Daily movements, habitat use, and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas* L.) within a foraging area in the Hawaiian islands

Richard W. Brill[a,*], George H. Balazs[a], Kim N. Holland[b],
Randolph K. C. Chang[a], Scott Sullivan[a], John C. George[a]

[a] *Southwest Fisheries Science Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396, USA*
[b] *Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1346, Coconut Island, Kaneohe, HI 96744, USA*

Abstract

Depth-sensitive ultrasonic transmitters monitored the horizontal and vertical movements of 12 juvenile (<65 cm carapace length) green turtles (*Chelonia mydas* L.) in Kaneohe Bay, Oahu (Hawaii, USA). This site was chosen because of its accessibility, its importance as a foraging area, and the high incidence ($\approx 50\%$) of fibropapillomatosis, a tumor disease of unknown etiology. Our objectives were to determine the daily movements, habitat use, and submergence intervals of normal and tumor-bearing animals. The presence of tumors had no obvious effects on movement patterns or habitat use. All turtles remained within a small portion of the bay where patch reefs and shallow coral-covered areas are common, and algal growth most abundant. During daylight, two normal and two tumor-bearing animals remained within known feeding areas, all other turtles studied stayed within deep mud bottom channels or within crevices on the sides of reefs. All, except one tumor-bearing turtle, moved up on to shallow patch reefs or shallow coral-covered areas at night. Submergence intervals for both groups were short (over 90% were 33 min or less and none exceeded 66 min) compared to maximum breath-hold times (up to 5 h) measured in the laboratory by earlier workers. Juvenile green turtles in Hawaii, therefore, most likely maintain aerobic metabolism while submerged and surface before oxygen stores are significantly depleted. Tumor-bearing turtles had a higher frequency of longer submergence intervals during the night, indicating they may have been somewhat less active at night. Normal turtles showed no such day-night difference.

Keywords: Behavior; Diving; Fibropapilloma; Fibropapillomatosis; Sea turtle; Tumor

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* Corresponding author.

1. Introduction

Green turtles (*Chelonia mydas* L.) eat mainly benthic algae and sea grasses (e.g. *Halophila hawaiiana* Doty & Stone, in the Hawaiian archipelago) and spend most of their lives in shallow bays and nearshore areas where these plants are present (Balazs, 1980; Bjorndal, 1985; Balazs et al., 1987; Bjorndal et al., 1991; Collazo et al., 1992; Morreale et al., 1992). Some data on behavior of green turtles in the Hawaiian Islands are available (Balazs, 1980; Dizon & Balazs, 1982; Balazs et al., 1987; Forsyth & Balazs, 1989; Balazs, 1994b), but detailed information on daily movements, specific habitat use, and submergence intervals within foraging and resting areas are lacking. Green turtles are currently listed as "threatened" under the U.S. Endangered Species Act and protection of essential habitats is considered critical for marine turtle conservation and species recovery (National Research Council, 1990; Hawaiian Sea Turtle Recovery Team, 1992).

Another possible threat to recovery of green turtle populations may be the rising incidence of cutaneous fibropapillomas. These tumors consist of hyperplastic epidermis and thickened, well vascularized dermis (Jacobson et al., 1989; Harshbarger, 1991) and most commonly involve the soft tissues of the cervical region, axillary and inguinal regions of the fore- and hindlimbs, eye lids, mouth, and conjunctivae (Balazs, 1986; Jacobson et al., 1989; Balazs, 1991). Although first described in Caribbean green turtles in 1938 (Luke, 1938; Smith & Coates, 1938) and in Pacific green turtles (Malaysia) in 1958 (Henderickson, 1958), the incidence of tumors was very low until the early to mid-1980s when it increased dramatically and almost simultaneously in Florida and Hawaii (Balazs, 1991; Ehrhart, 1991). The problem has become particularly acute in Kaneohe Bay (Island of Oahu, Hawaii), the Indian River Lagoon System (Florida), and the Florida Keys where over 50% of the green turtles now exhibit tumors (Balazs, 1991; Balazs, 1993; Ehrhart, 1991). Etiology and causative agent(s) of the disease are unknown (Aguirre, 1991; Balazs & Pooley, 1991; Aguirre et al., 1994). Moreover, it is not known if fibropapillomas effect the ability of green turtles to dive, exploit specific food resources, use shelter areas, avoid predation, etc. Although a majority of stranded green turtles in Florida and Hawaii have tumors (Balazs, 1991; Teas 1991), it is unknown if tumor-bearing turtles become stranded at higher rates then normal turtles.

