median 50% kernel utilisation distribution for the full track (all behavioural modes combined) for individual turtles was 295 km^2 (range = 64 to 4260 km^2) (Table 1). The range was large due to large variations in the migration distance from the nesting site to each of the foraging grounds (18 to 1326 km). The total combined areas encompassed by all the 50 and 95% utilisation distributions for the full track were 7829 and 75 060 km^2, respectively (Table 1).

The Cape Lambert Port shipping channel extends for approximately 40 km from the port. The 95% utilisation distribution overlapped with the Cape Lambert Port shipping channel and the area associated with dredging for a new wharf for 33 (94%) turtles during the inter-nesting period (Fig. 3A), 9 (26%) turtles during outward transit and only 1 (3%) turtle during foraging (Fig. 3B,C). During nesting and outward transit behaviours, 95 and 100%, respectively, of the shipping channel overlapped with the 95% utilisation distribution of all turtles combined. For the
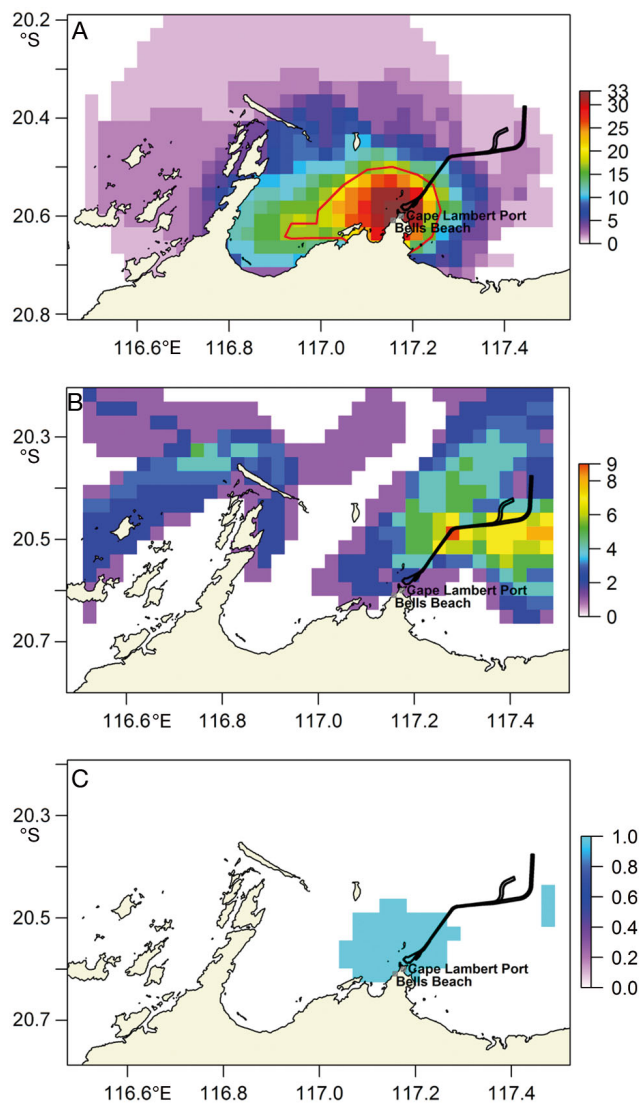

Fig. 3. Zoomed in detail (from Fig. 2) of the overlap between the number of turtle 95% Brownian Bridge utilisation distributions (UD) in each 3 km grid cell with the Cape Lambert shipping channel (large, continuous black contour) and the dredging for the new wharf (very small black contour next to the port) during (A) nesting, (B) outward transit and (C) foraging. Red contour in (A) represents the 50% UD contour for all turtles during nesting
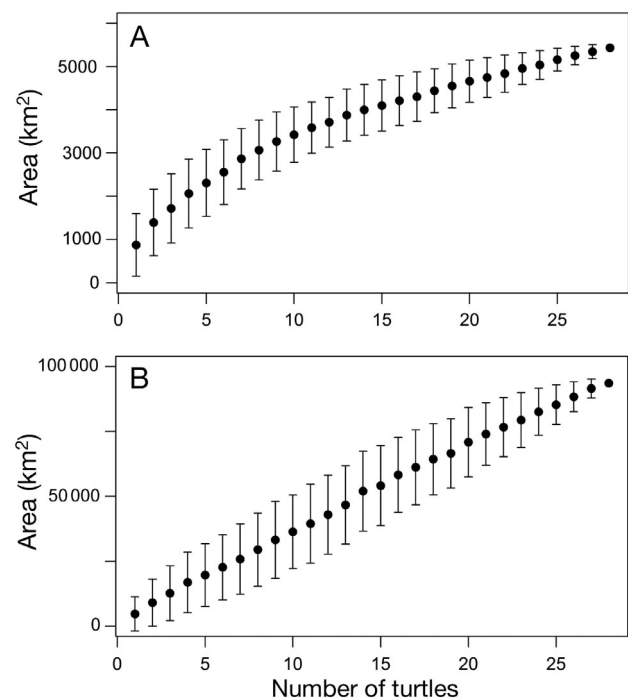

