



Diving at the shallow end: Green turtle behaviour in near-shore foraging habitat

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ABSTRACT

Green turtles *Chelonia mydas* of immature and adult size ($n=19$, curved carapace length 49 to 118 cm) were equipped with time-depth recorders for short periods (≤ 7 d) to investigate diel and seasonal variation in diving behaviour. Research sessions were distributed over 2 years to cover seasonal variation in sea temperature from 14 °C to 30 °C. Diurnal dives were shallower and shorter than nocturnal dives, with diel patterns also evident in dawn and dusk peaks in occupation of depths within 1 m of the surface, elevated diurnal occupation of depths 1 to 2 m below the surface and elevated nocturnal occupation of depths >2 m. Dive duration increased as sea temperature decreased, showing strong negative correlation by day and by night. Study turtles made resting dives that were 3 to 4 times longer in median duration, and six times longer in maximum duration, at cool temperatures than they were at warm temperatures, but there was no evidence of winter diapause or location shift to avoid cold water. The large majority of turtles spent 89 to 100% of their time at depths ≤ 5 m below the surface, three individuals did not exceed 3 m and the maximum depth recorded by any turtle was 7.9 m, although deeper water was available. Furthermore, the dive data indicated that study turtles collectively spent more than 80% of their time at charted (low tide) depths of 3 m or less, indicating that they consistently used the shallow margins of the bay where human activities tend to be concentrated, thereby potentially increasing their exposure to anthropogenic threats.

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1. Introduction

The green turtle *Chelonia mydas* has long been regarded as a species of conservation concern, with declining stocks in all major ocean basins being ascribed primarily to harvesting of eggs, juveniles and adults (IUCN Marine Turtle Specialist Group, 2004). Harvest mortality is augmented by inadvertent human impacts (Lutcavage et al., 1997) whose accidental nature demands mitigation strategies informed by knowledge of turtle behaviour. For example, regulation of beach lighting in Florida followed studies that revealed the harmful effects of artificial lighting on the behaviour of both nesting turtles and turtle hatchlings (Witherington, 1992, 1997), while research into dive-depth distributions of pelagic turtles may assist in reducing accidental capture of turtles by ocean long-line fisheries (Polovina et al., 2003).

Inadvertent impacts must also be addressed in near-shore foraging grounds because, among the diverse environments that the species occupies at different life-stages, the neritic is where individual green turtles spend the major part of their lives (Musick and Limpus, 1997; Plotkin, 2003). Threats recently recognised in the neritic environment include entanglement of turtles in near-shore fishing gear (nets, traps and discarded equipment) and mortality due to vessel strike (Greenland et al., 2004; Hazel and Gyuris, 2006; Hazel et al., 2007). These threats

also affect other vulnerable species, including dugong (Greenland and Limpus, 2005), manatee (Ackerman et al., 1995) and whales (Laist et al., 2001). However, mitigation is particularly challenging because the causative human activities are too economically and socially important to permit their broad scale restriction. Hence narrowly-targeted mitigation measures must be devised. Their design requires detailed and location-specific information about the behaviour and fine-scale movement patterns of turtles in areas affected by accidental mortality.

Such fine-scale behavioural data remain scant, particularly for green turtles in foraging areas, since much field research on this species and other chelonians has been conducted at breeding sites. The relative paucity of studies can probably be ascribed to the elusive habits of turtles in foraging areas, which severely constrain direct observation and hamper deployment and recovery of animal-attached telemetry devices. Furthermore, seawater blocks the transmission of radio signals and thereby limits the opportunities for obtaining satellite-tracking data to intermittent brief intervals when a turtle surfaces. Technology advances have alleviated some difficulties in this area of research. For example, novel GPS devices have recently been used to record the locations of inter-nesting loggerhead turtles more frequently and more accurately than was possible with earlier equipment, allowing review of critical habitat in relation to protected area boundaries (Schofield et al., 2007b). In an alternative approach, time-depth recorders can provide a very high-resolution record of a turtle's vertical movements, thereby revealing diving behaviour and at the same time allowing inference about habitat utilisation, especially where water depth varies spatially in a predictable manner (e.g. depth

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increasing with distance from shore). We adopted this method to investigate the ‘shallow end’ of turtle diving behaviour.

Early research into turtle diving investigated physiological responses and recorded extremes in depth and duration of submergence (see Lutcavage and Lutz, 1997 and references therein). Subsequent advances in telemetry equipment have greatly expanded the scope of turtle diving studies. Many studies have addressed behaviour in inter-nesting habitats and during post-reproductive movement in offshore waters, but only a few present dive data for green turtles in near-shore foraging grounds (e.g. Makowski et al., 2006; Seminoff et al., 2001; Southwood et al., 2003b) and these represent reef habitats and deeper bathymetry dissimilar to areas where accidental turtle mortality in eastern Australian waters is of most concern. It would be inappropriate to assume similar behaviour in disparate environments, given that green turtle diving behaviour has been shown to vary notably between different breeding sites (Hays et al., 2002).

Inference from stranding data suggests accidental turtle mortality in eastern Australian waters has occurred predominantly in shallow turbid water close to urban centres (Greenland et al., 2004; Haines and Limpus, 2001; Hazel and Gyuris, 2006). Accordingly, we chose a representative study site adjacent to an Australian capital city where significant marine wildlife populations, including green and loggerhead turtles, dugong and dolphins depend on shallow foraging habitat (Chilvers et al., 2005; Limpus et al., 1994). At this site we deployed time-depth recorders on green turtles during multiple short sessions spread over two years, to obtain sufficiently comprehensive data to

detect diel and seasonal variations in diving patterns and depth occupation.

2. Materials and methods

2.1. Field research

The study was conducted in semi-sheltered waters within Moreton Bay, a large tidal embayment in Queensland, Australia, surrounded on its southern and western shores by residential suburbs of Brisbane, the state capital (Fig. 1). Our preliminary surveys confirmed the presence of green turtles from large immature to adult-size at the intended study site located on the western side of Moreton Bay. This range of size-classes was similar to long-term research sites in different habitat on the eastern side of the bay (Limpus et al., 1994). Since individual green turtles have demonstrated long-term associations with localised areas of the eastern bay and with other coastal foraging sites in Queensland (Chaloupka et al., 2004; Limpus et al., 1994), the green turtles we observed were considered likely to be resident at our site.

