

Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia

Amanda L. Southwood, Richard D. Reina, Vivienne S. Jones, and David R. Jones

Abstract: This study compared diving patterns of juvenile green turtles, *Chelonia mydas*, in a coral reef habitat during summer and winter. Dataloggers were deployed on green turtles at Heron Island, Australia, during December 2000 and August 2001 so that dive variables and ambient water temperature (T_W) could be monitored. Cloacal temperatures (T_B) were recorded from green turtles upon capture to assess their ability to maintain a thermal gradient between T_B and T_W . Data show that green turtles altered diving behaviour seasonally. Green turtles spent significantly more time in shallow water (<1 m) during winter than during summer. Dive depth for dives that exceeded 1 m was 2.9 ± 0.4 m (mean \pm SEM) during summer and 4.4 ± 0.6 m during winter. Dive duration in summer (13.1 ± 1.2 min) was approximately half the dive duration in winter (24.3 ± 1.6 min), and surface interval in summer (0.6 ± 0.1 min) was one-third that of the surface interval in winter (1.8 ± 0.1 min). The observed changes in behaviour may be due to seasonal changes in environmental and physiological factors. There was no statistically significant difference between T_B and T_W during summer or winter.

Résumé : Notre étude compare les patterns de plongée chez de jeunes tortues vertes, *Chelonia mydas*, dans un habitat de récif corallien durant l'été et l'hiver. Des appareils enregistreurs fixés à des tortues à l'île Heron, en Australie, en décembre 2000 et août 2001, ont permis de suivre les variables de la plongée ainsi que la température de l'eau ambiante (T_W). La mesure de la température du cloaque (T_B) chez des tortues capturées a servi à déterminer la capacité des tortues à maintenir un gradient thermique entre T_B et T_W . Les tortues modifient leurs patterns de plongée selon la saison. Elles passent significativement plus de temps en eau peu profonde (<1 m) en hiver qu'en été. La profondeur moyenne de plongée, pour les plongées de plus de 1 m, est de $2,9 \pm 0,4$ m (moyenne \pm erreur type) en été et de $4,4 \pm 0,6$ m en hiver. La durée moyenne d'une plongée en été ($13,1 \pm 1,2$ min) est à peu près la moitié de la durée en hiver ($24,3 \pm 1,6$ min) et la durée de l'intervalle en surface en été ($0,6 \pm 0,1$ min) est le tiers de la durée en hiver ($1,8 \pm 0,1$ min). Les changements observés dans le comportement peuvent être dus à des changements dans les conditions environnementales et physiologiques. Il n'y a pas de différence statistiquement significative entre T_B et T_W , ni en été, ni en hiver.

[Traduit par la Rédaction]

Introduction

Historically, green sea turtles, *Chelonia mydas* (hereinafter referred to as green turtles), were abundant in the world's tropical and subtropical seas (Bjorndal 1980). This species was used as a source of meat for indigenous populations (Felger et al. 1976), as well as a source of soup stock for restaurants worldwide. Early attempts to understand the behaviour of green turtles in their natural habitat were motivated by commerce rather than conservation. Anecdotal information about seasonal movements and behavioural patterns of green turtles was passed on among indigenous hunters, fishermen, and eventually biologists (Carr and Ogren 1960; Felger et al. 1976). Sadly, uncontrolled harvesting of

green turtle eggs, overexploitation of adult green turtle stocks, and increased adult mortality owing to incidental capture in fishing gear has reduced the world-wide population of green turtles to the point where they are now an endangered species (King 1982). As a result, conservation considerations have replaced commercial interests, and an understanding of green turtle behaviour is regarded as an integral aspect in the campaign to minimize or prevent human interaction with this species. Efforts by the scientific community to determine habitat utilization and diving patterns have increased over the years as tracking methodology (sonic and satellite telemetry) and remote-monitoring technology (archival dataloggers) have improved and become widely available.

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The majority of information about the diving behaviour of green turtles has been collected from reproductively active adult females, owing to the relative ease with which these green turtles may be captured as they lumber along on a nesting beach. Consequently, most of our knowledge of green turtle diving behaviour is limited temporally to the nesting season (Hochscheid et al. 1999; Hays et al. 2000) or postnesting migration (Luschi et al. 1998; Hays et al. 1999; Hays et al. 2001) and categorically to adult females. Few studies have been conducted with juveniles, as young green turtles inhabit reefs, lagoons, and estuaries and do not haul out on land. The challenge of capturing and recapturing juvenile sea turtles for instrument deployment and retrieval at sea has rarely been undertaken.

Juvenile green turtles typically remain in their coastal, shallow-water habitats year-round, and experience seasonal fluctuations in environmental conditions. As with other reptiles, green turtles may alter their behaviour in response to seasonal changes in temperature, photoperiod, and food availability; however, the degree to which diving patterns and activity levels are affected is not well understood. Felger et al. (1976) made direct observations of adult and juvenile Pacific green turtles, *Chelonia mydas agassizii*, in the Gulf of California and found that they were lethargic and unresponsive when handled during the winter months. In contrast, sonic-tracking studies conducted with juvenile green turtles in a lagoon in Florida showed that they remained active year-round and actually increased distances travelled per day during winter (Mendonca 1983). Mendonca (1983) suggested that the increase in daily movements by green turtles during winter might represent an attempt to leave the lagoon and seek warmer temperatures offshore or, alternatively, the increased metabolic heat production concurrent with higher activity levels might allow them to elevate their body temperature (T_B) in relation to the ambient water temperature (T_W).

Adult green turtles can maintain core T_B 1–3°C above ambient T_W (Heath and McGinnis 1980; Standora et al. 1982; Sato et al. 1998), presumably owing to retention of metabolically produced heat via thermal inertia and circulatory adjustments such as decreased peripheral blood flow and an accompanying decrease in heart rate (Spotila et al. 1973; Smith et al. 1986; Hochscheid et al. 2002). However, juvenile green turtles may be considerably smaller than adults and less effective at maintaining a thermal gradient between T_B and T_W , owing to a reduced capacity for heat storage (Spotila et al. 1973). Read et al. (1996) captured 50 juvenile green turtles in a shallow subtropical bay in southern Queensland, Australia, during winter and found that there was no significant difference between T_B and T_W over 15.0–22.7°C. Despite low T_B , green turtles from this population rapidly fled approaching research boats and had food in their buccal cavities when captured. Although results from this study and others (Mendonca 1983) suggest that juvenile green turtles from some populations remain active year-round and that elevated T_B is not a requirement for maintaining activity, detailed records of seasonal diving behaviour and ambient T_W experienced seasonally are lacking. Seasonal alterations in variables such as dive duration, dive depth, and postdive surface intervals may herald fundamental changes

in metabolic status, thermoregulatory behaviour, or shifts in habitat preference or food availability.