Fig. 4. Cumulative mean and SD of the area (km^2) of the 95% utilisation distribution, calculated from 100 iterations of randomly selecting the turtles to be included in the sample (from 1 to the total) (A) for the inter-nesting period and (B) on the foraging grounds

Table 2. Dive summary statistics calculated from individual flatback sea turtle dive events. For max. duration we present the most conservative value between that which we calculate from the individual dive events and the value reported by the satellite relay data logger (SRDL) summary page

ID	Duration (min)	Max. duration (min)	Surface duration (min)	Descent rate (m s^{-1})	Ascent rate (m s^{-1})
123155	20.4 ± 10.8	60	3.2 ± 4.5	0.23 ± 0.17	0.15 ± 0.15
123156	37.1 ± 21.0	130	3.3 ± 3.0	0.29 ± 0.18	0.13 ± 0.15
123157	31.4 ± 30.3	180	2.9 ± 2.4	0.31 ± 0.29	0.17 ± 0.13
123158	34.2 ± 31.4	180	3.0 ± 3.2	0.28 ± 0.28	0.14 ± 0.14
123159	22.0 ± 15.4	75	3.0 ± 3.3	0.22 ± 0.18	0.15 ± 0.13
123160	19.6 ± 16.7	140	2.1 ± 2.6	0.30 ± 0.26	0.14 ± 0.15
123161	45.9 ± 34.7	200	4.3 ± 4.2	0.32 ± 0.23	0.19 ± 0.14
123162	32.1 ± 20.0	120	2.9 ± 3.3	0.21 ± 0.19	0.13 ± 0.13
123163	30.6 ± 24.1	140	4.2 ± 4.8	0.27 ± 0.17	0.18 ± 0.18
123164	24.9 ± 13.2	75	2.6 ± 1.8	0.28 ± 0.19	0.17 ± 0.17
Mean ± SD	29.8 ± 8.3	130.0 ± 48.5	3.2 ± 0.7	0.27 ± 0.04	0.15 ± 0.02

Table 3. Dive summary statistics calculated from the individual flatback sea turtle dive events. TAD: time allocation at depth index. See Table 2 caption regarding calculation of maximum max depth. Note: in some cases dive depth is greater than the bathymetry, which occurs because some turtle positions were very close to shore and bathymetry is recorded at lowest astronomical tide. Prop.: proportion

ID	Mean max. depth (m)	Maximum max. depth (m)	Mean time at max. depth (min)	% dives with TAD ≥ 0.75	Mean bathy- metry (m)	Max. bathy- metry (m)	Prop. within 10% of bottom
123155	14.3 ± 7.7	38	41.2 ± 39.3	0.57	10.5 ± 7.9	34	0.80
123156	42.5 ± 22.8	130	33.2 ± 36.3	0.48	52.7 ± 20.0	133	0.63
123157	11.0 ± 4.7	33	45.9 ± 42.0	0.81	2.8 ± 3.1	17	0.96
123158	12.5 ± 5.2	40	34.4 ± 40.0	0.69	6.9 ± 5.5	35	0.86
123159	15.9 ± 11.3	63	44.3 ± 39.4	0.60	13.5 ± 15.2	83	0.77
123160	8.5 ± 4.0	24	38.9 ± 39.2	0.60	8.9 ± 3.8	25	0.46
123161	39.4 ± 29.3	120	50.5 ± 40.9	0.72	44.8 ± 33.7	172	0.72
123162	22.7 ± 15.0	75	30.5 ± 38.1	0.62	15.6 ± 21.4	65	0.83
123163	40.6 ± 28.0	120	32.9 ± 36.9	0.45	57.5 ± 28.0	122	0.53
123164	21.9 ± 9.3	60	44.5 ± 39.1	0.60	23.5 ± 10.3	57	0.75
Mean ± SD	22.9 ± 13.1	70.3 ± 39.7	39.7 ± 6.7	0.61 ± 0.10	23.7 ± 20.3	74.3 ± 52.3	0.73 ± 0.15

one turtle with overlap with the shipping channel during foraging, only 25% of the shipping channel overlapped with the 95% utilisation distribution.

The plot of the cumulative utilisation distribution shows that we had near sufficient samples for documenting spatial use during the inter-nesting period (Fig. 4A), but not while on the foraging grounds (Fig. 4B). This is likely related to the finding that the turtles did not use a common foraging ground and had minimal spatial overlap among individuals.

