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Diving behavior of the Hawaiian green turtle (*Chelonia mydas*) during oceanic migrations

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Abstract

The diving behavior of an adult female and two adult male green turtles was recorded during their roundtrip breeding migration from Laniakea, Oahu, to French Frigate Shoals in the Northwestern Hawaiian Islands. These data represent the first detailed records of diving behavior of green turtles as they migrate to their breeding grounds. All three turtles exhibited a biphasic diving behavior. During the daylight hours, diving depth was shallow (1–4 m) and duration was short (1–18 min). It was assumed that the turtles were moving deliberately toward their destination during this time. Between 1900 and 1930 h daily, the turtles began a diving pattern consisting of deep dives with a mean maximum dive depth of 35–55 m and a mean duration of 35 to 44 min. The shallow diurnal diving began between 0600 and 0700 h, after the nocturnal deep-diving pattern ended. The adult female made two dives in excess of 135 m and one male made several dives in excess of 100 m. These are the deepest dives ever recorded for a naturally diving green turtle. It took an average of 36 days for the turtles to make the trip to French Frigate Shoals and an average of 30 days to make the return trip. The deep nocturnal diving was unexpected and this behavior is in need of further investigation.

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1. Introduction

Diving plays a central role in the lives of all air-breathing marine vertebrates, including sea turtles. With the advent of small, reliable data-loggers that can record diving behavior, there has been a profusion of studies examining the dive performance of a range of marine animals including mammals, reptiles and birds. For sea turtles, most dive studies focus on the interesting period between successive clutches, as instruments can be deployed relatively easily and removed when turtles are ashore nesting (Hays et al., 2002). More difficult is obtaining dive information when turtles are away from their nesting beaches, for example, on foraging grounds or while migrating. Some satellite tags allow dive information to be relayed from such environments (e.g., Hochscheid et al., 2005a,b; Myers et al., 2006), but higher resolution, continuous dive data could potentially be supplied from data-loggers that are not constrained by the limited bandwidth of the Argos satellite system (McMahon et al., 2007).

Satellite tracks of Hawaiian green turtles (*Chelonia mydas*) returning from their breeding grounds have shown that they take between 20 and 50 days to make the 800–1100 km trip with an average speed between 1.5 and 2 km/h (Balazs, 1994; Balazs et al., 1994; Balazs and Ellis, 2000). This is a generalized picture of their behavior during the migration necessitated by the long time interval between accurate Argos fixes and the lack of fine resolution diving data. As a consequence, we do not know if the turtles are traveling at the same rate of speed throughout the day, if they are swimming at the surface or at depth, and if they are feeding during the trip. Displacement studies at Ascension Island (Hays et al., 2001) have shown that adult green turtles exhibit diel variations in diving patterns during their breeding migration. There are currently, however, no published accounts of migration tracks or diving behavior for green turtle migrations to their breeding grounds. This is a result of the difficulty of determining when a turtle will migrate to breed without using techniques such as laparoscopy for gonad evaluation involving a relatively large number of animals.

Our study examines the diel diving behavior of three adult green turtles during their roundtrip breeding migrations between

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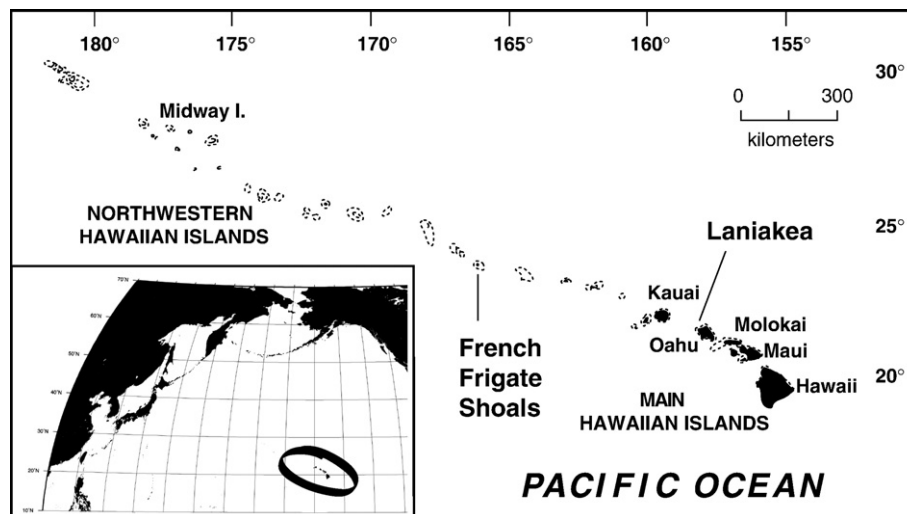