The primary objectives of this study were (i) to document the diving patterns of juvenile green turtles during summer and winter to determine if seasonal shifts in diving behaviour occur, (ii) to investigate a possible relationship between diving behaviour of green turtles and ambient T_W , and (iii) to determine if juvenile green turtles maintained a gradient between core T_B and T_W and if the magnitude of this gradient varied seasonally. Dataloggers were used to remotely monitor dive variables and ambient T_W while green turtles were at sea, and cloacal T_B was recorded upon capturing a green turtle. Heron Island, Queensland, Australia (23°26'S, 151°55'E), was chosen as our study site, as the waters surrounding this island support a resident population of green turtles that includes juveniles (Limpus and Walter 1980). Heron Island lies at the southern end of the Great Barrier Reef and is bisected by the Tropic of Capricorn. Water temperature at Heron Island varies from a minimum of 16°C in winter to a maximum of 29°C in summer, and green turtles from this population remain active year-round.

Materials and methods

Field procedures

Field research took place in December 2000 (austral summer) and August 2001 (austral winter). All of the green turtles for this study were captured by hand (free-diving) in the boating channel and harbour on the south side of the island. Turtles were taken directly to the Heron Island Research Station (University of Queensland) where measurements and instrument attachment took place. If we could not begin working with the green turtle immediately after capture, the green turtle was kept in a pool (4.6 m long × 4.6 m wide × 0.6 m deep) with seawater pumped in from the outer edge of the reef crest.

Extensive tag-and-recapture studies have been conducted with the Heron Island population of green turtles (Limpus and Walter 1980), so many of the green turtles we captured had numbered titanium flipper tags that could be used to identify individuals. The Queensland Parks and Wildlife Service provided additional flipper tags so that our research team could tag green turtles that had not been identified from previous studies. Tags were placed along the medial edge of the right front flipper. Curved carapace length (± 0.1 cm), curved carapace width (± 0.1 cm), and body mass (± 0.1 kg) were determined. The body mass for green turtles in this study was 10.0–23.6 kg.

Dataloggers to record at-sea diving behaviour and T_W (± 0.2 – 0.5 °C) were attached directly to the carapace with epoxy glue (SuperMend, Titan Corporation, Lynnwood, Wash.). Placement of a datalogger on the shell varied between the 2nd and 4th vertebral scutes (see Instrumentation). A sonic transmitter (model V16-5HR-01, Vemco Ltd., Shad Bay, N.S.; model CHP87L, Sonotronics, Tucson, Ariz.) was attached to the right rear marginal scutes of the carapace with epoxy glue. Sonic tags (1.5 cm diameter, 9–11 cm long) transmitted at a frequency of 38–57 kHz and could be detected within a range of 1.5 km. VHF-radio beacons (model SI-2sp, Holohil Systems, Carp, Ont.) were attached

either directly to the datalogger or to the left rear marginal scutes of the carapace with epoxy glue. The radio beacons transmitted a 149-MHz signal at a frequency of 1 Hz and had a range of approximately 3 km in air.

Green turtles were released within 500 m of the capture site after 14–65 h of captivity. The holding period for green turtles was 25.8 ± 4.2 h (mean \pm SEM) (33.8 ± 6.6 h in summer, 16.6 ± 0.7 h in winter). Following release, green turtles were tracked at sea periodically using both radio and sonic telemetry. Turtles were located and recaptured by hand in the boating channel and harbour after 4.8–5.4 days at sea in summer and 7.3–12.6 days in winter. Cloacal T_B ($\pm 0.1^\circ\text{C}$) was measured within 5–10 min of capture using a model 8700 thermocouple digital display meter and a 2 mm diameter rubber-coated thermocouple probe (Mallinckrodt Inc., Glens Falls, N.Y.). The probe was inserted to a depth of approximately 15 cm into the cloaca and readings were taken after an equilibration time of 1 min (Mrosovsky 1980). Dataloggers and tracking devices were removed from the green turtle's shell, and data were downloaded from the dataloggers onto a laptop computer. Green turtles were released in the harbour within 2 h of recapture.

All procedures were approved by the University of British Columbia Committee on Animal Care (in accordance with guidelines set by the Canadian Committee on Animal Care), the Queensland Parks and Wildlife Service, and the Great Barrier Reef Marine Park Authority (permit No. G00 568).

Instrumentation

Several types of instruments were used to record diving behaviour and ambient T_W from green turtles freely diving at sea (Table 1). Custom-built time–temperature–depth recorders (TTDRs) (180 g, $12.0 \times 6.0 \times 1.4$ cm) previously described for use with elephant seals, *Mirounga angustirostris* (Andrews et al. 1997; Andrews 1998), and leatherback sea turtles, *Dermochelys coriacea* (Southwood et al. 1999), were used with seven green turtles during the summer field season and with three green turtles during the winter field season. TTDRs had a memory of 512 kilobytes and could record depth and temperature every 5 s for 10.1 days. Depth resolution of the TTDRs varied from 0.2 to 0.5 m, depending on the pressure-transducer components and the analog-to-digital mode of sampling. Before instrument deployment, pressure transducers were calibrated with a compressed gas pressure gauge comparator and a National Institute of Standards and Technology (NIST)-traceable precision gauge. The TTDRs recorded T_W with a resolution of 0.4°C . Datalogger thermistors (Fenwal Electronics, Milford, Mass.) and the thermocouple reader used to record cloacal T_B were calibrated against the same NIST-traceable thermometer (0.05°C gradations) over $15\text{--}35^\circ\text{C}$.

During the winter field season, commercial time–depth recorders (model Mk6 TDR, Wildlife Computers, Redmond, Wash.) were used with two green turtles. The Mk6 TDRs (70 g, $7.4 \times 5.7 \times 3.0$ cm) were precalibrated by the manufacturer and had a depth resolution of 2 m over 0–500 m and a temperature resolution of 0.2°C over $0\text{--}22.7^\circ\text{C}$. The manufacturer's temperature calibrations were confirmed over $15\text{--}20^\circ\text{C}$ using a NIST-traceable thermometer. Depth was recorded every 10 s and T_W was recorded every 60 s.

A small (1.5 cm diameter, 0.5 cm high) temperature logger (model DS1921, Dallas Semiconductor Corporation, Dallas, Tex.) was used to record T_W from one green turtle during the winter field season. This temperature logger had a resolution of 0.5°C over -55 to 100°C and recorded T_W every 60 s. The logger was calibrated over $15\text{--}35^\circ\text{C}$ using a NIST-traceable thermometer.

