

Informing the interpretation of dive profiles using animal-borne video: A marine turtle case study

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ABSTRACT

It is often of interest to infer the behavior of air-breathing aquatic taxa (i.e., divers) based on the characteristics of dive profiles, which are relatively affordable and easy to obtain. However, dives that appear similar in shape or other attributes can reflect multiple activities, confounding their interpretation. Here, we used animal-borne video and environmental data recorders (AVED) to examine correlations between the dive-surfacing patterns and behavior of green (*Chelonia mydas* Linnaeus 1758) and loggerhead turtles (*Caretta caretta* Linnaeus 1758) and evaluate our ability to make behavioral inferences from stand-alone dive data. Commonly performed dive types, which have been previously defined, were behaviorally diverse but some generalizations about their function could be made. Furthermore, within Type 1 dives (i.e., square-bottom, U-shaped dives), which are often assumed to reflect benthic resting, dive features (maximum dive depth, duration and variation in depth during the bottom phase) correlated with the proportion of bottom time spent resting versus engaged in other activities. Statistical clustering of Type 1 dives based on these dive metrics identified groups of dives differing in function (i.e., the degree of rest versus traveling or feeding) but some behavioral overlap occurred. The probability of a dive reaching the sea floor varied by dive type, which has important implications if dive profile data are used to infer habitat depth for benthic foragers in the absence of tracking data. Finally, the number of breaths taken while at the surface between dives varied closely with surface interval duration, particularly for loggerhead turtles, suggesting surface times in dive profiles may be useful for estimating oxygen loading prior to a dive. This case study emphasizes the value of AVED technology for increasing the level of ecological insight obtainable from stand-alone dive profiles.

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1. Introduction

Large-bodied, diving taxa such as marine mammals and sea turtles can play important roles in marine ecosystems (Bjorndal and Jackson, 2003; Bowen, 1997). However, these species are challenging to study because they often range widely and engage in important activities (e.g., foraging) while submerged and out of view. Time-depth recorders (TDR) are commonly used to study dive-surfacing patterns and infer submerged activities (e.g., Frid et al., 2007; Hindell et al., 1991; Le Boeuf and Crocker, 1996; Thompson et al., 1991). Dive characteristics during foraging, such as bottom time relative to dive depth (i.e., travel time), may indicate the distribution of important prey species (Mori and Boyd, 2004; Mori et al., 2005). Furthermore, insight may also be gained into conservation issues such as the potential for interactions with, and behavioral responses to, boat traffic (e.g., Hazel et al., 2009; Stensland and Berggren, 2007) or protected area

requirements (e.g., Schofield et al., 2007). Thus, dive profiles are valuable for addressing a variety of ecological and applied questions.

For most species, dives can be coarsely grouped into a set of dive types based on their two-dimensional (i.e., time-depth) shape. These dive types, or dive characteristics within a type such as depth and duration, may correlate with particular activities such as foraging, traveling or resting (e.g., Hindell et al., 1991; Hochscheid et al., 2007; Houghton et al., 2002; Le Boeuf et al., 1988; Schreer and Testa, 1996; Thompson et al., 1991). However, such associations are unlikely to be perfect, which hinders our ability to make reliable inferences from stand-alone dive data. For example, an increased proportion of U-shaped dives by female harbor seals (*Phoca vitulina*) correlated with increased food intake based on water flux data (Baechler et al., 2002; Bowen et al., 2001). However, animal-borne video footage for male harbor seals revealed that U-shaped dives can also reflect traveling and reproductive vocalizations (Baechler et al., 2002). Therefore, relationships between dive-surfacing patterns and behavior should be evaluated with additional data in order to inform inferences from dive profiles (e.g., Davis et al., 2003).

In coastal foraging areas, chelonid (i.e., hard-shelled) sea turtles can spend as much as 95% of their time submerged (Lutcavage and

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Lutz, 1997) and engage in many activities (e.g., foraging, resting, traveling and social interactions) on or near the sea floor where direct observation is not possible (but see Houghton et al., 2000). Dive profiles are an important means of assessing the behavior of free-ranging sea turtles but behavioral inferences based on dive data can be challenging (Schofield et al., 2006). For example, square-bottom, U-shaped dives are commonly performed by several chelonid species (e.g., hawksbill turtles, *Eretmochelys imbricata*, van Dam and Diez 1992; green turtles, *Chelonia mydas*, Hays et al., 2000a; loggerhead turtles, *Caretta caretta*, Houghton et al., 2002) and have often been assumed to reflect benthic resting due to their extended, relatively flat bottom phase. However, behavioral data linked to dive profiles indicate that these dives can also reflect benthic activity (Hays et al., 2000b) including foraging and traveling (Seminoff et al., 2006). Houghton et al. (2002) observed that Type 1 dives could be further classified into two subtypes (1a and 1b) based on dive duration, depth, bottom phase characteristics and vertical velocity during descent and ascent. Briefly, Type 1a dives comprised long dives with a flat bottom phase while Type 1b dives were shorter with a more erratic bottom phase. While such groupings suggest differences in dive function (i.e., Type 1b dives more likely reflect benthic activity while Type 1a dives more likely reflect resting), behavioral data linked to dive profiles are required to test this hypothesis (e.g. Hays et al., 2000b).

Other valuable information may be contained in dive profiles but require assessment with complementary data. For example, for some taxa, particularly benthic foragers, it may be possible to infer habitat depth from dive profiles when tracking is not possible, allowing for inference of habitat use patterns (e.g., Hays et al., 2002; Houghton et al., 2002; Jay et al., 2001; Le Boeuf and Crocker, 1996). However, marine turtles and other benthic foragers routinely perform dives that do not reach the sea floor (e.g., Hochscheid et al., 1999). Therefore, the reliability of habitat characterizations from dive profiles requires assessment, for which animal-borne video and environmental data recorders (AVED) are well-suited (e.g., Reina et al., 2005). Furthermore, breath rate data can provide insight into energy expenditure during a dive (e.g., Goldbogen et al., 2008) and the energetic cost of particular activities (e.g., travel, Sumich, 1983). While it may be reasonably assumed that oxygen uptake increases with surface time measured in dive profiles, video data can be used to quantify the relationship between surface time and the number of breaths taken, providing a basis for directly estimating oxygen use.

