Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle

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ARTICLE INFO

ABSTRACT

Understanding food web functioning through the study of natural bio-indicators may constitute a valuable and original approach. In the context of jellyfish proliferation in many overexploited marine ecosystems studying the spatio-temporal foraging patterns of the giant "jellyvore" leatherback turtle turns out to be particularly relevant. Here we analyzed long-term tracking data to assess spatio-temporal foraging patterns in 21 leatherback turtles during their pluri-annual migration in the Northern Atlantic. Through an analytical approach based on the animal's own motion (independent of currents) and diving behavior distinct zones of high and low foraging success were identified. High foraging success occurred in a sub-equatorial zone spanning the width of the Atlantic and at high ($>30°$N) latitudes. Between these zones in the centre of North Atlantic gyre there was low foraging success. This "ocean desert" area was traversed at high speed by leatherbacks on their way to more productive areas at higher latitudes. Animals traveled slowly in high foraging success areas and dived shallower (17.2 ± 8.0 km day^{-1} and 53.6 ± 33.1 m mean $\pm$ SD respectively) than in low foraging success areas (51.0 ± 13.1 km day^{-1} and 81.8 ± 56.2 m mean $\pm$ SD respectively). These spatio-temporal foraging patterns seem to relatively closely match the main features of the integrated meso-zooplankton distribution in the North Atlantic. Our method of defining high foraging success areas is intuitive and relatively easy to implement but also takes into account the impact of oceanic currents on animal's behavior.

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1. Introduction

With climate change, overfishing and fisheries bycatch currently jeopardizing the sustainability of marine environments and natural resources worldwide (Pauly et al., 1998), there is a growing need for better understanding of marine food webs (e.g. Frank et al., 2007; Travers et al., 2009). A topical worrying example is notably the jellyfish proliferation to the detriment of other marine organisms in overexploited marine ecosystems which may have high ecological and economical consequences (Lynam et al., 2006). In view of the complexity of ecosystem functioning, an original approach is the use of natural bio-indicators (e.g. Boyd and Murray, 2001). The spatio-temporal distribution pattern of resources indeed drives the spatio-temporal behavioral patterns of specialist predators (e.g. Weimers-kirch et al., 2005). High-trophic level predators notably integrate and amplify the effects of environmental forcing on lower levels throughout food chains while migrants are integrators of global processes as they may feed in some parts of the world and reproduce

in others. The "jellyvore" migrant leatherback turtle may therefore be a particularly relevant bio-indicator of short- and long-term changes in food webs and resource availability in overexploited marine ecosystems (e.g. Saba et al., 2008). We thus surmise that the leatherback's spatio-temporal foraging patterns will match the gelatinous zooplankton global distribution with a lot of time spent successfully foraging on continental shelves which are known to be highly overexploited areas where gelatinous zooplankton may be abundant (Pauly et al., 2002).

In order to test this prediction, one of the first steps is to clearly identify the foraging strategies of leatherback turtles and objective methods of quantifying the time spent foraging are thus needed. Yet for highly migratory marine species, data on foraging success are difficult to obtain. Arguably the best approach might be to record prey ingestion over long periods using internal temperature sensor or sensors that record mouth opening (i.e. IMASEN, Wilson et al., 2002) as has been done for some other groups such as marine birds (e.g. Wilson et al., 2002), pinnipeds (Liebsch et al., 2007; Kuhn et al., 2009) and fish (e.g. Itoh et al., 2003; Bestley et al., 2008). However, to date successful studies using IMASEN to directly measure prey ingestion by leatherbacks have been limited to a few days only (Myers and Hays, 2006; Fossette et al., 2008a) due to the difficulty of long-term deployment of any loggers on this species. So for leatherback turtles a

