Behavior of juvenile green turtles in a coastal neritic habitat: Validating time–depth–temperature records using visual observations

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ABSTRACT

There are inherent limitations to inferring green turtle (Chelonia mydas L.) diving behavior from time–depth recorders (TDRs). Validating TDR data with independent observations of turtle behaviors is imperative to derive behavioral inferences from these archival data. Logistic regressions of video observational data and corresponding TDR data from six juvenile green turtles at the Kawai'nui Marsh Estuary (KME) in Kailua Bay, O'ahu, Hawai'i, were used to determine the extent to which TDR records capture six specific behaviors recorded using a submersible video camera. While foraging, food searching, hovering, and breathing could be explained using a combination of TDR-derived metrics, the records could not describe swimming and resting. The habitat associations of turtle activity patterns (activities) were also evaluated, with some behaviors being more commonly encountered in specific habitat types, including resting and breathing. Comparison of video-recorded in situ observations of juvenile green turtles to concurrent TDR records indicated that TDR data alone can accurately describe certain turtle behaviors at KME, but are insufficient to describe a turtle's full range of behavior. Therefore, we contend that direct behavioral observations augment TDR deployments by ensuring the full behavioral repertoire of juvenile green turtles is captured. The integration of these disparate datasets can enhance the understanding of juvenile green turtle behaviors, especially within shallow heterogeneous habitats like the Kawai'nui Marsh Estuary.

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1. Introduction

Time–depth-recorders (TDRs) provide insights into the diving behavior of air-breathing marine vertebrates, including green turtles (Chelonia mydas; e.g., Hays et al., 2000a, 2000b; Glen et al., 2001; Rice and Balazs, 2008; Salmon et al., 2004; Seminoff et al., 2001). TDRs are beneficial in providing data on depth utilization, surfacing behavior, and dive durations of turtles in confined areas (Hays et al., 2007; Rice and Balazs, 2008; Witt et al., 2010) by providing advances in our understanding of diving behavior (e.g., Blumenthal et al., 2010; Brill et al., 1995; Hays et al., 2000a; Hazel et al., 2009). However, there are limitations to inferring behavior from TDR data. Short dives with continuous

minor depth fluctuations during the bottom phase are normally considered foraging events (e.g., Brill et al., 1995; Makowski et al., 2006) while longer dives to a fixed depth are considered resting events (e.g., Hays et al., 2000a; Southwood et al., 2003a). Turtles may also perform multiple activities on a single dive (Hochscheid et al., 1999), making it difficult to assign behaviors to dives without independent visual confirmation (Heithaus et al., 2001; Houghton et al., 2000). Dives with extended periods spent along the seafloor can involve resting (Hochscheid et al., 1999; Seminoff et al., 2006) or horizontal movement, suggesting the turtles are searching for food (Hazel et al., 2009). Other behaviors, such as rubbing against rocks and sponges to self-clean, yield dive profiles similar to foraging turtles (Heithaus et al., 2002). Along with possible confusion from attempting to infer behaviors, setting the TDR sampling rate with a low sampling frequency also can lead to false results, leading to unrealistic dive statistics.

Turtle behavior can also change over time, making it problematic to detect the onset of new behaviors from TDR data alone. Chaloupka et al. (2008) observed changes in the behavioral patterns of green turtles as populations recover in Hawaii. For example, in some locations turtles switched from nocturnal to diurnal foraging, basking behavior expanded to new locations and increased in frequency at known basking sites, and turtles gathered at previously unknown underwater cleaning stations

(Balazs, 1996). Behavioral changes and the onset of new behaviors are nearly impossible to discern from TDR data alone.

In some cases, TDRs are supplemented with other body movement sensors that facilitate a more informed interpretation of the dive profiles (e.g., Fossette et al., 2012; Gallon et al., 2012; Gleiss et al., 2011; Houghton et al., 2008; Yasuda and Arai, 2009). In particular, accelerometers provide information on energy expenditure alongside diving data, allowing researchers to infer specific behaviors (Gleiss et al., 2011), often more precisely than with TDRs. However, specific behaviors are inferred, not confirmed, from the analysis of data from these archival tags.

Inferring behavior from TDR and accelerometer data is also hampered by the lack of knowledge of the specific location where the behaviors are taking place (Blumenthal et al., 2010; Witt et al., 2010). This lack of spatial context is particularly problematic for green turtles, since their diving behavior varies both within and amongst habitats (e.g., Bjorndal, 1997; Blumenthal et al., 2009; Brill et al., 1995; Hatase et al., 2006; Hays et al., 2000a; Hazel, 2009; Schofield et al., 2006; Seminoff et al., 2006). Therefore, comparing diving behavior using TDR data without spatial information may require subjective judgments or arbitrary decisions (Fedak et al., 2001).

While TDRs have revolutionized the study of turtle diving, many studies have highlighted the benefits of integrating visual observations with TDR data for studying turtle behavior (Houghton et al., 2002, 2003; Schofield et al., 2006). This study seeks to quantify the extent to which TDRs can be used to infer specific juvenile green turtle behaviors (e.g., resting, foraging, breathing) by comparing TDR data and behavioral video observations taken concurrently in the Kawai'nui Marsh Estuary on O'ahu, Hawai'i.

2. Methods

2.1. Study area

The Kawai'nui Marsh Estuary (KME) study area is located at the northern end of Kailua Bay on the island of O'ahu, Hawai'i (21° 25′ N, 157° 44′ W, Fig. 1), spanning approximately 0.5 km² and encompasses six different habitats: cove, channel, ledge, canal, rocky shore, and bay. The shallow (0.5–1.5 m) cove with pavement-type coral reef and carbonate rock substrate and 50–90% coverage of macroalgae and benthic invertebrates (NOAA CCMA, 2007), lies at the northern edge of KME. Bordering the cove is a 3.0–4.0 m deep dredged channel connecting to a manmade 2.75 km-long canal, both containing sandy-to-muddy substrate and leading to the 336 ha Kawai'nui Marsh. On either side of the channel is a vertical wall, made up of basaltic rock, calcium carbonate substrate with macroalgae, and sessile invertebrate cover which will be referred to as the "ledge." In this study, the channel and ledge are considered the same habitat. The south end of the channel empties into Kailua Bay, a relatively shallow (0.5–3.0 m) flat reef/rock habitat which also supports abundant macroalgae and sessile invertebrates (NOAA CCMA, 2007). The shallowest portion (0–0.5 m) of the bay will be referred to as the rocky shore (Fig. 1). Visibility was typically poor (<1.0 m) within the canal, based on highly eutrophic and silty fresh water input from the marsh, with visibility improving (2.0–10.0 m) in all other habitats.

2.2. Turtle capture and marking

Turtles were captured by hand while snorkeling in the channel or by scoop net while walking in the cove habitat. Turtles were immediately placed in a circular rubber float and brought to shore for tagging, weighing, body measurements, and a general health assessment. A unique identification number, approximately 3 × 3 cm and 1 mm deep, was etched into the left and right sides of each turtle's carapace and painted white to aid in visual identification of the turtle, as described in Balazs (1995). Turtles were also tagged with Passive

Integrated Transponder tags injected into the dorsal musculature of both the left and right hind flipper.

2.3. Time–depth recorders (TDRs)

Six turtles (4 in March — T2, T15, T16, T17; 2 in June of 2010 — T34, T37) were equipped with time–depth recorders (TDRs; Lotek, model LAT 1500 — pressure resolution of 0.05% of 1 dbar [minimal measuring increment], pressure accuracy of ± 1% of actual measurement [based on water temperature], temperature resolution of 0.05 °C, temperature accuracy <0.2 °C).