We used AVED technology to investigate correlations between dive profile characteristics and the behavior of green and loggerhead turtles on a feeding ground in Shark Bay, Western Australia. The analyses serve as a case study to illustrate the application of AVED systems to aid in interpretation of marine turtle dive profiles (see also Reina et al., 2005; Seminoff et al., 2006), which are more affordable and easily obtained. We assessed marine turtle behavior among and within commonly performed dive types, which have been described previously (Hochscheid et al., 1999; Houghton et al., 2002; Minamikawa et al., 1997; Seminoff et al., 2006; Fig. 1). Specifically, we addressed the following questions: 1. What generalizations can or cannot be made about the function of dive types commonly performed by green and loggerhead turtles in

coastal foraging habitat? 2. Does the probability of a dive reaching the sea floor vary by dive type and, if so, what are the implications for using maximum dive depth as a proxy for habitat depth in the absence of positional data? 3a. Within Type 1 dives (square-bottom, U-shaped dives), which may be behaviorally diverse, do features such as dive depth, duration and depth variability during the bottom phase correlate with activity level during the dive? 3b. Does a statistical method of subdividing Type 1 dives based on dive profile characteristics correspond with variation in turtle behavior? 4. Can the duration of a surface interval between dives be used to predict the number of breaths taken and, thus, estimate oxygen loading?

2. Methods

2.1. Study site and field methods

Shark Bay, Western Australia (~25°45' S, 113°44' E), is a shallow (mostly <15 m), subtropical bay located approximately 800 km north of Perth. The study area in the bay's Eastern Gulf is characterized by a series of shallow (<4.5 m), offshore seagrass banks separated and surrounded by deeper (>6.0 m) sand-dominated habitat, in addition to expansive sand-seagrass flats near shore. Sub-adult and adult green and loggerhead turtles use this area of Shark Bay as a feeding ground year round (Heithaus et al., 2002a, 2005). Green turtles may feed on a variety of seagrasses, algae, scyphozoan jellyfish and ctenophores (Burkholder et al., 2011; Heithaus et al., 2002b; Seminoff et al., 2006) while loggerhead turtles are known to consume diverse benthic invertebrates, particularly molluscs and crustaceans (e.g., reviews in Dodd, 1988 and Bjorndal, 1997; Limpus et al., 2001; Lazar et al., 2011; Thomson et al., unpublished).

Fieldwork took place between March and July, 1999, April and June, 2000 and during April, 2003. Turtles were captured by hand (Heithaus et al., 2002a; Heithaus et al., 2005) during haphazard searches and transect surveys of the study area. Turtles were brought aboard the vessel, curved carapace length (CCL) was measured (± 0.5 cm) and turtles were tagged using titanium flipper tags (Department of Environment and Conservation, Western Australia) applied to a proximal foreflipper scute. Turtles were considered male if tail length was ≥ 25.0 cm or unclassified, which would include immature males and all females, if tail length was <25.0 cm (Heithaus et al., 2002a; Heithaus et al., 2005; Limpus et al., 1994a,b).

To study turtle behavior and diving patterns, AVED systems (National Geographic's CRITTERCAM®; Marshall, 1998) were deployed (see Heithaus et al., 2002b). These units included a video recorder and recorded time, depth (± 0.5 m) and water temperature (± 0.1 °C) every 2.4 s. A plexi-glass plate was affixed to the carapace using cool-setting epoxy (Ten-Set™) and AVEDs were attached to this plate using a small wire and magnesium washer. Units were programmed to stay attached to the turtle for 3–24 h after which they would detach using a burnwire mechanism or when the magnesium washer dissolved. AVED packages were designed to be positively buoyant to facilitate retrieval at the surface using a VHF radio beacon.

2.2. Video data transcription

The first 30 min of each deployment was excluded from analysis to reduce the effects of capture stress on behavior. This brief acclimation period was specified due to the short nature of our video deployments (i.e., to ensure adequate data remained for analysis following the exclusion). Turtle behavior during this period comprised rapid escape swimming followed by a gradual return to swim speeds and behaviors typical of the rest of the deployment. Foraging was observed in the first 30 min of some green turtle deployments suggesting that, for some individuals, capture stress was not prolonged. Similarly, Seminoff et al. (2006) observed several typical behaviors upon release of green turtles equipped with video recorders in the Gulf of Mexico (e.g., Seminoff et al., 2006).

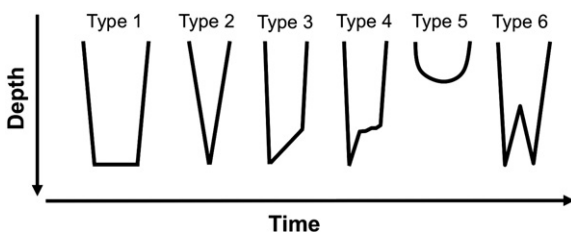


Fig. 1. Generic dive types: Generic dive types commonly performed by green and loggerhead turtles. Reproduced with permission from Seminoff et al. (2006, Fig. 3).

However, others have suggested post-capture stress periods, based on dive frequency, of several hours in longer time-depth recorder deployments (Hazel et al., 2009; Thomson et al., in press). This issue is addressed more thoroughly in the Discussion.

Video data were transcribed using a computer event recorder and behavior durations were measured to the nearest second. Behaviors measured included: 1) breathing (i.e., time at the surface with head above water); 2) descent; 3) swimming along the bottom; 4) resting (i.e., remaining motionless on the bottom except for occasional head movements); 5) swimming at a constant depth in the water column; 6) gradual ascent through the water column consisting of infrequent and gentle swimming strokes; 7) active ascent; 8) feeding; and 9) other behaviors including social interactions and sponge-rubbing (Heithaus et al., 2002b). We assumed that, while at the surface, turtles made a single exhalation and inhalation each time the head emerged above the water (Lutz and Bentley, 1985; Reina et al., 2005). During a dive, if the vertical direction of movement could not be easily discerned in the video footage, the duration of descents, ascents and mid-water swims was confirmed using the dive profile. Foraging tactics and prey data are presented elsewhere (Heithaus et al., 2002b; Burkholder et al., 2011; Thomson et al., unpublished) and are not addressed in detail here.