Statistics and analysis

Submergence to a depth of 1 m or greater was counted as a discrete dive and analysed for maximum depth and dive duration. A dive cycle was defined as an individual dive and the accompanying postdive surface interval. Green turtles spent extended periods of time at depths less than 1 m, and high-resolution dive records showed that green turtles could actually be submerged and not solely at the surface during these periods at shallow depths. Therefore, criteria were established to distinguish postdive surface intervals from prolonged submergence at shallow depths. The mean surface interval for all dive cycles was calculated, and dive cycles with surface intervals that were 3 times greater than the mean surface interval were eliminated from the dive analysis (Southwood et al. 1999). This method eliminated from the dive analysis $4.6 \pm 0.7\%$ of dive cycles for individual green turtles. Surface intervals that were 3 times greater than the mean surface interval were counted as “shallow depth” periods, and the percentage of time at sea spent at shallow depths was calculated.

Different dive types were distinguished using criteria established in previous studies of green turtle diving behaviour (Hochscheid et al. 1999). U-dives were dives in which green turtles made a steady descent to a maximum depth ($0.12 \pm 0.01 \text{ m}\cdot\text{s}^{-1}$) and remained within 75% of the maximum depth for an extended time (“bottom time”) before making a steady ascent ($0.12 \pm 0.01 \text{ m}\cdot\text{s}^{-1}$) back to the surface. At least 70% of the total dive duration had to consist of bottom time for a dive to be classified as a U-dive. V-dives were dives in which the green turtle descended to a maximum depth ($0.08 \pm 0.02 \text{ m}\cdot\text{s}^{-1}$) and then immediately began an ascent back to the surface ($0.07 \pm 0.01 \text{ m}\cdot\text{s}^{-1}$). Dives that did not fit either of these criteria were classified as “other”. The percentage of U-dives, V-dives, and other dives that occurred during dive bouts was calculated.

Descriptive statistics for mean dive depth, dive time, postdive surface interval, dive frequency, and the amount of time spent at shallow depths were calculated for each green turtle. Paired *t* tests were used to compare diving variables of green turtles for which data were available in both summer and winter ($N = 2$).

The mean ambient T_W was calculated for each green turtle and for all green turtles in each season (Table 1). The Mk6 TDRs used during the winter season only recorded T_W up to a maximum of 22.7°C . Portions of the temperature records obtained from both of the retrieved Mk6 TDRs were flat-lined at 22.7°C (8.5% of turtle 35104's file and 13.4% of turtle 35133's file), which indicates that T_W may have exceeded the upper limit of the datalogger's thermal range during this time. Data that were out of range were not used in the calculations of mean T_W for these records. Mean ambient T_W for summer and winter were compared using Student's *t* test ($N = 4$). Temperature data from turtle 38311 were avail-

Table 1. Water temperature and dive variables for juvenile green sea turtles, *Chelonia mydas*, during summer and winter at Heron Island, Australia.

Season and turtle No.	CCL [†] (cm)	Mass (kg)	Recording time (h)	Data logger	T _w (°C)	No. of dives analysed [‡]	Dives per day	Dive depth (m)	Dive duration (min)	Surface interval (min)	Percent time at depth <1 m
Summer											
38309	57.5	21.6	129.6	TTDR	—	314	47 ± 6	2.9 ± 0.1	14.3 ± 0.6	0.7 ± 0.03	40.2
38311	48.5	15.0	117.1	TTDR	27.9 ± 1.0	300	58 ± 1	2.1 ± 0.1	11.9 ± 0.6	0.5 ± 0.02	45.8
5276	—	15.5	—	TTDR	—	—	—	—	—	—	—
38306	50.6	15.6	127.2	TTDR	25.3 ± 0.8	300	50 ± 3	4.4 ± 0.2	15.2 ± 0.9	0.7 ± 0.03	37.7
38305	45.3	11.7	126.7	TTDR	25.6 ± 1.3	443	87 ± 3	2.3 ± 0.1	12.6 ± 0.6	0.5 ± 0.02	20.4
35982	45.9	11.6	127.7	TTDR	26.6 ± 1.6	289	46 ± 5	2.1 ± 0.1	12.8 ± 0.6	0.7 ± 0.03	50.2
94946	54.0	16.9	115.3	TTDR	25.8 ± 1.0	434	92 ± 11	3.7 ± 0.2	11.9 ± 0.5	0.6 ± 0.02	24.2
Mean ± SEM	50.3 ± 1.9	15.4 ± 1.3	123.9 ± 2.5		26.2 ± 0.5	346 ± 29	63 ± 8	2.9 ± 0.4	13.1 ± 0.5	0.6 ± 0.04	36.4 ± 4.8
Winter											
38309	59.0	23.6	175.9	TTDR	21.9 ± 1.4	180	22 ± 3	4.9 ± 0.4	22.7 ± 1.4	1.7 ± 0.2	60.7
38311	52.0	17.1	224.3	TTDR	21.7 ± 1.4	156	14 ± 2	3.8 ± 0.2	25.9 ± 2.2	1.9 ± 0.5	67.9
5276	52.1	15.9	178.2	DS1921	21.2 ± 0.1	—	—	—	—	—	—
38306	52.3	17.5	301.2	TTDR	—	—	—	—	—	—	—
35104	47.8	13.2	228.1	Mk6TDR	20.7 ± 0.1	—	—	—	—	—	—
35133	44.0	10.0	195.2	Mk6TDR	20.9 ± 0.1	—	—	—	—	—	—
Mean ± SEM	51.2 ± 2.1	16.2 ± 1.9	217.2 ± 19.1		21.3 ± 0.2	168 ± 12	18 ± 0.4	4.4 ± 0.6	24.3 ± 1.6	1.8 ± 0.07	64.3 ± 3.6

Note: Values for T_w and dive variables presented are means ± SEM.

[†]Curved carapace length.

[‡]Dives with depths >1 m.

able for both summer and winter but were excluded from the analysis in order to not violate the Student's *t* test requirement of independence of samples.

Pearson's correlation was used to test for a relationship between maximum dive depth of U-dives and ambient T_W at maximum depth. Four U-dives were chosen at random from 4 different depth categories (1–3, 3–5, 5–7, and 7–9 m) for each green turtle during summer ($N = 6$) and winter ($N = 2$). The mean T_W during bottom time of the dives was calculated and plotted against the depth category.

Diel patterns in diving behaviour and T_W were analysed by dividing the data into day and night periods based on seasonal sunrise and sunset times. Summer days lasted from 0500 to 1829, while winter days lasted from 0630 to 1729. Paired *t* tests were used to compare dive frequency, dive depth, dive duration, and time spent at shallow depths (<1 m) during the day and night in summer ($N = 6$) and winter ($N = 2$).

Linear regression was used to test for a relationship between cloacal T_B recorded at the time of green turtle capture and ambient T_W at the time of capture (obtained from the analysis of the datalogger output). A Student's *t* test was used to test for a significant difference in the thermal gradient ($T_B - T_W$) between summer and winter ($N = 4$).

Statistical analyses were performed using SigmaStat software (SPSS Inc., Chicago, Ill.). Differences were considered to be significant at $P < 0.05$. Values are presented as the mean \pm standard error of the mean (mean \pm SEM).