As do other diving vertebrates, green turtles show pronounced reductions in heart rate and cardiac output during submergence (Berkson, 1966). It is most likely that only the brain, heart, and lungs are continuously perfused (Berkson, 1966; Butler & Jones, 1982; West et al., 1992). The brain and heart receive blood to maintain aerobic metabolism and the lungs because they are an oxygen store (Prange & Jackson, 1976; Lapennas & Lutz, 1982; Lutz & Bentley 1985). In contrast, blood flow to the well vascularized fibropapillomas is probably not controlled. There are no published data on the total mass of fibropapilloma tissue in green turtles, their blood flow rates, or tissue metabolic rate. Jacobson et al. (1989), however, describe individual tumors as large as $11 \times 8.5 \times 6.5$ cm, and Balazs (1980) recorded tumors up to 25 cm in diameter. Human tumors can have mass-specific blood flow rates equal to or exceeding those of brain or heart and mass-specific oxygen consumption rates significantly higher than resting skeletal muscle, and equivalent to those of brain tissue (Vaupel et al., 1990). If

continuously perfused, large fibropapillomas (or a large number of small tumors) could, therefore, place a significant drain on oxygen stores and thereby reduce the ability of turtles to remain submerged, use shelter, graze on benthic plants, etc.

Blood oxygen stores are important to prolong breath hold diving, and diving animals generally have high blood hemoglobin levels. Some tumor-bearing green turtles, however, are anemic (Norton et al., 1990; Jacobson et al., 1991). Anemia could be a direct pathology or could result from fibropapillomatosis reducing the ability to dive and feed. If the latter is the case, there could be a positive feedback loop. In other words, fibropapillomatosis causes anemia, which reduces the ability to dive and feed, which exacerbates the anemia. Such a positive feedback loop could explain the emaciation seen in afflicted turtles where tumors have not yet affected the eyes, mouth, or throat.

The rationale for our research was 2-fold. One, understanding daily movements and specific habitat use of green turtles is needed to define and eventually to justify protection of, or limiting human activity in, important foraging and resting areas. Two, understanding changes in turtle behaviors (especially submergence intervals) caused by fibropapillomas is necessary to predict morbidity, mortality, interactions with actively fishing or derelict gear, and use or avoidance of specific habitats.

2. Methods

The work was conducted in Kaneohe Bay because of its importance as a turtle foraging area, its accessibility, and the high incidence ($\approx 50\%$) of animals bearing fibropapillomas (Balazs, 1993). We employed small depth-sensitive ultrasonic transmitters (VEMCO, Halifax, Nova Scotia, Canada) to track horizontal movements and submergence intervals. Transmitters were cylindrical (1.6 cm in diameter, ≈ 8–13 cm long depending on the battery pack), weighed ≈ 28–40 g in air, ≈ 12–17 g in seawater, and broadcast a 50 kHz signal pulsed at a rate proportional to depth. Transmitters increased the turtles' mass by less than 0.2% and transmitted a signal outside the hearing range of green turtles (30 Hz–1 kHz, Ridgway et al., 1969).

We used the same small-vessel tracking system (16-ft Boston Whaler) employed by Holland et al. (1992) to follow hammerhead shark (*Sphyrna lewini*) pups. The equipment to record, plot, and analyze the telemetered depth data was that used previously for tunas (Brill et al., 1984; Holland et al., 1986, 1990). The position of the tracking vessel was determined by triangulation on known landmarks using a hand-bearing compass. Efforts were made to stay as far away from the turtle as possible so as not to alter behavior. Whenever possible, the outboard motor was shut off and the boat anchored. Moreover, the sound of the tracking boat's motor was unlikely to be more disturbing than the ordinary frequent boat traffic in Kaneohe Bay.

Turtles were hand-captured by swimmers moving over the patch reefs or sandbars that are known resting and foraging areas. Animals were weighed, carapace lengths measured, and tumor severity scored (0 = no visible tumors, 1 = no tumors greater than 1 cm in diameter, 2 = tumors greater than 1 cm but less than 4 cm, 3 = tumors greater than 4 cm but less than 10 cm, 4 = tumors greater than 10 cm). Transmitters were attached dorsally on the carapace above the left or right rear flipper with two nylon

straps (tie-wraps) inserted through 3 mm holes drilled in the marginal scutes. Transmitters did not interfere with rear flipper movement. Turtles were released within 2 h near the point of capture and followed either for 48 h (4 tumor-bearing and 4 normal turtles), or for an initial 36 h, and then during daylight hours every other day for approximately the next 13 days (2 tumor-bearing and 2 normal turtles). Transmitters were retrieved from recaptured turtles at the completion of a track. Handling required to capture, weigh, measure, and attach the transmitters produced transient behavioral effects. During 3 h following release, submergence intervals were usually short (mean 5.6 min) and irregular (SD 5.1 min) as animals dispersed. Data from the first 3 h of a track have, therefore, been excluded from submergence interval and time at depth summaries.