2.3. Dive profile analysis

Dives were classified visually following Seminoff et al. (2006); see also Hochscheid et al., 1999; Minamikawa et al., 2000; Houghton et al., 2002; Fig. 1). Briefly, Type 1 dives were characterized by steep ascent and descent angles and a distinct, relatively flat bottom phase. At this stage, we did not attempt to distinguish between Type 1a and 1b dives (Houghton et al., 2002) due to the subjective nature of visually differentiating these shapes (but see below). Type 2 dives were V-shaped, with minimal time spent at the maximum depth of the dive prior to ascent. Type 3 dives had steep descents prior to an extended, gradual ascent followed by a steep final ascent to the surface. Type 4 dives comprised a steep descent and a brief initial ascent followed by a prolonged, gradual ascent through the water column and a steep final ascent to the surface. Type 5 dives were parabolic in shape (i.e., lacking abrupt inflection points) and typically short and shallow. Type 6 dives were defined by Seminoff et al. (2006) as having a W shape with a depth change during the bottom phase of at least 2 m. To adjust this criterion to suit the shallow depth regime in Shark Bay, we used a value of 1.5 m.

The software Multi Trace Dive (Jensen Software Systems, Laboe, Germany) was used to analyze dive profiles. Dive cycles were detected and surface and dive times measured using a combination of vertical velocity and depth thresholds. Dives began when depth exceeded 0.75 m and inflection points separating dive phases (descent, bottom phase, ascent, surface interval) were detected using a vertical velocity threshold of 0.03 m s^{-1} . End of diving was detected when vertical velocity dropped below -0.03 m s^{-1} and the turtle returned to a depth shallower than 10% of the maximum dive depth. This depth threshold was necessary because green and loggerhead turtles often perform gradual ascents making a vertical velocity threshold alone insufficient for detecting the end of dives (e.g., Houghton et al., 2002). Video data were used to distinguish actual surfacing events from near-surface movements, which was not possible in extremely shallow water using the dive profiles alone. Each individual dive was inspected visually during analysis to ensure that the software settings consistently detected inflection points in the dive profile.

2.4. Statistical analysis

Data were analyzed in R v. 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria). We first compared several dive metrics

(maximum dive depth, duration and whether a dive reached the sea floor) among dive types using mixed effect models in the R package 'lmer'. This involved treating individual dives as data points and specifying turtle identity as a random effect. Depths and durations were log-transformed to reduce heteroscedasticity and post hoc Tukey tests were performed to test for pair-wise differences between dive types. Dives reaching or not reaching the sea floor constituted a binary response variable and were analyzed using generalized linear mixed models specifying a binomial error structure.

Within Type 1 dives, we tested whether dive characteristics correlated with time spent resting on the seabed. These included dive duration (min), maximum depth (m), proportion of the dive comprising the bottom phase, standard deviation of depth during the bottom phase (m) and vertical velocity during descent and ascent. These dive parameters correspond to those used by Houghton et al. (2002) to distinguish Type 1a and 1b dives. Resting duration data were zero-inflated and zeros in the data set were 'true' zeros (i.e., zeros resulting from no resting occurring as opposed to non-detection of resting). Thus, we opted for two-part (i.e., hurdle) models, employing zero-adjusted models in the R package 'pscl' (Zuur et al., 2009). These models involve, first, treating the entire data set as binary (i.e., coding positive durations as ones) and performing a binomial logistic regression to assess factors influencing the probability of resting occurring during a dive (referred to here as the binary model). Then, the zeros are discarded and a Poisson regression is performed on the non-zero component to assess factors influencing the duration of resting during a dive, given that resting did occur (referred to here as the conditional model). Due to low sample size, dives were pooled for all turtles in this analysis.

Preliminary examination of the data using a correlation matrix revealed strong collinearity between dive duration and the proportion of the dive comprising the bottom phase (Pearson's correlation coefficient = 0.53 for green turtles and 0.67 for loggerhead turtles). Collinearity between independent variables can result in unstable parameter estimates and reverse the sign of coefficients in regression analyses (Slinker and Glantz, 1985), which was observed in preliminary binary logistic models using this data set. We therefore opted to exclude the bottom phase variable from the regression analysis in favor of dive duration, which might be expected to vary more closely with resting behavior due to the positive relationship between activity and metabolic rate (i.e., potential for longer dives with lower activity).

We fitted a maximal model with a Poisson and negative binomial error structure and compared these using likelihood ratio tests and AIC scores to test for overdispersion in the non-zero component of the data (Zuur et al., 2009). Once the appropriate error structure was determined, we simplified the maximal model by sequentially removing non-significant terms, starting with the least significant, and confirmed the validity of each step using a likelihood ratio test.

Subsequently, we performed a k-means cluster analysis on Type 1 dive data using the six variables listed above. We specified two clusters to correspond with Type 1a and 1b subtypes identified by Houghton et al. (2002). We then summarized dive parameters from the dive profiles and behavioral data (i.e., resting versus benthic activity) from the video in each cluster to examine differences and similarities in their two-dimensional shape and function. We also explored whether an additional cluster in this analysis would lead to more reliable functional dive classification.

Finally, we wanted to determine whether the number of breaths taken while at the surface varied predictably with surface time. To maintain model simplicity for predictive purposes in this analysis, all dives were pooled for each species and analyzed using a generalized linear model, specifying a Poisson error structure. Following Zuur et al. (2009), we used the regression models to predict the number of breaths, along with 95% confidence bands, across the range of surface interval durations observed for each species.

Where appropriate, pseudo-R² values were calculated via regression of predicted on observed values to provide an estimate of the proportion of variance in a dependent variable explained by a model. Diagnostics for all models were checked following Crawley (2007) or Zuur et al. (2009).

