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## Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): are they obligately neritic herbivores?

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**Abstract** Satellite telemetry and stable isotope analysis were used to confirm that oceanic areas (where water depths are >200 m) are alternative feeding habitats for adult female green sea turtles (*Chelonia mydas*), which have been thought to be obligate herbivores in neritic areas (where depths are <200 m). Four females were tagged with satellite transmitters and tracked during post-nesting periods from Ogasawara Islands, Japan. Three females migrated to neritic habitats, while transmissions from another female ceased in an oceanic habitat. The overall mean nighttime dive depths during oceanic swimming periods in two females were <20 m, implying that the main function of their nighttime dives were resting with neutral buoyancy, whereas the means in two other females were >20 m, implying that they not only rested, but also foraged on macroplankton that exhibit diel vertical migration. Comparisons of stable carbon and nitrogen isotope ratios between 89 females and the prey items in a three-source mixing model estimated that 69% of the females nesting on Ogasawara Islands mainly used neritic habitats and 31% mainly used oceanic habitats. Out of four females tracked by satellite, two females were inferred from isotope ratios to

be neritic herbivores and the two others oceanic planktivores. Although post-nesting movements for four females were not completely consistent with the inferences from isotope ratios, possibly due to short tracking periods (28–42 days), their diving behaviors were consistent with the inferences. There were no relationships between body size and the two isotope ratios, indicating a lack of size-related differences in feeding habitat use by adult female green turtles, which was in contrast with loggerhead sea turtles (*Caretta caretta*). These results and previous findings suggest that ontogenetic habitat shifts by sea turtles are facultative, and consequently, their life histories are polymorphic.

**Keywords** Life history · Ontogenetic habitat shifts · Reptile · Satellite telemetry · Stable isotope analysis

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### Introduction

Animals often shift habitats to meet their changing needs during ontogeny, e.g., to maximize growth rates, to minimize mortality risk, or to minimize the ratio of mortality risk to growth rate (e.g., Werner and Gilliam 1984; Dahlgren and Eggleston 2000). These shifts are not obligate but facultative, because if the needs of an individual are met in a habitat, it may continue to use the habitat throughout its life. Individual variation in habitat use can result in intrapopulational polymorphism in life history. This has often been reported in relatively small, abundant, easily handled/observed, or commercially important animals such as insects (Harrison 1980), fishes (Tsukamoto et al. 1998; Maekawa and Nakano 2002), amphibians (Wilbur and Collins 1973), and birds (Lundberg 1988), and various mechanisms that evolve and maintain the life-history polymorphism within populations have been proposed in studies of these animals (e.g., Gross 1996; Brockmann 2001).

Because sea turtles do not have any of these attributes, studies on their behavior and ecology are challenging and typically qualitative except during nesting

periods (and subsequent hatchling stages) when they land on sandy beaches. For example, although recent technological advances in satellite telemetry have enabled the foraging behavior of sea turtles to be observed in remote locations far from land during non-nesting periods (e.g., Hays et al. 2004a), the sample sizes of these observations are still small due to their high cost. This makes it difficult to generalize their behavior and ecology quantitatively (i.e. as a population). However, a recent study has overcome this difficulty by simultaneously using direct (telemetry) and indirect (biogeochemical analysis) methods (Hatase et al. 2002).

Stable isotope analysis has increasingly been used to infer animal movement patterns from invertebrates to higher vertebrates (Rubenstein and Hobson 2004). This technique is generally based on the fact that isotope ratios of animals reflect those of their diets with some enrichment. Thus, if isotope ratios in diets from different geographical origins are highly separated, comparison between isotope ratios in animals and diets can tell us where the animals came from. Although fractionation factors (enrichment values) between isotope ratios in animals and diets, and the turnover rates of isotope ratios in animals, are different both among tissues within an individual and among species, those for sea turtles are not yet available (but see Seminoff et al. 2006). Fractionation factors and turnover rates determined for other species have been applied to sea turtle studies (Godley et al. 1998; Hatase et al. 2002). In the present study, egg-yolks were used for analysis. Since vitellogenesis of sea turtles is presumed to begin 4–6 months prior to the mating season and to be completed prior to mating (Rostal et al. 1998), the isotope signatures of their egg-yolks should reflect the prey consumed in foraging areas before migration to nesting beaches.

Green sea turtles (*Chelonia mydas*) spend their early life history stages in open ocean pelagic habitats (where water depths are >200 m), feeding mainly on planktonic animals (Musick and Limpus 1997; Bjørndal 1997). After several years of the early developmental stage, they leave oceanic/pelagic habitats and recruit to neritic/benthic habitats (where depths are <200 m) in which they shift to herbivorous diets consisting of macroalgae and seagrasses (Kurata et al. 1978; Miyawaki 1994; Musick and Limpus 1997; Bjørndal 1997). After reaching sexual maturity, they start seasonal migrations between the neritic feeding habitats and distant nesting beaches (e.g., Tachikawa and Sasaki 1990; Baba et al. 1992, 1993; Luschi et al. 1998; Cheng 2000; Godley et al. 2002), which are undertaken every few years (Hirth 1997).

In contrast to this general understanding of the green turtle life history, recent satellite telemetry revealed that, during post-nesting seasons, adult females not only migrated into neritic habitats, but also wandered in oceanic habitats for several months (Japan Fisheries Resource Conservation Association 1999). They feed presumably on planktonic animals in the oceanic habitat as the juveniles do. This suggests that not all green turtles shift

habitats ontogenetically, but that their habitat shifts are facultative. The same phenomenon has recently been documented in loggerhead sea turtles (*Caretta caretta*) nesting in Japan, because both oceanic and neritic areas were quantitatively confirmed to be used as feeding habitats (Hatase et al. 2002). These behavioral differences influence several life history traits of female loggerheads, and this was considered as a life-history polymorphism within populations (Hatase et al. 2004).

In this study, we tested whether oceanic areas are alternative feeding habitats for adult female green turtles, which have been believed to be obligate herbivores in neritic areas. First, post-nesting movements and diving behavior of tagged individuals were directly measured using satellite telemetry. Green turtles have been thought not to feed either during the migration to and from a nesting ground or during their stay at a nesting ground (Mortimer and Carr 1987). From dive information during the migration, they were considered to simply alternate between travelling just beneath the surface and resting within the depths where they could attain neutral buoyancy (Hays et al. 2001). Thus, if green turtles forage during migration, it is predicted that they would show different diving behaviors from those above. For example, they may frequently dive deeper beyond the maximum depth of neutral buoyancy to exploit planktonic prey. Therefore, we focused on dive data during oceanic swimming periods and analyzed them in light of the use of neutral buoyancy associated with resting. Second, stable isotope analysis was used to infer the feeding habits of adult female green turtles. Synthesizing these findings, we determined their feeding habitat use and evaluated their apparent life history in relation to those of other sea turtle species.