The diving statistics are summarised in Tables 2 & 3. The mean diving duration for the turtles was 29.8 ± 8.3 min but the absolute maximum diving duration was 130.5 ± 48.5 min with the absolute maximum recorded for an individual being 200 min. Descent rates (0.27 ± 0.04 m s^{-1}) were faster than ascent rates (0.15 ± 0.02 m s^{-1}) (Table 2). Mean maximum diving

depth was 22.9 ± 13.1 m and 39.7 ± 6.7% of dive time was spent at the maximum depth. The absolute maximum depth reached across all turtles was 70.3 ± 39.7 m. The proportion of dives within 10% of the bottom (i.e. benthic) was 0.73 ± 0.15 and the proportion of dives that were U shaped (TAD ≥ 0.75) was 0.61 ± 0.10 (Table 3). There was large variation in the mean (23.7 ± 20.3) and maximum (74.3 ± 52.3) bathymetry and it was more or less in line with the mean and maximum diving depths (Table 3). The maximum dive duration and depth recorded by the SRDL in the summary file was sometimes different than the maximum duration and dive depth we calculated from the individual dive events per turtle (Figs. S6 & S7). This can occur because the summary statistics are based on all data recorded by the SRDL and are not prone to distortion by variations in the efficiency of transmission

via ARGOS (as per information provided by the manufacturer). However, to be conservative, we report the maximum dive duration and depth (Tables 2 & 3) as the lower of the 2 values.

All dive statistics varied with behavioural mode, with the slope model in all cases having majority support (wAIC = 0.92 to 1.0) (Table S3). However only a small amount of variance was explained by the fixed component of the models (R^2 = 0.01 to 0.11), with random effects accounting for most of the variance in all models, except for dive duration (Table S3). Dive depth, duration and surface duration were highest when in foraging mode and lowest when in the inter-nesting phase; descent rate was similar across all modes and ascent rate was lowest in outward transit mode (Fig. 5). There was also a tendency for time at maximum depth and the TAD index to be lowest in outwards transit mode, whereas the percent of bottom reached was highest in the inter-nesting phase (Fig. 5).

The mean maximum depths tended to be lower in between around 16:00 and 19:00 h, whereas diving duration started to increase after this time and was highest around 22:00 to 04:00 h, and surface duration highest around 10:00 to 11:00 h (Fig. S4).

We were not able to undertake statistical modelling of salinity data collected by CTD-SRDL tags as they were erroneous (same values recorded profile after profile), indicating a technical issue with the sensors. For linear models with water temperature collected by CTD-SRDL tags as the response variable, the model with day-of-year and maximum diving depth had the highest statistical support (wAIC = 1.0) and explained 46% of the deviance (Table S3). Most of the deviance was explained by day-of-year (45%), indicating that there was only minor evidence for a change in water temperature by depth and thus the water that these 10 turtles were diving in was, on average, well mixed. For some turtles, very little CTD data was returned (123155,

