Surface behavior of pelagic juvenile loggerhead sea turtles in the eastern North Atlantic

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ABSTRACT

Sea turtles bask at the ocean surface, but little is known about the patterns and ecological context of surface behavior in the wild. This study investigated the surface behavior of ten juvenile loggerhead sea turtles (34 - 58 cm straight carapace length) satellite tagged in Madeira, in the pelagic eastern North Atlantic. During a total of 2273 tracking days, turtles moved through oceanic areas with a mean depth of ~3400 m. On average, turtles spent one third of the time at the surface (0 - 1 m depth), spending 43% of the time at the surface during the day and 29% of the time during the night. Generalized linear mixed modelling showed that the proportion of time at the surface was significantly larger during the day, particularly during spring and summer. Time spent at the surface during the day increased with elevated air temperatures and weak winds, probably to maximize the benefits of solar absorption. Conversely, the probability of being at the surface during the day decreased as horizontal search effort increased, suggesting a trade-off between basking and daytime foraging activities. At night, time spent at the surface was not associated with air temperature or wind speed but was instead positively associated with moon illumination. As turtles tend to dive deeper during clear nights, increased surface time may be needed to recover from deeper dives. This study presents important aspects of the behavioral ecology of the species during the oceanic juvenile phase. The findings reported here may be relevant for species management and conservation, including correction of census data and management of interactions with surface fishing gear and other anthropogenic activities.

1. Introduction

Basking is a frequent activity for most reptiles, exposing them to solar radiation (see Zug et al., 2001). Basking has been associated primarily to thermoregulation (Boyer, 1965), but it may also benefit epidermis health, synthesis of vitamin D and reduction of plant and animal parasites (Boyer, 1965; Spencer et al., 1998; Stephen, 1982).

As well as the apparent benefits, basking behavior has associated costs. Time spent basking may reduce foraging time and increase exposure to predators (Heithaus and Frid, 2003; Huey and Slatkin, 1976). The pressure for other activities, such as foraging and predator avoidance, may offset the need for basking (Crawford et al., 1983). Basking behavior may thus represent a compromise between demands and benefits. For example, under low thermal quality conditions, such as winter or early morning, the costs of basking may outweigh its thermal benefits (Blouin-Demers and Nadeau, 2005; Crawford et al., 1983; Rowe et al., 2014).

Sea turtles bask at the ocean surface (Carr, 1952; Sapsford and van der Riet, 1979; Schofield et al., 2017) and some populations of green turtles also bask on land (Van Houtan et al., 2015; Whittow and Balazs, 1982). Captive sea turtles elevate their body temperature by basking at the water surface (Sapsford and van der Riet, 1979) or on land (Swimmer, 2006). Field studies indicate that sea turtles in pelagic and nearshore habitats spend more time at the surface during the day than at night, probably to benefit from solar radiation (Hochscheid et al., 2010; James et al., 2005; Ogden et al., 1983; Polovina et al., 2003;

Revelles et al., 2007). Surface behavior in sea turtles may also be needed to recover from anaerobic activity (Hochscheid et al., 2010), as well as be used as a form of resting/sleeping, particularly in deep areas where turtles cannot reach the sea bottom (Dujon et al., 2017). Basking in documented both for juveniles and adults, including adult females in nearshore areas prior to egg laying (Schofield et al., 2006; Schofield et al., 2017). Maternal basking probably increases body temperature and maximizes energy conservation, favoring egg development (Hays et al., 2002; Wapstra, 2000).

Like other sea turtle species, loggerhead sea turtles hatch on coastal beaches. Soon after hatching, juveniles enter the ocean and move off-shore to pelagic habitats (Bolten, 2003; Carr, 1987; Mansfield and Putman, 2013; Scott et al., 2014). In the North Atlantic, juvenile log-gerheads undertake a developmental migration through the North Atlantic Gyre (Bjorndal et al., 2003; Bolten et al., 1998; Monzón-Argüello et al., 2009). These juveniles, mainly originating from western Atlantic nesting beaches, can be observed off the archipelagos of Azores and Madeira before they return to coastal habitats as large juveniles or adults (Bolten, 2003; Mansfield et al., 2009). While neonates remain mainly at the surface during the first year (Mansfield et al., 2014), ju-veniles with straight carapace length (SCL) over 34 cm seem to spend most of their time diving to depth (Freitas et al., 2018; Howell et al., 2010; Mansfield and Putman, 2013; Polovina et al., 2003; Varo-Cruz et al., 2016). The patterns and function of their surface behavior is little understood.