Submergence intervals and times at specific depths were measured from depth records. Data were partitioned into four groups: (1) normal animals (tumor score 0–1) during daylight, (2) normal animals during nighttime, (3) tumor-bearing animals (tumor score 2–4) during daylight, and (4) tumor-bearing animals during nighttime. Submergence intervals were grouped into three minute bins. Times at specific depths were based on 1 m depth intervals. Frequency distributions of submergence intervals and times at specific depths were calculated and subsequently expressed as percentages based on the total number of submergence intervals observed for each turtle during daylight or nighttime, and on the total observation time for each turtle during daylight or nighttime, respectively. Frequency distributions were compared using the nonparametric Kolmogorov-Smirnov two-sample test; p less than 0.05 was considered to show statistically significant differences.

Although depth-sensitive transmitters provide detailed information on daily movements, habitat use, and submergence intervals, they have shortcomings. Because direction, but not range, from the tracking vessel is measured, small-scale movements around the tracking vessel could not be determined and fine scale activity patterns could not be quantified. Submergence intervals do most likely reflect activity patterns because normal swimming increases resting oxygen consumption rates of sea turtles by 2–4 times (Jackson & Prange, 1979; Lutz et al., 1989). Feeding, however, must be surmised from submergence interval data. In addition, the precision of the transmitters is insufficient to ascertain when turtles broke surface, nor are any data provided on the number or frequency of breaths. Because we could not follow turtles into very shallow (< 1 m) areas (especially at night), submergence intervals were not sampled continuously nor equally under all circumstances.

3. Results

Tracking was conducted between June 1991 and June 1992. Carapace length-mass relationship for the 12 turtles used in this study are given in Fig. 1 ("T" designates tumor-bearing animals, "N" normal animals). Since all turtles except for T5 fell within the 95% confidence interval of the carapace length-mass regression, none except T5 was emaciated. T5 was specifically chosen to determine the behavior patterns of a severely emaciated individual.

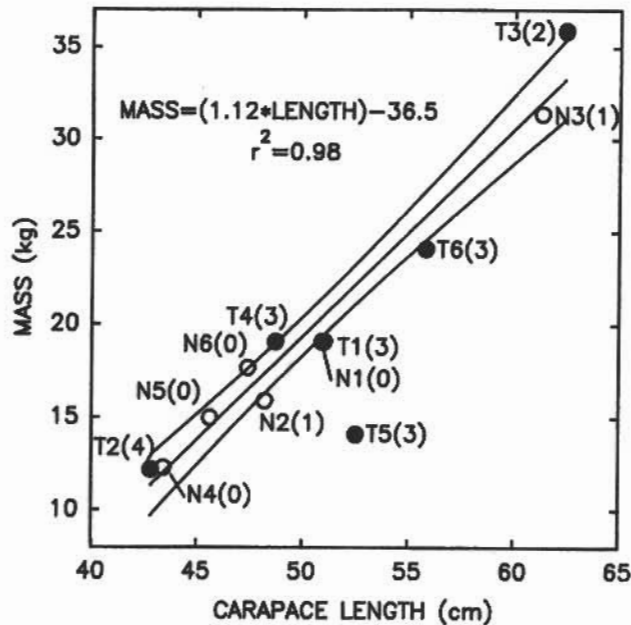Study location is shown in Fig. 2. N4 and T5 were captured in the shallows imme-

Fig. 1. Linear regression ($\pm 95\%$ confidence limits) of body mass on carapace length for eleven of the 12 green turtles used in this study. (T5 has been excluded from the regression as an outlier.) Tumor scores are shown in parentheses. "T" indicates tumor-bearing turtles (tumor score 2–4), "N" normal animals (tumor score 0–1).

diately southwest of the sandbar. All other turtles were captured in the vicinity of Mark Reef or the cleaner station. The latter is a site where turtles regularly present themselves to be cleaned by the wrasse *Thalassoma duperrey* (Losey et al., 1994).

3.1. Daily movements and habitat use

A relatively small fraction of Kaneohe Bay was used by the tracked turtles (Figs. 2 and 3). No turtle moved farther than ≈ 3 km from its point of release, ventured into the area south and west of Coconut Island, further north than the northern end of the sandbar, nor left the bay while being followed.

Turtles could be grouped into one of three categories based on horizontal movements:

(1) those moving only immediately after release then remaining stationary,
(2) those making extensive movements which included repetitively traversing channels separating shoreline reef flats, patch reefs, and sandbar, and
(3) those moving around the shallows where they were captured and released, areas where there is significant coral cover and heavy algal growth (500–1000 g dry weight per square meter, Smith et al., 1973).