Fig. 1. Hawaiian Archipelago showing locations of French Frigate Shoals and Laniakea.

an algal foraging area and French Frigate Shoals (FFS) (23.79° N, 166.29° W) (Balazs, 1976; Balazs and Chaloupka, 2004, 2006) (Fig. 1). The data were gathered during the 2004 breeding season (April to October 2004). The three turtles in this study were part of an ongoing evaluation of adult green turtles' diel diving behavior at a foraging area. They fortuitously migrated to FFS and back while carrying data-loggers that recorded their dive behavior. The unexpected migration of these three turtles meant that we were unable to attach satellite tags to track their spatial movements.

Laniakea (21.62° N, 158.09° W), on the North Shore of Oahu in the Hawaiian Archipelago, is a foraging ground and basking area for subadult and adult green turtles (see <www.turtles.org/laniakea.htm>). This unique basking behavior (Whittow and Balazs, 1982; Rice et al., 2002) was used to facilitate attachment and recovery of archival Time Depth Recorders (TDR) while the turtles were onshore. This also meant that for the first time, TDRs recording continuous diving behavior could be used on adult turtles naturally migrating from forage areas to nesting areas, showing their normal migratory behavior and not requiring artificial displacement studies.

2. Materials and methods

Two MK9 TDRs and an older model MK7 TDR (Wildlife Computers, Inc., USA) were placed into small polyvinyl chloride carriers mounted on the carapace of two adult male green turtles and one adult female green turtle (Fig. 2). The carriers were safely and securely attached to the carapace using a base of soft setting Silicone elastomer and thin layers of fiberglass cloth and polyester resin as described by Balazs (Balazs et al., 1996). The TDRs were placed into the carriers and the lid was attached using two stainless steel screws. Water flowed freely through openings in the base of the carriers. When the turtles crawled out of the water to bask, the tags were recovered by unscrewing the lid and removing the TDR. Replacement TDRs were put back into the carriers and the lid screwed on to continue data acquisition. The exchange normally took less than 5 min and did not require restraint of the animal.

One of the adult male green turtles (M1) was outfitted with an MK7 on December 16, 2003, and the other adult male green turtle (M2) was instrumented with an MK9 on September 26, 2003. An MK9 was attached to an adult female green turtle (F1) on September 25, 2003. All tags were set to sample time, depth (± 0.5 m), temperature (± 0.5 °C) and electrical resistance (wet/dry condition) at 60-s intervals. Tags from all turtles were retrieved and new tags deployed on several occasions both prior to and after their breeding migration to FFS.

The beginning and end of the migrations were determined based on changes in diving behavior and the occurrence of sustained 'U'-shaped resting dives in shallow water (<20 m) and/or basking behavior. Visual confirmation of arrival was sometimes possible.

Dives that occurred during the migration were classified into four categories (Fig. 3a–d) based on the work of Hays et al. (2000) and Hays et al. (2001). Type 1 dives (Fig. 3a) were shallow dives to less than 5 m. Type 2 dives (greater than 5 m deep and longer than 10 min in length) (Fig. 3b) were characterized by a steep descent to depth and a gradual ascent back to the surface. Type 3 dives (greater than 5 m deep and longer than 10 min in length) (Fig. 3c) were similar to Type 2 dives except that the initial descent was to a



Fig. 2. Turtle M2 (adult male) seen basking at Laniakea, Oahu shortly after its return from FFS. The TDR carrier is located on the third left lateral scute. Note the missing scales (white margin) along the posterior margin of the left front flipper. This is the result of other male turtles biting while M2 was mating.