The present study investigated the surface behavior of juvenile sea turtles (34 - 58 cm SCL) satellite tagged in Madeira, Portugal, in the pelagic eastern North Atlantic. We tested the hypothesis that surface behavior was associated with warm temperatures, wind-free and cloud-free conditions, to maximize the benefits of solar absorption. Further, we tested the relationship between surface behavior and foraging effort, with the hypothesis of a trade-off between solar absorption, rest and foraging activity. The possible effect of other individual and extrinsic parameters on surface behavior, such as season, moon illumination and body size, was also investigated to better understand the context and function of surface behavior.

2. Materials and methods

2.1. Animal telemetry data

A total of 10 loggerhead sea turtles were equipped with Argos sa-tellite transmitters (Wildlife Computers SDR-T10, 360 g on air) at Madeira Island, Portugal (Fig. 1), during spring and fall 1998 (Table 1). Turtles were captured while basking off the south coast of Madeira. Turtles were approached by boat from behind and captured by hand. Turtles were brought to captivity for tagging and released offshore, 4 to 13 days later. Turtles ranged in size from 33.9 cm to 57.6 cm SCL and weighed between 7.5 kg and 29.5 kg (Table 1). Satellite transmitters were attached to the turtle's carapace with fiberglass using a "backpack" attachment method adapted from Balazs et al. (1996).

Satellite transmitters provided location and dive data. Dive data were collected continuously (range 0 - 251 m, 1 m resolution) and later transmitted via Service Argos when turtles were at the surface. Data transmission limitations required diving data to be compressed into four 6-h histograms per day: night (21 - 03 h local time = GMT), dawn (03 - 09 h), day (09 -15 h) and dusk (15 - 21 h). Three types of histo-grams were obtained: the number of dives to maximum depth layers (maximum-depth histograms), number of dives to dive duration cate-gories (duration histograms) and the proportional time within each depth layer (time-at-depth histograms). Diving data contained in these histograms have been analyzed in detail by Freitas et al. (2018), while this study focused on surface behavior. Turtles were considered to be at the surface when at 0 - 1 m depth. Time-at-depth histograms contained the proportional time within 10 depth layers: 0-1 m, 1-3 m, 3-6 m, 6-10 m, 10-25 m, 25-50 m, 50-75 m, 75-100 m, 100-150 m and > 150 m. Time spent at the surface (0 - 1 m depth) was therefore extracted from each time-at-depth histogram.

Time-at-depth histograms were provided with an associated time, so location could be estimated from the track of the animals. Animal lo-cations were provided by Service Argos and therefore had an accuracy ranging from 150 to > 1500 m, depending on the location quality class (Vincent et al., 2002). In order to eliminate the low-accuracy locations
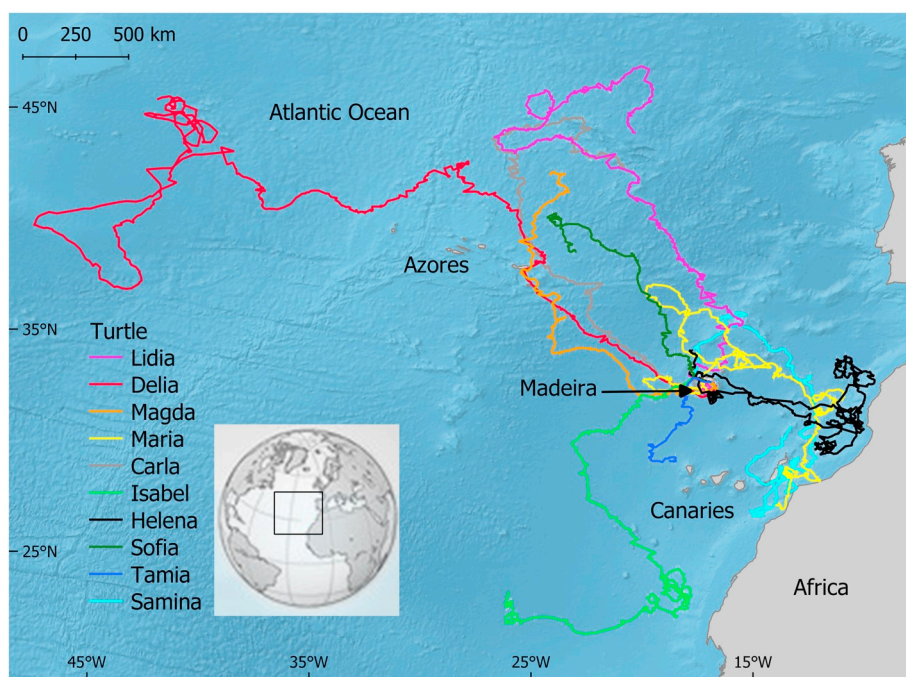

Fig. 1. Satellite track of ten juvenile loggerhead sea turtles captured, tagged and released in Madeira, Portugal, in 1998. Tracks are coloured according to turtle ID. White vertical marks along the tracks show the locations where surface data is available from 6-h dive histograms.