Results

Diving behaviour and water temperature

Six of the seven dataloggers deployed during the summer season were retrieved, and dive data from all six of these instruments were analysed. The seventh datalogger was retrieved during the winter field season, but batteries were dead and data could not be downloaded from this instrument. The thermistor in the datalogger deployed on turtle 38309 malfunctioned, so T_W data from only five green turtles were analysed for the summer season. Five of the six dataloggers deployed during the winter season were retrieved. Turtle 38306 dislodged her datalogger at some point before recapture. Unfortunately, a combination of low depth resolution of the Mk6 TDRs and shallow diving behaviour of the two green turtles (35104 and 35133) equipped with Mk6 TDRs made dive traces unusable. The DS1921 datalogger used with turtle 5276 recorded T_W only (not depth), so dive records were only obtained from two green turtles (38309 and 38311) during the winter season. Fortunately, data were collected from these same two green turtles during summer as well (Table 1), so a comparison of seasonal diving patterns could be made for these individuals. The T_W data from all five of the instruments retrieved during the winter field season were analysed.

Green turtles experienced T_W of 23.3–31.6°C ($26.2 \pm 0.5^\circ\text{C}$) during summer (Table 1). During winter, green turtles experienced T_W of 17.8–26.1°C ($21.3 \pm 0.2^\circ\text{C}$). Mean winter T_W was significantly lower than mean summer T_W ($P < 0.001$). Diel fluctuations in ambient T_W were apparent during both field seasons (Fig. 1). Mean nighttime T_W experienced by the green turtles was significantly lower than mean

daytime T_W during summer ($P = 0.007$) and winter ($P = 0.007$).

Descriptive statistics for dive frequency, maximum depth, dive duration, and postdive surface interval for dives made by all green turtles during summer and winter are listed in Table 1. The green turtles made 63 ± 8 dives per day during summer and 18 ± 4 dives per day during winter. Mean dive depth was within 2.1–4.4 m during summer and 3.8–4.9 m during winter. Dive duration in summer (13.1 ± 1.2 min) was approximately half the dive duration in winter (24.3 ± 1.6 min). The surface interval in summer (0.6 ± 0.1 min) was one-third that of the surface interval in winter (1.8 ± 0.1). During summer, green turtles spent $36.4 \pm 4.8\%$ of the recording period at shallow depths (<1 m). In comparison, green turtles spent almost twice as much time at shallow depths ($64.3 \pm 3.6\%$) during winter.

Since data were available for turtle 38309 and 38311 during both summer and winter, paired *t* tests were used to compare dive variables for these two green turtles between seasons. There was no statistically significant seasonal difference in dive frequency ($P = 0.171$), dive depth ($P = 0.051$), dive duration ($P = 0.156$), or surface interval ($P = 0.089$). However, a significantly greater amount of time was spent at shallow depths during winter than during summer ($P = 0.023$). Figure 1 demonstrates the seasonal differences in diving patterns displayed by turtle 38311.

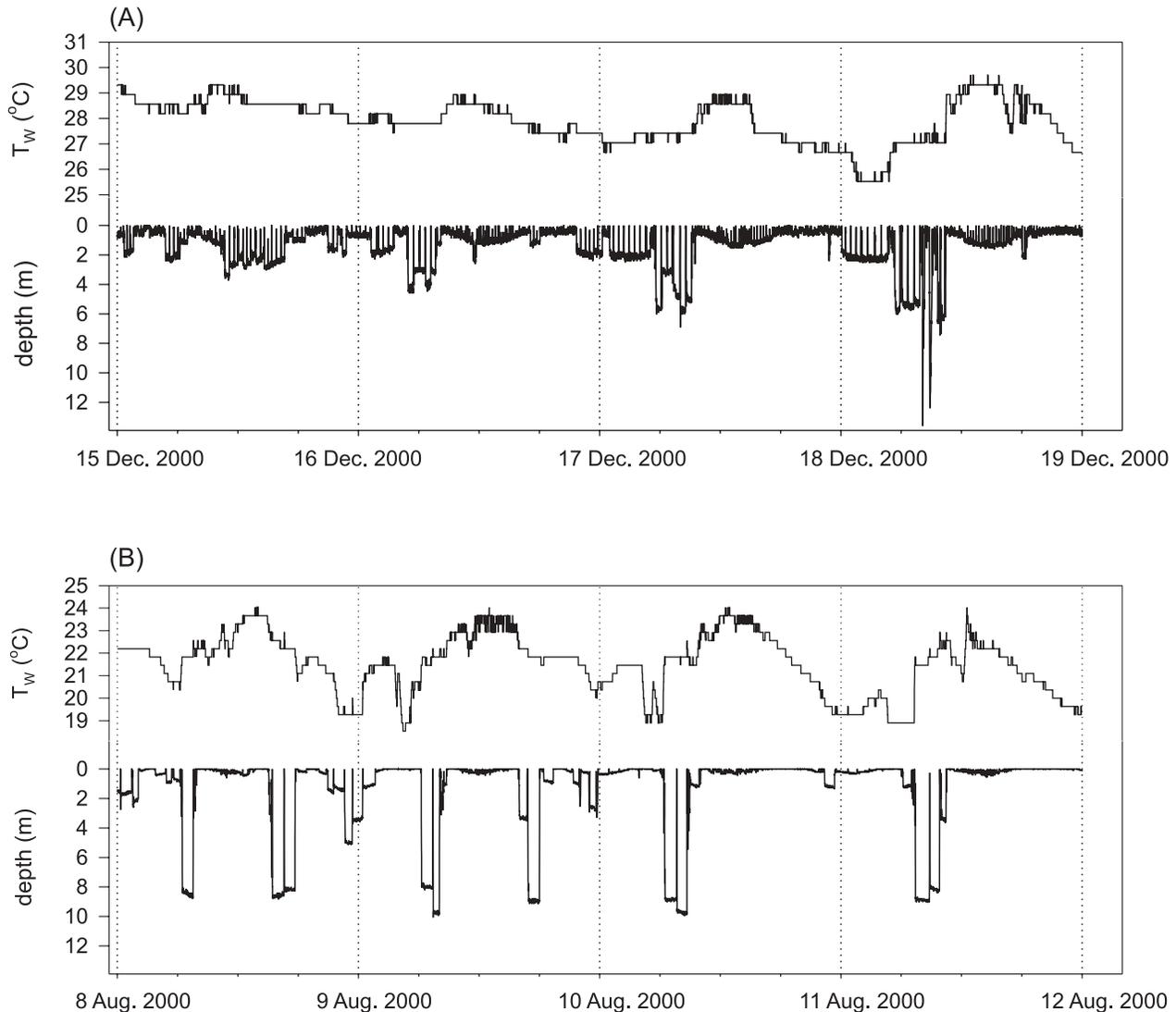
There was no significant correlation between dive depth and T_W over the range of depths most frequented by green turtles during summer ($r^2 = 0.1476$, $P = 0.104$) or winter ($r^2 = 0.1047$, $P = 0.396$). Figure 2 shows a 24-h excerpt from turtle 38309's T_W and dive records during the winter field season. Individual dives greater than a depth of 1 m occasionally resulted in a decrease in ambient T_W experienced by the green turtle. However, green turtles also experienced large fluctuations in ambient T_W during periods of shallow diving. Ambient T_W at shallow depths was relatively warm during the day, but decreases in T_W were noted for prolonged periods of shallow diving at night.