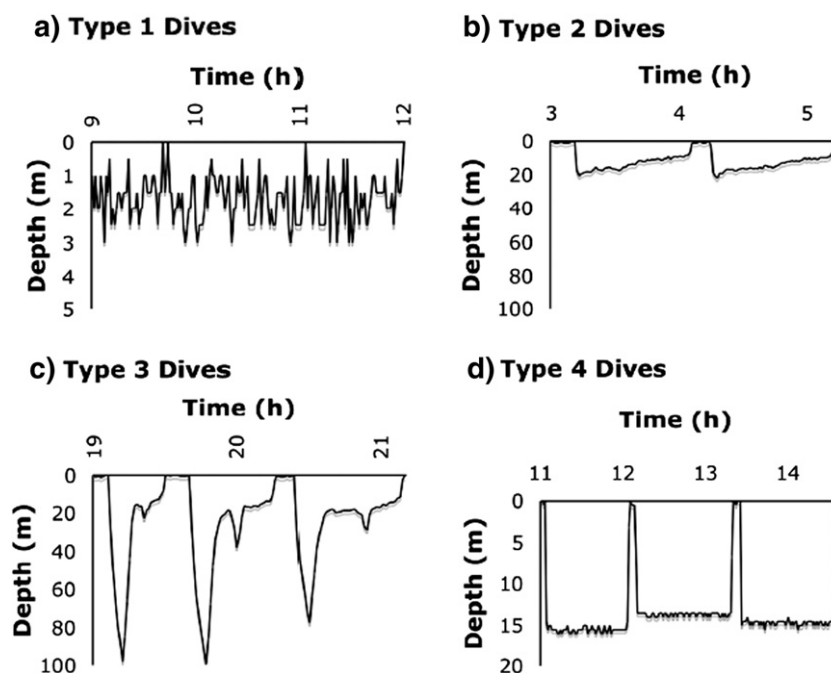


Fig. 3. Four dive types identified in migrating turtle dive profile data: a) Type 1 dive is a shallow surface dive from 1.5 to 4 m; b) Type 2 dive has a steep descent to depth with a slow gradual ascent; c) Type 3 dive shows a steep descent to depth and a rapid ascent followed by a gradual ascent to the surface; d) Type 4 dive is a ‘U’-shaped resting dive where 90% of the bottom time is spent at the maximum dive depth.

much greater depth with a correspondingly rapid ascent prior to a gradual ascent to the surface. Type 3 dives constituted more than 95% of the nocturnal diving conducted by all three turtles during what we believe is the deepwater phase of the migration. Type 4 dives (Figs. 3d and 5) were U-shaped dives to >5 m and had at least 90% of the bottom time spent at the maximum dive depth. Type 4 dives were considered to represent resting dives where the turtle could reach the bottom although other behaviors have been shown to occur during U-shaped dives (Seminoff et al., 2006). All Type 1, 2, and 3 dives were most likely carried out in the pelagic environment (Balazs, 1994; Balazs and Ellis, 2000).

3. Results

For F1 and M2, diving profiles were obtained for the complete trip from Laniakea to FFS and back. In the case of M1, the MK7 tag archived data on the migration from Laniakea to FFS, the entire breeding season at FFS and a portion of the trip back to Laniakea before the tag memory filled and data recording stopped on June 16, 2004. Table 1 shows the estimated travel times for the three turtles.