Category 1 included normal turtles N3 and N4 and tumor-bearing turtle T1 (Fig. 3A). While remaining in small areas, all three animals were closely associated the vertical edges of reefs.
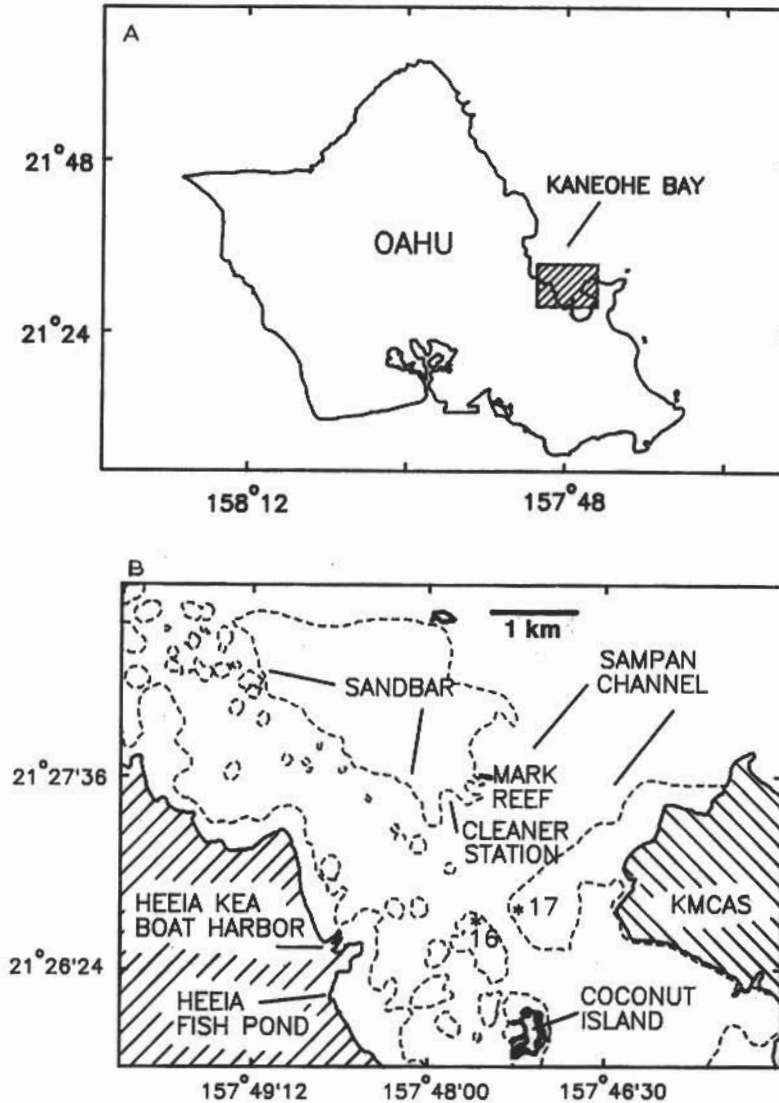
Fig. 2. Island of Oahu (Hawaii) (A) and Kaneohe Bay (B) showing reefs (1 m contour), shoreline, commonly used place names, and two channel markers. In (B) and all subsequent maps, dry land areas are indicated by cross hatching.

Category 2 included T4 and T6 (Fig. 3b) and tumor-bearing/normal turtles N2 and N5 (Fig. 3c). T4 traversed the channel between its release site and the patch reefs in front of Heeia Kea Boat Harbor. The latter appeared to be its preferred daytime area and the former its shallow preferred nighttime area. T6, equipped with a 14-day transmitter, initially moved southeast to the area immediately south of the active runway of KMCAS. However, for days 3–9 (numbers refer to days tracked, not consecutive days) the turtle moved in a repetitive pattern similar to that of T4. In the mornings, it would move southwest across the channel between the cleaner station to the shoreline reef flat immediately north of Heeia Kea Boat Harbor. It would remain in the deep mud bottom boat anchorage area until late afternoon ($\approx$ 1500–1600) when it would move back
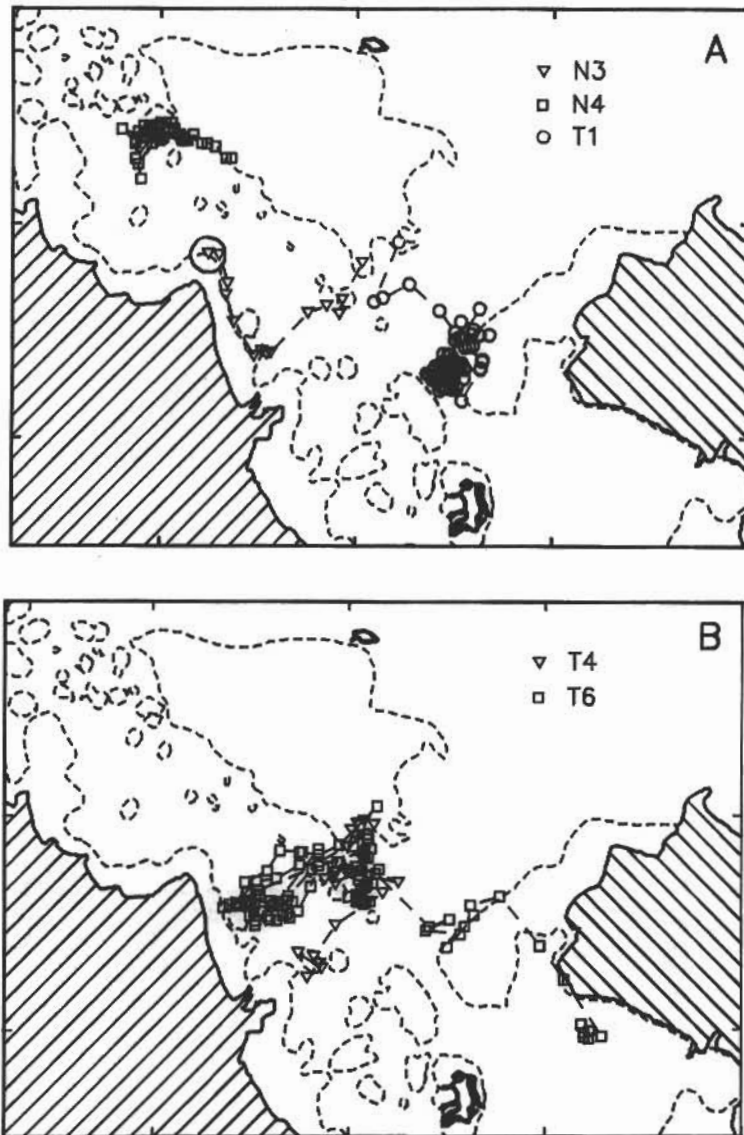
Fig. 3a, b.