Table 1
Summary of tracking records of 10 juvenile loggerhead sea turtles tagged in Madeira in spring and fall, 1998. Abbreviations: CCL, curved carapace length; SCL, straight carapace length.

Turtle ID	Turtle name	CCL (cm)	SCL (cm)	Released	N days tracked	N raw locations	N filtered locations	N dive histograms
97-946	Lidia	45.7	41.3	1998-04-01	274	1454	996	997
97-947	Delia	63.1	57.6	1998-05-18	278	1258	1005	958
97-948	Magda	50.5	46.1	1998-05-18	109	639	438	402
97-949	Maria	51.2	46.2	1998-05-27	342	1090	852	1050
97-950	Carla	37.9	33.9	1998-05-27	158	730	459	538
98-291	Isabel	57.7	52.3	1998-09-10	311	1212	853	972
98-292	Helena	51.2	48.3	1998-09-10	341	1101	744	993
98-293	Sofia	48.6	44.5	1998-09-10	123	577	431	417
98-294	Tamia	44.9	39.9	1998-09-10	57	192	123	161
98-295	Samina	44.0	40.0	1998-09-10	280	1069	874	869
Total					2273	9322	6775	7357

associated with unrealistic swimming speeds (> 2 m/s) and sharp turning angles, Argos locations were filtered using a speed and turning angle algorithm (Freitas et al., 2008). Filtering was performed using the library 'argosfilter' (function 'sdafilter' with all default parameters) in R software (R_Core_Team, 2015). The number of raw and filtered locations per location quality class is presented on Table S1. The location of dive histograms (at 00:00, 06:00, 12:00 and 18:00, for night, dawn, day and dusk histograms, respectively) was estimated by linear interpolation of the filtered track (Fig. 1).

2.2. Individual and environmental data

In order to investigate how time at the surface was affected by extrinsic and intrinsic variables, the following variables were obtained for each 6-h histogram: diel period (night, dawn, day and dusk), season (winter, spring, summer and fall), sea bottom depth (m), sea surface temperature (SST, ℃), air temperature (℃), wind speed (m s $^{-1}$), cloud coverage (%), moon illumination (%), turtle carapace size, SCL (cm) and turtle first-passage time (FPT, h). FPT is defined as the time required for a tracked animal to cross a circle of a given radius (Fauchald and Tveraa, 2003) and was used as a measure of search effort. All variables were obtained for each histogram location and time, at courser resolution than location data, to ensure unbiased extraction of these variables. Seasons were defined as: winter (December to February), spring (March to May), summer (June to August) and fall (September to November). Sea bottom depths were extracted from GEBCO 2014 grid data, with 30 arc-second resolution. SST, air temperature, wind speed and cloud coverage data were extracted from daily, 14 km resolution climate reanalysis data (ERA-Interim) from the European Center for Medium-Range Weather Forecasts (ECMWF). Moon illumination, ranging from 0 (during new moon) to 1 (during full moon) was extracted using the R software library ´Lunar´. Analysis of the foraging behavior of the study animals revealed that turtles performed area-restricted search at scales of approximately 10 km radius, i.e. 20 km diameter, within their home range (Freitas et al., 2018). To obtain a measure of horizontal search effort, FPT at 10 km radius was therefore calculated for each dive histogram location. FPTs were calculated in R software, using the library 'adehabitatLT' (Calenge, 2006).

2.3. Statistical analyses

Data exploration techniques were applied as described in Zuur et al. (2010). The presence of outliers in the response and continuous covariates was investigated with Cleveland dotplots. Collinearity (relationships between covariates) was assessed with Pearson correlation coefficients, scatterplots and boxplots.