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more sensible approach for delineating when and how foraging actually occurs remains for the moment through the analysis of long-term tracking data. To this end various approaches have been used, based on simultaneous changes in traveling rate and diving behavior (James et al., 2005; Hays et al., 2006), on movement patterns (i.e. using a switching state space model, Jonsen et al., 2005; Shillinger et al., 2008) or on changes in the animal's own motion (i.e. without the influence of oceanic currents, Gaspar et al., 2006). As demonstrated by Robinson et al. (2007), these approaches are all proxies for foraging and assume that animals will spend more time in areas of high foraging success and that travel rate decreases during foraging compared to transiting from one feeding area to another. The link between slower travel rate and increased foraging success has been directly shown in king penguins (*Aptenodytes patagonicus*, Bost et al., 1997) and bottlenose dolphins (*Tursiops truncatus*; Bailey and Thompson, 2006) and more recently in northern elephant seals (*Mirounga angustirostris*; Kuhn et al., 2009). But for many species the extent of successful feeding that occurs when animals are in inferred foraging areas when compared to periods defined as transit is still unknown. Nevertheless, while the different approaches of defining foraging success each has limitations (e.g. White and Sjöberg, 2002), importantly these techniques may be internally consistent, allowing objective delineation of temporal and spatial differences in foraging.

Gaspar et al. (2006), based on the analysis of the travel rate and the trajectory straightness of an Argos-tracked leatherback, suggested that the influence of oceanic currents on an animal's own motion should be taken into account for properly assessing where and how animals forage. The necessity of a current correction has also been acknowledged in several other species (e.g. king penguins: Cotté et al., 2007; Wandering Albatrosses *Diomedea exulans gibsoni*: Murray et al., 2002; northern fur seals *Callorhinus ursinus*: Ream et al., 2005; loggerhead turtles *Caretta caretta*: Girard et al., 2009). Here we implemented this approach of correcting animal movements by contemporaneous currents on a large sample size to calculate the time spent achieving high foraging success in the leatherback turtle. We then use the technique, combined with information about diving behavior, to identify the temporal and spatial patterns of leatherback turtle foraging in the Atlantic, identify zones of high foraging success and compare these zones with the distribution of zooplankton.

2. Methods

2.1. Turtles and satellite tracking

Our study involves a meta-analysis of some previously published tracks (Hays et al., 2006; James et al., 2006; Doyle et al., 2008, Fossette et al., submitted for publication) plus three new tracks, resulting in 21 study individuals (19 females and 2 males, Table 1). Study animals were fitted with a satellite transmitter (Series 9000 Satellite Relayed Data Loggers SRDLs, Sea Mammal Research Unit, St. Andrews, United Kingdom) deployed between July 2002 and September 2006 (Table 1): at Levera beach in Grenada (12.1°N–61.7°W, $n = 9$), Samsambo beach in Suriname (5.8°N–54.0°W, $n = 1$), Awala-Yali-mapo beach in French Guiana (5.7°N–53.9°W, $n = 5$), at sea off Nova Scotia coasts (44°N–64°W, $n = 4$) and off the Dingle Peninsula in County Kerry, Ireland (52.2°N, 10.3°W, $n = 2$). For 18 turtles, SRDLs were attached using custom-fitted harness systems integrating corrodible links to ensure release and for three turtles (FG05-4, FG05-5 and IR06-1), SRDLs were directly attached to the carapace (see Fossette et al., 2008b).

2.2. Turtle movement analysis

In the present study, only the post-nesting portions of the tracks were considered. Turtles' movements were reconstructed using the Argos satellite location system (www.cls.fr). Each Argos location is provided with a class of accuracy, called the location class (LC). LCs 3, 2, and 1, have nominal standard deviations around the tag's true position of 150 m, 150–350 m, and 350–1000 m respectively, while LCs 0, A and B have no location error estimate. All tracks were processed in a similar way as in Gaspar et al. (2006): all locations of all accuracies were analyzed, however Argos locations implying an apparent speed above 2.8 m s^{-1} (i.e. >10 km h^{-1}) were discarded as travel rates above this threshold are considered as biologically unlikely (James et al., 2005). Tracks were then smoothed and re-sampled every 8 h (corresponding to the mean daily raw Argos location frequency for all the turtles). This sampling interval is biologically relevant and provides a spatial resolution sufficient for sampling the mesoscale variations of the ocean current fields and thus correctly

Table 1
Summary of the movements and time spent achieving high foraging success of 21 Argos-tracked leatherback turtles during their migration in the North Atlantic Ocean. The percentage of time spent achieving high foraging success was calculated on the segments of the tracking period considered in the analysis and not on the entire migration. During their migration, turtles adopted three main strategies: the round-trip (R), the Northern (N) and the equatorial (E) strategies.