123157, 123158, 123160), possibly due to the shallow diving depths of these turtles (Table 3). For the turtles with long enough records, it is possible to see that there were times where the turtles were diving in stratified water (Fig. 6). For those with 2 summer periods recorded, it can be seen that the water tem-
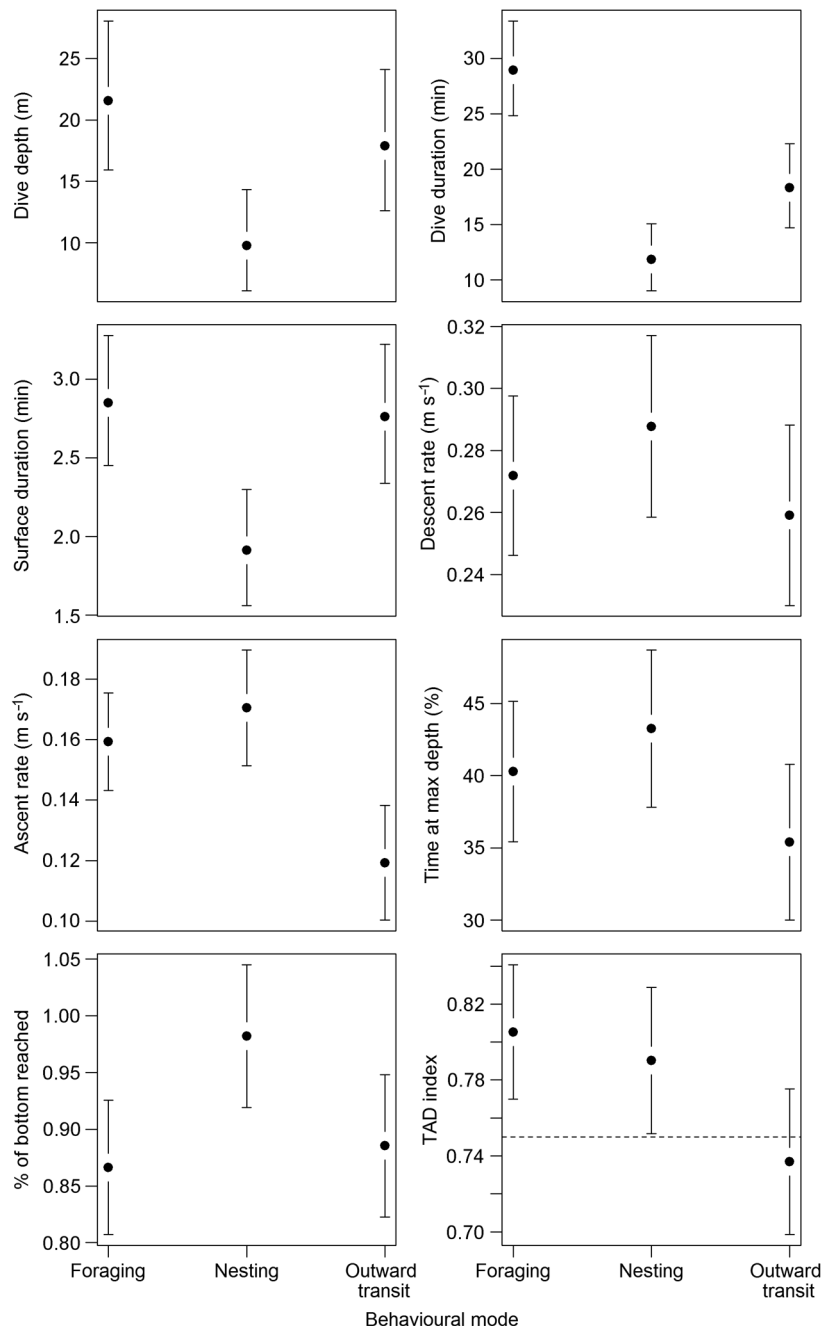

Fig. 5. Predicted values and confidence interval for each flatback sea turtle dive statistic from linear mixed effects models fitted to examine the relationship between dive statistics and behavioural mode. TAD: time allocation at depth, with the dashed line indicating the value of TAD above which dives are considered U-shaped
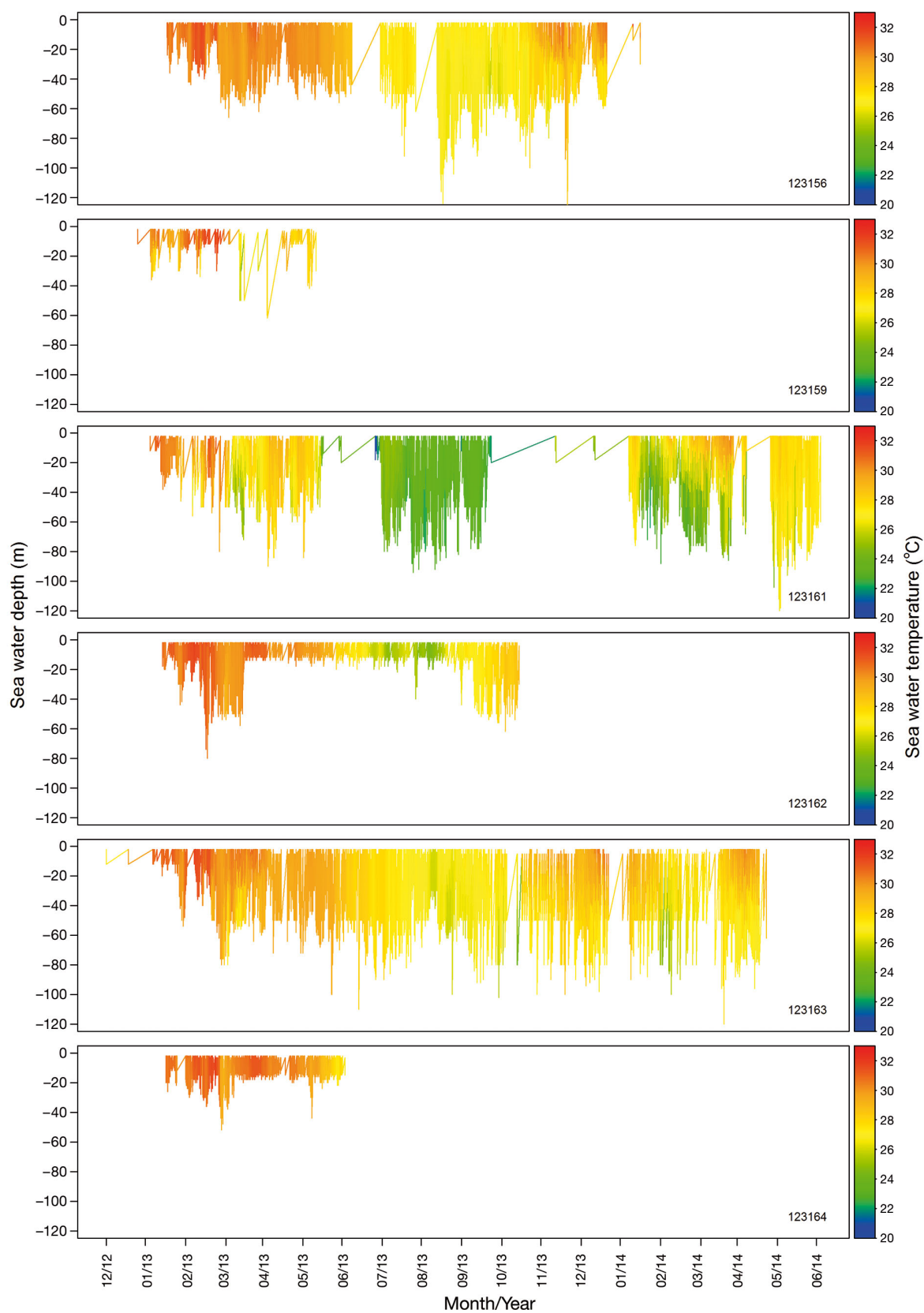
Fig. 6. Time depth profiles of flatback sea turtles colour coded by temperature recorded by conductivity-temperature-depth-satellite relay data loggers (CTD-SRDL) for 6 turtles (turtle ID in bottom right)