The proportion of time at the surface, at a given 6-h sampling period, was modelled using a generalized linear mixed model (GLMM), with quasibinomial distribution. This distribution was used instead of binomial distribution given over-dispersion in the data. We

hypothesized that surface behavior was affected by time of the day, season, meteorological conditions (SST, wind speed, cloud coverage and air temperature), as well as by the search behavior by turtles (FPT) and turtle body size (SCL), and therefore considered these variables as covariates. Turtle ID was used as a random intercept variable to account for random variation between individuals. SST and air temperature were highly correlated ($r = 0.9$) and were therefore not used simultaneously in the models to avoid collinearity issues. We chose to use air temperature with the hypothesis that turtles would spend more time at the surface during warm days to maximize the benefits of solar absorption. The model took the following form:

$$\text{Logit}(p_{ij}) = \alpha + \beta_1 \text{Diel}_j + \beta_2 \text{Season}_j + \beta_3 \text{FPT}_{ij} + \beta_4 \text{Wind}_j + \beta_5 \text{Cloud}_j + \beta_6 \text{Temp}_j + a_{ij} + \varepsilon_{ij}$$

The term p_{ij} denotes the proportion of time at the surface by individual i at the 6-h sampling period j. Diel_j is the time of the day at sampling period j and Season_j is the corresponding season. FPT_{ij}, is FPT of individual i at sampling period j, while Wind_j, Cloud_j and Temp_j are wind speed, cloud coverage and air temperature at sampling period j. β_1 to β_6 are the model coefficients. The random intercept a_i allows for a random variation around the intercept α and is assumed to be normally distributed with mean 0 and variance $\delta^2_{\text{individual}}$. The term ε_{ij} is independently normally distributed noise.

We further investigated whether environmental conditions affected differently the proportion of time at the surface during the day or during the night. For instance, if surface behavior during the day was associated with solar exposure, then we would expect that air temperature, wind speed and cloud coverage had a significant effect on the amount of time spent at the surface during the day, but not during the night. Further, if nighttime basking was associated with recovery from foraging dives or surface feeding of prey that undertake diel vertical migration (DVM), we would expect a significant association with moon illumination, as prey are expected to stay deeper during light nights (Stanley, 1990). To test these hypotheses, the following models were fitted:

$$\text{Logit}(p_{ij\,day}) = \alpha + \beta_1 \text{Season}_j + \beta_2 \text{FPT}_{ij} + \beta_3 \text{Wind}_j + \beta_4 \text{Cloud}_j + \beta_5 \text{Temp}_j + a_{ij} + \varepsilon_{ij}$$

$$\text{Logit}(p_{ij\,night}) = \alpha + \beta_1 \text{Season}_j + \beta_2 \text{FPT}_{ij} + \beta_3 \text{Wind}_j + \beta_4 \text{Cloud}_j + \beta_5 \text{Temp}_j + \beta_6 \text{Moon}_j + a_{ij} + \varepsilon_{ij}$$

where p_{ij} denotes the proportion of time at the surface during daytime or nighttime by individual i at the 6-h sampling period j and Moon_j represents moon illumination at the sampling period j. All models were fitted using the R package mgcv, function gamm (using the quasibinomial family and no smooth factors). Because model covariates used in this study were from widely different scales, all covariates were centered and scaled (centered to mean zero and variance of one), by

subtracting the mean to each value and dividing by the sample standard deviation (function scale in R). This standardization aimed to improve model computation and make comparison between model coefficients possible (Zuur et al., 2007).

3. Results

Sea turtles were monitored for 57 to 342 days (Table 1). In total, 9322 locations and 7357 time-at-depth histograms were obtained during a total of 2273 tracking days (Table 1). Turtles moved through deep oceanic areas, with a mean sea-bottom depth of 3372 m (max 5644 m), while few observed locations (6%) were in areas shallower than 1000 m (Fig. 1). During the tracking period, animals faced a variety of environmental conditions, with wind speed ranging from 0.2 to 22 m s^{-1}, air temperature of 7.0 to 26.8 °C and SST between 14.4 and 25.5 °C. Air temperature was highest during summer and fall, while wind speed was lowest during those seasons (Fig. S1). FPT, i.e., time spent in a 10 km radius area, ranged from 4 to 276 h (Fig. S1).

Analysis of time-at-depth histograms indicated that complete diving information (i.e., 4 time-at-depth histograms) was available for 1210 days (approximately 50 % of the tracking days, Fig. S2). The daily amount of time spent at the surface (0 - 1 m depth) ranged from 0.4 to 24 h. On average, turtles spent one third of the time at the surface (mean ± SE = 35 ± 4%, n = 10). Turtles were observed at the surface during the day (09:00-15:00), night (21:00-03:00), dawn (03:00-09:00) and dusk (15:00-21:00) but spent on average more time at the surface during the day (43 ± 5%) than at night (29 ± 4%) (Fig. 2). A seasonal analysis showed the highest amount of time spent at the surface was during spring and summer, during the day (Fig. 3). Surface activity was higher during the day across all seasons except winter, when turtles spent more time at the surface during the night (Fig. 3).