Turtle ID	Equipped in	Sex	Strategy	Date of departure in migration (dd/mm/yyyy)	Number of days tracked (d)	Number of days considered in the analysis	Time spent achieving high foraging success (%)	Number of recorded 6 h-summaries dives
GR02-1	Grenada	F	E	10/07/2002	376	109.0	91	358
GR02-2	Grenada	F	E	05/07/2002	323	162.0	51	352
GR03-1	Grenada	F	N	28/06/2003	406	160.7	39	154
GR03-2	Grenada	F	R	01/06/2003	358	120.3	22	220
GR03-3	Grenada	F	R	11/05/2003	322	197.0	28	504
GR03-4	Grenada	F	R	21/05/2003	517	83.0	35	160
GR03-5	Grenada	F	R	09/07/2003	241	204.7	30	502
GR03-6	Grenada	F	N	15/06/2003	180	153.7	27	319
GR03-7	Grenada	F	R	18/06/2003	247	221.0	30	436
NS05-1	Nova Scotia	F	R	21/07/2005	86	70.7	52	139
NS05-2	Nova Scotia	F	R	16/07/2005	127	97.7	40	0
NS06-1	Nova Scotia	F	R	14/09/2006	280	149.0	51	213
NS06-2	Nova Scotia	M	R	08/09/2006	73	72.3	7	70
IR05-1	Ireland	F	N	01/09/2005	313	92.0	27	232
IR06-1	Ireland	M	N	29/06/2006	233	203.3	55	380
SU05-1	Suriname	F	E	25/06/2005	714	79.0	68	200
FG05-1	Fr. Guiana	F	R	26/07/2005	247	48.7	10	44
FG05-2	Fr. Guiana	F	R	26/07/2005	383	102.7	17	166
FG05-3	Fr. Guiana	F	N	28/07/2005	257	104.0	15	71
FG05-4	Fr. Guiana	F	N	27/07/2005	122	82.7	6	99
FG05-5	Fr. Guiana	F	R	25/07/2005	129	100.0	11	134

estimating the currents along the tracks (see below). A local linear regression with a time window of one day was used to re-sample the tracks. Epanechnikov kernel was used to weight observations in that window. The size of the window should be adjusted according to the quality of the data in order to avoid over-smoothing the tracks. When there were less than 5 positions available in one time window, positions at 8-hourly intervals were obtained by simple linear interpolation between adjacent fixes. Linearly interpolated track's segments longer than 3 days were not taken into account in the subsequent analysis as travel rate and straightness index calculated from linearly interpolated locations were, respectively, underestimated and overestimated.

The observed track of an animal at any given time results from the animal's own movement (swimming) and its displacement due to ocean currents (drift). Thus by removing the influence of currents on the animal's trajectory, the 'true' locomotion behavior (the "motor track") of an animal can be obtained (Gaspar et al., 2006; Girard et al., 2006). In short, for each 8-h re-sampled location, we calculated the apparent turtle velocity (i.e. the velocity over the ground) and subtracted from it an estimate of the surface current velocity. The turtle swimming velocity is then simply obtained as the vector difference between the apparent and the current velocities. Following Gaspar et al. (2006), the surface current velocity is estimated to be the sum of the surface geostrophic current deduced from altimetric measurements (available from www.aviso.oceanobs.com) and the wind-induced Ekman current computed using the Rio and Hernandez (2003) model. Details concerning the computation and validity of these current estimates can be found in Pascual et al. (2006) and Gaspar et al. (2006). Note that this current correction was not performed for track segments located in the equatorial band (i.e. between 0° and 5°N) where both the geostrophic and Ekman approximations break down.

The straightness of an animal's path can be calculated as the ratio of the beeline distance D between the first and the last points, and the traveled path length L (Batschelet, 1981). Each motor track was thus re-sampled in a form of a sequence of n steps with a constant length l ($l = 15$ km corresponding to the average distance between our successive Argos locations), and the ratio D_i/L was successively calculated for each location (x_i, y_i) at the centre of a 10-steps ($L = 150$ km) window.

2.3. Turtle diving behavior

Modifications in the horizontal and vertical behaviors are often concurrent (e.g. James et al., 2005). In addition, diving patterns may provide information on the distribution of the prey in the water column. Therefore, the diving behavior was analyzed during leatherback's migrations. SRDLs provided measurements of diving behavior from a pressure sensor, which sampled depth every 4s with an accuracy of 0.33 m. Data were statistically summarized onboard over 6-h collection periods providing the number of individual dives performed during the period, their mean ($\pm$SD) duration and mean ($\pm$SD) maximum depth (see McMahon et al., 2005 for details).