3. Results

3.1. Data summary

Video and dive profile data were successfully obtained for 12 green turtles (10 unclassified, 2 male, mean CCL = 89.9 ± 3.79 cm SE) and 14 loggerhead turtles (9 unclassified, 5 male, mean CCL = 93.4 ± 2.58 cm SE). For green turtles, the duration of the linked segments of data, excluding the first 30 min following release, ranged from 0.20 to 2.43 h (mean = 1.77 ± 0.23 SE) while the number of dives in each deployment ranged from 3 to 52 (mean = 24.75 ± 4.46 SE). For loggerhead turtles, the duration of the linked segments ranged from 0.33 to 5.15 h (mean = 2.07 ± 0.31 SE) while the number of dives in each deployment ranged from 5 to 79 (mean = 24.07 ± 5.29 SE). Video data without accompanying dive profiles were obtained for a further four green and four loggerhead turtles and were included only to assess the proportion of all dives reaching the sea floor for each species.

For green turtles, Type 1 and 4 dives comprised the majority (68%) of total dive time with all other dive types each representing <8% of the total (Table 1). Dives that did not conform to the visual classification scheme represented 9.4% of total green turtle dive time. For loggerhead turtles, Type 1, 4 and 5 dives comprised the majority of total dive time (87%) with other dive types each representing <5% of the total (Table 1). Dives that did not conform to the visual classification scheme comprised 5.5% of total loggerhead dive time. Type 2 (V-shaped) dives were performed frequently by both species (ca. 18% of green and loggerhead turtle dives by frequency) but, due to their short durations, represented only 7% and 4% of green and loggerhead dive time, respectively.

3.2. Dive depth, duration and the probability of reaching the sea floor

The duration and maximum depth of dives varied by dive type for green turtles (duration, F_{5,265} = 60.81, P < 0.001; depth, F_{5,265} = 14.73, P < 0.001; Fig. 2A, C) and loggerhead turtles (duration, F_{5,302} = 61.29, P < 0.001; depth, F_{5,302} = 43.41, P < 0.001; Fig. 2B, D). Feeding was

observed during all dive types for green turtles but not during Type 3 or 6 dives for loggerhead turtles, although only six Type 3 and Type 6 dives were performed by loggerheads (Table 1). Benthic resting was observed during Type 1, 4 and 6 dives for green turtles and Type 1, 3 and 4 dives for loggerhead turtles (Table 1). Approximately 70% of all dives reached the sea floor and the probability of a dive reaching the bottom varied by dive type for both species (green turtles, χ² = 11.9, df = 5, P = 0.036; loggerhead turtles χ² = 50.5, df = 5, P < 0.001). Type 3 and 5 dives were least likely to be benthic for green turtles (although only 13 Type 3 dives were observed) while Type 2 and Type 5 dives were least likely to be benthic for loggerhead turtles (Table 1).

3.3. Benthic resting and Type 1 dive characteristics

Green and loggerhead turtles spent 1.3% and 8.2% of total dive time resting, respectively, with 64% and 95% of this time, respectively, occurring during Type 1 dives. For green turtles, the maximal model with a negative binomial error structure (AIC = 197.4, df = 13) fit the data significantly better than the model with a Poisson error structure (AIC = 296.5, df = 12; χ² = 101.1, df = 1, P < 0.001). The probability of resting occurring increased with dive duration and decreased with greater depth variation during the bottom phase (Table 2, Fig. 3A). When resting did occur, resting duration increased with dive depth (Table 2, Fig. 3A). Examination of model residuals indicated two problematic observations. Exclusion of these data points improved model fit based on pseudo-R² values, which increased from 0.540 to 0.753, and did not alter the significance of model parameters but did have a modest influence on parameter coefficients. Here, and for the loggerhead model below, results in Table 2 are based on the best-fit models while Fig. 3 shows all data. Since resting by green turtles was minimal and almost no dives comprised predominantly resting behavior, we did not attempt to identify groups of active versus resting Type 1 dives using cluster analysis.

For loggerhead turtles, the maximal model with a negative binomial error structure (AIC = 226.0, df = 13) fit the data significantly better than the model with a Poisson error structure (AIC = 876.7, df = 12; χ² = 652.7, df = 1, P < 0.001). Dive duration had a strong, positive effect on the probability of resting occurring during a dive. Maximum dive depth had a weak, positive effect on the probability of resting occurring while the standard deviation of depth during the bottom phase had a weak, negative effect (Table 2, Fig. 3B). When resting did occur during a dive, resting duration increased strongly

Table 1

Descriptive statistics for dives performed by 12 green and 14 loggerhead turtles fitted with AVED units. Means of individual means are presented with 1 SE in parentheses. Feeding and resting rows indicate whether these behaviors were observed, with the fraction of dives including each behavior in parentheses. Where indicated, cells in the same row not sharing the same superscript letter are significantly different based on Tukey's post hoc tests.

Green turtles	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
No. turtles performing dive type	11	9	6	10	6	5
No. dives with video	132	51	13	37	38	11
Mean proportion of total dive time	0.43 (0.08)	0.07 (0.03)	0.07 (0.03)	0.25 (0.06)	0.07 (0.03)	0.03 (0.01)
Mean maximum dive depth (m)	6.03 (0.48) ^b	4.82 (0.89) ^c	5.98 (1.01) ^{a,b}	6.77 (0.93) ^a	3.85 (0.68) ^c	5.30 (0.63) ^{b,c}
Mean dive duration (min)	5.29 (0.62) ^b	1.62 (0.42)	6.20 (1.05) ^{a,c}	6.67 (1.28) ^a	2.29 (0.65)	3.97 (0.86) ^{b,c}
Proportion reaching sea floor	0.71 (0.08)	0.78 (0.13)	0.39 (0.20)	0.83 (0.08)	0.53 (0.19)	0.83 (0.11)
Feeding observed?	Yes (21/132)	Yes (4/51)	Yes (2/13)	Yes (7/37)	Yes (3/38)	Yes (4/11)
Resting observed?	Yes (13/132)	No	No	Yes (4/37)	No	Yes (2/11)
<i>Loggerhead turtles</i>						
No. turtles performing dive type	11	10	4	11	12	2
No. dives with video	87	59	6	41	122	6
Mean proportion of total dive time	0.32 (0.06)	0.04 (0.01)	0.02 (0.01)	0.24 (0.06)	0.31 (0.09)	0.02 (0.01)
Mean maximum dive depth (m)	4.76 (0.61) ^a	2.45 (0.33)	4.92 (1.02)	5.73 (0.52)	2.61 (0.57)	1.49 (0.42)
Mean dive duration (min)	7.08 (0.92) ^b	1.24 (0.12)	6.64 (1.23) ^{a,b}	10.86 (1.65) ^a	3.80 (0.51) ^c	3.40 (0.08) ^{b,c}
Proportion reaching sea floor	0.86 (0.07)	0.32 (0.11) ^c	0.63 (0.24) ^{a,b}	0.85 (0.06) ^b	0.52 (0.14) ^c	1.00 (0.00) ^c
Feeding observed?	Yes (15/87)	Yes (1/59)	No	Yes (3/41)	Yes (15/122)	No
Resting observed?	Yes (14/87)	No	Yes (1/6)	Yes (2/41)	No	No