across the channel. N2, except for a brief excursion to the area near the active runway of KMCAS, spent daylight hours associated with edges of the patch reef near channel marker no. 16 and the nighttime hours in the shallow areas of this reef. N5, equipped with a 14-day transmitter, made a brief excursion (on the second day after release) to the patch reef where N2 had spent significant amounts of time. It then moved to the area of large patch reefs immediately northwest of Coconut Island for days 3–5. The turtle remained relatively stationary during any one day and strongly associated with the edges of patch reefs or shoreline reef flat. At the completion of the track (Day 6), the turtle had moved back to the patch reels south of the sandbar and eventually to the shallow area seaward of the sandbar, an area very close to where it was originally captured.
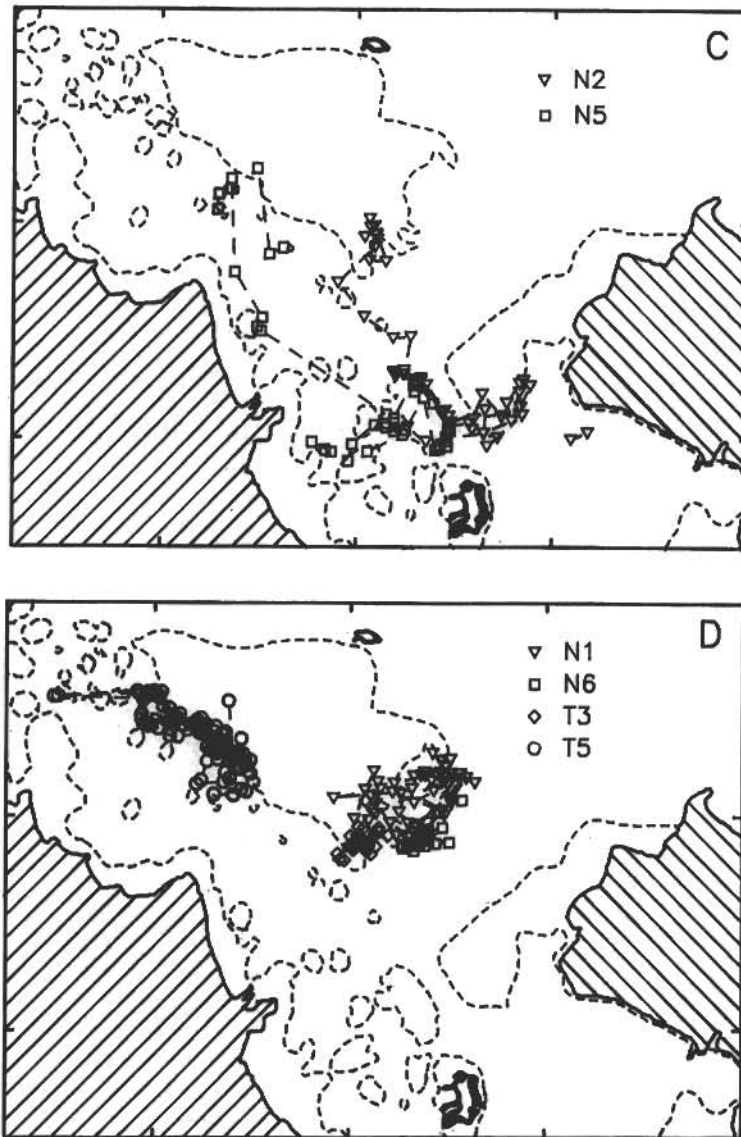
Fig. 3c, d.