Figure 3 demonstrates diel differences in dive patterns displayed by green turtles in summer and winter. Green turtles made significantly more dives to depths greater than 1 m during the day than during the night in summer ($P < 0.001$) and winter ($P = 0.042$). Daytime dive durations were significantly shorter than nighttime dive durations during both summer and winter ($P = 0.001$ and $P = 0.031$, respectively). Dives tended to be deeper during the daytime, but there was no statistically significant diel difference in dive depth during summer ($P = 0.164$) or winter ($P = 0.310$).

Several different dive types were displayed by green turtles (Fig. 4). The U-dives predominated dive records during both summer (53.4–73.0% of all dives) and winter (51.0–62.1% of all dives). The V-dives were less common, comprising only 0.4–6.1% of dives made during summer and 0–0.6% of dives made during winter. Dives with highly variable depth could not be defined as either U-dives or V-dives. These dives comprised 26.6–45.9% of dives made during summer and 37.3–49.0% of dives made during winter.

Figure 5 shows a series of nocturnal U-dives made by turtle 38305 during the summer field season. Maximum dive depth progressively decreased until 0100, and began to increase again at approximately 0200. The changes in dive

Fig. 1. Time/depth and water temperature (T_W) data for the green turtle, *Chelonia mydas*, 38311 for 4 days during summer (A) and 4 days during winter (B) at Heron Island, Australia. Green turtles spent significantly more time at shallow depths, and dive durations tended to be longer during winter than during summer. The T_W fluctuated between 19 and 24°C during winter and 26 and 30°C during summer. A diel pattern in T_W fluctuations occurred during both seasons, with daytime T_W significantly higher than nighttime T_W .



depth were in synchrony with the timing and magnitude of the falling and rising tides for that evening. This pattern was noted for five of the six green turtles monitored during summer and for one of the two green turtles monitored during winter.

Body temperature

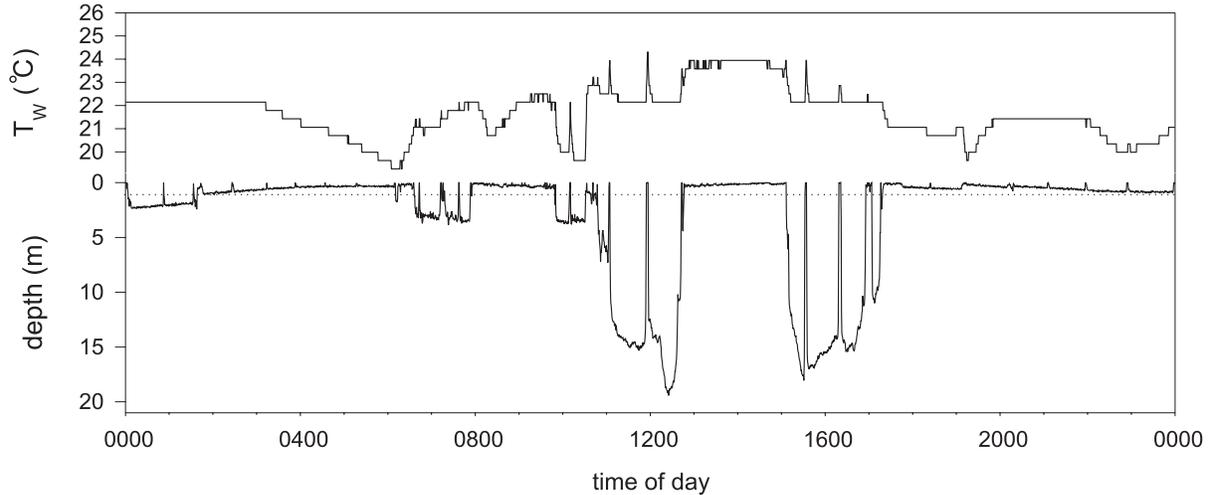
There was a strong and significant relationship between T_B and T_W over the range of temperatures experienced year-round ($T_B = 1.06T_W - 0.66$, $r^2 = 0.96$, $P < 0.001$). Figure 6 shows T_B plotted as a function of T_W during both summer ($T_W = 25.3$ – 26.6°C) and winter ($T_W = 21.1$ – 21.9°C). When data from summer and winter were separated, the relationship between T_B and T_W was not statistically significant (summer: $r^2 = 0.70$, $P = 0.185$; winter: $r^2 = 0.87$, $P = 0.056$). The slope of the regression line for T_B and T_W was not significantly different from 1 ($t_{0.05(2),7} = 0.662$, $P > 0.50$), and the Y intercept for the regression was not significantly differ-

ent from zero ($t_{0.05(1),7} = 0.312$, $P > 0.25$). On average, green turtle T_B was $0.6 \pm 0.2^\circ\text{C}$ higher than T_W . There was no statistically significant difference in the mean thermal gradient between T_B and T_W during summer ($0.9 \pm 0.4^\circ\text{C}$) compared with winter ($0.4 \pm 0.2^\circ\text{C}$) ($P = 0.261$).

Discussion

Circannual changes in temperature, food and water availability, and photoperiod are the major environmental factors that contribute to seasonal modifications in metabolism, physiology, and behaviour of ectotherms. The response to changing environmental conditions varies greatly depending on species and geographic distribution. Green sea turtles are primarily distributed in tropical and subtropical latitudes, and generally are not exposed to extremely cold temperatures. Even so, there have been reports of winter dormancy in green turtles from certain populations. Felger et al. (1976)

Fig. 2. A 24-h segment of time/depth and T_w data for green turtle 38309 recorded on 8 August 2001 (austral winter) at Heron Island. The dotted line through the dive trace represents a depth of 1 m. Large fluctuations in T_w occurred during individual dives to depths greater than 1 m, and also during extended periods at shallow depths.



noted that Pacific green turtles in the Gulf of California partially bury themselves in the muddy substrate on the sea floor and are lethargic and easily captured during winter. However, recent data obtained from sonic-tracking studies (Seminoff 2000) show that green turtles at Bahia de los Angeles in the Gulf of California may reside year-round at foraging pastures and maintain activity even during the winter months. Based on sea surface temperature data and movement patterns of green turtles, Seminoff (2000) suggested that the “inactivity threshold” for green turtles at this site was 15°C, and that green turtles may enter a state of torpidity when temperatures drop below this threshold.