Table 1
Travel times and dates of travel for three adult green turtles between their forage grounds at Laniakea and their breeding grounds at French Frigate Shoals

Turtle #	Laniakea departure date	FFS arrival date	Travel time to FFS	FFS departure date	Laniakea arrival date	Travel time to Laniakea
M1 (male)	3/08/04	4/23/04	47 days	6/14/04	*	–
F1 (female)	3/13/04	4/19/04	35 days	8/10/04	9/17/04	38 days
M2 (male)	2/28/04	3/24/04	25 days	6/3/04	6/24/04	21 days

*Memory chip filled, stopped recording on 6/16/04.

All three turtles were noted as being absent from their normal forage and basking grounds in early to mid-March and all three were observed at FFS during the 2004 breeding season. F1 was observed on the beach at FFS and her TDR was removed at that time (April 19, 2004). Subsequently, a new tag was placed in the carrier while she was nesting at FFS on June 1, 2004. All three turtles’ tags were removed on the beach at Laniakea after their return trip from FFS when they came out to bask.

3.1. Female F1 dive results

F1 began the journey to FFS at approximately 1200 h on March 13, 2004 and settled into a pattern of primarily nocturnal Type 3 deep diving (Fig. 3c) from ca 1900 h until ca 0630 h the next day for 20 days with an average of 13.9 (SD=4.1) dives per day. Ninety-six percent of the dives were made at night. The average number of dives per day was 16.2 (SD=8.7). The dives during the migration to FFS had a mean maximum depth of 34.5 m (SD=10.9) and a mean duration of 43.2 min (SD=13.3). The maximum depth achieved during this period was 135 m during an 18-min dive that occurred at 1836 h on March 13, 2004. While the mean maximum dive depth was 34.5 m, the mean depth of Type 3 dives was 18.9 m (SD=3.8) (Table 2).

Twenty-two days into the migration to FFS, F1’s diving patterns became irregular, ending in a 6-day period (April 3–8, 2004) of shallow resting dives and a 24 h basking event. After the 6 days, F1 resumed Type 3 diving and, presumably, continued on her journey. She made an average of 27.8 dives/day during the next 10 days prior to being observed basking at FFS on April 19, 2004. The mean dive depth was 20.7 m (SD=6.3) and mean maximum dive depth was 35.6 m (SD=8.5). The mean duration of these dives was 35.0 min (SD=8.1).

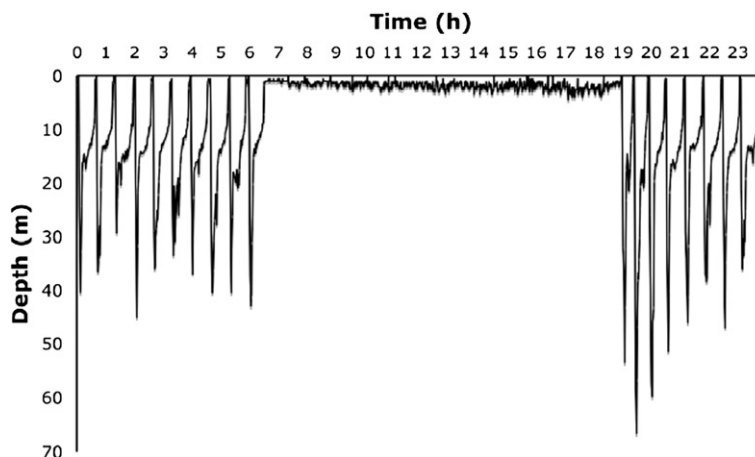


Fig. 4. Dive profiles for F1 on March 16, 2004 showing a typical day of nocturnal Type 3 dives and diurnal Type 1 dives.