GLMM modelling (Table 2) confirmed that the proportion of time at the surface was higher during the day than at night, and significantly higher during spring and summer compared to winter. Further, the proportion of time spent at the surface during the day increased with air temperature and decreased with wind speed (Table 2, Fig. 4A). Under calm wind conditions and air temperatures above 20°C, the model predicted that turtles would spend over 50% of the time at the surface (Fig. 4A). Interestingly, the proportion of time at the surface during the day decreased in areas where FPT was higher, i.e., areas of higher horizontal search effort (Table 2, Fig. 4B). As hypothesized, time spent at the surface during the night was not associated with air temperature or wind speed, and positively associated with moon illumination (Table 2). Turtle body size and cloud coverage did not have a significant effect on the probability of being at the surface (Table 2).

4. Discussion

Surface behavior of sea turtles is expected to be the result of a trade-off between competing benefits and needs. Turtles in this study stayed at the surface mainly during daytime, in particular during spring and summer, probably to benefit from solar absorption. On the other hand, the probability of being at the surface during daytime decreased in areas of high horizontal search effort, suggesting a trade-off between basking and foraging activities. The need for resting or recovery from diving activity may also affect patterns of surface behavior. Turtles spent more time at the surface during full moon nights, which may be related to recovery from foraging at deeper depths.

The ecology of basking behavior in terrestrial, freshwater and sea turtles has been studied for decades (e.g. Boyer, 1965; Sapsford and van der Riet, 1979; Spotila and Standora, 1985), but has only recently been made possible in the natural habitat of sea turtles with advances in monitoring technologies (e.g. Braun-Mcneill et al., 2010; Cardona et al., 2005; Hochscheid et al., 2010; James et al., 2005; Polovina et al., 2003; Revelles et al., 2007). Turtles in this study were monitored year-round and found to spend on average one third of the time at the surface; slightly more than reported for juvenile loggerheads in the Pacific (Howell et al., 2010), but approximately the same as reported for juveniles in the Mediterranean Sea (Cardona et al., 2005). Turtles spent more time at the surface during the day than during the night, consistent with previous studies (e.g. Hochscheid et al., 2010; James et al., 2005; Ogden et al., 1983; Polovina et al., 2003; Revelles et al., 2007), suggesting an association with solar exposure. The positive association with air temperature and negative association with wind speed adds to evidence for a link between surface behavior and absorption of solar energy. Solar exposure may be important for the health of the epidermis, for the synthesis of vitamin D and for reducing the incidence of plant and animal parasites (Boyer, 1965; Stephen, 1982). However, the bulk of the evidence suggests that the primary benefit of basking is elevated body temperature (Boyer, 1965; Dubois et al., 2009). Experiments in captivity have shown that sea turtles can increase their body temperature by behavioral means, either by basking at the water surface (Sapsford and van der Riet, 1979) or on land, in the case of green turtles (Swimmer, 2006). Based on field observations, we expected loggerheads to spend more time basking at the surface on warm, sunny days with no wind. The significant relationship between air temperature and wind speed on time spent at the surface shows that these variables affect basking behavior, and not only the ability of an observer to detect a turtle. Contrary to expected, we found no significant effect of cloud coverage. This could be partially due to the horizontal resolution of the environmental data used (Putman and He, 2013) or to the fact that our study considered turtles to be at the surface when
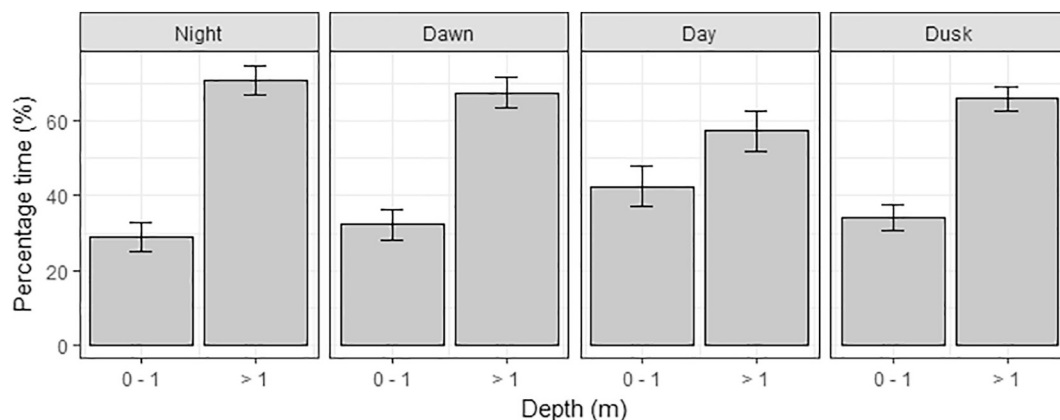