perature in the second summer (when the turtles were in foraging mode) was mostly lower than that for the first summer (during the inter-nesting period) (Fig. 6). This is probably related to the fact that on the foraging grounds, these 3 turtles were typically much further from shore and in much deeper water than when they were on the nesting grounds (Table 3).

Surface water temperatures recorded by Kiwisat tags ranged between 21.5 and 35.5°C during inter-nesting, 22 and 32.5°C during outward transit and between 16 and 37.5°C during foraging (Fig. S8). There was a clear seasonal pattern and some indication of fluctuations between years (Fig. S8). We found no evidence for an effect of year during nesting, with the model containing day-of-year alone having majority support (Table S4); however, we did find evidence for an effect of year during foraging, with the slope model having majority support ($wAIC = 1$) and explaining 60% of the deviance (Table S4). Predictions showed that turtles experienced warmer sea surface temperatures (by ~2°C) in the 2010–2011 season (Fig. S9). In total, 51% (17) of the turtles with transmitters have now been re-sighted, with an average (±SD) return rate of 1178 ± 374 d (~3 yr). Only one of these still had the harness attached but no transmitter (almost 2 yr later), due to biofouling along the harness (this was 1 of 3 that were not treated against fouling). The plastron ring had evidence of corrosion but had yet to completely corrode. Of these turtles, the majority (14) were recorded as having minor damage which consisted of 2 notches 1 to 2 cm long from the rear straps where the harness had rubbed on the carapace (Fig. S11). A further 3 were recorded as having no damage.

DISCUSSION

Our analysis provided an objective and quantitative assessment of the spatial and temporal extent of biologically important areas for flatback turtles. Importantly, we found that flatback turtles from the Cape Lambert region did not use a discrete migratory corridor and dispersed widely to foraging grounds that had minimal spatial overlap. The lack of common spatial areas for foraging and transit make protection outside the nesting season more challenging. By overlaying turtle utilisation distributions with industrial activities (shipping channels and port infrastructure), we have provided important data for conservation and management planning for this species. We also provide the first information on the diving behaviour and *in situ* water temperature data of flatback turtles during the post-nesting migration, showing that turtles forage both on the benthos and within the water column, and that some turtles forage in relatively deep and stratified water far from shore.

The median kernel utilisation distribution we calculated during the inter-nesting phase (131 km^2) was similar to that calculated for nearby Barrow Island (143 ± 171 km^2) (Whittock et al. 2014). This is a larger area than has been reported for other adult female marine turtles such as loggerhead turtles (10 km^2; Schofield et al. 2010) but much less than for Kemp's ridley turtles (600 to 1000 km^2; Seney & Landry 2008). The different ranges may reflect the size of adjacent available nesting beaches or be related to species-specific requirements such as foraging to supplement stored energy reserves (Schofield et al. 2010) as has been reported for other marine turtles (Hochscheid et al. 1999, Hays et al. 2002, Georges et al. 2007).