With the turtle restrained in an animal carrier, its carapace was cleaned with heavy duty green scouring pads to remove algae and other fouling material, then wiped dry and slightly sanded to prepare the carapace for adhesive. Silicone elastomer (Nephew and Nephew Rolyan, Inc., Menomonee Falls, WI) mixed with methyl ethyl ketone catalyst was shaped around the TDR while still moldable, leaving the pressure and temperature sensors of the TDR exposed. The TDR/elastomer combination was then pressed onto the sanded portion of the turtle's carapace to fit the curvature of the carapace, and left to harden. Once hard, fiberglass cloth was laid over the TDR/elastomer, and a mixture of surfboard (polyester) laminating resin and catalyst was applied to protect and glue the device in place to the turtle's carapace (Balazs et al., 1996). The scute to which the device was attached was varied to assist in turtle identification in the water. The device and its housing were easily removed without damaging the carapace by prying them off with a screwdriver at the end of the study, or would fall off naturally as the turtle grew. Attempts to recapture tagged turtles occurred approximately once per month, between March and September 2010, with the goal of retrieving and redeploying the TDRs repeatedly on the same individuals throughout the spring and summer. Each turtle received one tag that sampled water pressure and temperature every 15 s for approximately 33 days, until the device's memory was filled. A sampling frequency of 15 s was chosen due to physical limitations of collecting in-water visual observation data.

Following Hazel et al. (2009), the minimum depth value recorded for each TDR dataset was added to all depth values to correct inter-tag calibration differences making each turtle's minimum depth value "zero." This correction assumes that the 15-second sampling regime captured the turtle breathing at the surface at least once, during each 33-day deployment. A further analysis binning all full TDR datasets into 6-h intervals demonstrated that minimum depth did show a statistically significant drift within TDR deployments. However, the largest average difference in minimum depth between the last full and first full day of deployment was biologically insignificant — smaller than the size of any juvenile green turtle encountered at KME during this study.

2.4. Behavioral survey videos

To complement and validate the TDR data, focal-animal behavioral surveys were performed following Altmann (1974), in which individual turtle subjects were observed, recording their behaviors on 15-second intervals. Individual turtles equipped with TDRs were filmed by one snorkeler (DF) using an Olympus Stylus 1010 digital camera with underwater housing. Video length was constrained to the camera battery life and memory card space. Shorter videos occurred when sight of the turtle was lost because of poor visibility (filming did not resume if the turtle was resighted later within the survey) or when the focal turtle rested in the same position for 5 min. The full duration of each video was considered in subsequent analyses.

The video observations targeted turtles in 3 distinct habitats within KME (the cove, the adjacent channel/ledge, and Kailua Bay) and used 3 sets of potential starting points (labeled 1, 2, and 3; Fig. 1) within each habitat, the order of which was chosen using a random number table.
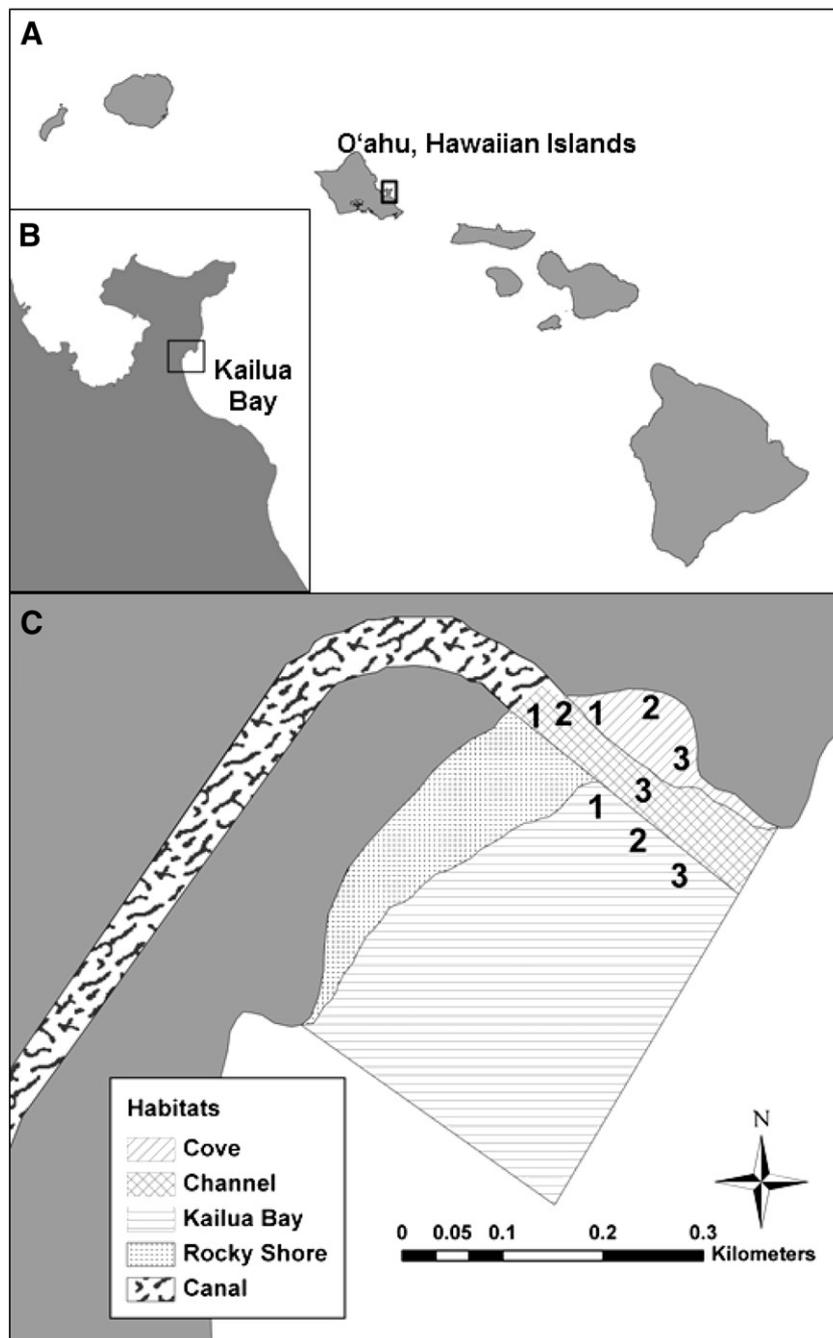
Fig. 1. Location of the Kawai'nui Marsh Estuary (KME) study site. A) O'ahu, 7 main Hawaiian Islands. B) Kailua Bay on the windward side of the island of O'ahu. C) KME: Locations of 5 specific habitats within the study site. Video behavioral surveys occurred in the cove, channel, and Kailua Bay habitats, with randomized starting positions labeled as 1, 2, and 3 within each habitat.

The first turtle sighted within the targeted habitat was selected as our focal individual, and filming started immediately. All surveys occurred between 10:00 and 16:00 local time, when turtle abundance was highest (Asuncion, 2010) and when a high sun angle provided the best visibility. These surveys covered four tidal phases (flooding, ebbing, high, low) spanning six consecutive 28-day lunar cycles, sampling each tidal phase twice during each lunar cycle (once in each 14-day period). During each 2-hour sampling period, a maximum of 6 turtles were filmed; 2 within each of the 3 habitats. Whenever poor visibility or low turtle abundance resulted in fewer than 2 turtles being filmed in a given habitat, more turtles were filmed in other habitats to reach the goal of recording 6 focal individuals per sampling session.