Fig. 2. Mean (± SE) percentage time spent at the surface (0 - 1 m) versus diving (> 1 m) as a function of diel period for ten juvenile loggerhead sea turtles tracked off Madeira. Diel periods: Night, 21:00-03:00; Dawn, 03:00-09:00, Day, 09:00-15:00, Dusk, 15:00-21:00.
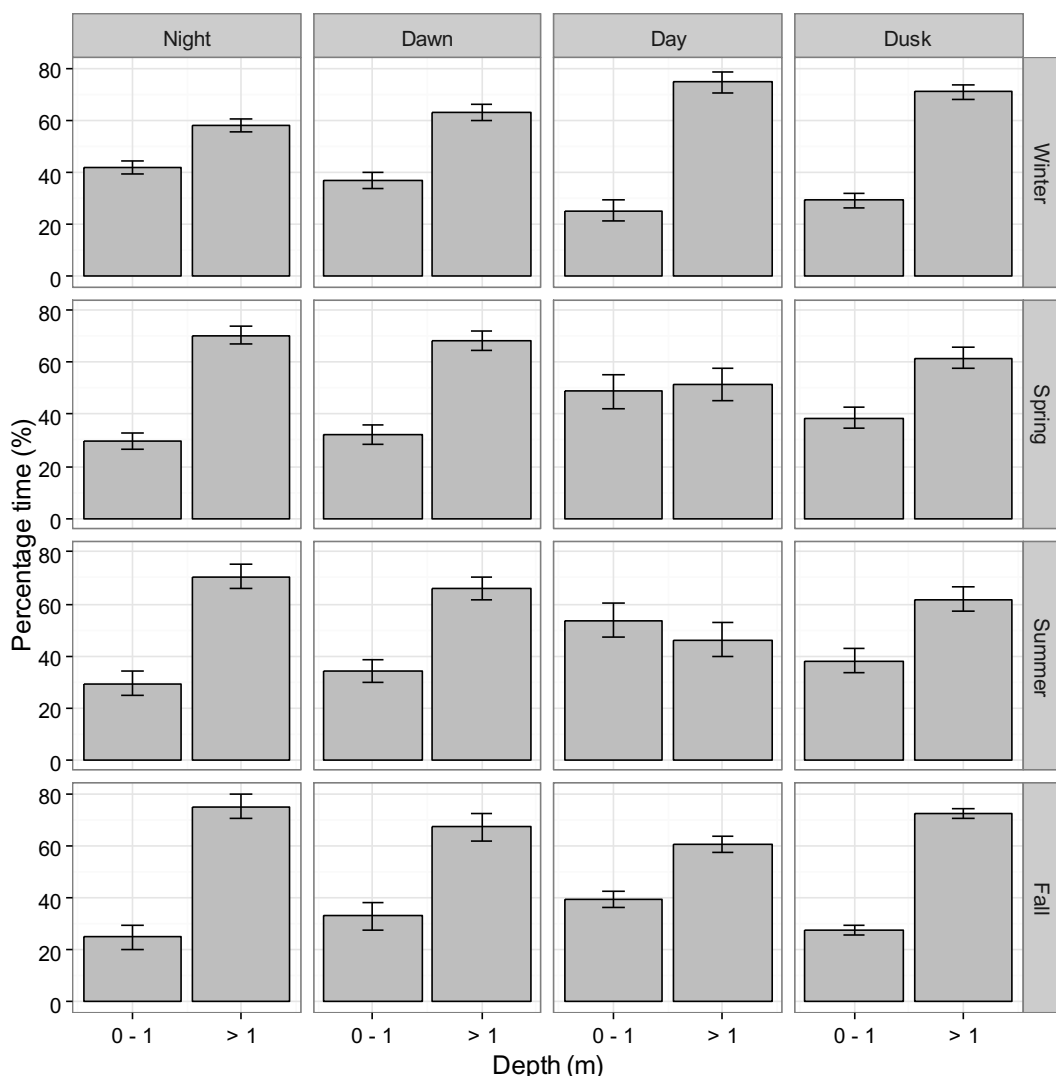
Fig. 3. Percentage of time (mean ± SE) spent at the surface (0 - 1 m) versus diving (> 1 m) by ten juvenile loggerhead sea turtles tagged off Madeira per time of the day and season.