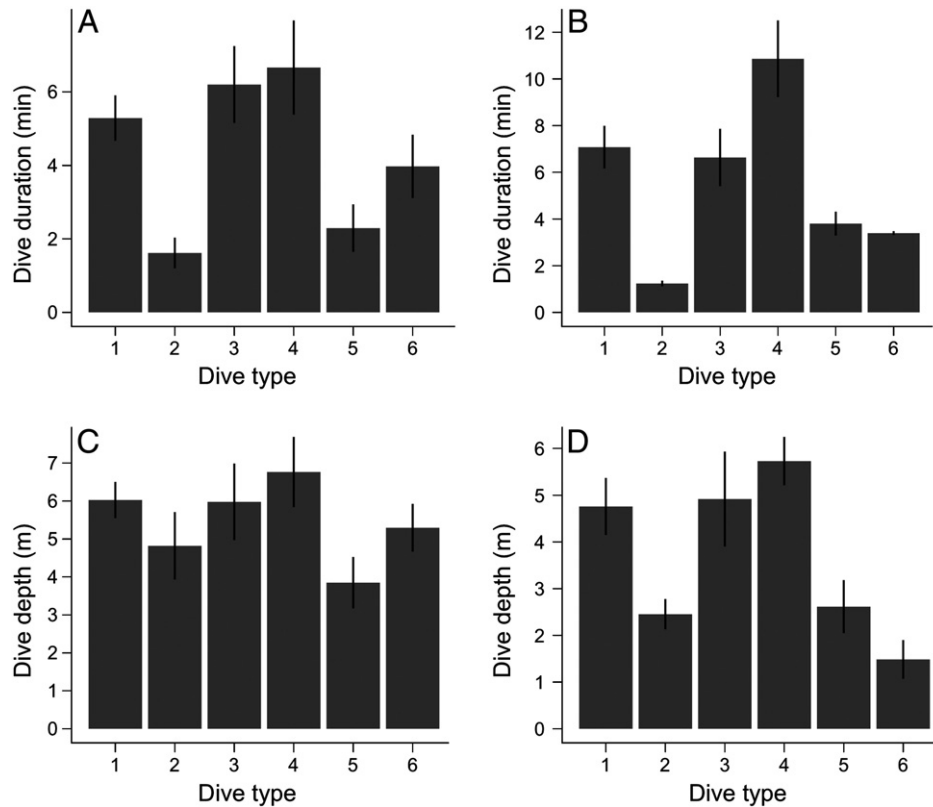


Fig. 2. Dive duration and depth: Dive duration and maximum depth of dive types commonly performed by green (A, C respectively) and loggerhead (B, D respectively) turtles. Means of each turtle's deployment mean are presented with 1 SE, while statistical analyses treated individual dives as data points with turtle identity included as a random effect.

with dive duration and decreased strongly with increasing depth variation during the bottom phase (Table 2, Fig. 3B). Examination of model residuals and plots of fitted versus observed values revealed two problematic observations. Exclusion of these data points improved model fit (pseudo- R^2 increased from 0.771 to 0.902), but did not change the significance of parameters in the model and had minimal influence on parameter coefficients.

The k-means cluster analysis with two groups identified 18 loggerhead dives in the first cluster (referred to as 1a) and 69 loggerhead dives in the second cluster (referred to as 1b). Dives in cluster 1a were distinguished from those in cluster 1b primarily by longer duration and a higher proportion of the dive comprising the bottom phase (Table 3). Video data revealed that more resting occurred during dives in cluster 1a, and a higher proportion of the bottom phase was spent resting, than during dives in cluster 1b (Table 3). However, dives in cluster 1a included roughly equal proportions of resting and traveling during the bottom phase. Furthermore, six long dives (>9.5 min) in cluster 1a did not include any resting; these dives

comprised predominantly swimming along the bottom or benthic foraging. Two dives in cluster 1b included short bouts of resting (<1 min).

When three clusters were specified, the first cluster (1a) included 12 long dives with bottom phases representing a high proportion of dive time and an average of 66% of the bottom phase spent resting (Table 4). Video revealed that these dives included a much higher proportion of bottom time spent resting than the other clusters. Moreover, all dives with periods of resting exceeding two minutes were included in this cluster. However, this cluster also included one dive comprising mostly benthic travel and one involving mostly feeding. The other two clusters (here, 1b and 1c) comprised progressively shorter dives with bottom phases representing lower proportions of dive time; minimal resting behavior was observed in these clusters, which were dominated by traveling (Table 4).

3.4. Surface interval as a proxy for oxygen loading

While at the surface, green turtles spent an average of 89.0% (SE = 4.70) of their time breathing with an average of 1.10 (SE = 0.04) breaths per surface interval and a mean surface interval duration of 3.74 s (SE = 0.50). Loggerhead turtles at the surface spent 63.1% (SE = 4.0) of their time breathing with an average of 2.79 (SE = 0.48) breaths per surface interval and a mean surface interval duration of 20.25 s (SE = 5.41).