Research was conducted in 10 separate sessions between July 2005 and April 2007. Each session commenced with a boat expedition to capture study turtles and attach tracking equipment. After deployment of the equipment, boat expeditions were undertaken on subsequent days when favourable wind and sea conditions permitted. The objective was to re-locate study turtles by means of ultrasonic signals because knowledge of recent locations could facilitate recovery

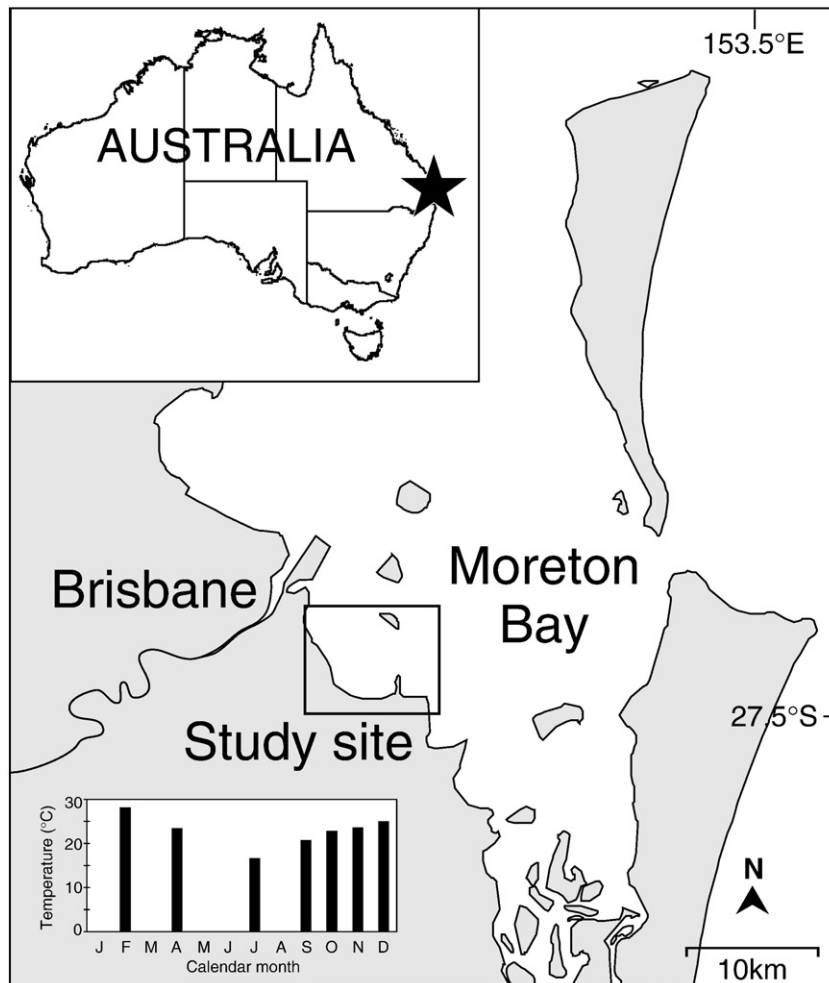


Fig. 1. The study site was located within Moreton Bay on the east coast of Australia. The city and suburbs of Brisbane, state capital of Queensland, surround the western and southern shores of the bay. Inset lower left shows mean sea temperature experienced by study turtles, for detail see Table 1.

of tracking tags after their automatic detachment (see Tracking equipment below). In addition we wished to observe turtles' emergence at the surface when possible.

2.2. Study turtles

Green turtles were captured individually in a net (stretched mesh 20 cm) using a method designed to minimise accidental capture of other species. Capture sessions were restricted to winds $< 18 \text{ km h}^{-1}$ to facilitate visual searches for cryptic surface movements by turtles. When a suitable turtle was detected at close range the net was deployed over the stern of the boat (a 6 m net-fishing vessel operated by an experienced professional fisher) and rapidly laid out in a large circle (diam. ~50 to 100 m) around the location where the turtle had been seen. Thereafter the net was closely monitored for signs that the turtle had become entangled, usually revealed by sudden movement of small floats attached to the upper margins of the net. If no movement occurred over an extended period we concluded that the turtle had escaped and proceeded to retrieve the net before searching for another candidate. Once a turtle was entangled we promptly lifted it into the boat for inspection, measurement and attachment of tracking equipment. In all cases turtles were returned to the water at the same location within 5 to 15 min of capture.

2.3. Tracking equipment

We used custom-made tracking tags, each comprising electronic devices mounted in a streamlined housing with sufficient buoyancy to rise to the sea surface after detachment from the turtle. Each tag was fitted with a link made of fast-corroding metal (Galvanic Timed Release, International Fishing Devices Inc, Pompano Beach FL, USA) designed to release the tag within approximately 7 days of deployment. The corroding link was attached to the posterior margin of the turtle's carapace by a plastic cable tie (tie wrap) secured through a 2 mm diameter hole drilled in the extreme edge of the carapace. The cable tie, with breaking load 8 kg, served as a safety link to ensure the turtle could break free if the equipment snagged on an obstruction. We considered it important to ensure our equipment did not disturb the study turtles' natural buoyancy, since experimental manipulation of buoyancy has been shown to influence turtle behaviour (Hays et al., 2004; Minamikawa et al., 2000). Therefore, to achieve neutral buoyancy for each tag while attached to the turtle, small steel washers were connected to the attachment link to serve as counterweights, the size and number of washers being determined by individual testing.

Our standard tags, used on the majority of turtles, were 120 mm long with maximum diameter 55 mm and contained a miniature time-depth recorder (TDR) (model DST Milli, Star-Oddi, Reykjavik, Iceland, depth accuracy $\pm 0.08 \text{ m}$, temperature accuracy $\pm 0.1 \text{ }^\circ\text{C}$) and an ultrasonic transmitter (model CHP-87-L, Sonotronics, Tucson AZ, USA). Three turtles (T22, T25, T28) received a larger tag (155 mm long, 105 mm max. diam.) containing the same items as a standard tag plus a second TDR and additional equipment for a separate study. On both types of tags the flexible attachment linkage allowed movement ($\pm 10 \text{ cm}$) of the TDR pressure transducer relative to the carapace margin and consequently we regarded the depth data as approximate representations of the turtle's body position. We programmed the TDRs to record depth every 15 s and temperature every 225 s, a schedule that allowed continuous recording for up to 7 days before filling the data storage capacity. The second TDR, present in the larger tag only, operated concurrently with the first TDR for two separate 12-hour periods during which it recorded depth every 2 s. High-frequency 2 s data were compared to 15 s data for periods of dual recording, as described in Data analysis below. The ultrasonic transmitters emitted an individually coded signal, detectable at close range with a boat-mounted hydrophone and receiver (DH-4 and USR-96, Sonotronics, Tucson AZ, USA). These signals allowed

intermittent identification of individual turtles and assisted in recovery of tracking tags after detachment.