Table 2
Estimated coefficients (β) and corresponding standard errors (SE) and significance levels (P), from three generalized mixed-effects models used to quantify how the proportion of time spent at the surface (0 - 1 m depth) was affected by intrinsic and extrinsic variables. The first model was fitted using all data, while the second and third models were fitted to daytime and nighttime data respectively.

	Overall			Day			Night		
	β	SE	P	β	SE	P	β	SE	P
Intercept	**-1.081**	**0.129**	**< 0.001**	**-1.111**	**0.166**	**< 0.001**	**-0.697**	**0.172**	**< 0.001**
Diel (dawn)	**0.120**	**0.038**	**0.001**						
Diel (day)	**0.398**	**0.038**	**< 0.001**						
Diel (dusk)	**0.113**	**0.037**	**0.002**						
Season (spring)	**0.127**	**0.042**	**0.003**	**0.802**	**0.087**	**< 0.001**	**-0.569**	**0.091**	**< 0.001**
Season (summer)	**0.239**	**0.049**	**< 0.001**	**0.983**	**0.102**	**< 0.001**	**-0.397**	**0.107**	**< 0.001**
Season (fall)	**-0.155**	**0.054**	**0.004**	**0.235**	**0.110**	**0.033**	**-0.630**	**0.116**	**< 0.001**
SCL	0.073	0.122	0.546	0.011	0.151	0.943	0.140	0.156	0.372
FPT	**-0.046**	**0.014**	**0.001**	**-0.137**	**0.030**	**< 0.001**	0.018	0.029	0.527
Wind	-0.014	0.015	0.346	**-0.077**	**0.031**	**0.013**	-0.030	0.034	0.369
Cloud	-0.022	0.014	0.118	-0.030	0.029	0.304	-0.045	0.028	0.104
Temp	0.024	0.021	0.256	**0.092**	**0.042**	**0.029**	-0.067	0.048	0.159
Moon							**0.157**	**0.029**	**< 0.001**

Abbreviations: Diel, diel period (night as base level); Season, season of the year (winter as base level); SCL, straight carapace length; FPT, first passage time; Wind, wind speed; Cloud, cloud coverage; Temp, air temperature; Moon, moon illumination. Significant effects are presented in bold.
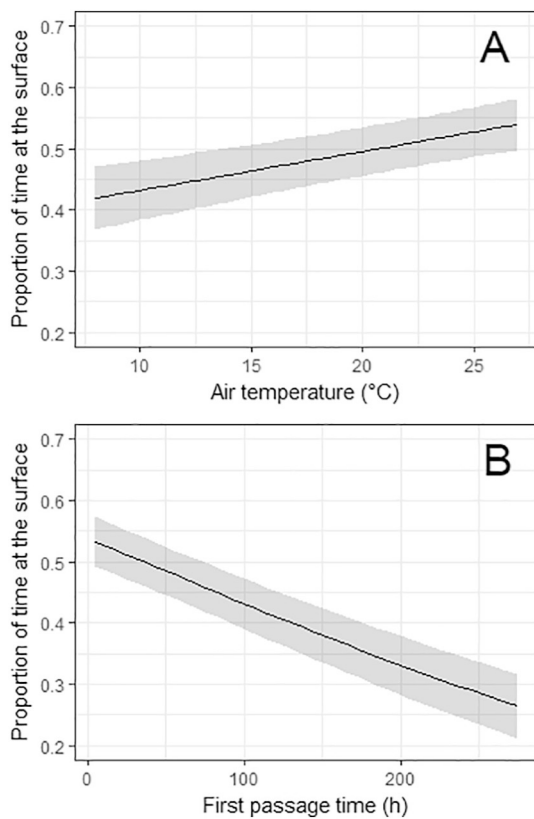
Fig. 4. Predicted proportion of time spent at the surface (0 - 1 m depth) by a loggerhead sea turtle as a function of air temperature (A) and first passage time (B). Predictions are given for summer, during the daytime (09:00 - 15:00) and calm wind conditions (3 m s $^{-1}$). First passage time (FPT) was set as 40 h in panel A and air temperature was set as 20 °C in panel B.

between 0 and 1 m deep and not exclusively when basking at the surface.