Turtles at KME are habituated to snorkelers, which allowed for observation with minimal disturbance. During filming, the observer remained at least 3 m from the turtle and moved with slow and deliberate movements to minimize influencing the turtles' behaviors. If a turtle appeared to be disturbed by the presence of the observer, the recording was terminated and the video was not included in this study.

2.5. Analysis of behavioral videos

Based on preliminary behavioral observations, *a priori* to data collection, a set of behavioral parameters were defined which were then used in the analysis of each video observation (Table 1). Instantaneous behaviors were recorded at 15-second intervals (the temporal resolution of the TDRs) through each entire video. As date/time was known for all behavioral survey observations and all TDR data points,

Table 1
The definitions of each behavior and environmental parameter recorded during video behavioral surveys.

Behavior	Definition
Foraging	
Food searching	Actively moving along bottom substrate, head moving around looking down for food, using flippers to steady self
Foraging	Turtle takes a bite of the vegetation on the substrate, or food is in its mouth and the jaw is moving up and down
Resting	
On substrate	Motionless, no flipper movement while in contact with bottom substrate, turtle's overall position does not change
Assisted	Motionless, no flipper movement while in contact with bottom substrate, turtle's overall position does not change, using a structure to maintain its position
Swimming	
Hovering	Motionless, or minimal amount of flipper movement while in water column, turtle's horizontal position relative to the substrate does not change
Posing	Motionless, or minimal amount of flipper movement while in water column, turtle's position relative to the substrate does not change; turtle's flippers and neck are outstretched, likely in vicinity of cleaning station
General swimming: direction	Turtle is actively using its flippers to change its position relative to the substrate. Classified as either movement up (nearer the surface), down (further from the surface), or horizontal (distance from surface does not change)
Relative speed	Distance traveled (m)/time (s), in km/h — calculated by GPS
Breathing	Turtle is at surface of water, its head clears water surface, bubbles and expulsion of water may or may not be seen
Body swiping	Turtle uses its front flipper(s) to deliberately wipe its face, plastron, or carapace

Table 2
Description of the 7 TDR parameters compared with 26 behavioral observation videos.

TDR parameter	Description
Depth displacement	The total vertical distance (m; recorded by the TDR) moved by the turtle during the length of the video
Depth coefficient of variation (CV)	The coefficient of variation (CV) of the turtle's depth (m; recorded by the TDR) during the length of the video
Maximum depth	The turtle's maximum reached depth (m; recorded by the TDR) during the length of the video
Average depth	The turtle's average depth (m; recorded by the TDR) during the length of the video
Surface proportion (arcsine transformed)	The proportion, or percent, of the video in which the turtle was within the top 0.5 m (recorded by the TDR) of the water column
Average temperature	The average water temperature (°C; recorded by the TDR) during the length of the video
Temperature CV	The CV of the water temperature (°C; recorded by the TDR) during the length of the video

the 2 datasets could be closely synchronized for analysis, separated by no more than 8 s — the halfway point between 15-second intervals. These time differences between behavioral observations and TDR data were determined to be insignificant. Many food searching events were not followed by active feeding, therefore separating food searching and foraging events as separate classifications, although foraging events included food searching behavior. The locations of subjects were recorded every 15 s using a floating Geographic Positioning System (GPS; Garmin, model eTrex Legend) instrument attached to the observer.

2.6. Comparison of TDR data to behavioral survey video data

A custom Matlab (v. R2007a) program was used to summarize 12 different depth and temperature characteristics of the TDR data for each video, including: maximum, average, and median depth, total depth displacement, proportion of time spent between the surface and 0.5 m depth, proportion of time spent below 0.5 m depth, the coefficient of variation (CV) of depth, average, median, maximum, and minimum temperature, and the CV of temperature. In addition to the mean/median metrics used to quantify the depth/temperature experienced by the tagged turtles, the CVs quantify variability in depth/temperature, indicative of activity levels (e.g., Blumenthal et al., 2009). Dive duration was not used as a TDR parameter because the shallow nature of the site made it difficult to define dives based on shape or duration. Instead, turtle vertical position was classified by depth strata (0.5 m bins), similar to the methods of Hazel et al. (2009). Seven of these 12 variables were compared with behavioral video observations (Tables 2 and 3), after removing 5 variables that were very highly cross-correlated or redundant (Table 4). This analysis involved 6 behaviors that occurred in at least 2 of the analyzed videos: food searching, active foraging, resting, general swimming, hovering, and breathing. Posing and body swiping behaviors were excluded because they occurred only once.

Similar to the methods employed by Barnett-Johnson et al. (2007) we used binary stepwise (forward and backward, $\alpha = 0.1$) logistic regressions (SYSTAT v11.0) to determine if these TDR parameters could predict the occurrence of these six behaviors. Stepwise logistic regressions were followed by complete logistic regressions for those behaviors with significant results. A second set of stepwise logistic regressions determined if the length of the behavioral survey video affected the occurrence of specific behaviors, while considering all seven TDR variables. These logistic regressions provided a "logit" value defined as:

$$L_i = \log\left(p_j / \left(1 - p_j\right)\right) = \sum\left(a_{ij} \times b_{ij}\right) + c;$$

where

L_i	logit value, or inverse of the logistic function, or significant linearly predicted value for the associated behavior based on the combination of TDR parameters;
i	the number of videos (ranging from 1–26);
j	the number of TDR parameters significantly related to the behavior;
p_j	the probability (0–1) of the occurrence of a particular behavior;
a_{ij}	TDR parameter value significantly related to the behavior;
b_{ij}	the logistic regression estimated value, or "weight," associated with each TDR parameter;
c	a calculated constant, the line intercept.

Finally, to investigate finer-scale associations of the individual behaviors with specific habitats, each video was split into 2-minute segments, involving 8 consecutive 15-second observations. The GPS tracks of each 2-minute segment were used to assign each 15-second location to a specific habitat. To address specific habitat associations, only those 2-minute segments contained solely within one habitat (channel/ledge, Kailua Bay, cove, or rocky shore) were considered. A G-test was used to analyze the association of the 6 specific fine-scale behaviors and the 4 habitats (Zar, 1984). For the subset of behavior/habitat combinations with a minimum of 3 occurrences, stepwise (forward and backward, $\alpha = 0.1$) and complete logistic regressions were used to relate the behaviors with specific TDR parameters.

3. Results

3.1. Paired TDR and video datasets

Over the 6-month study period, 16 TDR datasets (recorded on 15-second intervals) were uploaded from the six tagged turtles, 15 of which had usable, uncorrupted data (T2 = 2 datasets, T15 = 3,

Table 3
Depth and temperature TDR parameters calculated by Matlab computer software for the length of each of the 26 visual observation videos. Disp = Depth Displacement (m), CV = Coefficient of Variation (%), Max = Max Depth (m), Avg = Average (depth: m; temperature: °C), Surface Prop = Proportion of video spent within the top 0.5 m of the water column (surface), arcsine transformed.