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## Materials and methods

### Satellite telemetry

On 10 August 2003 and 17 August 2004 (the end of the nesting season), satellite transmitters (Satellite Relayed Data Loggers, Series 7000, Sea Mammal Research Unit, University of St Andrews, St Andrews, UK) were attached to four adult female green turtles (the smallest and largest turtles in each year: turtles 1 and 2 in 2003, turtles 3 and 4 in 2004; Table 1), which were kept in a breeding pool of the Ogasawara Marine Center (27°05'N, 142°12'E) on Chichijima Island, Ogasawara Islands, Japan. Every year, some adult female green turtles are legally captured by fishermen early in the breeding season and kept in the pool to collect eggs for headstarting projects (Sato et al. 1998). The data loggers were attached to the carapaces of the turtles with epoxy resin and glass-fiber cloth. Their eggs were also collected for stable isotope measurements. Turtle 1 was brought offshore, 8.5 km west of Chichijima Island, by a boat and released there, while Turtles 2, 3, and 4 were released at a beach adjacent to the breeding pool.

**Table 1** Summary of information on adult female green turtles (*Chelonia mydas*) tracked by satellite from Ogasawara Islands, Japan

Turtle	Straight carapace length (mm)	Body mass (kg)	Release data	Last transmission	Tracking duration (days)	Distance covered (km)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1	905	115.2 <sup>a</sup>	10 Aug 2003	21 Sep 2003	42 (14)	1,962	-17.7	8.3
2	1,068	200.0	10 Aug 2003	13 Sep 2003	34 (18)	1,546	-18.4	11.4
3	927	125.2 <sup>a</sup>	17 Aug 2004	19 Sep 2004	33 (19)	1,627	-17.3	11.4
4	1,092	211.0	17 Aug 2004	14 Sep 2004	28 (15)	966	-18.2	9.3

Numbers in parentheses next to the tracking durations are the days during which turtles swam in oceanic areas and the dive data were analyzed

<sup>a</sup>Estimated from straight carapace length

The data loggers were located with the Argos system, which classified locations into seven classes of decreasing accuracy (<150 m, 350 m, 1 km for the first three classes: 3, 2, 1; and with no limits of accuracy for the remaining four classes: 0, A, B, Z). Because there were insufficient locations of high-accuracy classes to reconstruct migratory routes, all locations, except for the locations that required a high speed of travel (>7.2 km/h), were used for the route reconstruction. The total distance covered was calculated as the sum of the shortest distances between successive locations.

The data loggers recorded depth every 4 s with a resolution of 0.33 m (range: surface to 10 m) or 1 m (range: 10–486 m). The start of dives was defined by the time that the saltwater switch on the data logger perceived that the transmitter was submerged and the depth became below 2 m for 30 s, and the end of the dives was defined when either the depth became less than 2 m, or the saltwater switch recorded the transmitter breaking the surface. When dives were completed between 2 and 10 m, the data logger transmitted only the maximum depth, the time of the end of the dive, and dive duration. When dives exceeded 10 m, the data logger transmitted the time and depth of the five most significant points of inflection during the dive, the time of the end of the dive, and dive duration. Because of the limited bandwidth of the Argos system, not all dive data were obtained. In addition to relaying individual dives, the data logger also summarized the dive information, such as the percentage of time spent deeper than 2 m into 6-h summaries. Individual dives were used as a proxy for the proportion of time spent diving over the 24-h cycle, and these proxy values were converted into absolute units using the mean percentage of time spent diving supplied in the 6-h summaries (Hays et al. 2004a).

Sea turtles often show midwater resting dives with neutral buoyancy (e.g., Minamikawa et al. 2000; Hays et al. 2001). During these dives they spend most of their time in the gradual ascent phase following the occasional steep deep drop so mean dive depth should be a better indicator of the dive (Hays et al. 2001). Thus, both maximum and mean dive depths were used for analysis in this study. For a dive exceeding 10 m, the mean dive depth was calculated by reconstructing the dive profile from the five inflection points and the start and end

points. Depths of the start and end points were defined as 2 m, and depths at every 10% of dive duration were calculated using equations between the seven points. Mean dive depth was then calculated averaging these 11 depths (including start and end depths).

The data loggers also recorded water temperatures on selected dives. In each of these dives, 12 coordinate pairs of pressure and temperature were obtained. The temperature sensor in the data logger has long-term stability (McMahon et al. 2005).

#### Samples for stable isotope analysis

Eggs of captive green turtles were collected during nightly watches at enclosed sandy beaches adjacent to breeding pools, which are managed by the Ogasawara Marine Center on Chichijima Island, and the Hahajima Fisheries Cooperative (26°38'N, 142°09'E) on Hahajima Island, Ogasawara Islands, from late May to late July in 2003 and 2004. Their body mass was measured by fishermen with a hanging scale when the turtles were captured, and they were not fed while being held captive during the nesting season. Eggs were also collected during nightly patrols at the natural Hatsune (300 m length) and Kitahatsune (100 m) Beaches (27°05'N, 142°14'E) on Chichijima Island during the latter half of June 2004. Turtles were identified by placing tags on one front and both rear flippers, or from existing tags. Their straight carapace lengths were measured with calipers. A total of 89 females (42 from breeding pools and 47 from natural beaches) were sampled. Green turtles lay several clutches of eggs (about 100 eggs per clutch) during a nesting season. In 2003 and 2004, they laid 800–900 clutches annually at Ogasawara Islands (Ogasawara Marine Center, unpublished data). Since their mean clutch frequency at the Ogasawara Islands is 4.1 (Suganuma et al. 1996), the annual number of nesting females was estimated to be 200–220. Thus, the 89 sampled females represented 40–45% of the annual nesting females.

One egg was collected per individual female except for one female, which was kept in a breeding pool of the Ogasawara Marine Center in 2003. Five eggs were collected per clutch from five serial clutches laid by this

female in order to examine inter- and intra-clutch variation in stable isotope ratios of egg-yolks. Eggs were frozen at  $-20^{\circ}\text{C}$  until analytical preparation.

### Stable isotope measurements

Egg-yolks of green turtles were used for isotopic analysis. Subsamples of well-mixed yolks were dried at  $60^{\circ}\text{C}$ . Lipids were removed with a chloroform–methanol (2:1) solution, and lipid-removed yolks were ground to a fine powder. Lipids were again removed with a chloroform–methanol solution from the powder. Isotope ratios were determined using a mass spectrometer (Finnigan DELTAplusXP, Thermo Electron, Mass., USA) interfaced with an elemental analyzer (FlashEA1112, Thermo Electron). Approximately 0.8–1.3 mg of powdered sample was used for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  measurements. Ratios,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , were expressed as per mil deviations from the standard as defined by the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000(\text{‰}), \quad (1)$$

where  $R$  is  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ .

Belemnite (PDB) and atmospheric nitrogen were used as the carbon and nitrogen isotope standards, respectively. L-alanine and sodium L(+)-glutamate monohydrate standards with known isotope ratios were used for every six or eight samples in sequence to assess the analytical precision and correct the drift in isotope ratios of the samples. The analytical precision was  $\leq 0.17\text{‰}$  for  $\delta^{13}\text{C}$  and  $\leq 0.07\text{‰}$  for  $\delta^{15}\text{N}$ . The complete data of isotope ratios in the samples are available as an appendix in the Electronic Supplementary Material.