During the return trip similar behavior was apparent. F1 settled into a regular diving pattern shortly after leaving FFS on August 10, 2006. She typically began her nocturnal Type 3 deep diving at 1900 h until approximately 0630 h the next day for a 28-day period. The mean maximum dive depth was 55.1 m (SD=11.5) and the average dive duration was 38.2 min (SD=13.4). The mean dive depth of Type 3 dives (Fig. 4c) was 26.6 m (SD=2.3). F1 made an average of 14.4 (SD=3.0) dives per day of which 94% (392 dives) were conducted during the night (Table 2). As F1 neared the end of her journey from FFS to the North Shore of Oahu, the dive patterns became irregular and there were several days of numerous shallow Type 1 dives (Fig. 3a) both day and night. After this foray into repetitive Type 1 dives, F1 resumed the regular nocturnal Type 3 dive pattern for a 3-day period prior to arriving at shallow water where she started making U-shaped resting dives.

3.2. Male M1 dive results

M1 began the journey to FFS at ca 0900 h on March 8, 2004, as it moved over deeper water. M1 immediately settled into a pattern of primarily nocturnal Type 3 deep diving beginning at ca 1900 h and ending at ca 0630 h the next day for 40 days with an average of 15.8 (SD=6.6) dives per day. Eighty-five percent of all Type 3 dives were made during the night ($n=526$) and 15% during the day ($n=91$). The dives during this time had a mean maximum depth of 42.3 m (SD=7.1) and a mean duration of

38.7 min (SD=13.2). The mean depth of the Type 3 dives during the trip was 25.3 m (Table 2). The maximum depth achieved was 103 m during a 17-min dive that occurred at 1838 h on March 3, 2004. M1 made a series of Type 4 U-shaped resting dives (Fig. 3d) that were unusually long (Fig. 5). There were two different sessions of 'U' resting dives; one occurred on the 14th–15th day of the migration and one on the 26th–30th day of the migration. Dives from these days were not counted in the totals above. These dives (Fig. 5) show M1 remaining at a constant depth and probably means that he found the bottom at 35 to 40 m. The longest of these dives was 215 min (3.6 h). During these two periods there were six Type 4 'U' dives that each lasted more than 3 h. These are the longest dives we have ever recorded for Hawaiian green turtles. It is of some note that both F1 and M1 carried out Type 4 resting dive behavior for several days during a similar time in their trip. F1's resting dives were between 15 and 20 m deep and M1's were 40 m deep.

On June 14, 2004, M1 departed FFS. The memory chip on the MK7 tag that M1 was carrying filled and stopped storing data prior to the completion of M1's return migration. M1 was first sighted back on Laniakea Beach on August 24, 2004, and a portion of its left hind flipper had been amputated by a shark. The 4 days of data recorded after M1 left FFS showed behavior very similar to that exhibited during M1's migration to FFS.

3.3. Male M2 dive results

M2 began its journey to FFS at ca 0900 h on February 28, 2004, as it moved into deeper water. M2 immediately settled into a pattern of primarily nocturnal Type 3 deep diving beginning at ca 1900 h lasting until ca 0700 h the next day for 25 days with an average of 13.1 (SD=2.3) dives per day. Eighty-five percent of all dives were made during the night ($n=327$) and 15% during the day ($n=59$). The dives during this time had a mean maximum depth of 39.5 m (SD=10) and a mean duration of 44 min (SD=11.7). The mean depth of the Type 3 dives during the trip was 28.1 m (Table 2). The maximum depth achieved was 86 m during a 22-min dive that occurred at 1945 h on March 15, 2004. M2, based on diving behavior, arrived at FFS on March 24, 2004.

Table 2
Summary of Type 3 diving carried out by M1, F1, and M2 during their migration to and from FFS in 2004

Turtle	Max dive depth (m)	Mean max dive depth (m)	Mean dive depth (m)	Mean dive duration (min)	% night dives
M1 to FFS	103	42.3 m	25.3	38.2	85
M1 from FFS	*	—	—	—	—
F1 to FFS	138	34.5	18.9	35	95
F1 from FFS	137	55.1	26.6	38.2	94
M2 to FFS	86	39.5	28.1	44	85
M2 from FFS	88	35.3	28.3	37.7	63

*Memory chip filled, stopped recording on 6/16/04.