Video no., turtle no.	Depth parameters					Temperature parameters	
	Disp	CV	Max	Avg	Surface Prop	Avg	CV
1, T2	7.87	54.27	1.73	0.77	0.18	27.68	1.85
2, T2	5.74	12.33	2.30	1.81	0.00	26.10	0.40
3, T2	9.87	59.29	1.80	0.79	0.16	26.95	2.74
4, T16	7.36	18.53	1.98	1.48	0.00	24.49	0.44
5, T16	10.58	23.43	2.68	2.08	0.02	23.40	0.00
6, T16	5.76	19.50	1.63	1.16	0.00	23.59	0.07
7, T16	3.59	32.25	0.80	0.54	0.22	26.73	0.47
8, T34	1.20	5.97	2.21	1.75	0.00	24.99	0.34
9, T37	7.69	27.24	1.71	1.02	0.00	26.88	1.37
10, T34	6.06	35.34	1.71	1.04	0.00	27.42	1.64
11, T37	6.45	30.53	2.13	1.50	0.02	27.22	0.18
12, T16	3.22	19.42	0.50	0.41	0.57	27.36	0.18
13, T37	7.48	48.01	1.94	1.21	0.12	26.69	0.89
14, T34	5.91	33.01	1.42	0.84	0.06	27.60	1.13
15, T37	0.72	2.00	1.50	1.45	0.09	28.06	0.07
16, T34	3.83	19.88	0.92	0.71	0.08	28.63	0.42
17, T37	4.54	62.50	1.92	1.26	0.18	26.89	0.90
18, T34	1.24	56.51	1.45	0.93	0.25	28.41	0.81
19, T34	6.24	26.21	1.57	1.10	0.04	27.27	0.33
20, T37	1.47	2.54	1.82	1.70	0.00	26.37	0.08
21, T37	12.53	55.28	2.35	1.20	0.10	26.53	0.34
22, T34	7.26	54.38	1.50	0.67	0.22	27.91	0.57
23, T2	8.48	23.41	2.28	1.87	0.00	27.91	0.26
24, T34	4.12	45.57	2.07	1.28	0.00	27.61	1.12
25, T2	8.68	30.32	2.03	1.46	0.00	28.00	0.53
26, T34	6.04	53.57	2.25	1.04	0.02	26.86	0.25

T16 = 3, T17 = 1, T34 = 3, T37 = 3). Twenty-six videos documented the behavior of turtles equipped with TDRs. Four of the 6 tagged turtles were captured in these 26 videos (T15 and T17 were not filmed while their TDRs were active). The videos were distributed throughout the 6-month study, covering all 4 tidal cycle phases and all 3 habitats. Videos ranged in duration from 2 to 10 min (avg of 7.71 min; SD 1.53).

To explore potential habitat-behavioral associations, the 26 videos of varying durations were split into 99 nonoverlapping 2-minute segments, 75 of which were restricted to a single habitat: 31 (41.3%) occurred in the channel/ledge, 11 (14.7%) in the cove, 23 (30.7%) in Kailua Bay, and 10 (13.3%) in the rocky shore. We used G-tests (Zar, 1984) to assess the independence between the presence/absence of 6 individual behaviors in the 4 habitats (Table 5). These tests identified 4 "specialized" behaviors with significant habitat-specific associations: foraging, food searching, resting, and breathing. Conversely, 2 generalized behaviors, hovering and swimming, occurred frequently and independently of habitat. These generalized behaviors were often interspersed with foraging and breathing, and followed resting behavior.

3.2. Comparison of TDR parameters with behavioral videos

Although the 7 TDR parameters were cross-correlated (Table 4), all were included in the analyses (Table 3) using stepwise logistic regression. Forwards and backwards logistic regressions revealed that 4 of the 6 behaviors documented in the videos were significantly related

to one or more TDR parameters (Table 6). Moreover, complete logistic regressions relating these 4 behaviors and their associated significant TDR parameters revealed the predictive ability of these models ('percent correct' values, Table 6), describing the nonlinear behavioral responses of the turtles (Fig. 2). Occurrences of turtle behaviors were not significantly associated with video length ($p < 0.1$), indicating no sampling biases across observations of varying duration.

Consistent with the approach of Barnett-Johnson et al. (2007) and Tinker et al. (2007), three metrics were used to quantify the ability of the TDR parameters to predict turtle behavior:

1. Sensitivity is defined as the proportion of positive events correctly identified, when a given behavior occurred in both the video and TDR observations;
2. Specificity is defined as the proportion of negative events correctly identified, when a given behavior did not occur in the video nor in the TDR observations TDR;
3. Sensitivity and specificity determine a 'percent correct' value, an overall assessment of the likelihood that any particular logit value will correctly predict a specific behavior's occurrence.

If the occurrence of a behavior was perfectly predicted by its associated logit value, the sensitivity, specificity, and percent correct values (Table 6) for this behavior would all equal 100%. Additionally, the resulting 95% confidence interval value of the odds ratio (OR, which describes the strength of association between two binary data values)

Table 4
Pair-wise Pearson correlation coefficients for all 7 TDR parameters. *p*-values are italicized; significant *p*-values are in bold.

	Depth disp	Depth CV	Max depth	Avg depth	Surface prop	Avg temp	Temp CV
Depth disp	–	**0.02 < p < 0.05**	**0.01 < p < 0.02**	*p > 0.10*	*p > 0.10*	*p > 0.10*	*p > 0.10*
Depth CV	0.41	–	*p > 0.10*	**0.02 < p < 0.05**	*p > 0.10*	*p > 0.10*	**p < 0.01**
Max depth	0.48	0.08	–	**p < 0.01**	**p < 0.01**	**0.02 < p < 0.05**	*p > 0.10*
Avg depth	0.10	−0.45	0.80	–	**p < 0.01**	**0.01 < p < 0.02**	**0.02 < p < 0.05**
Surface prop	−0.14	0.33	−0.65	−0.67	–	*p > 0.10*	*p > 0.10*
Avg temp	−0.20	0.30	−0.41	−0.47	0.27	–	*p > 0.10*
Temp CV	0.26	0.56	−0.06	−0.41	0.11	0.28	–

Table 5

G-tests for the occurrence of 6 behaviors across 4 habitats within ninety-nine 2-minute behavioral video segments. Behaviors were dependent on habitat if $p < 0.05$. Cells with superscripts (a or b) show the behaviors and habitats further tested with stepwise logistic regressions to determine if any TDR parameters were significantly related to the specific behavior within the specific habitat (only cells with occurrences in 3 or more 2-minute segments were tested).

Behavior	Habitat				G-score	p-value
	Channel/ledge	Cove	Kailua Bay	Rocky Shore		
Foraging[a]	0	5[a]	10[a]	1	17.57	$p < 0.001$
Food searching[a]	2	8[a]	13[a]	1	14.92	$0.001 < p < 0.005$
Resting[a]	12	0	0	0	18.89	$p < 0.001$
Hovering[b]	9[b]	7[b]	20[b]	3[b]	6.32	$0.10 < p < 0.25$
Swimming[b]	21[b]	11[b]	17[b]	10[b]	0.92	$p > 0.25$
Breathing[a]	8[a]	4[a]	0	3[a]	10.08	$0.01 < p < 0.025$
Total no. of 2-min segments	31	11	23	10	–	–

[a] Specialized behaviors — not independent of habitat.
[b] Generalized behaviors — independent of habitat.

value would not overlap with the value of 1.00, indicating that the probability of occurrence increases/decreases significantly in response to the changing logit value.