2.4. Data analysis

Data were downloaded from each recovered tag using proprietary software (StarOddi, Reykjavik, Iceland). A zero offset correction (ZOC) was applied to the depth data following established practice to adjust for small baseline discrepancies typical of depth recorders. A single ZOC value was applied to each time-series of depth values, rather than separate corrections to each dive (e.g. Hays et al., 2007) or to each hour of data (e.g. Myers et al., 2006) because posterior attachment of tags in the present study meant that the data loggers reached zero depth only rarely, when a turtle elevated the posterior end of its carapace on commencing an exceptionally abrupt dive (confirmed by field observations). Preliminary field tests confirmed transducer accuracy of $\pm 5 \text{ cm}$ after ZOC. To allow for initial responses to capture and handling, the data from the first 12 h post-release were not used in analyses. The adequacy of this exclusion period was confirmed by scrutiny of plotted data that indicated some turtles appeared to dive more frequently during the first 6 h while others showed no evident response.

Depth data were analysed both in terms of proportional time at depth and as discrete dives. Dives were defined as trajectories below a threshold depth of 1 m with maximum depth $\geq 2 \text{ m}$. Intervals between consecutive dives were evaluated as 'near-surface' events, comprising a series of records $\leq 1 \text{ m}$, since our equipment was not designed to measure true surface emergence. Because the actual duration between dives could be shorter than the recording frequency of 15 s, it was necessary to scrutinise plotted data (time on the x -axis, depth on the y -axis) for each turtle to ensure that discrete dives were recognised correctly. A dive start/end was inserted where a distinctive steep ascent-descent trajectory peaked just below 1 m. Plots of high-frequency (2 s) data confirmed, for periods of dual recording (3 turtles, $2 \times 12 \text{ h}$ each), that each of these distinctive 'missed peaks' reliably indicated the turtle had followed a trajectory that actually peaked above 1 m, close to the surface.

We calculated the proportion of time spent in depth strata of 1 m increments below the sea surface and allocated data to three categories of depth-below-surface occupation (0 to 1 m, 1 to 2 m and $> 2 \text{ m}$). These categories reflect progressively reduced exposure to potential contact with vessels in areas where traffic comprises vessels of varied draft (maximum depth of vessel hull and appendages). Turtles occupying greater depths can potentially be struck only by deeper draft vessels, whereas turtles occupying lesser depths can potentially be struck by vessels of deep and shallow draft (i.e. a larger sub-set of available vessels). Our categories make provision for future work to evaluate turtles' risk of contact with vessels, pending collection of data on vessel traffic that are not currently available.

We used time of sunrise and sunset to categorise data by day and night and to accommodate seasonal variation in day length. To estimate low-tide depths occupied by the study turtles, tide-adjusted depth data were derived by subtracting the current tidal height, measured at 10-minute intervals by Maritime Safety Queensland, Brisbane. Results reported include median, extreme range and mean $\pm \text{SD}$. Non-parametric statistical tests were used where the assumption of normality was untenable. T -tests were used for mean temperatures and for diel patterns in depth occupation. For the latter, proportional times were arcsine transformed and tests were one-tailed. For all tests $p < 0.05$ was considered statistically significant.

3. Results

From a total of 25 deployments we obtained depth and temperature data for 19 green turtles of curved carapace length (CCL) 49 to 118 cm with individual recording periods from 30.3 to 165.5 h, excluding the

first 12 h post-release (Table 1). One data logger yielded corrupted data due to an electronic fault and five tracking tags were not recovered. Sea temperature extremes over the entire study ranged from 13.8 °C to 30.3 °C (turtles T06 and T19 respectively) due to the seasonal spread of tracking sessions, but each individual turtle experienced a narrow range of sea temperatures during its tracking period (Table 1). Mean sea temperatures recorded in each turtle's data showed no statistically significant difference between day and night (paired *T*-test, $t=0.896$, $df=18$, $p=0.382$).

3.1. Depth occupation

The large majority of turtles (17 out of 19 individuals) spent 89 to 100% of their time at depths ≤5 m below the surface, three turtles did not exceed 3 m and the maximum depth recorded by any turtle was 7.9 m (Table 1). The proportion of time spent within 1 m of the surface showed a slight positive association with mean water temperature, both by day (Spearman's $r_s=0.53$, $p=0.021$) and by night (Spearman's $r_s=0.54$, $p=0.019$). Proportional time in other depth zones was independent of temperature. Proportional time in all depth zones showed no consistent trend with respect to turtle size (CCL).

Diel variation in depth occupation presented three distinct patterns. (1) Small peaks were evident at dawn and dusk for occupation of depths 0 to 1 m below the surface (Fig. 2a) with occupation of this depth zone significantly greater at dawn (sunrise ±1 h) and dusk (sunset±1 h) than it was during 2 h periods at the middle of the solar day and night, $t=4.8705$, $df=18$, $p<0.001$. (2) Elevated diurnal occupation of depths 1 to 2 m below the surface (Fig. 2b) was statistically significant, $t=6.734$, $df=18$, $p<0.001$. (3) Elevated nocturnal occupation of depths >2 m (Fig. 2c) was also statistically significant, $t=-3.7526$, $df=18$, $p<0.001$. Statistical tests at different temperatures were precluded by small sample sizes. However, the three diel patterns were also evident in subsets of data for warmer and cooler temperatures, partitioned at 22.1 °C, which was the grand mean for all tracking sessions.

3.2. Dives and near-surface events

Dives tended to be shorter and shallower by day for the large majority of study turtles, with median values showing longer nocturnal dives for 18 turtles, longer nocturnal near-surface events

between dives for 18 turtles and deeper nocturnal dives for 17 turtles (Fig. 3). Weak positive association between CCL and median dive depth for individual turtles suggested that smaller turtles tended to make shallower dives than larger turtles by day, but correlations were not statistically significant (day: Spearman's $r_s=0.4$, $p=0.09$, night: Spearman's $r_s=0.22$, $p=0.39$).

Dives became longer as sea temperature decreased. There was significant negative correlation between dive duration and mean temperature, both by day (Spearman's $r_s=-0.69$, $p=0.001$) and by night (Spearman's $r_s=-0.77$, $p<0.001$). The duration of nocturnal near-surface events was also inversely related to temperature (Spearman's $r_s=-0.54$, $p=0.02$). A potentially similar trend in diurnal near-surface events (Spearman's $r_s=-0.22$, $p=0.37$) might have been obscured in data recorded at 15 s intervals, since the majority of these events comprised a single record, representing duration ≤15 s. The depth of nocturnal dives tended to increase with temperature (Spearman's $r_s=0.51$, $p=0.03$) but dive depths during the day were independent of temperature (Spearman's $r_s=0.06$, $p=0.79$).

The influence of temperature was most notable for longer dives (Spearman's $r_s=-0.88$, $p<0.001$ for dives ≥15 min). Dives exceeding 1 h (max depth 2 to 7.9 m) occurred only at sea temperatures below 22 °C, both by night (150 out of 214 dives, 70%) and by day (64 out of 214 dives, 30%), and involved 8 individuals (T05, T06, T07, T08, T11, T13, T22, T23) that spanned the entire size range of study turtles. The longest dives (2.5 to 2.9 h, max depth 3 to 7.5 m) occurred at 16 to 17 °C. Near-surface events immediately following the longest dives did not exceed 4.25 min. Pooled data comprising the 10 longest dives for each turtle, inferred to represent resting behaviour by each individual, suggested a positive relationship between dive duration and depth as well as confirming the strong inverse relationship with temperature (Fig. 4). Small samples and disparate distributions precluded statistical evaluation of these opposing influences.