During non-nesting seasons, green turtles that nest on Ogasawara Islands inhabit two areas: coastal waters of Japan and the oceanic Pacific (e.g., Tachikawa and Sasaki 1990; Japan Fisheries Resource Conservation Association 1999). In coastal waters of Japan, they feed mainly on macroalgae (Kurata et al. 1978). Although their diet in the oceanic Pacific is unknown, they are thought to feed mainly on macroplankton, such as jellyfish and salps as in other regions (Bjorndal 1997). In general, stable isotope signatures of nearshore food webs are highly different from those of offshore food webs (Wu et al. 1997; Pinnegar and Polunin 2000; Brodeur et al. 2002; Smit et al. 2005). Thus,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of prey items (macroalgae, macroplankton, and also benthic animals) from or near these two areas (i.e., coastal waters of Japan and the oceanic Pacific) were cited from literature and compared with those of green turtle eggs using a three-source mixing model (Phillips and Gregg 2001) in order to identify feeding habitats for the individual turtles. There are no published values for fractionation factors between isotope ratios of prey and those of sea turtle eggs. In several avian species, fractionation factors between isotope ratios of diet and those of lipid-free yolks were  $-0.1$  to  $0.2\text{‰}$  for  $\delta^{13}\text{C}$  and  $3.1$  to  $3.6\text{‰}$  for  $\delta^{15}\text{N}$  (Hobson 1995). These values were

similar to generally reported values for diet-tissue fractionation in many animal species: ca.  $1\text{‰}$  for  $\delta^{13}\text{C}$  (DeNiro and Epstein 1978) and  $3\text{--}4\text{‰}$  for  $\delta^{15}\text{N}$  (Minagawa and Wada 1984). Thus,  $0\text{‰}$  for  $\delta^{13}\text{C}$  and  $3.4\text{‰}$  for  $\delta^{15}\text{N}$  were applied to the fractionation between isotope ratios of prey and those of sea turtle egg-yolks. In the mixing model, proportions (with 95% confidence intervals) of food sources in a turtle's diet were estimated. A turtle was considered to have mainly used the area with the highest contributing prey, i.e., if the highest contributing prey for a turtle was either macroalgae or benthic animals, the turtle would have foraged mainly in neritic areas, and if the highest contributing prey for a turtle was macroplankton, the turtle would have foraged mainly in oceanic areas. Alternatively, if the difference between proportions of prey was  $<10\%$ , the prey with smaller confidence intervals was adopted to determine the main foraging area for a turtle.

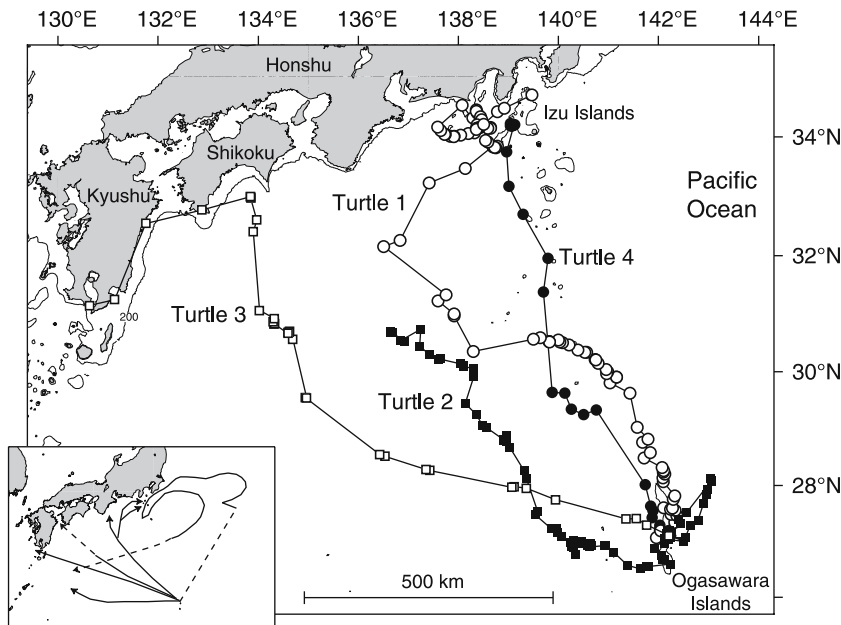
## Results

### Post-nesting movements

There was a highly significant positive correlation between straight carapace length and body mass for green turtles ( $r^2=0.74$ ,  $n=35$ ,  $P<0.0001$ ). Using the regression equation (body mass =  $0.452 \times$  straight carapace length  $-293.818$ ), the estimated body mass for turtle 1 with a carapace length of 905 mm was 115.2 kg and that for turtle 3 with a carapace length of 927 mm was 125.2 kg (Table 1). The carapace length and actually measured body mass for turtle 2 were 1,068 mm and 200.0 kg, and those for turtle 4 were 1,092 mm and 211.0 kg (Table 1).

Four turtles were tracked for 28–42 days and the total distances covered were from 966 to 1,962 km (Table 1). After release, turtle 1 was located around the Ogasawara Islands for 3 days (Fig. 1). She crossed oceanic areas northwards for 14 days, and then wandered around neritic areas of the Izu Islands for 25 days. Turtle 4 showed a similar migratory route (Fig. 1). She was located around the Ogasawara Islands for 1 day after release. She crossed oceanic areas northwards for 15 days, and then stayed at a fixed neritic area of the Izu Islands for 12 days. Turtle 2 stayed around the Ogasawara Islands for 16 days after release (Fig. 1). Since there were long haulout records near Chichijima Island at night on 13 and 20 August 2003 (3 and 8 h, respectively), she might have landed to nest on either day. She then moved northwestwards, and her transmission stopped in an oceanic area 18 days after departing from the Ogasawara Islands. Turtle 3 was located around the Ogasawara Islands for 2 days after release (Fig. 1). She crossed oceanic areas northwestwards for 19 days, and then wandered in neritic areas south of Shikoku and Kyushu for 12 days. Percentages of the days during which turtles 1–4 swam in oceanic areas were 33.3, 52.9, 57.6, and 53.6%, respectively.

**Fig. 1** Post-nesting migratory routes of four green turtles (*Chelonia mydas*) tracked by satellite from the Ogasawara Islands, Japan. Contour line 200 m depth. Inset a schematic map of post-nesting migratory routes of seven green turtles tracked by satellite from the Ogasawara Islands during 1994–1998 (Japan Fisheries Resource Conservation Association 1999). Broken lines indicate the periods during which transmissions were not received



### Post-nesting diving behavior

Dive data during oceanic swimming periods for the four turtles were analyzed (14–19 days; Table 1). Totals of 152, 140, 70, and 28 dives were obtained from turtles 1 to 4, respectively, and within those dives, totals of 142, 122, 51, and 24 dive profiles were obtained (Fig. 2). Most of their maximum dive depths were <80 m and their dive durations were <50 min (Fig. 3). The maximum dive depths for turtles 2 and 3 were greater than those for turtles 1 and 4 (Fig. 3). Differences in dive depth distributions among turtles were clearer in mean depth. Turtles 1 and 4 seldom showed mean dive depths greater than 25 m, whereas turtles 2 and 3 frequently showed mean dive depths greater than 25 m (Fig. 3). The percentages of dives with a mean depth greater than 25 m were 4.2, 10.7, 49.0, and 4.2% for turtles 1–4, respectively.