The total area used during inter-nesting mode by all turtles combined was, however, larger (1474 km^2) than that calculated previously (218.69 km^2) at the Lacepede Islands (Thums et al. 2017). This was due to the different ways that the utilisation distributions were calculated. Here, we overlapped all individual 50% utilisation densities and summed the area used, whereas the utilisation density for the Lacepede Islands was calculated across all turtle locations combined. In addition, our calculation included turtles from both Bells Beach and Delambre Island, and as the latter turtles utilised Nickol Bay, the total utilisation distribution was expanded.

Similar to that reported previously (Whittock et al. 2016b, Thums et al. 2017), we found huge variation in home range of individual turtles (range = 64 to 4260 km^2) due to the large variation in mean distance from the nesting site to the foraging sites used (18.2 to 1325.8 km). Here, the former turtle foraged near to the nesting grounds, whereas the latter turtle was 1 of 7 turtles (22%) that migrated over 1000 km from the nesting site.

There was low individual overlap in the 95% utilisation distribution for foraging mode, showing that over their wide ranges, the turtles did not have any common foraging grounds used by large numbers of individuals. The highest number of turtle utilisation densities overlapping was 3 (9%) at Eighty Mile beach, also found to be an important foraging site for flatbacks from other rookeries (Whittock et al. 2016b). This low overlap in flatback turtle home ranges has been found previously, with only 15% of turtles from across 4 rookeries in the northwest (n = 66) having

overlapping home ranges at a 20 km grid scale (Whittock et al. 2016b). These observations suggests that suitable foraging habitat is available along the entire length of the coast (Pendoley et al. 2014b), and perhaps also that flatback turtles do not have specialised diets (Limpus 2007). These results also have important implications for protecting the foraging grounds for this species, and suggest that marine protected areas are unlikely to be a solution — although in this case, the Eighty Mile Beach, Kimberley and Oceanic Shoals Commonwealth Marine Reserves afford some protection to foraging turtles. However, there was no overlap between the Dampier Commonwealth Marine Reserves and the total 95% utilisation distribution for all turtles during the nesting season (Figs. 2 & S10 in the Supplement at www.int-res.com/articles/suppl/m602p237_supp.pdf). Affording more protection to the inter-nesting utilisation distribution area with the largest individual turtle overlap could be considered, although for high-risk operations such as dredging, mitigation such as turtle excluder devices (TEDs) and fauna observers are used by industry in this area.

The cumulative mean plot of utilisation distribution shows that our sample size was representative for calculating the area used during the inter-nesting period; however, it might have been insufficient for documenting the foraging grounds. This is perhaps not surprising given that we did not find a common foraging ground used by large numbers of individuals.

As previously shown by Esteban et al. (2017), satellite transmitters are useful for estimating clutch frequency in sea turtles. Using haulout events >45 min reported by the CTD-SRDL tags, our data suggest an inter-nesting interval of around 16 ± 4 d. Unfortunately, we were not able to determine the location class for each of the haulout events, as haulouts are calculated by the tag via the wet and dry sensors and reported with the interpolated haulout location and start and end dates (Fedak et al. 2001). Thus, some of the location estimates used in the interpolation might have been those with higher spatial error. Even still, our calculated inter-nesting interval is similar to the inter-nesting interval calculated for flatback turtles in the same region, at 10 to 14 d (Pendoley et al. 2014a, Whittock et al. 2014), and similar to that reported for marine turtles in general (9 to 18 d) (Miller 1997).

Our data suggest that 3 turtles re-migrated to the nesting grounds, but only one of these (111633 at 690 d) showed evidence that nesting occurred (it spent 50 d there, whereas the other 2 spent ≤13 d).

Using our inter-nesting interval of 16 d, this would suggest that the turtle only nested 3 times (range = 2 to 4 considering the calculated SD). The re-migration interval at nearby flatback rookeries was also around 2 yr (Pendoley et al. 2014a). The fact that many (31%) of our tracked turtles had tracking durations longer than 1 yr but did not re-migrate, and another of our turtles had a tracking duration of 727 d but was still 751 km from the nesting grounds, suggests that re-migration intervals for flatback turtles at this site are likely to be ≥2 yr. But given that 75% of re-migrant flatback turtles at Eco Beach (in the Kimberley region) nested on a 1 yr cycle (McFarlane 2011), and 37% of the flipper tag re-sighted turtles at Delambre Island re-migrated within 1 yr (Thums 2015), 1 yr re-migration intervals are also possible, but perhaps not all re-migrants nest. Marine turtles generally return to breed at variable intervals of 2 yr or more (Miller 1997) and differences in re-migration intervals could be related to body condition and quality of the foraging grounds in addition to environmental conditions, as has been suggested in relation to fluctuations in the numbers of green turtles returning to breed among years (Limpus & Nicholls 1988).