Category 3 includes normal turtles N1, N6, and tumor-bearing turtles T3 and T5 (Fig. 3D). The first three remained in shallow areas near Mark Reef and the cleaner station, areas where they were originally captured and released. T5 (equipped with a 14-day transmitter) would remain associated with the patch reefs off the southwestern corner of the sandbar, the same area where N4 had spent the majority of its time. At mid-morning or early afternoon, however, it would repeatedly move to the sandbar and remain there until the track was abandoned at dusk. After recapture over the sandbar, esophageal flushing (technique described in Balazs 1994a) yielded sea grass (*Halophila hawaiiana*), indicating that the turtle had been feeding.

Only one tumor-bearing turtle (T2) exhibited movements that differed from all others. After release, T2 moved slowly and continuously almost due south (Fig. 3E). The
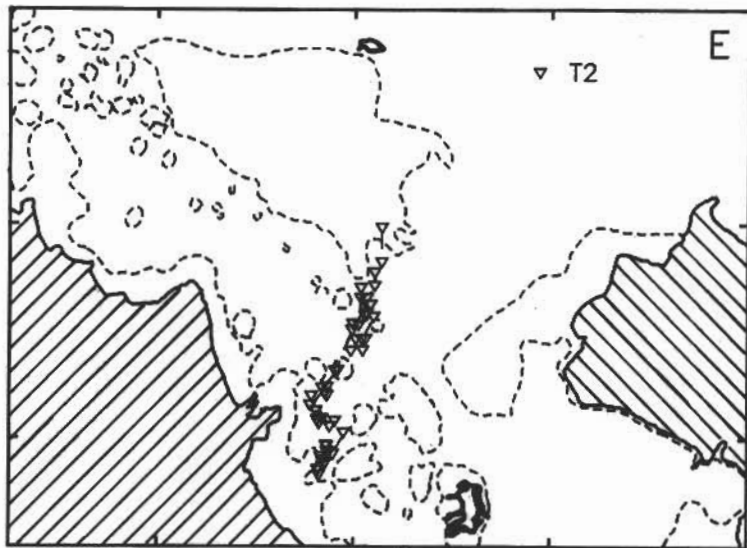
Fig. 3. Movements of the 12 turtles tracked in this study. Symbols show recorded positions of the tracking boat and are not connected when turtles were lost and relocated. (A) Turtles that moved after release then remained stationary (N1, N4, T1); (B) and (C) turtles that repeatedly crossed channels between patch reefs, shoreline reef flats and the sandbar (T4, T6, N2, N5); (D) turtles that showed frequent feeding activity N1, N6, T3, T5); and (E) the one tumor-bearing turtle that moved slowly and continuously, and had regular long submergence intervals (T2).

animal remained in the deep mud bottom channel between the patch reefs, except during the second night when its southerly course carried it over a small patch reef.

3.2. Submergence intervals

Submergence intervals were strongly related to activity in both tumor-bearing and normal turtles. Intervals were long and regular when the animals were stationary (i.e. when turtles were either in the mud bottom channels or associated with the sides of reefs) and shorter when they were swimming. This is clearly exemplified by N3. Submergence intervals were short immediately after release when the turtle was moving (93% of observed submergence intervals were 15 min or less), but lengthened once it stopped (47% of observed submergence intervals were 15 min or longer. T6 (days 3–6) also had long regular submergence intervals when stationary (mean $\pm$ 95% CI, 27.3 $\pm$ 6.2 min), but clearly shorter submergence intervals (14.0 $\pm$ 3.0 min) when repeatedly moving across the channel between the deep mud bottom area north of Heeia Kea Boat Harbor and the reef to the northeast. T4 showed similar changes in submergence intervals. While remaining stationary, mean ($\pm$ 95% CI) submergence intervals were 22.6 $\pm$ 3.1 min, but 8.9 $\pm$ 4.7 min while moving north across the channel from its daytime to its nighttime area.