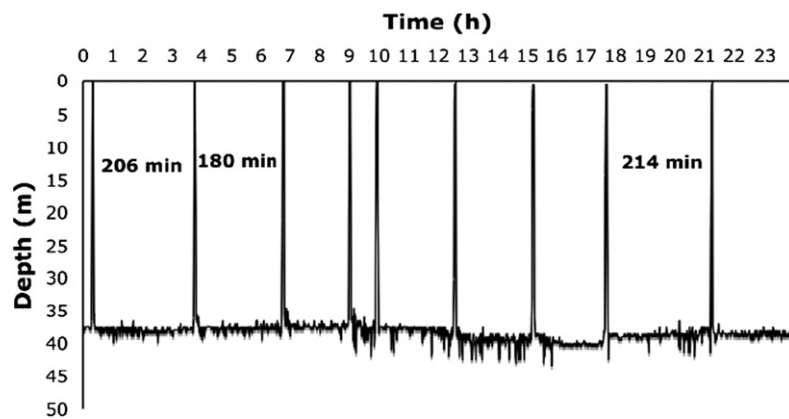


Fig. 5. Dive profiles for M1 on April 5, 2004 showing unusually long Type 4 resting dives.

On June 3, 2004, M2 began the return trip. He arrived at or near Laniakea on June 24, 2004. During the 21-day return trip, M2 made a total of 482 Type 3 dives with a mean duration of 37.7 min (SD=13.8) and a mean maximum depth of 35.3 m (SD=11.5). The mean dive depth for Type 3 dives was 28.3 m (SD=2.9). The average number of dives per day was 23, and 37% of the dives were made during daylight hours and 63% during the night (Table 2).

4. Discussion

The diving data for the three migrating green turtles indicate that diving behavior during migrations to and from the breeding area is varied in nature. What was most striking about their migratory dive behavior was the unexpected frequency and depth of Type 3 dives. Berkson (1967) showed that green turtles can survive dives to depths in excess of 200 m in the laboratory, but it has never been documented that they make such deep dives in the wild. F1 made several dives in excess of 120 m, a record for green turtles. It is clear that they did not swim continuously 1–3 m below the surface as might be expected to maximize efficiency and minimize energy costs (Hertel, 1966). Shallow diving behavior occurred almost exclusively during the daylight hours and, although we do not have location data to indicate that the turtles were moving during this time, we assume that they were swimming toward their destination. Balazs (1980) mentions that sun compass navigation might occur and that is one possible explanation for shallow diving during the daylight hours. It is difficult to say what the shallow diurnal dive duration was because of the relatively long sampling interval of 1 min. It is estimated, however, that the depth of the dives ranged from 1.5 to 4 m and the dive duration was from 3 to 18 min. These dive depths and times fit nicely with the idea that all three turtles were swimming consistently (short dive duration) and at the most efficient depth as indicated by Hertel (1966) during the daylight hours.

The duration of Type 3 nocturnal deep diving exhibited by all three turtles would significantly slow their movement towards their ultimate destination and may explain the observation that turtles move more rapidly during the daytime during breeding migrations (Luschi et al., 1996, 1998). The duration of

Type 3 nocturnal dives was similar to those reported for green turtles resting on the seabed (Hays et al., 2004). The duration of these Type 3 dives implies that the turtles were probably not swimming vigorously to achieve significant horizontal movement.