The time spent diving deeper than 2 m increased at night and decreased in the day for turtles 1, 2, and 3 (Fig. 4), while the pattern was not clear for turtle 4 due to a small sample size. All four turtles showed deeper dives at night than in the day (Fig. 4). At night, most of the mean dive depths of turtle 1 were <20 m, while those of turtles 2 and 3 were >20 m (Fig. 4). The trend in mean nighttime dive depths for turtle 4 was unclear because of the small sample size. The means ( $\pm$ SD) of the mean dive depths at night (the dives starting during 1900–0459 hours Japan Standard Time) for turtles 1 and 4 were  $18.5 \pm 2.7$  ( $n=81$ ) and  $19.6 \pm 1.8$  ( $n=14$ ), respectively, while the means for turtles 2 and 3 were  $21.3 \pm 3.0$  ( $n=69$ ) and  $24.8 \pm 2.7$  ( $n=41$ ), respectively. The body sizes of turtles were not related to their diving behaviors.

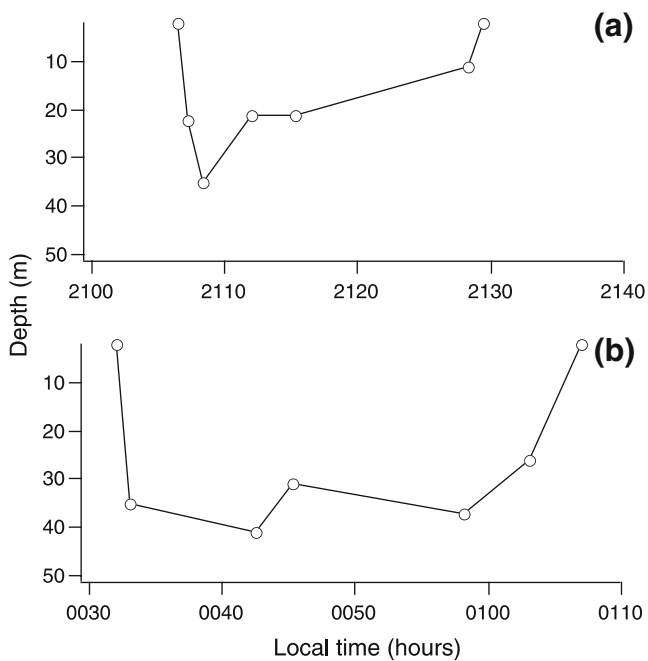
Water temperatures during oceanic swimming periods were obtained only from turtles 1 and 2 (in 14 and

16 dives, respectively). The mean ( $\pm$ SD) water temperature experienced by turtle 1 was  $26.9 \pm 3.8$  C ( $n=168$ ), while that for turtle 2 was  $28.4 \pm 1.2$  C ( $n=192$ ).

### Stable isotope ratios in green turtle egg-yolks

The  $\delta^{13}\text{C}$  in egg-yolks were not significantly different among the five serial clutches (five eggs per clutch) from one turtle (one-way repeated measures ANOVA;  $P=0.16$ ), although the  $\delta^{15}\text{N}$  were significantly different and increased with the clutch order (one-way repeated measures ANOVA;  $P<0.001$ ) (Table 2). The difference in mean  $\delta^{15}\text{N}$  between the first and last clutches was 0.9‰. We have no explanation for the significant enrichment in  $\delta^{15}\text{N}$  among clutches from the green turtle. In a loggerhead turtle, there was no similar trend in  $\delta^{15}\text{N}$  among clutches (Hatase et al. 2002). Significant enrichment in  $\delta^{15}\text{N}$  has been reported in several tissues (such as liver and muscle) of non-fed animals (Hobson et al. 1993; Doucett et al. 1999). However, because vitellogenesis of sea turtles is thought to be completed prior to the mating period when turtles presumably start to fast (Rostal et al. 1998), the observed enrichment in  $\delta^{15}\text{N}$  among clutches from a green turtle would not be attributable to nutritional stress from fasting. A larger sample size is needed to verify whether significant enrichment in  $\delta^{15}\text{N}$  among clutches is a general tendency in sea turtles.

The standard deviations of the isotopic values for the five eggs within each clutch were small ( $\delta^{13}\text{C}$ , 0.0–0.1‰;  $\delta^{15}\text{N}$ , 0.1–0.2‰; Table 2). In addition, the standard deviations of the isotopic values for a total of 25 eggs were also small ( $\delta^{13}\text{C}$ , 0.1‰;  $\delta^{15}\text{N}$ , 0.3‰, Table 2). Thus, a single egg-yolk from any clutch in a nesting season could be used to represent the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of a



**Fig. 2** Examples of dive profiles from two green turtles. Symbols are the start and end points (2 m depths) and the five most significant inflection points. **a** Data from turtle 1 collected on 26 August 2003. The maximum and mean depths were 35 and 16.4 m, respectively. This profile has a gradual ascent phase between 2112 and 2128 hours Japan Standard Time. **b** Data from turtle 2 collected on 3 September 2003. The maximum and mean depths were 41 and 28.4 m, respectively

nesting green turtle. For the turtle used to compare clutches, the mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of its 25 eggs were used in the following analysis.

The straight carapace lengths of 89 female turtles whose eggs were sampled for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ranged from 871 to 1,092 mm (Fig. 5). For statistical analysis, they were divided into 4 size groups: < 900 mm ( $n=6$ ), 900–950 mm ( $n=35$ ), 950–1,000 mm ( $n=39$ ), and  $\geq 1,000$  mm ( $n=9$ ) straight carapace length. The  $\delta^{13}\text{C}$  of the 89 green turtles varied from  $-23.1$  to  $-11.4\text{‰}$ , while their  $\delta^{15}\text{N}$  varied from 6.6 to 14.2‰ (Fig. 6a). The mean ( $\pm$ SD)  $\delta^{13}\text{C}$  values in the four size groups from small to large were  $-16.7 \pm 3.3$ ,  $-17.5 \pm 1.0$ ,  $-17.7 \pm 1.0$ , and  $-18.5 \pm 1.9$ , respectively, whereas the mean  $\delta^{15}\text{N}$  values in these groups were  $10.2 \pm 2.1$ ,  $9.3 \pm 1.7$ ,  $9.4 \pm 1.3$ , and  $9.9 \pm 1.7\text{‰}$ , respectively. There were no significant differences in both isotopic values among groups (Kruskal–Wallis test;  $\delta^{13}\text{C}$ ,  $P=0.18$ ;  $\delta^{15}\text{N}$ ,  $P=0.48$ ; Fig. 6a). No significant correlation was found between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of all females (Spearman's rank correlation = 0.14,  $n=89$ ,  $P=0.19$ ; Fig. 6a).