The number of breaths taken varied closely with surface interval duration for both species (Fig. 4). For green turtles, the initial model was strongly influenced by two extended surface intervals (>50 s) leading to highly uncertain predictions of the number of breaths taken. While these two data points should be considered biologically meaningful, they were inadequate to reliably assess the number of breaths during longer surface durations. Thus, these observations were excluded to generate predictions of the number of breaths

Table 2

Results of hurdle models of benthic resting behavior during Type 1 dives by green and loggerhead turtles. SD represents the standard deviation of depth during the bottom phase, duration refers to dive duration and depth is the maximum dive depth.

Species	Model	Fixed effect	Coefficient	SE	P-value
Green	Binary	SD	-15.234	5.622	0.007
		Duration	0.559	0.143	<0.001
	Conditional	Depth	0.670	0.139	<0.001
Loggerhead	Binary	SD	-14.720	10.909	0.177
		Duration	0.911	0.295	0.002
		Depth	0.943	0.423	0.026
	Conditional	SD	-9.107	1.986	<0.001
		Duration	0.272	0.038	<0.001

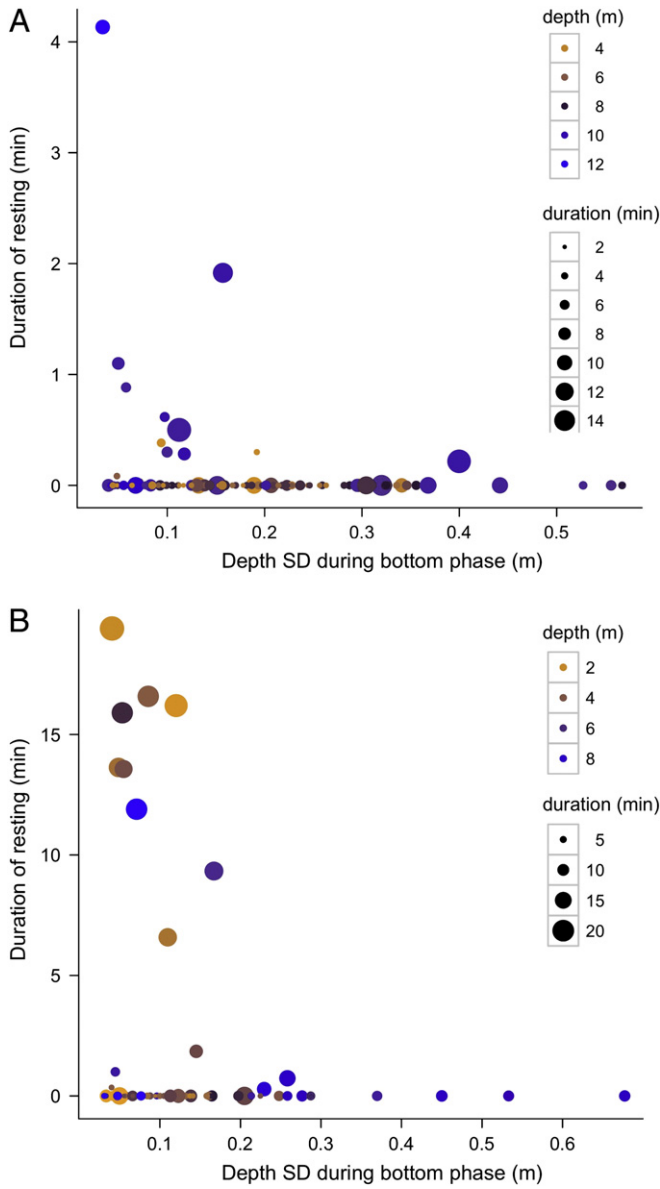


Fig. 3. Benthic resting and Type 1 dive characteristics: The proportion of the bottom phase of Type 1 dives spent resting by standard deviation of depth during the bottom phase for green (A) and loggerhead turtles (B). Symbol sizes reflect dive durations while the color gradient reflects maximum dive depths.

taken during other surface intervals, which were all <20 s long. For loggerhead turtles, examination of model residuals suggested the addition of a quadratic term could improve fit, which was confirmed by comparison of AIC values between models with and without this term. Based on comparison of observed versus fitted values for the final models, a smaller proportion of the variance in the number of

breaths taken was explained by surface interval duration for green turtles (co-efficient = 0.681, SE = 0.028, P < 0.001, pseudo-R² = 0.670) than for loggerhead turtles (co-efficient = 0.868, SE = 0.020, P < 0.001, pseudo-R² = 0.849).

4. Discussion

Animal-borne video imaging technology can be valuable for analyzing relationships between dive-surfacing patterns and behavior, allowing for more informed inferences based on stand-alone dive profiles, which are more affordable and easily obtained (e.g. Calambokidis et al., 2007; Davis et al., 2003; Heithaus et al., 2002b; Mori et al., 2005; Williams et al., 2000). Even in cases where detailed dive profiles are not available (e.g., satellite-linked tags that relay only dive durations), video data sets may be useful in enabling some generalizations about variation in dive function. Here, we have illustrated the value of AVED systems for informing the interpretation of sea turtle dive profiles in a coastal foraging area (see also Reina et al., 2005; Seminoff et al., 2006).

4.1. What generalizations can be made about the function of common dive types?

Behavior during Type 1 dives was diverse for green and loggerhead turtles, consistent with previous findings. For example, Seminoff et al. (2006) found that Type 1 dives by green turtles could include benthic traveling, resting and foraging. In the current study, the majority of Type 1 dives by both species were benthic and many included foraging, benthic traveling, resting or some combination of these activities. Despite this diversity in behavior, characteristics of Type 1 dives did provide insight into the extent of resting behavior during a dive (see below).

Type 2 dives are often assumed to be active exploratory or traveling dives for marine turtles (Hochscheid et al., 1999; Seminoff et al., 2006; van Dam and Diez, 1996). In Shark Bay, Type 2 dives comprised continuous swimming during descent and ascent, which is consistent with flipper beat data during V-dives reported for both species (Hays et al., 2004a). The majority of Type 2 dives reached the sea floor for green turtles (78%), which would support a benthic exploratory function, but not for loggerhead turtles (32%); these dives more often involved near-surface movements for loggerheads. Furthermore, Type 2 dives appear to play a role in foraging for green turtles, which frequently fed on gelatinous plankton suspended in the water column (Heithaus et al., 2002b; Burkholder et al., 2011). Only one feeding event occurred for loggerhead turtles during a Type 2 dive and it occurred on the sea bottom.