3.2.1. TDR predictors of foraging behavior

Foraging behavior was related to the combination of increasing TDR depth displacement (OR > 1.00, $p = 0.02$) and decreasing depth CV (OR < 1.00, $p = 0.06$) (Table 6). A positive response to increasing depth displacement indicated that vertical movement serves as a proxy for foraging activity. Foraging was also related to decreasing depth CV, suggesting that as a turtle's bottom depth became steadier, foraging behavior was more likely. Yet, the low sensitivity value (57.0%) underscored the poor predictive ability to correctly predict foraging behavior using the TDR logit model. However, the high specificity value (77.0%) suggested that the model correctly identified non-foraging behavior at a high rate. Overall, the high (70.0%) percent correct value indicated that the logit model inferred foraging/non-foraging behavior using TDR data with fairly high confidence (Fig. 2a).

3.2.2. TDR predictors of food searching behavior

Food searching behavior was related to the combination of increasing TDR depth displacement (OR > 1.00, $p = 0.05$), decreasing depth CV (OR < 1.00, $p = 0.07$), and increasing surface proportion (OR > 1.00, $p = 0.10$) (Table 6). As with foraging, food searching is positively related to depth displacement (more depth displacement indicates more food searching) and negatively related to depth CV (steadier bottom diving depth is associated with more food searching). While searching for food, the turtles skimmed along the substrate swimming at a fairly constant depth, except for intermittent surfacing to breathe. Because the food searching behavior primarily occurred within the shallow-cove habitat, a positive relationship with the proportion of time spent within the top 0.5 m of the water column is also evident. Overall, the logit model identified the food searching behavior more reliably than the foraging

behavior (food searching: sensitivity = 82.0%, specificity = 87.0%, percent correct = 84.0%) (Fig. 2b).

3.2.3. TDR predictors of hovering behavior

Hovering behavior was related to increasing TDR depth displacement (OR > 1.00, $p = 0.03$) (Table 6). As TDR depth displacement increased, the probability of hovering increased. Yet, despite the fairly high sensitivity (71.0%), the specificity value was rather low (53.0%) indicating that the logit model performed poorly because the TDR variables consistently predicted the presence of hovering behavior not confirmed by the videos (percent correct = 64.0%) (Fig. 2c).

3.2.4. TDR predictors of breathing behavior

Breathing behavior was related to the combination of increasing TDR average temperature (OR > 1.00, $p = 0.06$), increasing depth displacement (OR > 1.00, $p = 0.01$), and decreasing maximum depth (shallower; OR < 1.00, $p = 0.09$) (Table 6). The association of breathing behavior with average water temperature is likely caused by breathing in warmer surface water. Furthermore, because turtles rest in cooler and deeper water (larger maximum depths), they were less likely to surface for air than active swimming turtles; thus reinforcing the association of decreasing maximum TDR depth and breathing behavior. The logit model predicted the breathing behavior with 79.0% success, with both high sensitivity (80.0%) and high specificity (77.0%) (Fig. 2d).

3.3. Predicting habitat-specific turtle behaviors

Stepwise logistic regressions used to determine habitat-specific associations between TDR parameters and turtle behaviors revealed three significant relationships. Resting behavior was significantly related to increasing TDR average depth and decreasing maximum depth in the channel/ledge; breathing behavior was significantly

Table 6

Significant results from the complete logistic regression analyses. Models of resting, swimming, posing, and body swiping behavior did not provide any TDR parameters with which they were significantly related. Behavior = turtle behavior recorded from observational video; TDR Parameter = parameter(s) collected by the TDR, the linear combination (logit function) of which are significantly related to the listed behavior; Estimate = logistic regression estimated value given to the TDR parameter in the logit function; S.E. = standard error of the estimate; t-ratio = t-statistic of the estimate; p-value = significance level of the estimate; 95% CI = 95% confidence interval for the Odds Ratio; Sens. (%) = sensitivity, the percent of actual positives which are correctly identified as such; Spec. (%) = specificity, the percent of negatives which are correctly identified; Correct (%) = the likelihood that any specific logit function result of the listed TDR parameter(s) will indicate the behavior with which it is significantly related.

| Behavior	TDR parameter (a_i)	Estimate (b_i)	S.E.	t-ratio	p-value	Sens. (%)	Spec. (%)	Correct (%)
Foraging	Depth disp	0.61	0.26	2.34	0.02	57.0	77.0	70.0
	Depth CV	−0.08	0.04	−1.92	0.06			
Food searching	Depth disp	2.64	1.33	1.99	0.05	82.0	87.0	84.4
	Depth CV	−0.48	0.24	−1.83	0.07			
	Surface proportion	50.67	30.35	1.67	0.10			
Hovering	Depth disp	0.42	0.19	2.18	0.03	71.0	53.0	64.1
Breathing	Avg temp	1.20	0.65	1.86	0.06	80.0	77.0	78.8
	Depth disp	0.85	0.35	2.45	0.01			
	Max depth	−2.38	1.39	−1.71	0.09			
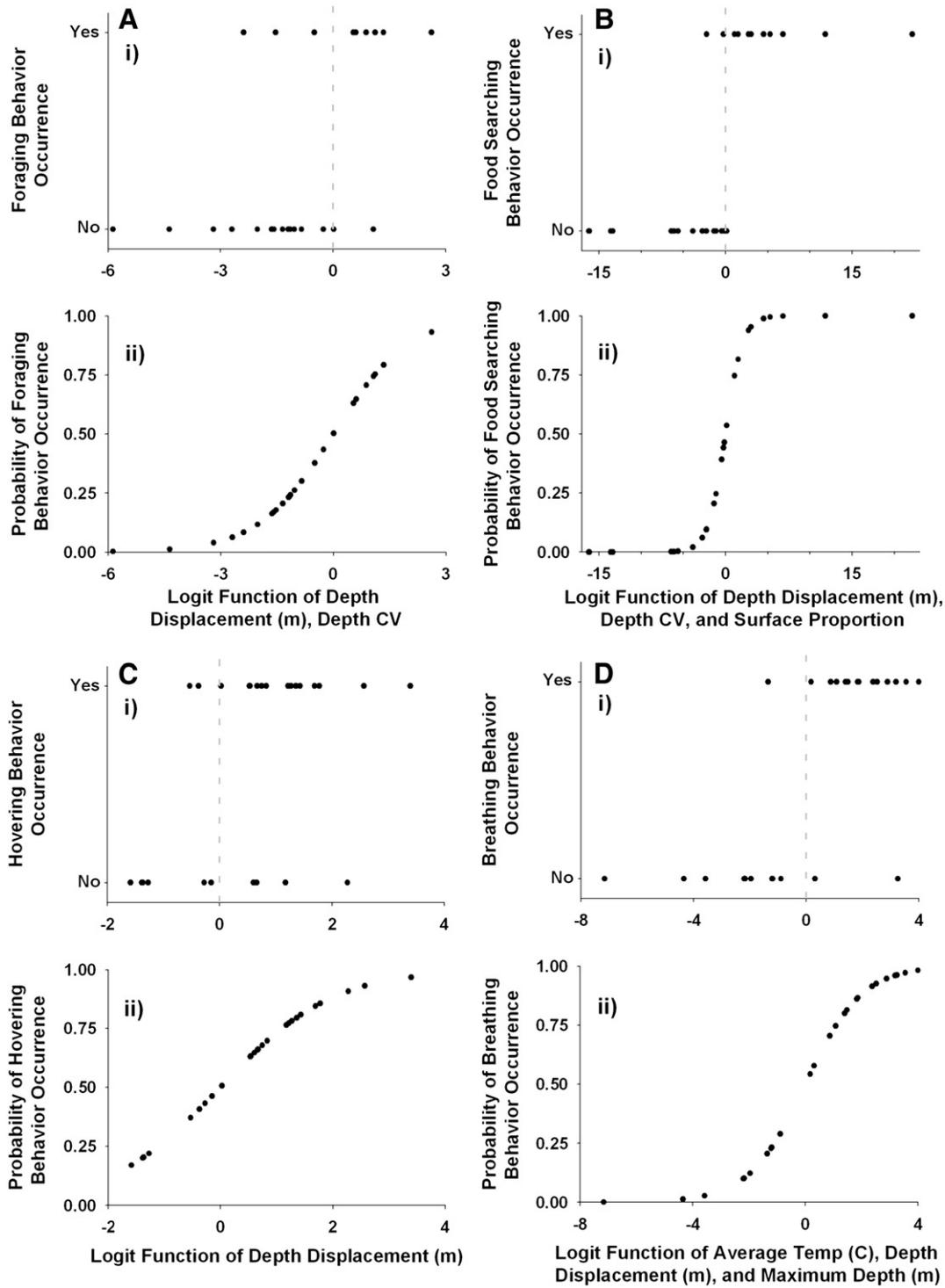
Fig. 2. Predicting the likelihood of the occurrence of specific behaviors using TDR data; A) foraging, B) food searching, C) hovering, and D) breathing. The upper graphs (i) represent the observations from 26 behavioral videos, of whether or not the specific behavior (A–D) occurred as a function of a linear combination, or logit function, of specifically defined TDR parameters (the combination of which is marginally significant with the behavior). The dashed gray line indicates the hypothetical line which the "yes" and "no" points should not cross if the logit function were to perfectly explain the presence/absence of foraging behavior. The lower graphs (ii) represent complete logistic regressions showing the probability of the occurrence of the specific behavior (A–D) as a function of the linear combination of its associated TDR parameters which (marginally) significantly describe its presence or absence.