#### Comparison between isotope ratios of prey items and green turtle eggs

The mean ( $\pm$ SD)  $\delta^{13}\text{C}$  of many macroalgae species in coastal waters of Taiwan was  $-16.8 \pm 4.3\text{‰}$  ( $n=33$ ;

Wang and Yeh 2003), and the mean  $\delta^{13}\text{C}$  of some macroplankton and many benthic animal species around Japan was  $-18.5 \pm 1.6\text{‰}$  ( $n=11$ ) and  $-15.0 \pm 1.3\text{‰}$  ( $n=120$ ), respectively (Hatase et al. 2002). The  $\delta^{13}\text{C}$  of the three prey groups overlapped somewhat with each other (Fig. 6b). The mean ( $\pm$ SD)  $\delta^{15}\text{N}$  of two macroalgae species-groups in coastal waters of Japan was  $3.9 \pm 1.6\text{‰}$  ( $n=155$ ; Umezawa et al. 2002), and the mean  $\delta^{15}\text{N}$  of some macroplankton and many benthic animal species around Japan was  $9.4 \pm 2.2\text{‰}$  ( $n=11$ ) and  $10.9 \pm 1.4\text{‰}$  ( $n=120$ ), respectively (Hatase et al. 2002). The  $\delta^{15}\text{N}$  of the three prey groups were distinct (Fig. 6b). There were significant correlations between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in both macroplankton and benthic animals (macroplankton:  $r=0.91$ ,  $n=11$ ,  $P<0.0001$ ; benthic animals:  $r=-0.23$ ,  $n=120$ ,  $P<0.05$ ), and these correlations were incorporated into a three-source mixing model (Phillips and Gregg 2001).

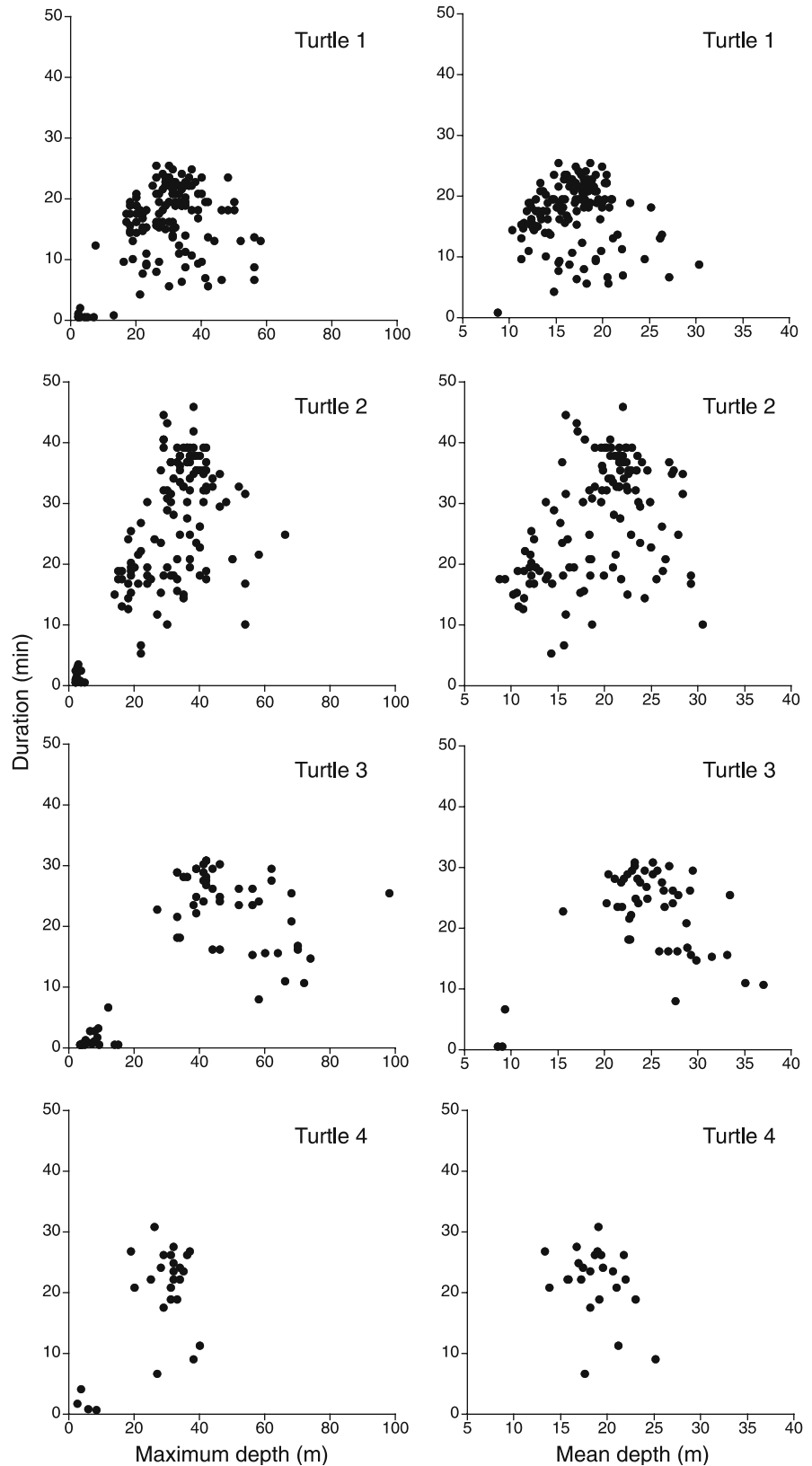
Using the mixing model, it was estimated that, among the 89 adult female green turtles, 56 turtles foraged mainly on macroalgae in neritic areas, 28 on macroplankton in oceanic areas, and 5 on benthic animals in neritic areas (Fig. 6b). Mean ( $\pm$ SE) proportions (with 95% confidence intervals) of the three prey items (macroalgae, macroplankton, and benthic animals) for the 56 turtles (neritic herbivores) were  $73.4 \pm 6.3\%$  (60.9–85.9%),  $30.8 \pm 19.1\%$  (0–69.3%), and  $-4.2 \pm 15.1\%$  (0–26.2%), respectively. Those for the 28 turtles (oceanic planktivores) were  $36.2 \pm 13.2\%$  (9.6–62.9%),  $84.2 \pm 21.9\%$  (40.5–100%), and  $-20.5 \pm 17.9\%$  (0–15.3%), respectively. Those for the five turtles (neritic carnivores) were  $42.7 \pm 15.4\%$  (5.1–80.2%),  $-19.1 \pm 34.1\%$  (0–68.6%), and  $76.4 \pm 27.1\%$  (6.9–100%), respectively. There were no significant differences in straight carapace length among the three groups (Kruskal–Wallis test:  $P=0.58$ ). These data suggested that 69% of the green turtles nesting on the Ogasawara Islands mainly used neritic habitats and 31% mainly used oceanic habitats.