Eight turtles recorded prolonged periods at depths ≤1 m with the maximum continuous duration for individuals ranging from 1.3 h (T27) to 5.7 h (T29). Close scrutiny of time-depth plots for each turtle indicated that these periods did not represent discrete events between two successive dives. Rather they appeared to be periods when turtles had occupied substrates ≤1 m below the surface and made extremely brief ascents and descents that could not be reliably detected by our data loggers. Therefore diving patterns during these periods could not be quantified.

Table 1

Chelonia mydas. Summary of proportional time spent in depth-below-surface categories (upper limits inclusive) by 19 green turtles of diverse curved carapace lengths (CCL)

Turtle	CCL (cm)	Sex	Date (MM/YY)	Dur (h)	Max dep (m)	Sea temp (°C) mean [min–max]	Proportional time at depth below surface							
							0–1 m	1–2 m	2–3 m	3–4 m	4–5 m	5–6 m	6–7 m	7–8 m
T05	105.0	M	07/05	165.5	7.9	17.3 [15.8–19.0]	4%	8%	18%	24%	21%	5%	9%	11%
T06	57.5	U	07/05	163.6	2.7	16.1 [13.8–19.3]	10%	63%	27%					
T07	49.3	U	07/05	142.2	5.1	16.7 [15.0–18.6]	3%	5%	29%	39%	24%	#		
T08	55.6	U	07/05	163.0	3.0	16.5 [14.6–19.3]	7%	56%	37%					
T10	69.5	U	09/05	98.4	4.6	21.1 [19.4–23.0]	5%	25%	38%	20%	12%			
T11	81.6	U	09/05	85.6	7.7	20.1 [19.3–21.5]	6%	17%	13%	16%	17%	18%	12%	1%
T13	117.9	LF	09/05	137.8	6.4	20.7 [19.1–23.0]	4%	16%	26%	21%	25%	7%	1%	
T14	82.8	U	10/05	109.6	5.0	23.6 [21.8–25.5]	8%	20%	32%	25%	15%			
T15	78.9	U	10/05	108.2	5.6	23.7 [21.7–25.6]	8%	22%	35%	22%	9%	4%		
T16	94.2	U	11/05	78.2	7.8	23.6 [22.8–25.5]	8%	38%	20%	26%	8%			#
T18	88.0	U	02/06	30.3	5.7	27.8 [27.1–30.2]	13%	22%	14%	21%	19%	11%		
T19	84.5	U	02/06	31.5	6.9	28.6 [27.8–30.3]	8%	25%	23%	21%	13%	10%	#	
T22	113.2	LF	09/06	161.3	6.5	21.1 [18.9–23.7]	13%	38%	21%	13%	10%	4%	1%	
T23	107.0	LF	10/06	161.3	5.7	21.9 [19.5–24.2]	16%	31%	26%	14%	11%	2%		
T25	108.8	LF	12/06	94.7	5.7	25.0 [24.3–25.8]	13%	14%	18%	27%	21%	7%		
T26	56.6	U	12/06	63.8	2.8	24.8 [22.4–27.6]	44%	39%	17%					
T27	92.6	M	12/06	150.2	5.9	25.1 [23.1–27.1]	20%	30%	20%	8%	15%	7%		
T28	96.0	LF	04/07	133.5	5.3	23.5 [22.1–26.4]	9%	27%	25%	21%	16%	2%		
T29	71.0	U	04/07	135.2	5.4	23.4 [22.0–25.4]	19%	27%	24%	17%	10%	3%		

Dur=duration of depth records excluding 12 h post-release. Sex was inferred by reference to the sexual dimorphism of adult turtles in eastern Moreton Bay (Limpus et al., 1994) as males (M – long tail), likely females (LF – short tail & CCL >95 cm) or undetermined (U). # indicates <0.5% of proportional time at max. depth.

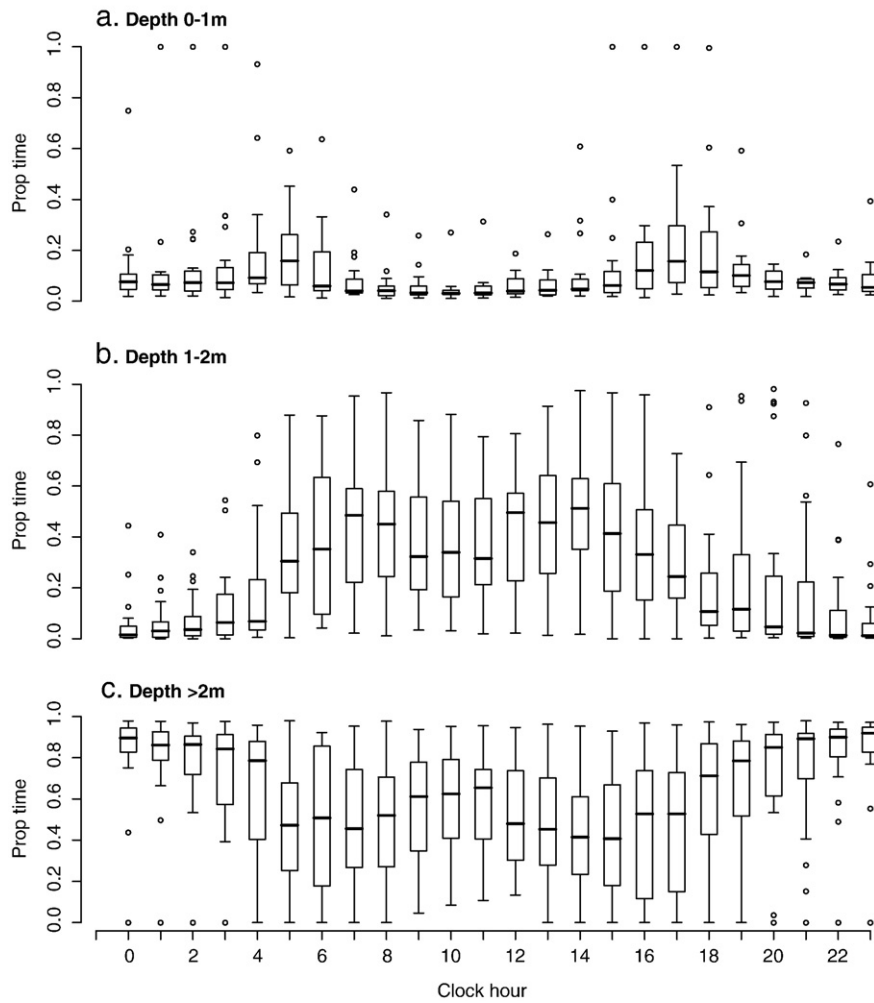


Fig. 2. *Chelonia mydas*. Diel patterns in depth occupation for 19 study turtles showed peaks at dawn and dusk for depths 0 to 1 m below the surface (panel a), elevated occupation of depths 1 to 2 m during the day (panel b) and elevated occupation of depths >2 m at night (panel c). Differences were statistically significant in all three instances. Box plots show the median (horizontal bar), inter-quartile range (box length), largest values within 1.5 x inter-quartile range (whiskers) and all data points beyond the whiskers (open circles).