The submergence intervals of the four turtles (N1, N6, T3, T5) we believed to be regularly feeding were relatively short. Mean ($\pm$ 95% CI) submergence intervals were 9.4 $\pm$ 2.6, 8.4 $\pm$ 5.9, and 12.0 $\pm$ 2.5 min for turtles N1, N6, and T3, respectively. For T5,
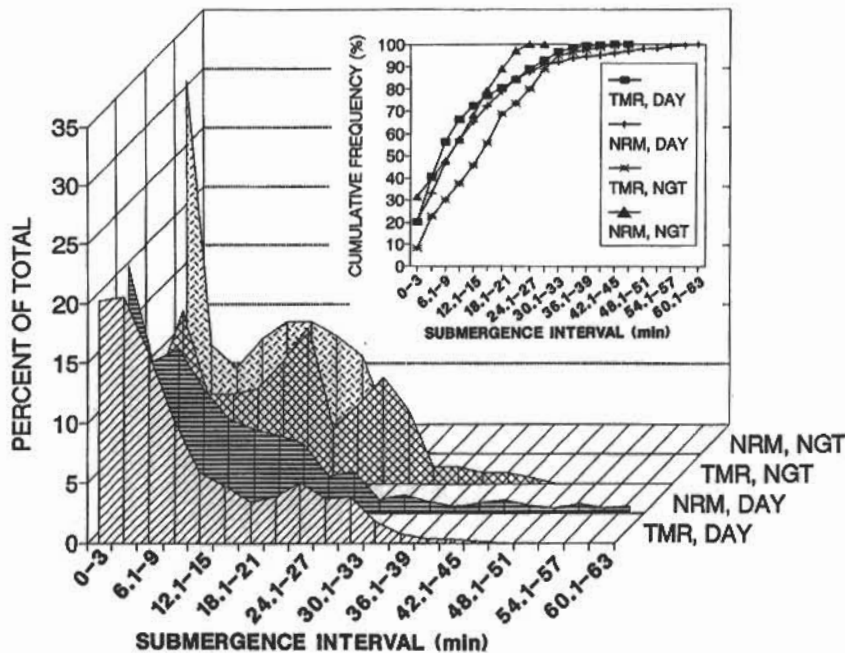
Fig. 4. Frequency distribution of submergence intervals, expressed as a percent of the total number of observed daylight and nighttime submergence intervals, for tumor-bearing turtles during daylight (TMR, DAY), normal turtles during daylight (NRM, DAY), tumor-bearing turtles during nighttime (TMR, NGT), normal turtles during nighttime (NRM, NGT). Insert shows cumulative distribution of submergence intervals.

submergence intervals were long (22.6 ± 5.8 min) when the turtle was inactive and associated with the patch reefs, but shorter (7.2 ± 0.6 min) and irregular when moving around the patch reefs and the shallower areas of the sandbar (where it was presumably feeding). The submergence intervals of T2, although continuously moving slowly south, closely resembled those of T1 and N3, animals which remained stationary for the majority of the time they were tracked. Mean ($\pm 95\%$ CI) submergence interval for T2 was 22.4 ± 4.2 min.

Frequency distributions of submergence intervals are shown in Fig. 4. For all possible pair-wise comparisons, statistically significant differences were found only between daylight versus nighttime submergence interval distributions of tumor-bearing turtles, and between the nighttime submergence interval distributions of normal and tumor-bearing animals.

3.3. Time at depth

Time at depth data is shown in Fig. 5. Both tumor-bearing and normal turtles occupied shallower depths during the night. There are no statistically significant differences between daylight depth distributions of tumor-bearing and normal turtles, nor between their nighttime depth distributions.
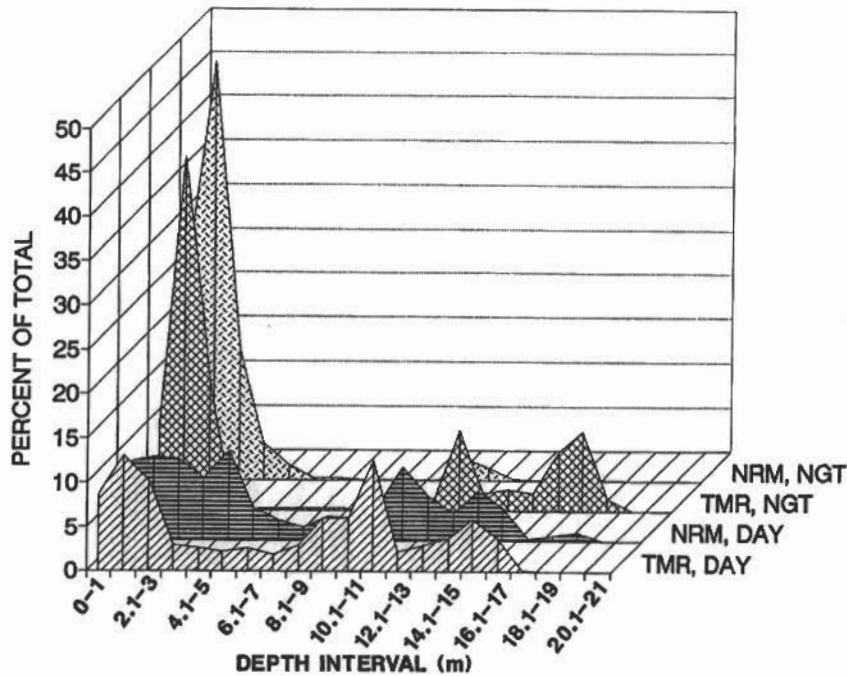
Fig. 5. Time at specific depths, expressed as a percent of the total time observed, for tumor-bearing turtles during daylight (TMR, DAY), normal turtles during daylight (NRM, DAY), tumor-bearing turtles during nighttime (TMR, NGT), and normal turtles during nighttime (NRM, NGT).