related to increasing TDR temperature CV in the channel/ledge; and hovering behavior was significantly related to decreasing TDR average temperature, increasing depth displacement, and increasing surface proportion across all habitats. Complete logistic regressions relating the occurrence of these behaviors to their associated TDR parameters within specific habitats revealed that behaviors were predicted more accurately without partitioning behavior by habitat (Table 7), as the 2-minute video segment logistic regressions yielded

smaller sensitivity, specificity, and percent correct values than the full video logistic regressions. The ability to predict hovering behavior decreased to 62.0% for all habitats (from 64.0% when considering full-length videos) and breathing behavior (within the channel/ledge) decreased to 69.0% (from 79.0% from all habitats). However, resting behavior was significantly related to specific TDR parameters within the channel/ledge, whereas it had no significant relationship with the analysis from the full videos.

Table 7

Results from the complete logistic regression analyses of the 2-minute video segments. All significant p-values are in bold. Behavior = turtle behavior recorded from observational video; TDR Parameter = parameter(s) collected by the TDR, the linear combination (logit function) of which are significantly related to the listed behavior; Estimate = logistic regression estimated value given to the TDR parameter in the logit function; S.E. = standard error of the estimate; t-ratio = t-statistic of the estimate; p-value = significance level of the estimate (values in bold are significant, $p \leq 0.10$); 95% CI = 95% confidence interval for the Odds Ratio; Sens. (%) = sensitivity, the percent of actual positives which are correctly identified as such; Spec. (%) = specificity, the percent of negatives which are correctly identified; Correct (%) = the likelihood that any specific logit function result of the listed TDR parameter(s) will indicate the behavior with which it is significantly related.

Habitat	Behavior	TDR parameter (a_i)	Estimate (b_i)	S.E.	t-ratio	p-value	Sens. (%)	Spec. (%)	Correct (%)
Kailua Bay	Foraging	Avg depth	−11.46	7.24	−1.58	0.11	65.0	70.0	68.0
Channel/ledge	Resting	Max depth	−6.41	3.26	−1.97	**0.05**	71.0	82.0	77.0
		Avg depth	9.90	3.52	2.82	**0.01**			
Channel/ledge	Breathing	Temp CV	4.30	1.97	2.18	**0.03**	40.0	79.0	69.0
All habitats	Hovering	Avg temp	−0.83	0.27	−3.04	**0.00**	63.0	60.0	62.0
		Depth disp	0.72	0.32	2.26	**0.02**			
		Surface proportion	2.47	1.42	1.74	**0.08**			

3.3.1. Resting

Resting was significantly related to decreasing maximum depth (OR < 1.00, $p = 0.05$) and increasing average depth (OR > 1.00, $p = 0.01$) within the channel/ledge, the only habitat where this behavior occurred (Table 7). In particular, the TDR average depth parameter had a larger influence on the logit value given its larger coefficient estimate as turtles would always rest among the benthos within this habitat. The ability to predict resting within the channel/ledge was fairly high (sensitivity = 71.0%, specificity = 82.0%, percent correct = 77.0%).

3.3.2. Breathing

Although breathing behavior occurred in three of the four habitats (channel/ledge, cove, and rocky shore) on the 15-second interval, it was only significantly related to the TDR temperature CV within the channel/ledge (OR > 1.00, $p = 0.03$) (Table 7). This behavior was predicted correctly 69.0% of the time (sensitivity = 40.0%, specificity = 79.0%).

3.3.3. Hovering

Hovering behavior, which was widespread and independent of habitat, was significantly related to decreasing average temperature (OR < 1.00, $p < 0.01$), increasing depth displacement (OR > 1.00, $p = 0.02$), and increasing surface proportion (OR > 1.00, $p = 0.08$) (Table 7). Of the three significant behavior/habitat combinations, hovering was the least predictable (sensitivity = 63.0%, specificity = 60.0%, percent correct = 62.0%).

4. Discussion

4.1. Comparison of TDR parameters with behavioral observation videos (logistic regressions)

The combination of increasing TDR depth displacement and decreasing depth CV (steady bottom depth) were ground-truthed as fairly reliable proxies for foraging and food searching activities, which require frequent surfacing to replenish oxygen stores (Houghton et al., 2003; Southwood et al., 2003a). Cheng (2009) similarly found that on such active-type dives, turtles exhibit frequent vertical movement, resulting in an erratic bottom profile with a large bottom depth standard deviation. Decreasing depth CV contrasts increasing TDR depth displacement. If turtles foraged often along the substrate, with minimal surfacing to breathe, a small depth CV value could result. But, as the CI overlaps 1.00 and its significance values are marginally greater than $p = 0.05$ ($p = 0.06$ for foraging and $p = 0.07$ for food searching; Table 6), foraging behavior could also occur with greater depth CV. Food searching was also described by a third TDR variable, increasing time near the water surface. The shallow cove had high algal cover and was consistently witnessed as foraging habitat. Green turtles are known to forage at shallow depths (Hart and Fujisaki, 2010; Salmon et al., 2004; Seminoff et al., 2001) and such a shallow depth could limit vertical movement, perhaps explaining the correlation with decreasing depth CV. Turtles often took multiple breaths while food searching, spending more time near the surface, contributing to this parameter's inclusion in describing food searching behavior. But, as the CI overlaps 1.00 (Table 6), increasing surface time was not always associated with increased food searching behavior. Thus, this TDR parameter must be combined with depth displacement and depth CV to predict food searching occurrence. Including a third TDR parameter allows more accurate prediction of food searching behavior than foraging behavior. These observations, taken together demonstrate that the more variables included in the logit function the better its predictive power.