3.3. Surface exposure

Our visual observations encompassed study turtles, identified by signals from their ultrasonic transmitters, and many non-study green turtles at our site, all of which displayed similar behaviour. Turtles made only fleeting appearances at the sea surface with no turtle remaining visible for longer than 2 s. Turtles usually exposed only the dorsal-anterior part of the head but occasionally exposed the dorsal posterior surface of their carapace when diving very suddenly. Turbid water precluded visual observation of submerged turtles.

4. Discussion

Green turtles in this study maintained occupation of relatively shallow depths throughout their respective tracking periods. Yet within their narrow depth ranges they displayed significant day–night differences in depth occupation and diving patterns, while their dive durations demonstrated the strong influence of sea temperature.

4.1. Behavioural patterns

The predominant pattern of shorter, shallower dives during the day and longer, deeper dives during the night (Fig. 3) suggested turtles were more active by day and rested by night. Short dives are consis-

tent with heightened activity involved in seeking and consuming forage, since activity increases metabolic demand (Schmidt-Nielsen, 1997). An active submerged turtle would therefore be expected to ascend to the surface more frequently for respiration. Reduced metabolic demand while resting would allow correspondingly longer periods of submersion and on this basis prolonged dives by green turtles are widely considered to represent resting behaviour (e.g. Hays et al., 2000; Southwood et al., 2003b).

Our behavioural inference was confined to differentiating active and resting periods because it was not possible to reliably identify the functions of individual dives. Under some circumstances the geometric shapes evident in plots of time–depth data can be informative, e.g. a turtle foraging on a reef makes small movements up- and down-slope that result in an irregular dive profile readily distinguishable from the square or U-shaped profile created when the turtle remains stationary on the substrate while resting (van Dam and Diez, 1997). However, in other habitat the correspondence between dive profile and dive function is uncertain. Studies using additional equipment together with depth recorders have shown that square or U-shaped dive profiles do not exclusively represent resting and can include movement activity (detected by a 3-D compass system, Hochscheid et al., 1999) as well as foraging behaviours (captured by carapace-mounted underwater cameras, Seminoff et al., 2006), and can encompass varying states of consciousness (inferred from jaw movements detected by a novel sensor, Houghton et al., 2008).

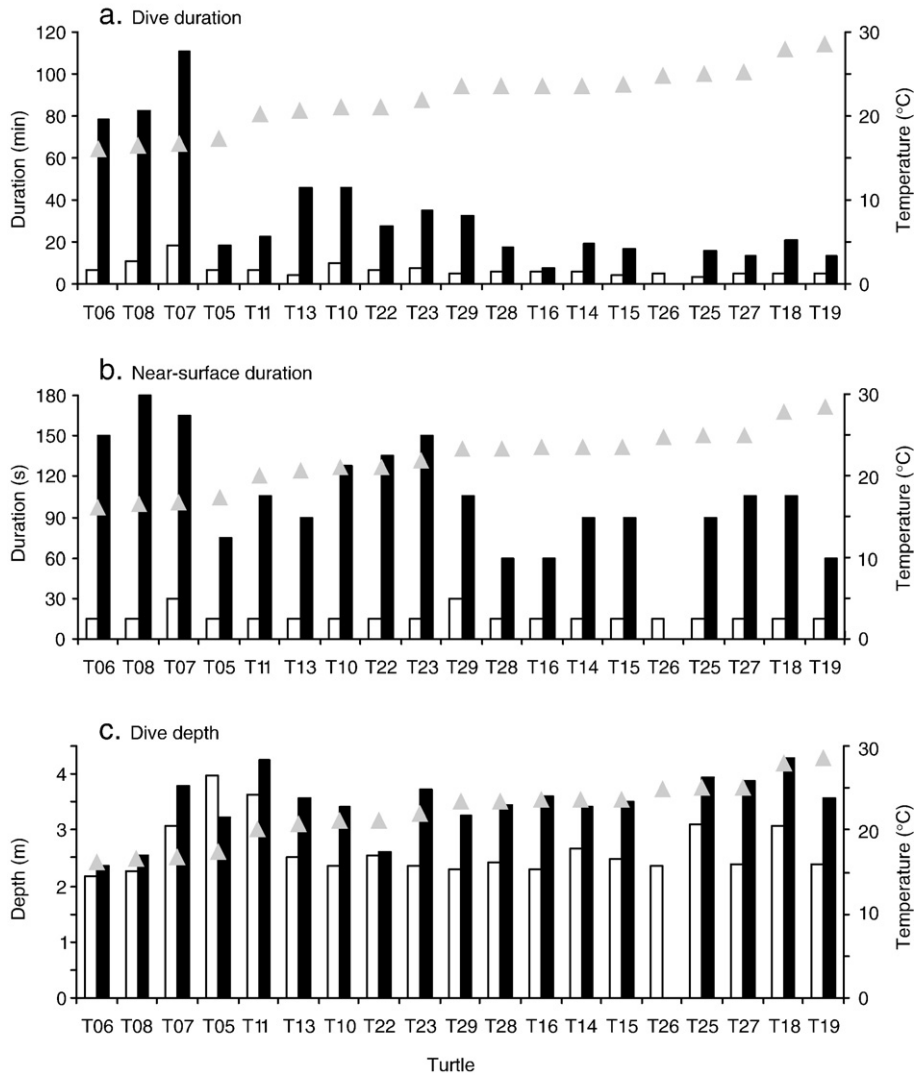


Fig. 3. *Chelonia mydas*. Median duration of dives (panel a) and near-surface events between dives (panel b) was shorter by day (white bars) and longer by night (black bars) for all turtles except T26. The latter made no qualifying dives at night as it remained at depths <2 m. With increasing sea temperature (grey triangles) durations tended to decrease, with the exception of diurnal near-surface events. Note left-hand y-axes of panels a and b use different units. Dive depth (panel c) was greater by night, and night depth tended to increase with temperature.