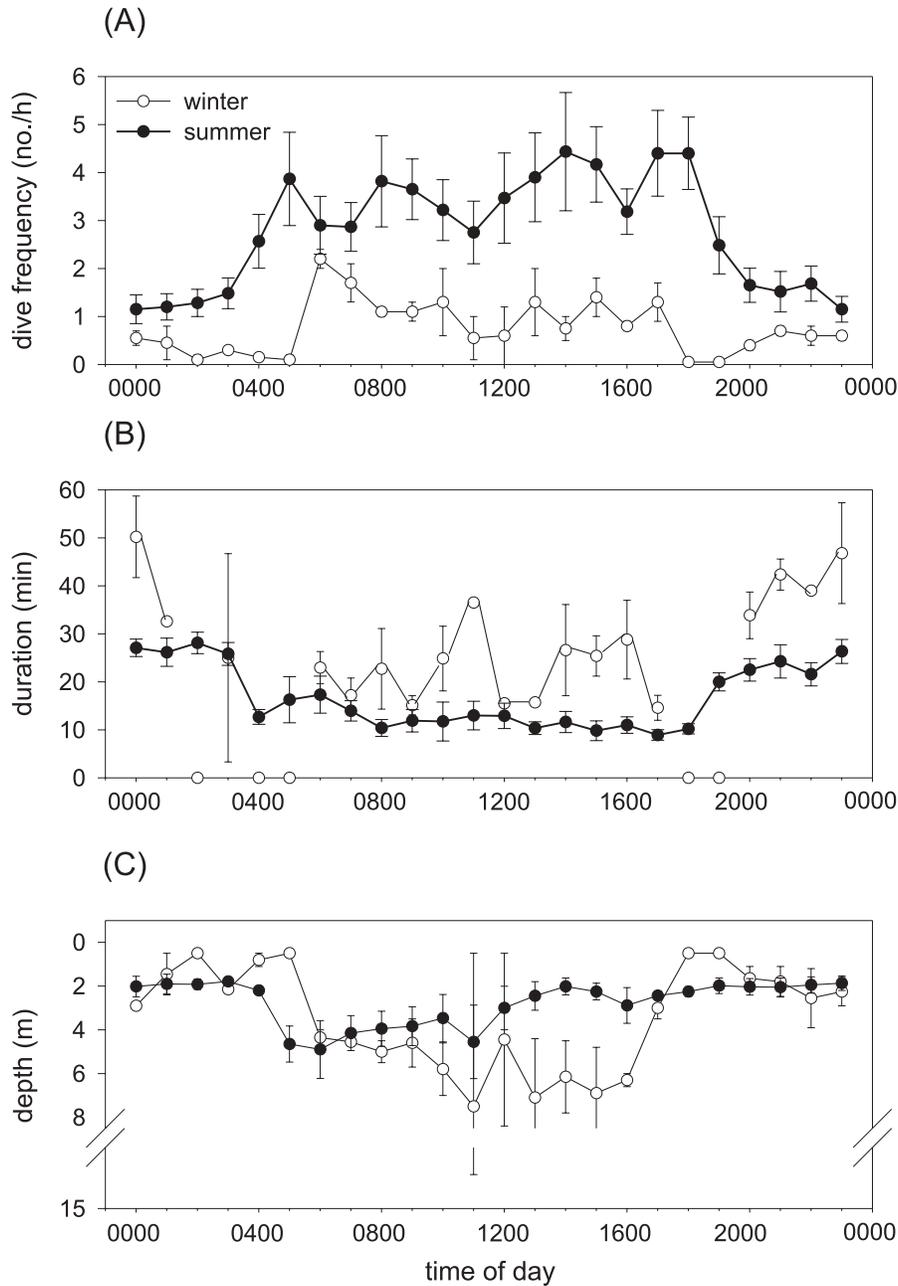
Green turtles from populations in Florida and Australia continue to forage and remain alert and active during seasonal cold exposure (Mendonca 1983; Read et al. 1996). Interestingly, T_w at these study sites rarely drops below 15°C in winter. The mean T_w experienced by green turtles during winter at Heron Island was 21.3°C, although T_w dropped below 18°C on occasion. Dive records and direct observation of green turtles at this study site indicate that green turtles remain active during winter; however, there were differences in diving behaviour displayed by green turtles during winter compared with summer.

There was a significant difference between seasons ($P = 0.023$) in the amount of time that green turtles spent at shallow depths (Table 1, Fig. 1). Turtles spent nearly twice the amount of time at depths less than 1 m during winter as they did during summer. During periods of shallow diving, green turtles may have been in areas where maximum water depth is 1 m or in the upper 1 m of a deeper water column. Utilization of shallow habitats may be based on thermal preference. Temperature data obtained from freely swimming green turtles showed that T_w at shallow depths is subject to large fluctuations. Nocturnal T_w at shallow depths dropped as low as 17.8°C during winter, yet green turtles typically spent a large proportion of nighttime at shallow depths during both winter and summer (Figs. 1 and 3). Brill et al. (1995) found that juvenile green turtles prefer shallow water at night when they are resting, and this preference is consistent with what we observed in the current study. Data from high resolution

dataloggers show that green turtles make an extended series of U-dives while at shallow depths, particularly at night (Fig. 2). It is likely that green turtles are resting on the sea floor during these shallow nocturnal U-dives. Intermittent sonic tracking of juvenile green turtles at Heron Island and direct observation of green turtles during late afternoon and evening snorkeling surveys of the harbour and surrounding reefs verified that green turtles returned to shallow areas nightly and rested motionless on the ocean floor. The low temperatures experienced during periods of nocturnal rest in shallow water may result in a temperature-induced decrease in metabolic rate (via Q_{10} effects) and energetic savings. On the other hand, T_w at shallow depths can be quite high during the daytime (Fig. 1), up to 31.6°C in summer and 26°C in winter. During summer, green turtles may avoid shallow water so as to avoid high temperatures. Mendonca (1983) found that juvenile green turtles in a Florida lagoon moved into deeper, cooler water during the mid-afternoon when temperatures at shallow seagrass foraging pastures exceeded 31°C. The lower proportion of time spent at shallow depths by green turtles at Heron Island during summer may reflect a similar thermoregulatory strategy. Maximum daytime T_w at shallow depths was lower during winter than during summer, and therefore thermal limitations would not prevent green turtles from utilizing shallow habitats.