The unusual number, distribution, depth, and consistency of the Type 3 dives were surprising findings. Nearly continuous nocturnal deep diving occurred for the majority of both trips for all three turtles. As suggested by Hays et al. (2001), it may be that these dives are 'resting' dives. It has been calculated that adult turtles with full lungs will achieve neutral buoyancy at <20 m depth (Minamikawa et al., 2000; Hays et al., 2000). During F1's migration to FFS, some of the Type 3 dives had the appearance of 'resting' dives as described in previous work. Yet, the fact that they were almost all initiated with a steep descent to an average depth well in excess of 20 m means that the turtles were often in a negative buoyancy situation for half of each dive. On F1's return trip, this is more dramatically demonstrated with a mean maximum dive depth of 55.1 m and a mean dive depth of 26.6 m (Table 2). During both migrations, the turtles spent nearly half of Type 3 dive time at depths where they would be negatively buoyant and would have to actively swim to keep from sinking. If they wanted to rest passively in the water column they probably would have remained in the 10–20 m depth range. Instead, they all spent a significant amount of their dive time at depths exceeding 30 m. This means that they are expending energy not only to get to greater depth, but also to make their way back to the surface. It should be noted that temperature measurements taken concurrently with depth measurements show only a minor change in water temperature (<0.5 °C) with increasing depth so water density changes would not counteract the negative buoyancy experienced beyond 20 m in depth.

So why did these three migrating Hawaiian green turtles dive so deeply during the night? It could be that diving to those depths is simply done so that favorable currents are used to assist in the migration. Since this type of behavior occurs in both directions of the migration, it is unlikely that this is the reason. Another possibility is that these deep dives might be exploratory dives as seen in sea snakes (Graham et al., 1975, 1987). It should be noted that in several instances when the

migrating turtles neared an island or shallow area where they could “find” bottom, the frequency of Type 3 dives went up dramatically and the bottom time decreased correspondingly. Were these exploratory dives made in anticipation of reaching shallow water? Hays et al. (2001) suggested that migrating turtles might be diving to greater depth to avoid predators like large pelagic sharks. Recent work (Heithaus et al., 2007) has shown that the risk of predation can play a significant role in diving behavior of green turtles in coastal waters although the role of the threat of predation on diving behavior during migration is not known.

While the diurnal behavior of the turtles largely matched the displacement studies of the Ascension Island turtles (Hays et al., 2001) in that they appeared to travel at shallow depths (<4 m) during the day, the nocturnal diving patterns were much deeper. To counteract the energy expenditure this deep diving entails, it seems possible that these turtles were going deep to find the upward migrating mesopelagic layer to exploit macroplanktonic food, as is thought to be the case for deep-diving leatherback turtles (Luschi et al., 2006) and olive ridley turtles (Polovina et al., 2003). It is commonly believed that green turtles do not feed during their migrations, but this has not been clearly demonstrated. Feeding on mesopelagic organisms could be the ‘counter-balancing’ factor in deep-diving energy expenditure. Hatase et al. (2006) has shown that green turtles in Japan are not always obligate herbivores and some may indeed opt for a pelagic carnivorous existence. Our own personal observations indicate that Hawaiian green turtles are sometimes opportunistic carnivores in their forage grounds and certainly during their juvenile pelagic phase (Parker and Balazs, in press).

In summary, adult green turtles in Hawaii make migrations to FFS, a one-way distance ranging from 800 to 1100 km. The trips normally take between 20 and 50 days. The variation in travel time on this journey can be the result of different paths of migration, variation in environmental factors, and differences in behavior. For example, the resting periods exhibited by M1 and F1 most likely extended their trip to FFS by 4 to 9 days. It appears that they may travel primarily by day and spend much of the night making deep dives beyond what is thought to be the depth of neutral buoyancy for adult green turtles. While it may indeed be true that they are resting within the water column some of the time during the night dives, and they may be exploring the water column or avoiding predators, it seems likely that there is some other function (e.g., exploiting a planktonic food resource) for these unusually deep, sustained diving behaviors. Additional studies will be required to resolve this question, perhaps through different technologies such as miniature archival camera systems carried by turtles during their migration to measure swimming effort (Hays et al., 2007), or sensors that could measure ingestion through jaw activity such as inter-mandibular sensors (Hochscheid et al., 2005a,b) or high resolution Global Positioning System loggers to resolve diel patterns in speed of travel (Schofield et al., 2007).

The occurrence of deep nocturnal diving in migrating Hawaiian green turtles, deeper than any previously reported for this species, indicates that this behavior is an important life history characteristic that deserves further study.

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