Slight gradients in bathymetry across much of our study site meant that the dive profile created by a turtle foraging across a near-level patch of seagrass could match that of a turtle resting immobile on the substrate for a similar duration, and such inherent ambiguity precluded functional interpretation of dive profiles in our depth data. Similarly, it was impossible to determine from the depth data exactly where a turtle had selected deeper water. A series of square or U-shaped dive profiles with progressively increasing or decreasing depth (after adjustment for tide height) clearly indicated when the turtle moved down or up a slope. However the micro-location of the slope remained uncertain because corresponding slopes in the substrate occurred in many parts of the site, as recorded in detailed bathymetry data from hydrographic surveys provided by Maritime Safety Queensland, Brisbane.

The finding that diurnal-biased activity prevailed across the range of study turtles (immature and adult-sized) supported generalisation of the pattern reported elsewhere, predominantly for immature green turtles. For example, diurnal activity has been visually observed (Bjorndal, 1980), inferred from movement between distinct feeding and resting sites (Mendonca, 1983; Taquet et al., 2006) and inferred from diving behaviour (Makowski et al., 2006; Seminoff et al., 2001; Southwood et al., 2003b). However, the selection of deeper water at

night appears less amenable to generalisation. Deeper water was favoured at night in our study and in several others (e.g. Bjorndal, 1980; Makowski et al., 2006; Taquet et al., 2006) but the converse, nocturnal selection of shallower depths, has also been reported (Brill et al., 1995; Southwood et al., 2003b), as has individual variation in diurnal/nocturnal depth selection (Seminoff et al., 2001). Reasons for these divergent trends in depth selection remain unclear but may reflect disparate availability of forage resources and differences in foraging behaviour, variations in predatory pressures (Heithaus et al., 2007) and possible interactions with conspecifics (Schofield et al., 2007a).

4.2. Sea temperature effects

The significant negative correlation between dive duration and sea temperature was expected in its direction but novel in the strength of the relationship and the scope of resting dive duration demonstrated within a shallow depth range. Laboratory and field studies (Southwood et al., 2003a; 2006) have shown reduced metabolic rates for green turtles occupying colder water. Consequently green turtles would be expected to replenish oxygen less frequently at lower temperatures. A slight trend towards longer dives in winter has been

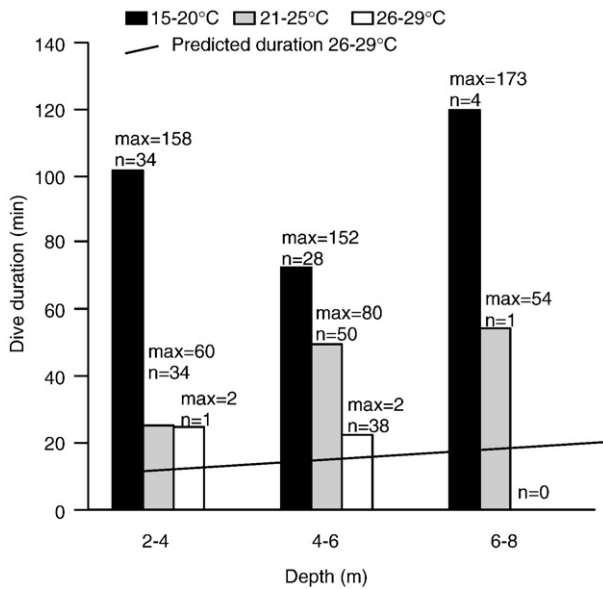


Fig. 4. *Chelonia mydas*. Median duration of resting dives showed both depth and temperature dependence. Pooled data for the 10 longest dives (inferred resting) by each of 19 study turtles were classified by depth and sea temperature (white bars 15–20 °C, grey bars 20–25 °C, black bars, 25–29 °C). Maximum duration (min) and number of dives in each category are indicated above bars. Line represents predicted dive duration for warm sea temperature derived from equation provided by Hays et al. (2004) extrapolated beyond the original depth range and life-stage, hence this comparison must be regarded with caution.

noted for juvenile green turtles in a coral reef environment (Southwood et al., 2003b) and post-nesting females in temperate coastal habitat have demonstrated an abrupt increase in the proportion of dives >25 min when sea temperature dropped below 25 °C. The latter change in diving behaviour, accompanied by a location shift to deeper water, was interpreted as a mid-winter diapause (Broderick et al., 2007; Godley et al., 2002). In contrast, our results showed no evidence of diapause or location change. Study turtles remained at the study site (detected by acoustic signals) during the coldest tracking session and depth data showed that bouts of activity (frequent short dives) occurred intermittently despite the predominance of prolonged dives at low temperatures. Foraging was likely to have occurred during this activity, consistent with the observation that green turtles elsewhere in Moreton Bay continued to forage at water temperatures down to 15 °C (Read et al., 1996).

Prolonged dives at shallow depths (Fig. 4) were notable in view of green turtles' reliance on their lungs to regulate their buoyancy. By diving with fully inflated lungs a turtle can rest passively at its maximum depth of neutral buoyancy, and by diving with lungs partially inflated (to varying degrees) it can rest passively at various lesser depths (Hays et al., 2000; Milsom, 1975; Minamikawa et al., 2000). However, partially inflated lungs provide a smaller volume of oxygen than fully inflated lungs, thereby reducing the duration of submergence. Consequently resting dives, when metabolism is assumed to be relatively stable, would tend to be shorter at shallower depths if turtles surface when oxygen reserves are depleted to approximately similar levels. The expected depth–duration relationship has been confirmed for mature female green turtles at Ascension Island, where they rested predominantly in deeper water within the range 5 to 20 m (Hays et al., 2004).

This buoyancy-related constraint must apply to all green turtles when they rest on open substrates, as at our study site where reefs and other structures were not available. Therefore the following aspects of our findings were notable. Firstly, study turtles selected shallow resting depths despite the availability of deeper water nearby that would have allowed them to dive with greater oxygen stores (due to

greater lung inflation) and remain submerged for longer periods. Secondly, their resting dive durations were longer than expected from published data, although disparate life-stages, habitat and depth ranges require that this comparison be regarded with caution. As shown in Fig. 4, our data for resting dives by study turtles at warm temperatures (26 to 29°) were 1.5 to 2.1 times longer, for depths 2 to 4 m and 4 to 6 m respectively, than values predicted by extrapolation of the duration–depth relationship reported for Ascension Island green turtles (Hays et al., 2004, p 1142). For lower temperatures no comparison with published data was feasible as sources could be not found with sufficient detail. However our data demonstrate that turtles made resting dives that were 3 to 4 times longer in median duration, and six times longer in maximum duration, at cool temperatures than they were at warm temperatures (Fig. 4).