The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for satellite-tracked females were as follows:  $-17.7$  and  $8.3\text{‰}$  for turtle 1,  $-18.4$  and  $11.4\text{‰}$  for turtle 2,  $-17.3$  and  $11.4\text{‰}$  for turtle 3, and  $-18.2$  and  $9.3\text{‰}$  for turtle 4 (Table 1). In the mixing model, turtles 1 and 4 that showed shallow dives in oceanic areas and migrated into neritic areas were inferred to be neritic herbivores, while turtles 2 and 3 that showed deeper dives in oceanic areas were inferred to be oceanic planktivores, although turtle 3 migrated into neritic areas.

## Discussion

This study provided some evidence that adult female green turtles, which have been thought to be obligate herbivores in neritic areas, also used oceanic areas as their feeding habitats. Intrapopulation variation in habitat use is widely reported in many animal species from invertebrates to higher vertebrates. In some

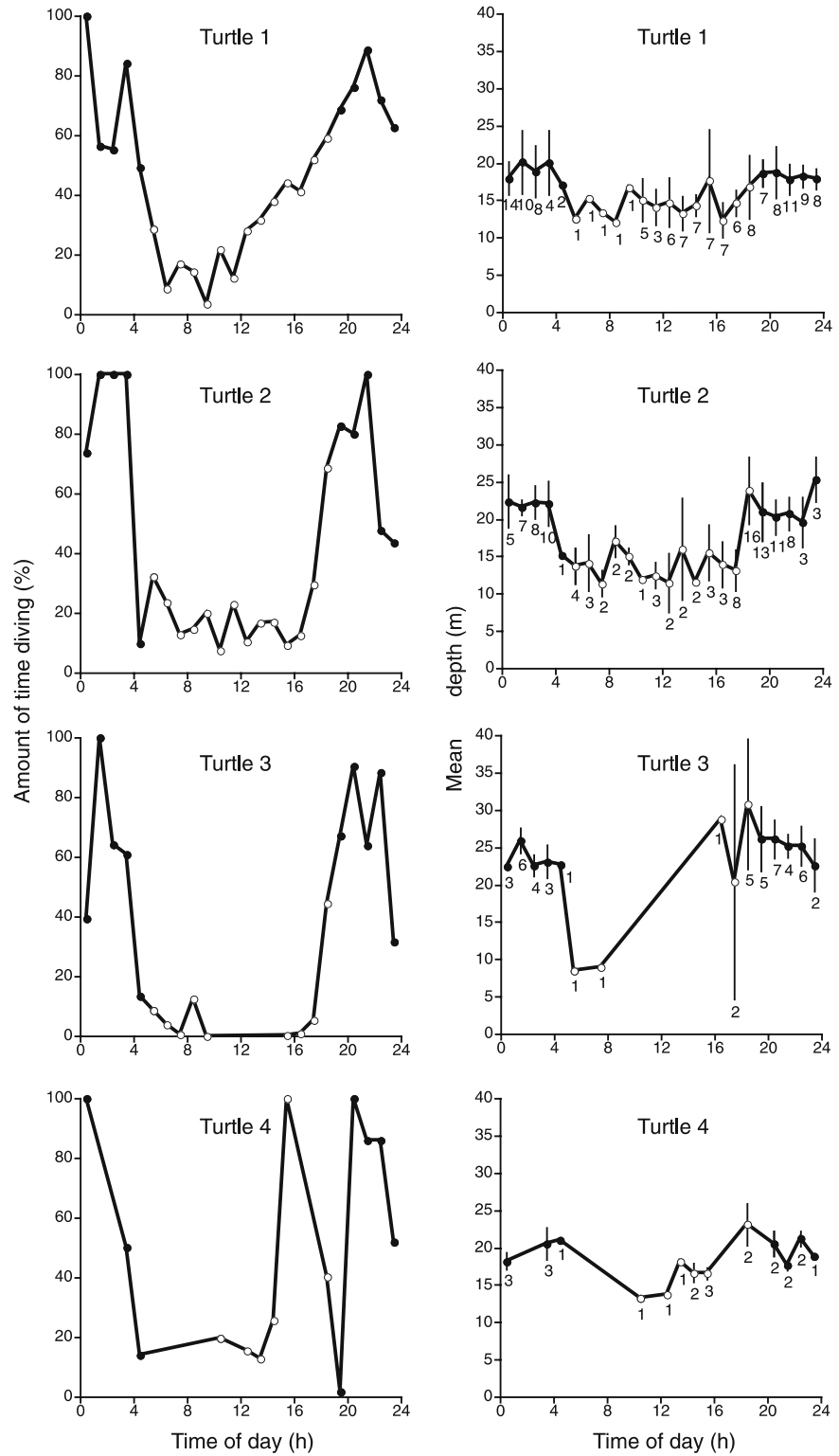
**Fig. 3** Relationships between maximum dive depth and dive duration (*left*) and between mean dive depth and dive duration (*right*) for four green turtles during oceanic swimming periods. Mean dive depth is the mean of 11 depth values in a dive profile whose maximum depth was deeper than 10 m



marine birds and mammals that exhibit long-distance migration, habitats are different by age and sex (e.g., Minami and Ogi 1997; Burton and Koch 1999;

Le Boeuf et al. 2000). In sea turtles, most studies are conducted on adult females that land to nest, and the generalization of their behavior and ecology at sea has

**Fig. 4** *Left* the time spent diving deeper than 2 m in each hour throughout the day (*open circle*) and night (*filled circle*) for four green turtles during oceanic swimming periods. *Right* the mean of mean dive depths in each hour of the day for the turtles. *Error bars* show standard deviations. *Numbers below symbols* are sample sizes. Some hours lack data



long been challenging due to the difficulty in obtaining information about them. However, recent technological advances in telemetry and simultaneous use of several methods have made it possible to elucidate their feeding habitat use.

Post-nesting movements and feeding habits

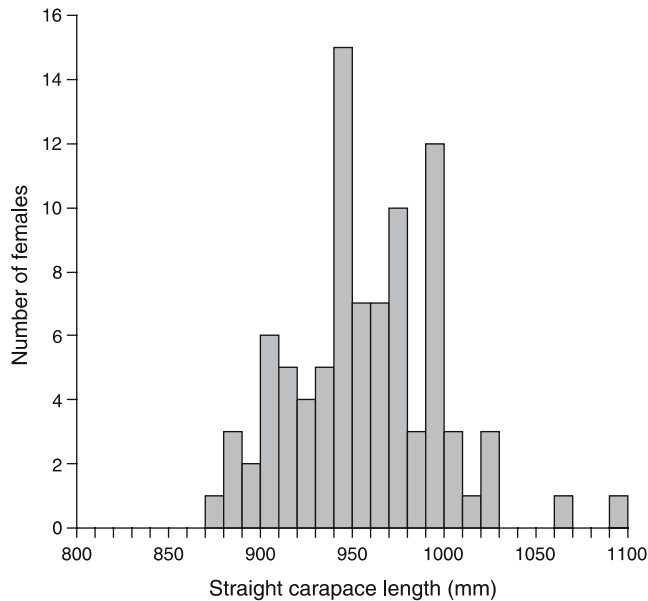
Satellite telemetry recently conducted in Japan has suggested that green turtles may not be obligate herbivores in neritic areas. The Japan Fisheries Resource