Seasonal changes in food availability or location of preferred food may also contribute to shifts in depth preferences between summer and winter. Green turtles are facultative herbivores and can thrive on a variety of plant matter. Juvenile green turtles from the Heron Island population forage primarily on algae, and show a preference for red (*Rhodophyta* spp.) and brown (*Phaeophyta* spp.) algae (Forbes 1994). However, green turtles are opportunistic in their foraging patterns and sudden dietary shifts have been observed for green turtles in this population when species of green algae (*Chlorophyta* spp.) become abundant (Forbes 1994). Necropsy of an untagged juvenile green turtle found dead during the winter field season at Heron Island revealed large amounts of green algae in the green turtle’s esophagus and stomach (A.L. Southwood, personal observation). A survey of sea-

Fig. 3. Diel patterns in dive frequency (A), dive duration (B), and dive depth (C) for dives deeper than 1 m made by green turtles at Heron Island during summer ($N = 6$, ●) and winter ($N = 2$, ○). Each point represents the mean \pm SEM. Green turtles made significantly more dives during the day than during the night in both summer and winter, and daytime dive durations were significantly shorter than nighttime dive durations in both seasons. Dive depths tended to be deeper in the daytime than in the nighttime, but there was no statistically significant difference.



sonal algal abundance at different depths was not conducted for the current study, but this information would be valuable for assessing the role of food availability in determining seasonal diving patterns.

Green turtles typically forage throughout the day, but peak foraging times are just after dawn and in the late afternoon (Mendonca 1983; Bjorndal 1980; Davis et al. 2000). Foraging dives tend to be of shorter duration than resting dives, and this is presumably a consequence of higher metabolic rates associated with activity. The common view of diving in air-breathing marine vertebrates is that dives are aerobic and

the animal returns to the surface before oxygen stores are depleted (Kooyman et al. 1983; Butler and Jones 1997). Faster utilization of oxygen stores would result in shorter dive durations, assuming that dives are primarily aerobic in nature. In this study, green turtles began to make more dives (depth >1 m) with shorter dive durations at daybreak, and this trend persisted throughout the day. Dive frequency during the day was significantly higher than dive frequency at night, and daytime dive durations were significantly shorter than nighttime dive durations during both summer and winter (Fig. 3). Based on behavioural data obtained from other

Fig. 4. A 10-h segment of time/depth data recorded from green turtle 94946 on 18 December 2000 (austral summer) at Heron Island. The dotted line represents a depth of 1 m. The majority of dives deeper than 1 m were U-dives (51.0–73.0%). Dives of variable depth (“other” dives) were also common (26.6–49.0%), whereas V-dives were relatively rare (0–6.1%). Individual green turtles spent 20.4–67.9% of the time at sea at shallow depths.

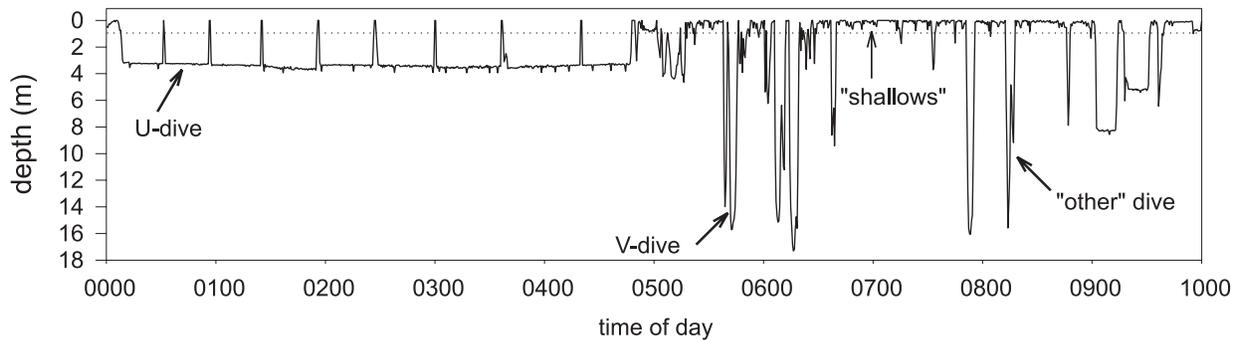
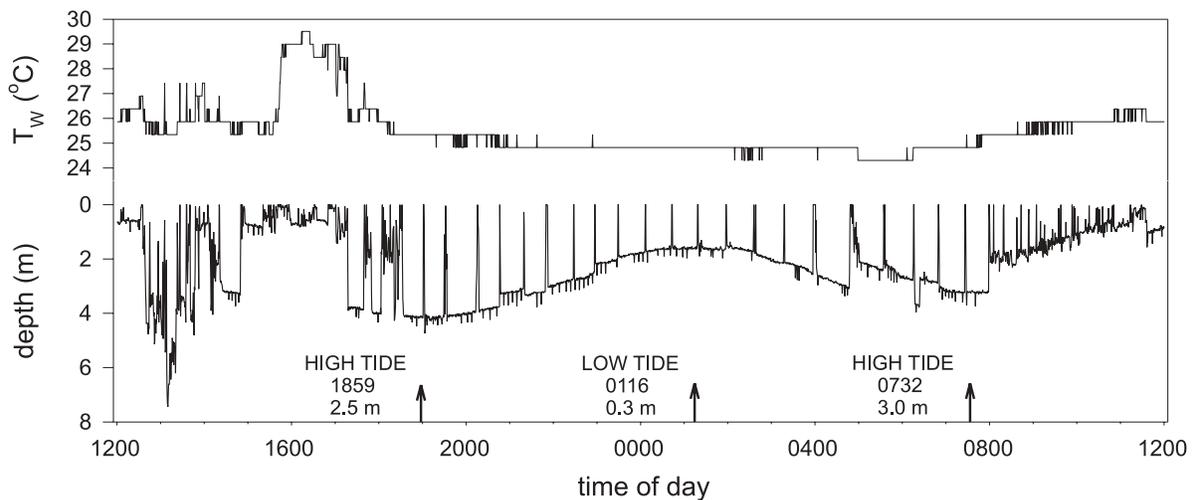


Fig. 5. A 24-h segment of time/depth data recorded from green turtle 38305 on 9–10 December 2000 (austral summer) at Heron Island. Variability in dive depth of U-dives throughout the night was in synchrony with the falling and rising of the tide. The magnitude of the changes in dive depth closely mirrored the difference between high and low tide for that evening. This pattern suggests that green turtles remained stationary at a certain location during the U-dives, and changes in depth reflect the ebb and flow of the tides rather than movements made by the green turtle.



studies with green turtles (Bjorndal 1980; Mendonca 1983; Brill et al. 1995) and hawksbill turtles (*Eretmochelys imbricata*; van Dam and Diez 1996), this dive pattern is suggestive of foraging behaviour.