To our knowledge, dives of similar and even more prolonged duration by green turtles have been recorded only in deeper water (Broderick et al., 2007; Rice and Balazs, 2008). Thus in relation to their shallow depths the longest dives by our study turtles appear to have no precedents in the literature. However, we infer that our study turtles were diving within their aerobic limits, following the norm for voluntary dives (Lutcavage and Lutz, 1997). Near-surface events between dives remained relatively short (≤ 4.25 min) even after the longest dives (up to 2.9 h) and, as noted above, the turtles intermittently undertook short bouts of activity (potentially including foraging) and remained within the study area while making their longest dives. Therefore these prolonged dives do not appear to indicate a distinct physiological state such as diapause. Rather, we infer that they represent one end of a temperature-related continuum of behaviour by green turtles in shallow foraging areas.

4.3. Depth selection

The study turtles' preference for deeper water at night is consistent with the established understanding that lung-related buoyancy (discussed above) means deeper sites allow longer periods of continuous rest than shallower sites. Why then did their recorded depths remain so modest, despite unobstructed access to deeper water? Distance may have discouraged regular use of substantially deeper sites, since charted depths >10 m (high tide depths >12.6 m) were 3 to 6 km distant from shallow areas in the study site that appeared to be preferred foraging sites. (The latter were inferred from our visual observations of frequent surfacing behaviour by turtles.) Yet distance did not preclude use of intermediate depths greater than those actually selected. Depths of 4 to 8 m were available within 1 to 1.5 km of the assumed foraging areas, and we observed that study turtles travelled equal and greater distances (confirmed by intermittent detection of individuals by their ultrasonic signals). Our extensive field observations, including substrate inspection by remote video, revealed no evident deterrents to the use of deeper areas in the study site. We therefore infer that other factors in addition to distance and depth must influence the choice of resting sites, but these remain to be elucidated.

4.4. Conservation implications

Our data clearly demonstrated the study turtles' dependence on shallow habitat (Table 1). This is even more evident when tidal range (max 2.6 m during tracking sessions) is taken into account. Tide-adjusted depth data indicated that study turtles spent most of their time (mean $82\% \pm 0.16$) at charted depths (lowest astronomical tide) of 3 m or less. Since locally dominant seagrass species in south-western Moreton Bay (which includes our study site) are severely depth-limited by turbid water (Abal and Dennison, 1996) the use of shallow habitat was likely to enhance turtles' forage intake. However this habitat preference means turtles occupy the broad shallow margins of the bay and thereby have greater exposure to human activities that are typically more frequent near the shoreline than in waters more distant

from shore. For example, the margins of Moreton Bay margins are favoured for some forms of recreational and commercial fishing, including the deployment of various types of nets and traps. Furthermore, bay margins include areas of vessel traffic concentration because vessels transit at least twice on each trip when leaving and returning to their points of origin at wharves, marinas, moorings and launching ramps.

Temporal patterns in turtle behaviour also appear to exacerbate risk. Diurnal and dawn/dusk biases in turtles' occupation of shallow depth strata (Fig. 2) coincide with a diurnal bias in vessel traffic (concomitant with human preferences for conducting outdoor activities by day) and thereby would be expected to increase turtles' risk of vessel strike. It appears that broadly similar levels of exposure to vessels persist year-round, as shallow water occupation and diel patterns were maintained at colder and warmer temperatures. However there may be a slight increase in exposure during the warmer months, since the proportion of time at 0 to 1 m below the surface showed a small positive association with mean water temperature, and this is the depth zone where turtles are potentially within vertical range of a large proportion of passing vessels (i.e. shallow and deeper draft vessels).

Our detailed data on green turtles' vertical movements might in principle be complemented by geographically-referenced data on their horizontal movements. Novel variants of GPS technology enable researchers to track turtles at a relatively fine scale (e.g. Schofield et al., 2007b) albeit not matching simple TDRs in spatial (<10 cm) and temporal resolution (<1 min). However, tracking turtles is a costly and logistically challenging task. In contrast, human activities associated with accidental turtle mortality can be directly monitored. Effort might therefore more usefully be applied to determine the spatial and temporal distributions of vessel traffic and various types of fishing activity within near-shore turtle habitat. Such data could be used in conjunction with the findings of our study, to accurately identify time- and location-specific risks, and hence enable mitigation through narrowly targeted strategies that could offer a dual benefit by maximising protection for green turtles and other vulnerable species while minimising constraints on human activities.