**Table 2** The sample sizes ( $n$ ) and intra- and inter-clutch variation in stable isotope ratios of egg-yolks laid by a green turtle

Clutch order	$n$	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
1st	5	$-18.3 \pm 0.1$ ( $-18.5$ to $-18.1$ )	$10.9 \pm 0.2$ ( $10.8$ to $11.1$ )
2nd	5	$-18.4 \pm 0.0$ ( $-18.4$ to $-18.3$ )	$11.2 \pm 0.1$ ( $11.1$ to $11.3$ )
3rd	5	$-18.4 \pm 0.1$ ( $-18.5$ to $-18.3$ )	$11.3 \pm 0.1$ ( $11.2$ to $11.4$ )
4th	5	$-18.4 \pm 0.1$ ( $-18.7$ to $-18.3$ )	$11.5 \pm 0.1$ ( $11.4$ to $11.6$ )
5th	5	$-18.3 \pm 0.0$ ( $-18.4$ to $-18.3$ )	$11.8 \pm 0.1$ ( $11.7$ to $11.9$ )
Total	25	$-18.4 \pm 0.1$ ( $-18.7$ to $-18.1$ )	$11.4 \pm 0.3$ ( $10.8$ to $11.9$ )

Values are means  $\pm$  SD. Ranges are also shown in parentheses



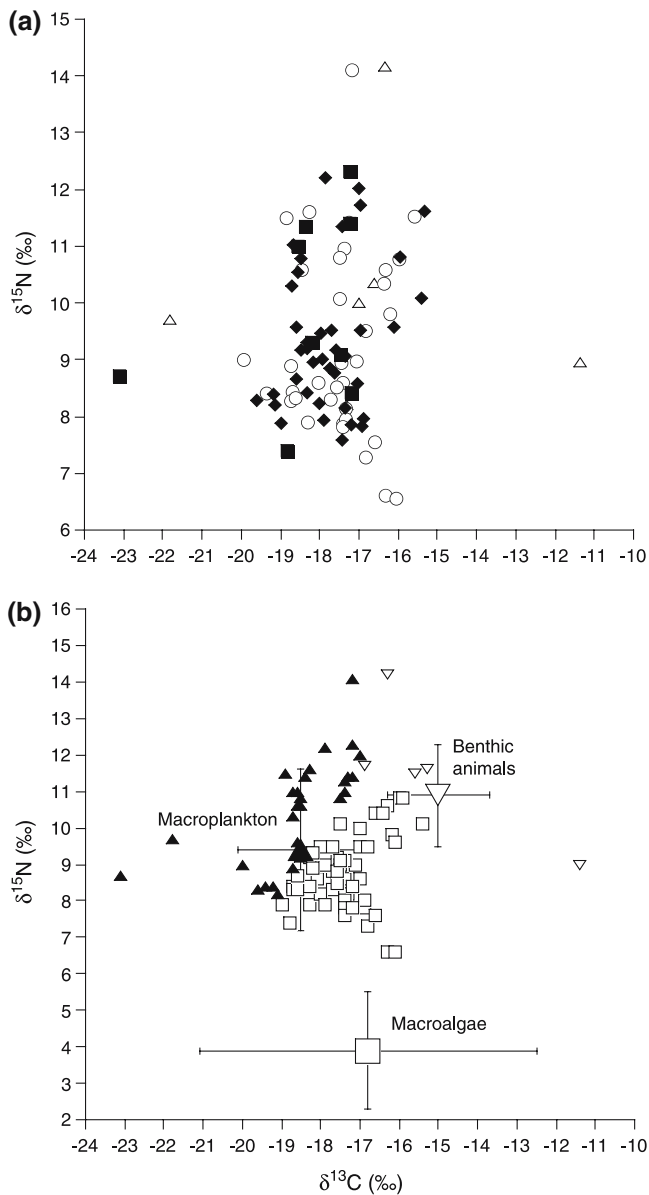
**Fig. 5** Size distribution of 89 adult female green turtles whose eggs were collected at the Ogasawara Islands, Japan

Conservation Association (1999) tracked seven adult female green turtles by satellite from Ogasawara Islands during post-nesting seasons and reported that four turtles moved into neritic areas south of Honshu, Shikoku, and Kyushu, whereas one turtle wandered in oceanic areas, temporarily approaching neritic areas (transmissions from two other turtles stopped in oceanic areas) (Fig. 1). Dive data were not available in these findings, but the oceanic wandering turtle was tracked for 8 months. After release, the turtle stayed around the Ogasawara Islands for 1 month, and then wandered in oceanic areas for 2 months. After that, the turtle was located around the Izu Islands for 2 months, and then she wandered again in oceanic waters for 3 months. In addition, it has been revealed that oceanic areas are alternative feeding habitats for adult female loggerhead turtles, which had been considered to be obligate carnivores in neritic areas (Hatase et al. 2002). The life history pattern for both green and loggerhead turtles has been considered to be the same, with immature turtles developing in oceanic areas during their early life history stages and then later recruiting to neritic areas (Type 2: Bolten 2003). These findings suggest that adult female green turtles also use oceanic areas as their alternative feeding habitats.

Simultaneous use of indirect and direct methods enables the feeding habitats of green turtles to be identified quantitatively. Stable isotope analysis provides information on pre-nesting foraging areas of turtles and satellite telemetry provides information on their post-nesting foraging areas. In this study, there was large variation in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the egg-yolks of green turtles, which can be compared to the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in various potential prey items. Using a three-source mixing model, it was estimated that 69% of green turtles nesting on Ogasawara Islands mainly used neritic habitats and 31% mainly used oceanic habitats. It was particularly unexpected that a few turtles were estimated to have foraged mainly on benthic animals in neritic areas, although a similar possibility of selective feeding on animal matter by green turtles was reported in the Mediterranean (Godley et al. 1998). The post-nesting movements of green turtles tracked by satellite were not completely consistent with these inferences. Although turtles 1 and 4 that were inferred from isotope ratios to be neritic herbivores did indeed migrate into neritic habitats, out of the two turtles inferred to be oceanic planktivores, turtle 3 also migrated into neritic areas. This inconsistency may be attributed to the short tracking durations, i.e., turtle 3 may have come back to oceanic areas after temporarily approaching neritic areas like a turtle in a previous study (Japan Fisheries Resource Conservation Association 1999; Fig. 1). Otherwise, this might imply that there are some turtles that change their main foraging areas between seasons. To improve the confidence of estimates from stable isotope analysis, feeding habits of wild turtles should be examined more thoroughly using conventional gut content analysis, and the diet-tissue fractionation factors for turtles should be determined by captive feeding experiments in future studies. In addition, isotope ratios of long-term satellite-tracked turtles that would remigrate to nest after several years should be measured and compared with their pre-nesting movements and diving behavior.