Hovering was positively related with TDR depth displacement. Currents or slight flipper movements may have caused changes in the turtles' depths while hovering. Breath volume may have also affected vertical movement. The number and volume of breaths sea turtles take along with lung compression determines the depth of neutral buoyancy (Hays et al., 2000a; Hochscheid et al., 1999). The lungs expand with slight upward vertical movement assisting the turtle to reach the surface, while expending less energy (Hays et al., 2007), leading to greater vertical depth displacement while hovering.

Breathing was significantly related to TDR increasing depth displacement and decreasing maximum depth. Turtle submergence intervals and diving depths are strongly related to activity level (Brill et al., 1995; Cheng, 2009). Hawaiian green turtles typically surface for a few seconds to take a single breath between shallow foraging bouts (Rice et al., 2000). Greater activity (increased depth displacement) requires more frequent surfacing to regulate oxygen (and carbon dioxide) gas balance (Hochscheid et al., 1999). Long duration dives in shallow sites are often associated with seafloor resting behavior (Hays et al., 1999), resulting in lower activity levels and thus fewer breaths in slightly deeper waters. However, in this study, video observations demonstrated that resting turtles did occasionally surface for extended breathing bouts followed by re-submergence. This behavioral pattern may have decreased statistical power when evaluating the relationship between breathing and TDR maximum depth. Brill et al. (1995) also found that long and regular green turtle dives were associated with minimal movement on the substrate (defined as resting), while more active dives were typically much shallower and shorter (defined as foraging), involving more surfacing events. Colder water temperatures have also been linked to longer dives, and therefore fewer breathing events (Hazel et al., 2009), making it more likely for breathing to occur in warmer water, as documented in this study. However here breathing did not only occur in warm surface water, but also when water with lower salinity and temperature from the Kawai'nui Marsh displaced ocean waters resulting in a negative relationship of water temperature and breathing behavior.

It is surprising that no other significant logistic regression relationships existed, particularly for resting and swimming behaviors. Five out of 8 videos with resting also involved other behaviors with substantial vertical displacement (breathing and swimming), likely obscuring resting with other behaviors. Swimming behavior was recorded in 22 of the 26 videos, possibly making it too pervasive to be described by

TDR parameters. Additionally, other studies which document repeated long flat-bottomed dive profiles, assumed to be resting behavior, occur predominantly at night (e.g., Hays et al., 2004). Hence future studies would benefit from behavioral observations made during both night and day.

The absence of an association of temperature parameters with behavior (other than breathing) may have been due to the shallow nature of the site with minimal vertical temperature gradients (maximum difference during video observations = 2.19 °C, avg = 0.56 °C (SD 0.54). Additionally, Southwood et al. (2003b) found no significant difference in juvenile green turtle behavior when exposed to a laboratory simulation of varying water temperatures (17–26 °C). Cheng (2009) found no relationship between water temperature and the inter-nesting interval length at Wan-an Island, Penghu Archipelago, Taiwan, suggesting minimal thermoregulatory behavior. Yasuda and Arai (2009) also found no effect of water temperature on green turtle diving behavior at Huyong Island, Thailand, over a narrow temperature range (mean ambient water temperature at diving depth ranged from 28.23 °C (SD 1.54) to 29.31 °C (SD 0.69). Small differences in water temperature also have minimal effects on buoyancy (Rice and Balazs, 2008), and therefore activity level and behavior. Thus, water temperature was unlikely to have affected turtle behavior in the current study, despite a significant relationship with breathing behavior.

The video length was not significantly related to the occurrence of any behaviors and it was not a confounding effect within the logistic regression analyses. We hypothesized that certain behaviors, such as breathing and swimming, may be positively related to video length as these generalized behaviors would be more likely to occur within a longer video. It is possible that the overall maximum video length was too short to differentiate behavioral events.

The current study used a smaller sample size (26 videos showcasing 4 turtles, 3.35 total hours of footage) than previous studies of turtle behavior (e.g., N = 25 turtles, 61.4 h, Heithaus et al., 2002; N = 34 turtles, 89.5 h, Seminoff et al., 2006), increasing chance for error in analyses. Additionally, posing and body swiping behaviors were not analyzed as their presence/absence data were not evenly distributed, each only occurring once in the 26 videos. Logistic regression analyses were used because of the shallow nature of the site — dive behaviors could not be assigned to typical dive profile 'shapes' as can be done in deeper water (Houghton et al., 2002). Given that dive profile shapes are used by researchers in describing turtle behavior in other studies, direct comparison of our results with other studies may be problematic. However, this study then demonstrates a novel methodology of analyzing dive data in locations where shallow depths limit typical dive data analyses.

In locations where turtles can dive deeper than in the KME, ascent and descent phases of the dive take longer, making it possible to record depth on a lower frequency (every 15 s) and still determine dive profiles. In the shallow KME, recording depth data at a more frequent rate may have improved the ability to determine the specific shape of dive profiles, as shown in Hays et al. (2002a). However, due to the physical and electronic limitations of the visual surveys, depth data could not be recorded any faster than at 15-second intervals in the current study.

4.2. Predicting behaviors within habitats (2-minute video segments)

Logistic regressions of 2-minute video segments yielded smaller percent correct values than of full-length videos, possibly due to a smaller dataset per video — 8 data points in the 2-minute video vs. 32 data points for an 8-minute video. For example, Tinker et al. (2007) found large variation between feeding bouts for sea otters, likely due to small TDR sample size when using logistic regressions. In the current study, increasing the video segment length within specific habitats would have greatly decreased the overall number of video segments, making analysis impractical. The 2-minute videos

were selected to separate the observations into 4 discrete segments, each within a unique habitat. It is important to note that the logistic regression analysis using the two-minute video segments is a novel approach to relate turtle behaviors to TDR parameters within specific habitats. Because this fine-scale analysis used multiple consecutive segments from the same videos and turtles, estimates of behavioral rates are susceptible to pseudoreplication, possibly inhibiting or biasing the results, potentially describing differences amongst turtles not habitats (Hurlbert, 1984).

Foraging, food searching, resting, and breathing behaviors were found to be habitat-dependent behaviors, with resting and breathing readily identified by TDR parameters. Brill et al. (1995) reported that green turtle foraging grounds include reef flats and shallow rocky shelves, often not exceeding 3 m in depth (like the cove and rocky shore). In contrast, turtles often rest in vertical crevices or vertical-walled channels within a reef flat, which are typically shallower than 8 m (like the channel/ledge; Balazs et al., 1987; Rice et al., 2000). It was therefore expected that foraging, food searching, and resting would occur within specific habitats. Indeed, the majority of foraging and food searching was observed within the cove, Kailua Bay, and rocky shore habitats, whereas resting was observed in the channel/ledge.

Breathing patterns were also site-specific, occurring in the channel/ledge, cove, and rocky shore habitats, but not in Kailua Bay (on 15-second intervals within the 2-minute videos). As turtles must surface to breathe frequently while foraging (Balazs, 1980; Rice et al., 2000), as commonly witnessed in Kailua Bay, it is by chance that this behavior was not recorded on any 15-second interval there. The significance of TDR temperature CV (with breathing) in the channel/ledge is likely related to swimming from depth after resting (2.0–3.0 m, colder water) to breathe at the surface (warmer water). However, a low sensitivity value (40.0%) suggests the relationship between TDR temperature CV and breathing behavior in the channel/ledge must be interpreted with caution.