The primary benefit of thermoregulation in reptiles is the improvement in physiological performances, including energy intake and locomotion (Dubois et al., 2009; Fossette et al., 2012; Schofield et al., 2009). For pregnant females, thermoregulation is also important for egg maturation (Wapstra, 2000). Juvenile turtles in our study surfaced longer during spring than autumn. In addition to prevailing air temperatures during these seasons, it is possible that a history of low body temperature during winter increased the demand to elevate body temperature through behavioral thermoregulation at the surface (Crawford et al., 1983).

Interestingly, our study found a significant association between surface behavior and horizontal search effort during daytime. Turtles spent less time at the surface during the day in area of high horizontal search effort, probably due to a trade-off between surface behavior and foraging activities. The foraging behavior of sea turtles if typically inferred from movement and/or diving data (e.g. Freitas et al., 2018; Jonsen et al., 2007; McCarthy et al., 2010). Previous analyses of the foraging behavior of the study animals indicated that such areas where turtles spent more time or travelled more sinuously, were associated with increased chlorophyll a concentration, a proxy of food availability (e.g. Freitas et al., 2018; McCarthy et al., 2010). The cost-benefit model of thermoregulation (Huey and Slatkin, 1976) predicts that thermoregulation should cease when the costs outweigh the benefits. Two costs of thermoregulation are predation risk (Huey, 1982; Pianka and Pianka, 1970) and the reduction in time for other non-thermoregulatory activities such as foraging (Gregory et al., 1999; Huey and Slatkin, 1976). Our study suggests a tradeoff between daytime foraging activity and surface behavior in productive areas.

As hypothesized, surface behavior during the night was not associated with air temperature or wind speed, but instead associated with moon illumination. Note that air temperature and SST were highly correlated and that the latter was not used in the models to avoid collinearity issues. Given this correlation between air temperature and SST, the relationship between surface behavior and air temperature could be driven by SST. If it was the case, we would expect that its effect was present both during the day and during the night, which was not the case.

The association between surface behavior at night and moon illumination may be related to foraging patterns. Pelagic loggerhead turtles feed on pelagic cnidaria and mollusca, as well as on flotsam-associated barnacles and crabs (Frick et al., 2009; Parker et al., 2005). Some of these prey items are strictly associated with the surface, while some gelatinous zooplankton are known to perform diel vertical movements (e.g. Nogueira Júnior et al., 2015). Freitas et al. (2018) found that these juvenile turtles forage deeper during the day (and during full moon) and shallower at night, probably due to DVM of their prey. If surface behavior at night was related to surface feeding at 0-1 m depth, we would expect that turtles would spend more time at the surface during dark nights, as their prey are expected to be closer to the surface. We found the opposite; that turtles spent more time at the surface during full moon. As turtles tend to dive deeper during clear nights (Freitas et al., 2018), increased surface time may be needed to recover from deeper dives. Recovery from anaerobic activity has been suggested as a function of surface behavior (Hochscheid et al., 2010). Factors other than moon illumination (e.g. mixed layer depth and temperature at depth) may also affect foraging depths and dive duration (and therefore the need for recovery from diving), but these data were not available for this study. Diving data used in this study, which were summarized in 6-h periods, did not allow direct analysis of the relationship between surface events and the depth and duration of the previous dives. Sea turtles probably need a minimum time resting at the surface, especially in oceanic areas where they cannot rest at the sea bottom (Dujon et al., 2017). Minimum time spent at the surface in this study was 0.4 h in a day.

Previous studies suggest that young juvenile loggerheads spend more time at the surface compared to larger juveniles, probably due to their limited diving capacities (Cardona et al., 2005; Mansfield and Putman, 2013; Mansfield et al., 2014). Within the size range analyzed in this study (34 - 58 cm SCL) and in Revelles et al. (2007; 39 – 63 cm SCL), no relationship was found between body size and surface behavior. As turtles get older, larger animals may spend more time basking, as large bodies take more time to heat (Boyer, 1965; Hochscheid et al., 2010; Standora et al., 1982).

Turtle bycatch in surface fishing gear, such as longlines, is a threat for sea turtles worldwide (Lewison et al., 2014). Understanding the patterns of surface behavior in pelagic turtles is essential for managing interactions with such fishing activities, as well as other commercial activities, such as turtle watching and ship traffic. Surface behavior data are also valuable for planning or correcting census of turtle populations based on aerial surveys. Besides its relevance for management and conservation, information on patterns and environmental context of surface behavior is important to clarify the behavioral ecology of sea turtles during the pelagic stage, as well as to predict potential impacts of climate change (see Van Houtan et al., 2015).

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2018.10.006.

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