Type 3 and 4 dives are unique among reptilian dives due to a gradual ascent phase preceding a short, final ascent to the surface (e.g., Graham et al., 1987; Minamikawa et al., 1997). It has been suggested that gradual ascents could represent stationary mid-water resting (Minamikawa et al., 2000) or, alternatively, an energy conservation tactic by turtles in transit (Hays et al., 2004b; Hochscheid et al., 1999; Houghton et al., 2002). In Shark Bay, green turtles spent an average of ca. 70% of bottom time during Type 4 dives actively swimming, while loggerhead turtles spent an average of ca. 82% of bottom time swimming. Turtles also typically maintained a low flipper stroke rate during

Table 3
Summary of dive profile characteristics and turtle behavior in two clusters of Type 1 dives. Means are presented with (1 SE).

Cluster	N dives	Dive profile characteristics						Behavior				
		Duration (min)	Depth (m)	Bottom phase as proportion of dive	Depth SD during bottom phase (m)	Descent rate (m s ⁻¹)	Ascent rate (m s ⁻¹)	Duration of resting (min)	Proportion of bottom phase resting	Proportion of bottom phase traveling	Proportion of bottom phase feeding	
1a	18	14.55 (0.82)	4.39 (0.56)	0.86 (0.02)	0.11 (0.02)	0.12 (0.01)	-0.08 (0.01)	7.00 (1.74)	0.45 (0.10)	0.44 (0.10)	0.11 (0.07)	
1b	69	4.73 (0.27)	4.73 (0.25)	0.51 (0.03)	0.13 (0.01)	0.13 (0.01)	-0.07 (0.00)	0.02 (0.02)	0.02 (0.02)	0.90 (0.03)	0.06 (0.02)	

Table 4
Summary of dive profile characteristics and turtle behavior in three clusters of Type 1 dives. Means are presented with (1 SE).

Cluster	N dives	Dive profile characteristics					Behavior				
		Duration (min)	Depth (m)	Bottom phase as proportion of dive	Depth SD during bottom phase (m)	Descent rate (m s^{-1})	Ascent rate (m s^{-1})	Duration of resting (min)	Proportion of bottom phase resting	Proportion of bottom phase traveling	Proportion of bottom phase feeding
1a	12	16.57 (0.65)	4.30 (0.73)	0.88 (0.03)	0.11 (0.02)	0.11 (0.01)	-0.08 (0.01)	10.32 (2.01)	0.66 (0.12)	0.25 (0.10)	0.09 (0.07)
1b	31	8.00 (0.30)	5.46 (0.43)	0.66 (0.04)	0.18 (0.03)	0.13 (0.01)	-0.06 (0.01)	0.10 (0.07)	0.03 (0.02)	0.85 (0.05)	0.12 (0.05)
1c	44	3.22 (0.15)	4.20 (0.24)	0.44 (0.03)	0.09 (0.01)	0.13 (0.01)	-0.07 (0.01)	0.01 (0.01)	0.02 (0.02)	0.92 (0.03)	0.03 (0.02)

gradual ascents, although camera positioning did not allow reliable observation of flipper motions in some videos. Overall, this suggests an energy conservation tactic while traveling. Like Type 2 dives, gradual ascents played a dual role for green turtles because they included mid-water foraging on gelatinous macro-plankton. Seven of nine foraging events during these dives by green turtles occurred in the gradual ascent phase. In contrast, all feeding by loggerheads in these dives occurred during the bottom phase on the sea floor.

Type 5 dives were behaviorally diverse but exclusively active dives for both species (i.e., no resting was observed). These dives included foraging and reached the sea bottom in just over 50% of cases for both green and loggerhead turtles. Generally, these dives were associated with searching-foraging behavior, travel along the sea bottom or in mid-water. The smooth, parabolic profile of these dives was consistent with dives attributed to traveling in other taxa (e.g., marine mammals, Williams et al., 2000). Type 6 dives occurred rarely and generalizations regarding their function require further data.

4.2. Can maximum dive depth be used to infer habitat depth?

Overall, turtles in this study dove to the sea floor approximately 70% of the time (including analysis of video data without linked dive profiles, which are not included in Table 1) and the probability of a dive reaching the sea floor depended on dive type. Therefore, when attempting to infer habitat depth from dive profiles it is important to consider the shape of individual dives. Green and loggerhead

turtles in Shark Bay frequently perform short, shallow Type 2 or 5 dives near the surface between consecutive longer, deeper dives with distinct bottom phases suggesting a benthic stage (Thomson et al., unpublished). To avoid habitat misclassifications, habitat depth should be estimated based on the maximum depth of likely benthic dives (e.g., Type 1, Type 4) and uncertainty in depth classifications based on other dive types should be recognized. Extended sequences of parabolic (i.e., Type 5) dives may be particularly problematic because these dives can reflect either benthic or mid-water travel and thus often do not reflect habitat depth.

4.3. Do dive characteristics reveal activity during Type 1 dives?

The standard deviation of depth during the bottom phase, dive duration and maximum dive depth correlated with resting behavior versus activity during Type 1 dives. The strong correlation between Type 1 dive duration and resting behavior was consistent with previous research (Hays et al., 2000b; Seminoff et al., 2006). Furthermore, a statistical means of subgrouping Type 1 dives based on dive profile characteristics (e.g., Houghton et al., 2002) did associate with functional differences. However, relatively long benthic traveling dives at a constant depth were grouped with resting dives, particularly when two dive clusters were specified. Furthermore, dives with resting behavior in our data set often also included other activities (e.g., foraging, traveling). Some of this behavioral overlap can likely be attributed to the fact that minimal resting was observed in our short AVED deployments. Neither long (i.e., >30 min), single Type 1 dives, nor extended sequences of Type 1 dives to a constant depth, were observed in this study. These features of diving behavior are characteristic of green and loggerhead turtles (e.g., Hochscheid et al., 1999; Hays et al., 2000a,b; Houghton et al., 2002; Seminoff et al., 2006; Thomson et al., unpublished). Instead, resting in our data set was consistent with the 'episodic resting' described by Seminoff et al. (2006). Longer dive profiles with video data are required to determine whether long bouts of resting behavior can be identified using dive characteristics. Furthermore, data are required to evaluate these relationships across different chelonid life stages. Dive profiles and turtle behavior may vary between feeding and breeding areas (e.g., Storch et al., 2005) or among breeding areas differing in resource availability (e.g., Hays et al., 2002). Dives appearing similar in shape may reflect different activities when performed during different life stages. Despite its limitations, our data set provides encouragement that such functional grouping of dives based on dive profile characteristics is possible with adequate data.