The 15-second sampling interval did not bias the absence of recorded breathing events within the Kailua Bay habitat. For a concurrent study, the timing of all breathing events was recorded on 1-second intervals. Within the 26 videos used in this study, of all habitats, breathing occurred least frequently in the Kailua Bay habitat, at an average of 1 breath every 110.11 s, and most frequently in the Cove habitat, occurring on average once every 58.00 s. This shows the rarity of breathing events in Kailua Bay, and thus the unlikelihood that it would be captured frequently on 15-second intervals. If it were a more common behavior and not recorded, our analyses would not have been valid. Additionally, for a concurrent study, 4 turtles were equipped with 2 TDRs — one sampling at 1-second intervals, and the other every 15 s. An analysis of these data suggests that a breathing event would be captured just as likely, despite the sampling frequency.

Hovering behavior, witnessed within all habitats, was found to be a generalized behavior, just as in the full video logistic regressions. Hovering turtles do not stay at one depth level, but rather move up and down, explaining its significant relationship with increasing TDR depth displacement. While hovering at slightly negative buoyancies (influenced by lung volume and depth), turtles experience cooler water temperatures in deeper water (decreasing TDR average temperature), and while hovering at slightly positive buoyancies, more time is spent within the top 0.5 m of the water column, increasing TDR surface proportion.

Swimming was not significantly related to any TDR parameters within the 2-minute video segments probably based on its common presence within each habitat, obscuring the ability of the logistic regressions to predict it. Foraging and food searching behaviors were also not significantly related with any TDR parameters within the cove or Kailua Bay, possibly based on the dispersion of these behaviors amongst other generalized behaviors (swimming and hovering).

4.3. Other studies comparing TDR data with direct observations

Few studies have used rigorous direct observations together with electronic devices to quantify green turtle diving behavior (Schofield et al., 2006). Many use the Crittercam, a video-TDR which records video or still images of the turtle and its environment, concurrently with standard diving and environmental data (time, depth, and water temperature) (e.g., Heithaus et al., 2002; Seminoff et al., 2006; Thomson et al., 2011). For example, Thomson et al. (2011) used animal-borne video cameras to confirm the absence/presence of behaviors assumed to be associated with particular dive profile shapes. However, the authors admit the short video duration and capture-related-stress may have biased their results. Because our study filmed subjects several days, or even weeks after release, we are confident we eliminated these potential biases. Ballorain (2010) used snorkel and scuba surveys to visually record dive behaviors (feeding, traveling, and resting) of green turtles later compared with 10 TDR dive parameters using a principal component analysis. But, their direct observations merely confirmed inferences made using the TDR data, not to determine the extent that TDR data describes behavior. In another study, researchers visually observed a green turtle's diving behavior, using these observations to associate specific TDR dive profiles with certain behaviors (Rice et al., 2000). However, as individual and subpopulations of turtles show great behavioral variability (Hays et al., 1999), multiple subjects should be analyzed to account for any inherent variability, as was done in the current study. Most commonly, sea turtle behavior studies involving TDR deployments include only casual or opportunistic direct observations (e.g., Blumenthal et al., 2009; Davis et al., 2000; Hays et al., 2002b; Houghton et al., 2000).

Studies comparing direct observations with electronic data have been performed with species other than green turtles. Davis et al. (2003) used video/data recorders on 10 adult Weddell seals (*Leptonychotes weddellii*) to describe 4 different dive types, determining that previous studies using TDRs alone had misclassified certain dive types. Tinker et al. (2007) compared TDR data on California sea otters (*Enhyrda lutris*) with observational data to validate using TDR data to detect differences in diet and foraging behavior. They found that TDR data can be used >90% of the time to identify specific diets and foraging behavior. In another study, Underwater Timed Picture Recorder (UTPR) cameras placed on 6 lactating female fur seals differentiated feeding and other dives with similar TDR-based two-dimensional dive shapes (Hooker et al., 2002).

When direct observations have not been possible, accelerometer devices have been used as another means of inferring behavior. For instance, Gallon et al. (2012) placed accelerometers on the heads of elephant seals (*Mirounga leonina*), analyzing each head movement upon prey encounters to infer foraging behavior. However, these devices are too large for attachment to juvenile green turtle heads, and therefore cannot be used to infer foraging behavior as done by Gallon et al. (2012). As another example, Fossette et al. (2012) attached tri-axial accelerometers to six loggerhead sea turtles (*Caretta caretta*) during the nesting season at Laganas Bay, Zakynthos, Greece to study seasonal effects of water temperature on loggerhead activity. The accelerometers showed inactivity during long, deep U-shaped dives, inferred by the authors as resting behavior. However, sporadic, unsuccessful foraging occurs during the nesting season at that location (Schofield et al., 2007). Without visual confirmation, one cannot be certain if these stationary turtles were indeed resting, or if they were foraging. Accelerometers have greater error in behavioral prediction not related to locomotion (Gleiss et al., 2011), especially if not placed on a turtle's head. Therefore, accelerometers are not a substitute for visually confirming a turtle's diving behavior.

4.4. Limitations of direct observations

The benefits of using direct observations are many. Direct observations of animal behavior are useful for studying an organism within its natural habitat, for understanding an animal's ecosystem function, and for confirming, or ground-truthing inferences using electronic tags or remote technology (Hochscheid et al., 1999; Houghton et al., 2003; Schofield et al., 2006). Field observations of behavior are critical to effective conservation of animals in their natural habitat (Mills et al., 2005). But, limitations to their use do exist. Direct observations are constrained by logistical limitations and environmental conditions (Hooker and Baird, 2001; Myers et al., 2006). Records are typically brief or opportunistic, and researcher presence may disrupt natural behaviors (Witt et al., 2010). Therefore, many studies rely on inferences from animal-borne devices, such as TDRs, to determine behavior (Schofield et al., 2006). Video equipment, such as Crittercam, is suitable only for larger animals, and is costly and memory constrained (Moll et al., 2007). Although electronic devices accurately depict diving behavior, despite their limitations direct observations still provide a more detailed picture.

5. Conclusions

While TDRs have revolutionized the study of turtle diving behavior, they cannot describe the full range of behavioral patterns (Houghton et al., 2002). By comparing video-recorded direct observations of juvenile green turtles on 26 separate incidences to concurrent time–depth recorder (TDR) data, this study concluded that TDR data describe turtle diving behavior in a shallow habitat well, but visual observations are needed to fully characterize diving behavior. Because this conclusion may not be applicable to other habitats (e.g., pelagic waters, internesting habitat) similar habitat-specific studies could be conducted in the future. An improved habitat-specific understanding of TDR-derived diving data will help to inform protective measures for juvenile marine turtles in specific sites where they are susceptible to anthropogenic impacts (e.g., ship strikes, fishing gear interactions) in heavily used neritic habitats.

Using binary logistic regression models within the KME, only 4 (foraging, food searching, hovering, breathing) of the 6 behaviors considered were significantly related to specific TDR parameters. When analyzing behaviors within 2-minute segments, the ability to predict any given behavior decreased. Therefore, analyzing behavior by specific habitat does not increase the likelihood of correctly identifying behaviors based on TDR data alone. To best understand juvenile green turtle behaviors, it is important that direct observations augment TDR deployment to ensure field studies are capturing and describing the full behavioral repertoire of green turtles in heterogeneous habitats.

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