#### Diving behaviors and feeding habits

The diving behaviors of green turtles during oceanic swimming periods were consistent with the inferences from stable isotope analysis in the present study. The two turtles that were inferred to be neritic herbivores from their isotope ratios showed shallow dives, while other two that were inferred to be oceanic planktivores



**Fig. 6** The  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  maps for green turtle egg-yolks and prey items. **a** Sizes (straight carapace lengths) of individual females that laid the eggs: *open triangle* <900 mm, *open circle* 900–950 mm, *filled diamond* 950–1,000 mm, and *filled square*  $\geq$ 1000 mm. **b** Groups that were divided by main prey in a three-source mixing model: *open square* neritic herbivore, *filled triangle* oceanic planktivore, and *inverted triangle* neritic carnivore. Values for prey items (*large symbols*) are means  $\pm$  SD. The values are cited from literature (macroplankton and benthic animals: Hatase et al. 2002; macroalgae: Umezawa et al. 2002 and Wang and Yeh 2003)

showed deep dives. Adult female green turtles around Ascension Island in the mid-Atlantic had a range of mean dive depths (excluding shallow dives) that were between 13.1 and 20.6 m during their oceanic migration (Hays et al. 2001). Because Ascension Island green turtles can attain neutral buoyancy within this range (maximum 17–20 m; Hays et al. 2000, 2004b), the main function of these dives was considered to be resting (Hays et al. 2001; although there might be other

functions in these dives: Hays et al. 2004c). These dives were conducted mainly at night (Hays et al. 2001), and in the present study, a longer time was spent making nighttime dives. Although the maximum depth of neutral buoyancy might change with body size in sea turtles (Hays et al. 2004b), the body sizes of satellite-tracked green turtles in this study (115–211 kg) were similar to those of green turtles at Ascension Island (130–225 kg; Hays et al. 2000), suggesting that green turtles at Ogasawara Islands could attain neutral buoyancy within the same range. In fact, the depths of resting dives (U-dives) for green turtles ( $n=6$ ; estimated body mass 105.8–161.3 kg) at the Ogasawara Islands during interesting periods almost never exceeded 20 m, and most of those were < 15 m (Sato et al. 1998; Japan Fisheries Resource Conservation Association 1999). Furthermore, although water temperature affects buoyancy (i.e., cooler temperature induces larger buoyancy, possibly leading to greater depth of neutral buoyancy, and vice versa), differences in water temperatures experienced by turtles between Ogasawara Islands and Ascension Island were not very large (Hays et al. 2002), supporting the above suggestion. There was also no observation of a turtle that had experienced lower temperatures showing deeper dives than a turtle that had experienced higher temperatures in the present study. The mean of nighttime mean dive depths (18.5 and 19.6 m) for turtles 1 and 4, which were inferred to be neritic herbivores from their isotope ratios, was similar to that of Ascension Island green turtles. These turtles are thus considered to have mainly rested at night. However, the mean of nighttime mean dive depths (21.3 and 24.8 m) for turtles 2 and 3, which were inferred to be oceanic planktivores, was beyond that of Ascension Island green turtles, implying that the function of nighttime dives for these turtles was not just resting. They may have foraged on zooplankton that exhibit diel vertical migrations, which occur near the surface at night and much deeper than turtles' range of dives during the day (Nishikawa et al. 2001), as do leatherback turtles (*Dermochelys coriacea*) that are specialized predators of gelatinous zooplankton in oceanic areas (Hays et al. 2004a). Similar foraging and diving behaviors in response to the vertical distribution of prey have often been reported in other marine animals such as penguins and seals (e.g., Wilson et al. 1993; Horning and Trillmich 1999). In addition, recent satellite telemetry of post-nesting movements and diving behavior by some adult female green turtles around Costa Rica similarly showed evidence of potential oceanic foraging (Troëng et al. 2005).

There is some indication that variation in prey quality might cause body size variation within populations of adult female sea turtles. Adult female loggerhead turtles used different feeding habitats as a function of body size around Japan (Hatase et al. 2002), with small females mainly using oceanic habitats and large females mainly using neritic habitats. It was suggested that nutritional differences in their main prey (macroplankton vs benthic animals) between the habitats were related to this

phenomenon (Hatase et al. 2002). Satellite telemetry and stable isotope analysis in the present study did not show similar trends in the use of feeding habitats (neritic vs oceanic) by green turtles, implying that nutritional differences in their main prey (macroalgae vs macroplankton) between the habitats might not be large enough to influence the body size of adult female green turtles.

#### Possible mechanisms behind individual variation in feeding habitat use

Why do some adult female green turtles mainly use oceanic habitats and others mainly use neritic habitats? We speculate that variation in ontogenetic habitat shifts by turtles may be related to this phenomenon. All juvenile Atlantic loggerhead turtles are considered to leave oceanic habitats and move to neritic habitats when their growth rates begin to slow (Bolten 2003). Given the relatively large size of juvenile sea turtles, differences in mortality (predation) risk between the habitats may be negligible. If the main function of habitat shifts by juvenile sea turtles is to maximize growth rates, turtles that do not shift habitats should be the turtles that have undergone better growth in previous (i.e., oceanic) habitats. However, Atlantic loggerheads are considered to compensate for early bad growth, lessening the individual variation in growth rates during oceanic stages (Bjorndal et al. 2003). Individuals that have undergone compensatory growth may incur a variety of costs (Metcalf and Monaghan 2001). Although, at present, it is not known whether there are some turtles that do not shift habitats in the Atlantic, turtles that have undergone compensatory growth in the Atlantic might not be able to grow and prepare for reproduction unless they recruit to neritic habitats and shift diets, while those that have not undergone compensatory growth might be able to grow and still reach sexual maturity in oceanic habitats. It is also not known whether Pacific turtles undergo compensatory growth during oceanic stages. In the Pacific, however, food availability early in life might have a disproportionate effect on an individual's later growth trajectory (silver spoon effect: Grafen 1988; Madsen and Shine 2000), as has been speculated in Japanese loggerheads (Hatase et al. 2004). In this case, turtles that have undergone better growth in oceanic habitats continue to use the habitats throughout their lives, while turtles with bad growth in oceanic habitats leave them and move to neritic habitats in order to maximize growth rates and prepare for reproduction (at a size of 300–400 mm straight carapace length in Japanese green turtles: Miyawaki 1994). Habitats where turtles have grown might be imprinted and this might affect habitat selection throughout their lives (Limpus and Limpus 2001).

Similar individual variation in feeding habitat use was reported by satellite telemetry in adult female hawksbill turtles (*Eretmochelys imbricata*) (Japan Fisheries Resource Conservation Association 1999), which

have been considered to possess the same life history pattern as loggerhead and green turtles (Type 2: Bolten 2003). Out of eight female hawksbills released from waters off Okinawajima (26°36'N, 127°48'E), Japan, six females moved into neritic waters, while two females wandered in oceanic waters during almost the whole tracking periods (3 and 9 months, respectively) (Japan Fisheries Resource Conservation Association 1999). It is therefore suggested that ontogenetic habitat shifts by sea turtles (at least Type 2 species) are facultative, and consequently, their life histories are polymorphic. Future research must address how alternative life histories are maintained in a population, i.e. (1) whether alternative life histories have a genetic basis, and (2) whether there are differences in fitness between alternative life histories. Solving these questions will help in understanding how sea turtles have survived and adapted to the marine environment during their evolutionary history of > 110 million years (Hirayama 1998).

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