Re-sight rates of flatback turtles at Bells Beach not instrumented with satellite tags were shorter on average (~2 yr) than those that were instrumented (~3 yr). There are, however, some important considerations here: (1) the rookery is only monitored for 2 to 3 wk over peak season, thus it is not possible to calculate re-migration intervals precisely with these data; (2) re-sight effort was higher during years where satellite tags were deployed; (3) we have a much smaller pool of re-sighted turtles that had satellite tags deployed compared to those that did not (17 vs. 180); and (4) turtles lose their flipper tags and any minor carapace damage might go unnoticed (thus some re-sightings of turtles that had satellite tags deployed would be recorded as new). We suggest that more data are needed to determine any effect of the harness, such as comparing satellite tags deployed with and without a harness as done for leatherback turtles (see Fossette et al. 2008).

As these are the first dive records of flatback turtles outside of the inter-nesting period, it is difficult to compare our results. Even for other species, most deployments of time-depth recorders are during the inter-nesting period where fidelity to nesting beaches allows for the recovery of instruments (and data). The mean maximum depth of turtles here for all behavioural modes combined (22.9 ± 13.1 m) was in line with that found for inter-nesting flatback turtles at Curtis Island, Queensland and Bare Sand Island,

Northern Territory (Sperling et al. 2010); however, inter-nesting turtles here had much shallower dives (9.6 ± 2.4 m). The mean dive duration at Curtis Island and Bare Sand was around 35 and 44 min, respectively, whereas inter-nesting turtles here had mean dive durations of around 14.0 ± 3.7 min, and for all periods combined was 29.8 ± 8.3 min. Our dive durations are similar to the post-nesting migrations of another benthic diving species from the region, the hawksbill turtle, which had mean dive and post-dive durations ranging from 31.2 to 57.9 min and 1.1 to 3.9 min, respectively (Hoenner 2012). The mean maximum dive duration recorded here was 130.5 ± 48.5 min, and an absolute maximum recorded of 200 min, greater than the maximum recorded for hawksbills in the region of 145 min (Hoenner 2012). Our procedure of selecting the more conservative maximum duration (comparing that calculated by us from the individual dive events versus that reported in the SRDL summary statistics) ensures that this result is not distorted by variations in the efficiency of transmission via ARGOS. In addition, a maximum duration of 200 min occurred twice (for turtle 123161) with the next longest value being 180 min recorded by this turtle 10 times and by 2 other turtles (123157 and 123158) on 4 and 3 occasions, respectively (Fig. S6). Although this is not the longest duration recorded for a marine turtle, e.g. the maximum recorded for a marine turtle was 410 min for a loggerhead turtle (Hochscheid et al. 2005), the loggerhead record was from temperate waters during winter, where dive duration might be extended by reduced metabolic rates (Hochscheid et al. 2005). While we also included some portion of winter in our dive records, the diving occurs in tropical waters. However, some of our turtles dived deeply (30% ≥120 m and 70% ≥60 m), and inspection of the temperature profiles for the turtle that recorded the longest dive duration (200 min for 123161) shows that the water temperature experienced by the turtle was as low as 20°C, with ~24°C commonly recorded. Taken together, the evidence suggests that flatback turtles here might also be able to extend dive duration beyond other species diving in tropical waters (e.g. hawksbill turtles) given these relatively deep dives to cooler waters.

Even though all dive statistics varied with behavioural mode, much of the deviance explained by the models was related to the random effects, except for dive duration. This is likely the result of small sample size, and that the 10 turtles tracked all went to different places with highly variable bathymetry, mostly related to distance from shore. Dive durations were longest on the foraging grounds and shortest on the nesting grounds, with the outward transit having intermediate durations. This might be the result of a combination of seasonal effects (cooler air and thus sea water temperature in winter) and deeper diving on the foraging grounds and thus a mechanism (via reduced metabolic rate) to extend dive duration (as explained above). We also found a similar pattern between diving depth and behavioural state. However this is largely related to differences in the bathymetry, with some turtles selecting areas for foraging with bathymetry deeper than that available during the inter-nesting period.