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References

- Abal, E.G., Dennison, W.C., 1996. Seagrass depth range and water quality in Southern Moreton Bay, Queensland, Australia. *Mar. Freshw. Res.* 47, 763–771.
- Ackerman, B.B., Wright, S.D., Bonde, R.K., O'Dell, D.K., Banowetz, D.J., 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. In: O'Shea, T.J., Ackerman, B.B., Percival, H.F. (Eds.), *Population Biology of the Florida Manatee*. National Biological Service, Washington, DC, pp. 223–258.
- Bjorndal, K.A., 1980. Nutrition and grazing behavior of the green turtle *Chelonia mydas*. *Mar. Biol.* 56, 147–154.
- Brill, R.W., Balazs, G.H., Holland, K.N., Chang, R.K.C., Sullivan, S., George, J.C., 1995. Daily movements, habitat use and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L) within a foraging area in the Hawaiian islands. *J. Exp. Mar. Biol. Ecol.* 185, 203–218.
- Broderick, A.C., Coyne, M.S., Fuller, W.J., Glen, F., Godley, B.J., 2007. Fidelity and overwintering of sea turtles. *Proc. R. Soc. Lond. B, Biol. Sci.* 274, 1533–1538.
- 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.
- Chilvers, B.L., Lawler, I.R., Macknight, F., Marsh, H., Noad, M., Paterson, R., 2005. Moreton Bay, Queensland, Australia: an example of the co-existence of significant marine mammal populations and large-scale coastal development. *Biol. Conserv.* 122, 559–571.
- Godley, B.J., Richardson, S., Broderick, A.C., Coyne, M.S., Glen, F., Hays, G.C., 2002. Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography* 25, 352–362.
- Greenland, J.A., Limpus, C.J., 2005. *Marine Wildlife Stranding and Mortality Database Annual Report 2004: 1. Dugongs*. Queensland Environmental Protection Agency, Brisbane. 29 pp.
- Greenland, J.A., Limpus, C.J., Currie, K.J., 2004. *Marine Wildlife Stranding and Mortality Database Annual Report, 2001–2 – III Marine Turtles*. Queensland Parks and Wildlife Service, Brisbane. 73 pp.
- Haines, J.A., Limpus, C.J., 2001. *Marine Wildlife Stranding and Mortality Database Annual Report, 2000 – III Marine Turtles*. Queensland Parks and Wildlife Service, Brisbane. 35 pp.
- Hays, G.C., Adams, C.R., Broderick, A.C., Godley, B.J., Lucas, D.J., Metcalfe, J.D., Prior, A.D., 2000. The diving behaviour of green turtles at Ascension Island. *Anim. Behav.* 59, 577–586.
- Hays, G.C., Glen, F., Broderick, A.C., Godley, B.J., Metcalfe, J.D., 2002. Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. *Mar. Biol.* 141, 985–990.
- Hays, G.C., Metcalfe, J.D., Walne, A.W., 2004. The implications of lung-related buoyancy control for dive depth and duration. *Ecology* 85, 1137–1145.
- Hays, G.C., Forman, D.W., Harrington, L.A., Harrington, A.L., Macdonald, D.W., Righton, D., 2007. Recording the free-living behaviour of small-bodied, shallow-diving animals with data loggers. *J. Anim. Ecol.* 76, 183–190.
- Hazel, J., Gyuris, E., 2006. Vessel-related mortality of sea turtles in Queensland, Australia. *Wildl. Res.* 33, 149–154.
- Hazel, J., Lawler, I.R., Marsh, H., Robson, S., 2007. Vessel speed increases collision risk for the green turtle *Chelonia mydas*. *Endanger. Species Res.* 3, 105–113.
- Heithaus, M.R., Frid, A., Wirsing, A.J., Dill, L., Fourqurean, J.W., Burkholder, D., Thomson, J., Bejder, L., 2007. State-dependent risk-taking by green turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J. Anim. Ecol.* 76, 837–844.
- Hochscheid, S., Godley, B.J., Broderick, A.C., Wilson, R.P., 1999. Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* 185, 101–112.
- Houghton, J.D.R., Cedras, A., Myers, A.E., Liebsch, N., Metcalfe, J.D., Mortimer, J.A., Hays, G.C., 2008. Measuring the state of consciousness in a free-living diving sea turtle. *J. Exp. Mar. Biol. Ecol.* 356, 115–120.
- IUCN Marine Turtle Specialist Group, 2004. 2004 Global Status Assessment: Green Turtle (*Chelonia mydas*). The World Conservation Union (IUCN).
- Laist, D.W., Knowlton, A.R., Mead, J.G., Collet, A.S., Podesta, M., 2001. Collisions between ships and whales. *Mar. Mamm. Sci.* 17, 35–75.
- Limpus, C.J., Couper, P.J., Read, M.A., 1994. The green turtle, *Chelonia mydas*, in Queensland: population structure in a warm temperate feeding area. *Mem. Queensl. Mus.* 35, 139–154.
- Lutcavage, M.E., Lutz, P.L., 1997. Diving physiology. In: Lutz, P.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*, vol. 1. CRC Press, Boca Raton, Fla, pp. 387–409.
- Lutcavage, M.E., Plotkin, P., Witherington, B., Lutz, P.L., 1997. Human impacts on sea turtle survival. In: Lutz, P.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*, vol. 1. CRC Press, Boca Raton, Fla, pp. 387–409.
- Makowski, C., Seminoff, J.A., Salmon, M., 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Mar. Biol.* 148, 1167–1179.
- Mendonca, M.T., 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. *Copeia* 4, 1013–1023.
- Milson, W.K., 1975. Development of buoyancy control in juvenile Atlantic loggerhead turtles, *Caretta caretta*. *Copeia* 1975, 758–762.
- Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T., Sakamoto, W., 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J. Exp. Biol.* 203, 2967–2975.
- Musick, J.A., Limpus, C.J., 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), *The Biology of Sea Turtles*, vol. 1. CRC Press, Boca Raton, pp. 137–163.
- Myers, A.E., Lovell, P., Hays, G.C., 2006. Tools for studying animal behaviour: validation of dive profiles relayed via the Argos satellite system. *Anim. Behav.* 71, 989–993.
- Plotkin, P., 2003. Adult migrations and habitat use. In: Lutz, P.L., Musick, J.A., Wyneken, J. (Eds.), *Biology of Sea Turtles*, vol. II. CRC Press, Boca Raton, pp. 225–241.
- Polovina, J.J., Howell, E., Parker, D.M., Balazs, G.H., 2003. Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: might deep longline sets catch fewer turtles? *Fish. Bull.* 101, 189–193.
- Read, M.A., Grigg, G.C., Limpus, C.J., 1996. Body temperatures and winter feeding in immature green turtles *Chelonia mydas* in Moreton Bay, south east Queensland. *J. Herpetol.* 30, 262–265.
- Rice, M.R., Balazs, G.H., 2008. Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations. *J. Exp. Mar. Biol. Ecol.* 356, 121–127.
- Schmidt-Nielsen, K., 1997. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, Cambridge. 607 pp.
- Schofield, G., Katselidis, K.A., Pantis, J.D., Dimopoulos, P., Hays, G.C., 2007a. Female–female aggression: structure of interaction and outcome in loggerhead sea turtles. *Mar. Ecol. Prog. Ser.* 336, 267–274.
- Schofield, G., Bishop, C.N., MacLean, G., Brown, P., Baker, M., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2007b. Novel GPS tracking of sea turtles as a tool for conservation management. *J. Exp. Mar. Biol. Ecol.* 347, 58–68.

- Seminoff, J.A., Resendiz, A., Smith, T.W., Yarnell, L., 2001. Diving patterns of green turtles (*Chelonia mydas agassizii*) in the Gulf of California. In: Coyne, M.S., Clark, R.D. (Eds.), Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation. NOAA, Philadelphia.
- Seminoff, J.A., Jones, T.T., Marshall, G.J., 2006. Underwater behaviour of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? *Mar. Ecol. Prog. Ser.* 322, 269–280.
- Southwood, A.L., Darveau, C.A., Jones, D.R., 2003a. Metabolic and cardiovascular adjustments of juvenile green turtles to seasonal changes in temperature and photoperiod. *J. Exp. Biol.* 206, 4521–4531.
- Southwood, A.L., Reina, R.D., Jones, V.S., Jones, D.R., 2003b. Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. *Can. J. Zool.* 81, 1014–1024.
- Southwood, A.L., Reina, R.R., Jones, V.S., Speakman, J.R., Jones, D.R., 2006. Seasonal metabolism of juvenile green turtles (*Chelonia mydas*) at Heron Island, Australia. *Can. J. Zool.* 84, 125–135.
- Taquet, C., Tacquet, M., Dempster, T., Soria, M., Ciccione, S., Roos, D., Dagorn, L., 2006. Foraging of the green sea turtle *Chelonia mydas* on seagrass beds at Mayotte Island (Indian Ocean), determined by acoustic transmitters. *Mar. Ecol. Prog. Ser.* 306, 295–302.
- van Dam, R.P., Diez, C.E., 1997. Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs* 16, 133–138.
- Witherington, B., 1992. Behavioural responses of nesting sea turtles to artificial lighting. *Herpetologica* 48, 31–39.
- Witherington, B.E., 1997. The problem of photopollution for sea turtles and other nocturnal animals. In: Clemmons, J.R., Buchholz, R. (Eds.), Behavioural Approaches to Conservation in the Wild. Cambridge University Press, Cambridge, UK, pp. 303–328.