4. Discussion

4.1. Daily movements and habitat use

The reasons turtles apparently restrict themselves to a relatively small portion of Kaneohe are unknown. Movements patterns may be influenced by the proximity of reefs and forage (i.e. the availability of food and benthic shelter). Shallow patch reefs and heavy algal growth are nearly absent from the extreme northern and southern ends of the bay (Smith et al., 1973). All turtles, except T1 and T2, used the shallow patch reefs, coral-covered areas, or sandbar as resting and forging areas, although even T1 spent the majority of its time immediately adjacent to a shallow reef flat. The movement distances of the turtles in Kaneohe Bay were similar to the average ($\pm$ SD) movement distances (2.62 $\pm$ 0.96 km) of green turtles recorded by Mendonca (1983) in a Florida Lagoon during the summer months, when water temperatures approximated those of Kaneohe Bay (i.e. 26–28 °C).

There were no obvious differences in movement patterns between tumor-bearing and normal turtles. All remained stationary from a few up to 46 h. (Only T2 was an exception, it moved continuously and slowly south for $\approx$ 48 h) Both tumor-bearing turtles (T1, T3) and normal turtles (N1, N4, N6) remained within small areas, and both tumor-bearing turtles (T2, T4, T5, T6) and normal turtles (N2, N5) moved across channels between shallow patch reefs, shore line reef flat, and the sandbar. Moreover, T5 and T6 clearly exhibited daily shuttling behavior between daylight and nighttime

the day is unknown, but may be a thermoregulatory behavior to help turtles avoid overheating in the shallow water (Mrosovsky, 1980; Whittow & Balazs, 1982). Bjorndal (1980) and Mendonca (1983) observed similar shuttling behaviors of green turtles (between shallow and deep water) in Florida and the Caribbean. The reason(s) that T2 showed no apparently directed movements remains unexplained.

Our data provide no support for our hypothesis that tumors significantly deplete oxygen stores and reduce submergence intervals. The statistically significant difference between nighttime submergence intervals of tumor-bearing and normal turtles is due to the former having a higher frequency of longer submergence intervals. The statistically significant difference between daylight and nighttime submergence intervals of tumor-bearing turtles further implies that tumors have no effect on diving behaviors.

Whether tumor-bearing or normal, turtles in our study rarely submerged long enough (> 60 min, Lutcavage & Lutz, 1991) to deplete oxygen stores; 90% of all observed submergence intervals were less than 33 min (Fig. 5, inset). Similar voluntary submergence intervals have been observed for green and loggerhead turtles (*Caretta caretta* L.) in captivity (Berkson, 1966; Lutcavage & Lutz, 1991). Although capable (in the laboratory) of surviving complete depletion of oxygen stores (up to 5 h of forced submergence in large turtles, Berkson, 1966), juvenile green turtles in Hawaii do not routinely exploit this ability. Prolonged anoxic submergence may occur, however, in temperate habitats when turtles are forced to overwinter (Felger et al., 1976; Morreale et al., 1992).

Submergence intervals were clearly longer when turtles were quiescent and short (generally less than 10 min) when turtles were confirmed to be swimming. Wood et al. (1984) found rapid decreases of blood oxygen saturation (from 90% to 45%) and plasma pH (0.4 units), and increases in blood lactate (from 0.6 to 10.4 mM) within 20 min in a swimming submerged green turtle. Stabenau et al. (1991) found similar changes within 8 min in Kemp's Ridley turtles (*Lepidochelys kempi* Garman) forced to swim in a submerged shrimp trawl. Recovery times were not measured in either study, but could have been up to 9 h (Lutz & Dunbar-Cooper, 1987). We assume similar changes occur during submerged swimming in the green turtles observed in our study. We infer, therefore, that green turtles in Kaneohe Bay maintain aerobic metabolism while submerged and come to the surface before large changes in blood acid-base status or lactate levels occur (as do loggerhead turtles, *Caretta caretta*, Lutcavage & Lutz, 1991). This may explain the lack of differences in dive times between normal and tumor-bearing turtles. Laboratory measurement of rates of oxygen depletion and recovery from prolonged submergence and exercise in tumor-bearing and normal turtles may be warranted in order to better understand the effects of fibropapillomatosis in green turtles.

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