The mean TAD index calculated suggested that dives on the foraging and nesting grounds only are U-shaped (relatively rapid descent and ascent with a long bottom time). As U-shaped dives are associated with foraging (Schreer et al. 2001, Thums et al. 2008) and resting on the bottom (Hays et al. 2000, Fossette et al. 2012), this is expected. The lower ascent rate recorded for the outward transit also fits, as traveling dives have been associated with a gradual ascent phase (Hochscheid et al. 1999). Our results suggest that flatback turtles do not transit at the surface, but rather at depths of 18 m on average. This has been suggested as a strategy to reduce silhouetting and thus predation (Hays et al. 2001). We also suggest that bathymetry features such as ancient coastlines might aid in navigation, as on average, turtles were within about 88% of the bottom (Thums et al. 2017). The majority (73 ± 0.15%) of dives were within 10% of the bottom, suggesting that flatback turtles are predominantly benthic, as indicated based on stomach content data and other observations (Limpus et al. 1988, Zangerl et al. 1988, Walker 1991). However, as the mean percentage of the sea floor reached during foraging mode was around 87%, we suggest that foraging both on the benthos and in the water column occurs. The association with the benthos highlights their vulnerability to activities such as dredging and other activities such as bottom trawling that are focussed on the seabed.

The foraging habitat of flatback turtles is thought to focus on shallow, turbid, inshore waters (Limpus et al. 1983). The results presented here mostly align with this hypothesis, with most of the individuals spending considerable time close to shore in relatively shallow average water depths of 26 ± 25 m. However, 18% of our tracks were off-shore, and the limited number of turtles we obtained water temperature profiles from showed that some forage in relatively deep (>100 m), stratified water as found for flatback turtles from the Lacepede Islands (Thums et al. 2017).

We found a strong diel signature in dive behaviour, namely with dive and surface durations, with dives longest at night and a longer period of time spent on the surface, increasing during the morning up to midday and declining thereafter. As reported for other turtles (Hays et al. 2000, Blumenthal et al. 2009, Witt et al. 2010), these longer durations could be related to resting on the bottom. As our diel calculations were made on diving behaviour during the entire deployment, they consist of dives during all stages (inter-nesting, transit and foraging), but the behaviours are likely more indicative of foraging mode, given that 75% of the time was spent in foraging mode.

The higher temperatures in 2010–2011 during foraging may have been the result of the low number of tags deployed in the summer of 2011 (n = 3) and shorter duration of tracks (approximately 5.7 mo on average) with most data recorded during austral summer and autumn. It could also have been related to a discrete warming event experienced in the southeast Indian Ocean, with sea water temperatures up to 5°C higher than usual along northwest Australia (Moore et al. 2012) and overlapping with the area that these turtles used.

The total utilization distribution calculated for the inter-nesting period and outward transit both had high (94 and 26% turtles, respectively) overlap with the shipping channel associated with Cape Lambert, but only 1 turtle (3%) had its foraging range around Cape Lambert. This suggests that outside of the nesting season and early part of the outward transit to foraging grounds, industrial activities in this area are not likely to be a risk to flatback turtles, at least for turtles nesting at Bells Beach. As we only tracked 5 turtles from Delambre Island, we cannot make this assertion as confidently for flatback turtles nesting there or other marine turtle species that use the area for foraging. The high overlap we found between turtle inter-nesting and outward transit utilisation distributions and the shipping channels and dredging associated with the Cape Lambert Port could pose risks to turtles from operational vessel movements in terms of dredging and boat strikes. TEDs and fauna observers were in place to reduce risk related to dredging and no interactions with turtles were observed during the study period. Ensuring these controls are in place during dredging operations appears to assist in preventing dredge related injury or mortality (Whittock et al. 2017). Although Hazel (2007) found that in research trials in a 6 m boat, the proportion of turtles that fled decreased as vessel speed increased above 4 km h^{-1}, this response has not been demon-strated in large vessels. The bulk carriers used in this area are relatively slow (usually not more than 10 knots) and large (250 m or more in length). It is expected that turtles would hear approaching vessels in advance and flee, given that the auditory range of turtles (Ketten & Bartol 2006) is within the broad frequency spectrum of vessel noise (Richardson et al. 1995). The fact that turtle tracks continued and did not stop after entering the channel (average deployment duration of 334 d) suggests that the turtles tracked here were not impacted by vessel strike; furthermore, 17 out of the 35 instrumented turtles have now been re-sighted (as mentioned above). The 3 turtles with short (14 to 22 d) deployment times were all re-sighted (after 738, 1122 and 722 d), lending further support to this assertion. With only 1 turtle having overlap with the shipping channel during foraging, our data suggest that flatback turtles that use the Cape Lambert area for nesting are at low risk from vessel strike associated with industrial activity in this area. However, we only tracked adult female flatback turtle nesters; flatbacks (or other species) that nest in other areas could use the area for foraging. Deployments on turtles (including males and juveniles) caught in water and/or aerial surveys would be able to assess the risk further and additional deployments on flatbacks from Delambre Island would be useful to this end given that Delambre is a significant rookery for the species.

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