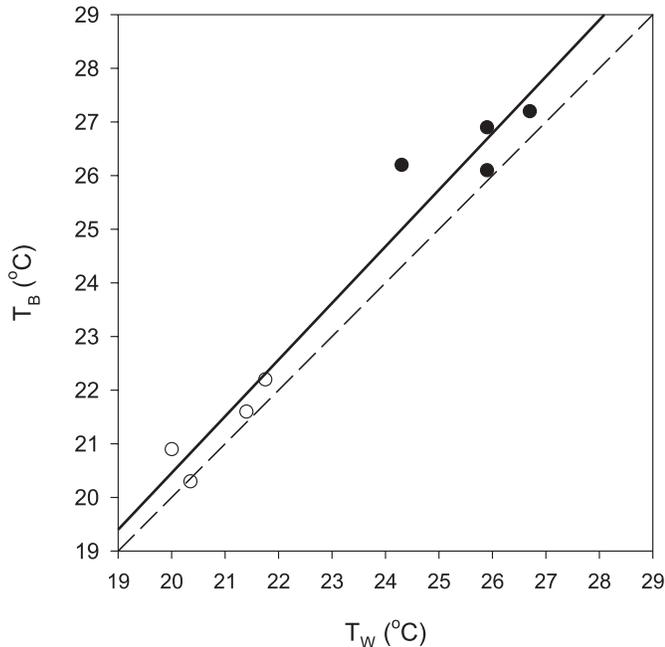
Review of dive traces for green turtles during winter and summer showed that nocturnal diving was strongly characterized by prolonged periods in shallow water and U-dives, which typically represent resting behaviour in sea turtles (van Dam and Diez 1996; Hays et al. 2000). Gradual changes in depth of individual nocturnal U-dives likely reflect the ebb and flow of the tides rather than movements made by the green turtle in the water column (Figs. 2 and 5). In contrast, there was a great deal of variability in dive depth and dive type during the daytime when green turtles are presumably foraging (Figs. 1, 2, 4). Green turtles from other populations typically forage in shallow water. Although juvenile green turtles at Heron Island do spend time at shallow depths during the daytime, they also make dives with variable depth (categorized as “other” by our dive criterion) as well as deeper U-dives during the daylight hours. This variation in diurnal diving behaviour may indicate that green turtles

are engaged in a variety of activities during the day (traveling, searching, foraging, resting), or alternatively that green turtles are foraging in many different types of underwater habitats.

The two green turtles for which we have dive traces for both seasons spent a larger proportion of time at sea in shallow water (i.e., depths <1 m) during winter than during summer. However, dive depth for dives that exceeded 1 m was deeper during winter (4.4 ± 0.6 m) than during summer (2.5 ± 0.4 m). There was also a tendency towards longer dive durations in winter (24.3 ± 1.6 min) than in summer (13.1 ± 1.2 min) for these two animals. The length of a dive depends on oxygen stores in the body, the proportion of oxygen stores that are used, and the rate of oxygen utilization (i.e., metabolic rate). The tendency towards longer dive durations during winter could be a result of alterations in any of these variables.

The lungs are the primary site of oxygen storage in green turtles, and alterations in the lung oxygen store may be achieved by changing the volume of air inspired before diving. The lungs are also used to control buoyancy (Milsom

Fig. 6. Linear regression of T_B vs. T_W at the time of recapture for green turtles in summer (●) and winter (○) ($r^2 = 0.96$, $P < 0.001$, $T_B = 1.06T_W - 0.66$). The thermal difference between T_B and T_W was $0.6 \pm 0.2^\circ\text{C}$. The dashed line represents a slope of 1. The slope of the regression was not significantly different from 1 and the Y intercept of the regression was not significantly different from 0.



1975; Minamikawa et al. 1997, 2000). Hays et al. (2000) proposed that green turtles alter the amount of air inspired at the surface to achieve neutral buoyancy at a selected depth. Neutral buoyancy would be achieved at a deeper depth with a larger inspiration. Therefore, green turtles diving to deeper water would have a larger lung oxygen store than green turtles diving to shallow water and would be able to remain submerged for a longer duration at a given metabolic rate. A comparison of U-dives (which are presumably resting dives) made by turtle Nos. 38309 and 38311 shows that dive depth of U-dives was deeper in winter (5.4 ± 0.4 m) than in summer (2.5 ± 0.5 m) and dive duration of U-dives was longer in winter (38.75 ± 5.85 min) than in summer (17.15 ± 1.45 min). If making this link between depth selection, buoyancy control, and lung oxygen stores is valid, then the longer dive durations in winter could be explained in part by increased lung oxygen stores.

An alternate, and perhaps more likely, explanation for the tendency towards longer dive durations in winter is a decrease in the rate of oxygen utilization. Mean T_W during winter was 4.9°C lower than mean T_W during summer. A change in temperature of only a few degrees Celsius can have a large impact on biological reaction rates and metabolic and physiological processes. A lower rate of oxygen utilization as a result of decreased ambient temperatures (and therefore T_B) during winter would allow green turtles to remain submerged for longer periods of time before oxygen stores were fully depleted (if O_2 stores remain constant between seasons). However, the increase in mean dive duration during winter was accompanied by an increase in mean postdive surface interval. It is possible that rates of oxygen

consumption during dives are similar in winter and summer, and the increased postdive surface interval in winter reflects the necessity to replenish oxygen stores that have been depleted to a greater extent. Additionally, the degree to which green turtles rely on anaerobic metabolism during diving and the effects of temperature on the balance between aerobic and anaerobic metabolism in this species have not been thoroughly investigated. The fact that longer dives are followed by longer postdive surface intervals during winter may reflect an increase in anaerobic means of energy production during submergence and a necessity to repay an oxygen debt at the surface.

As seen with other populations of juvenile green turtles in southern Queensland (Read et al. 1996), there was a strong relationship between T_B and T_W for juvenile green turtles from the Heron Island population. This relationship was only significant when data from both seasons were pooled together. The lack of significance for individual seasons is likely due to the small sample size ($N = 5$) and the small range of instantaneous cloacal T_B and T_W recorded in winter (21.1 – 21.9°C) and summer (25.6 – 27.9°C). The thermal difference between green turtle T_B and T_W was $0.6 \pm 0.2^\circ\text{C}$. The T_B of adult green turtles (110–121 kg) is typically 1– 3°C above ambient temperature (Mrosovsky 1980; Standora et al. 1982; Sato et al. 1998). Studies with adult loggerhead turtles have shown that as T_W decreases, the thermal gradient between T_B and T_W gets larger (Sato et al. 1994), but this was not the case with juvenile green turtles in the current study. There was no significant difference in the thermal gradient between T_B and T_W during winter ($0.4 \pm 0.2^\circ\text{C}$) compared with summer ($0.9 \pm 0.4^\circ\text{C}$). Adult green turtles may be able to maintain a greater thermal gradient owing to physiological adjustments, such as alterations in regional blood flow, and the benefits endowed by a large body mass, i.e., a low surface area to volume ratio and high heat storage capacity (Spotila et al. 1973; Standora et al. 1982). In any case, the present study and earlier work by Read et al. (1996) clearly show that elevated T_B is not a prerequisite for maintenance of activity by juvenile green turtles during exposure to lower T_W in winter. Further detailed investigations into the physiological and biochemical adjustments made by sea turtles in response to prolonged cold exposure may provide insight as to how green turtles adapt to seasonal variation in their thermal environment.

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