A potential problem with the use of standard deviation in depth during the bottom phase as an indicator of activity is the influence of tidal or, possibly, sea state variation. Tidal flux may be problematic if turtles are diving for extended periods in strong tidal environments. In Shark Bay the tide range is ca. 1.2 m (Burling et al., 2003) and there is minimal oceanic swell that could result in large depth fluctuations. However, extended sequences of Type 1 dives with cyclic depth changes corresponding to tidal period and amplitude have been observed in longer dive records (Thomson et al., unpublished). Such depth variation would need to be accounted for if using bottom phase characteristics to assess resting versus activity. One possible

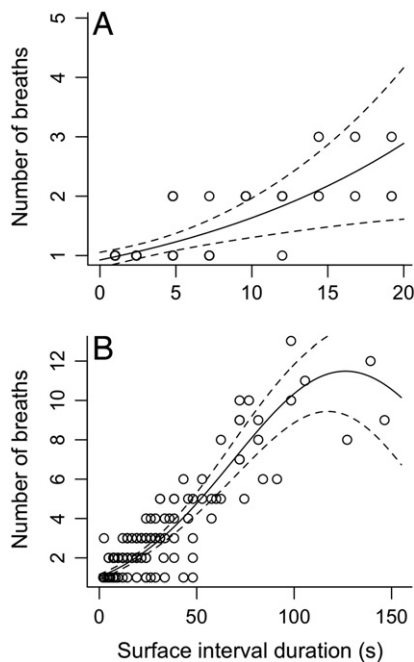


Fig. 4. Breathing and surface interval duration: The number of breaths taken by green (A) and loggerhead turtles (B) as a function of surface interval duration. Regression equations were: green turtles, $y = \exp(-0.07727 + 0.05690 \cdot x)$; loggerhead turtles, $y = \exp(0.03369 + 0.03810 \cdot x - 0.00015 \cdot x^2)$, where x is surface interval duration (s).

means of doing this would be to place a data logger on the seabed to directly measure tidal or sea state fluctuations (see Hays et al., in press).

4.4. Surface interval duration as a proxy for oxygen loading

The number of breaths taken while at the surface varied closely with surface interval duration, particularly for loggerhead turtles. Thus, if tidal volume data are available, it may be possible to directly estimate oxygen stores prior to a dive based on surface interval duration. Furthermore, the surfacing and breathing patterns of green and loggerhead turtles were quite different. Green turtles spent minimal time at the surface, most of which comprised time breathing during a small number of head emergences. Loggerhead turtles spent considerably longer at the surface with a lower proportion of that time spent breathing and more breaths taken. While most head emergences lasted a few seconds, in rare instances turtles appeared to keep their head above water long enough for a second breath, which would lead to error in estimated oxygen intake.

The differences in surfacing behavior between the two species likely reflect a combination of physiological and behavioral traits. Green turtle tidal volumes may be considerably greater than those of loggerhead turtles (Lutcavage and Lutz, 1997), meaning loggerhead turtles would require relatively more breaths to replenish O_2 and expel CO_2 than green turtles for a given dive duration, all else equal. Additionally, both species are under risk of predation from tiger sharks (*Galeocerdo cuvier*; Heithaus et al., 2002a; Heithaus et al., 2007). Between breaths, loggerhead turtles often submerge their heads and scan in all directions beneath them (J.T., personal observation), which could be a vigilance tactic. It is possible that these two surfacing tactics represent different methods of mitigating predation risk within species-specific physiological limitations. The effect of tiger shark density on surfacing patterns remains an important, unresolved question (Frid et al., 2007; Heithaus and Frid, 2003).

4.5. Possible effects of AVED units on diving behavior

It is important to consider the effects of capture stress and the AVED units on marine turtle behavior, particularly due to the short nature of the deployments. As one means of mitigating the effects of stress, the first 30 min of data were excluded from analyses. However, Thomson et al. (in press) and Hazel et al. (2009) observed a trend toward increased dive frequency in the first several hours of longer dive profiles for green and loggerhead turtles collected using stand-alone TDRs, suggesting more prolonged impacts of capture and instrumentation. To test the effects of AVED deployments on turtle behavior further, we compared dive durations from the AVED data set for each species with those predicted under similar temperature and depth conditions using hierarchical regression models of Thomson et al. (in press), which were based on dive records for 29 green and 46 loggerhead turtles. For green turtles in the AVED study, mean habitat depth was 5.60 m ($SE=0.59$), mean daily water temperature was $20.04^\circ C$ ($SD=3.62$) and mean observed dive duration was 4.83 min ($SE=0.67$). Predicted dive duration at this depth and temperature using the models from the TDR study was 6.92 min. For loggerhead turtles in the AVED study, mean habitat depth was 3.61 m ($SE=0.52$), mean daily water temperature was $24.67^\circ C$ ($SD=3.52$) and mean observed dive duration was 6.02 min ($SE=0.91$). Predicted dive duration for this depth and temperature from the TDR study was 10.00 min. Thus, AVED units appear to have reduced dive durations, which could arise as a result of elevated metabolism from capture stress, added buoyancy from the AVED or increased energy expenditure due to drag caused by the AVED. Progress in AVED technology (e.g., smaller unit size, increased memory allowing longer deployments) will reduce these effects in the future.

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