The point location values for high foraging success (Fig. 3) and the mean dive depth (Fig. 4) were imported into ArcMap 9.1 (ESRI, Redlands, California) and interpolated using inverse distance weighting to predict values for area where there was no data coverage on a $2° \times 2°$ and $1° \times 1°$ scale, respectively.

3. Results

3.1. General migration pattern

The 21 turtles were followed for between 73 and 714 days (Table 1, Fig. 1), but at different periods of their migration. Among the females of this study, the earliest date of departure from the nesting site was on the 11th of May. Accordingly, we considered that when females started their migration from Grenada, French Guiana or Suriname, they were in year 1 of migration starting on the 1st of May (noted May Year 1) and finishing on the 30th of April (noted April Year 1) one year later. We then assumed that turtles caught at their high-latitude sites in Nova Scotia in September were in year 1 of migration whereas turtles caught in Nova Scotia in July or in Ireland in June and September were in year 2 of migration beginning in May year 2 and finishing in April year 2. Indeed, as turtles need on average between 3 to 6 months to travel from their nesting beaches to these high-latitude summering sites, turtles should have left their nesting sites as early as March–April in order to arrive in Nova Scotia in July or in Ireland in June which is unlikely as March–April corresponds to the beginning of the nesting season for leatherbacks in the North
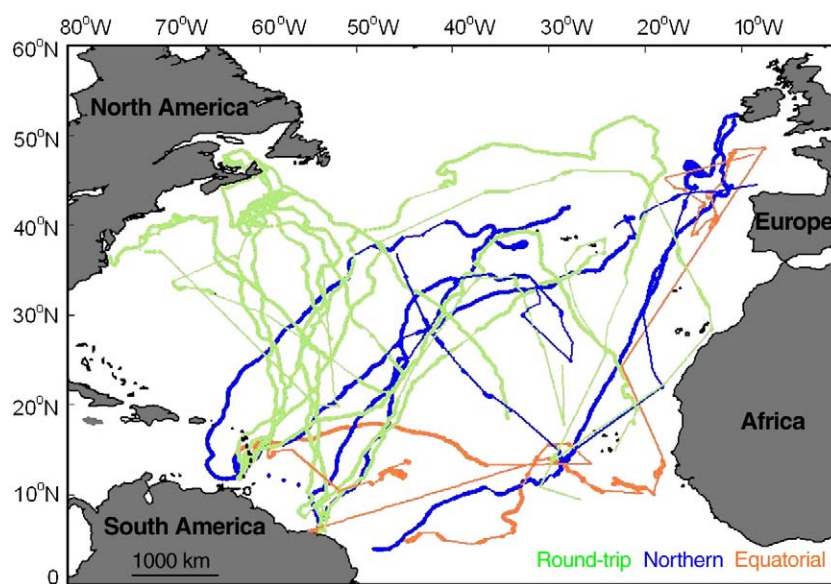

Fig. 1. Movements of 21 Argos-tracked leatherback turtles during their pluri-annual migration in the North Atlantic Ocean. Fifteen SRDLs were deployed on females nesting in Grenada, in French Guiana and Suriname while six were deployed on individuals captured in waters off Nova Scotia and off the west coast of Ireland, close to Dingle. During their migration, turtles adopted three main strategies: the round-trip (in green), the Northern (in blue) and the equatorial (in orange) strategies. Thinner lines: linearly interpolated portions of the tracks not considered in the subsequent analysis, see methods for details.

hemisphere. Two turtles (IR05-1; SU05-1) were tracked until year 3 of migration beginning in May year 3 and finishing in April year 3.

Turtles moved across the entire North Atlantic Ocean basin between 4.3°N (Turtle GR02-2) and 52.0°N (Turtle GR03-3) and 7.5°W (Turtle SU05-1) and 75.5°W (Turtle FG05-5). According to (1) their initial direction of migration, i.e. North or East, (2) the dates of arrival and departure at and from the high-latitude sites taking into account the distance from the nesting sites and (3) the fact that they head south or not at the end of the autumn, three main migrating strategies adopted by the turtles during their pluri-annual migration were defined (Fig. 1). The first strategy (hereafter called the "round-trip" strategy, 12 individuals) consisted in reaching high latitudes (35–50°N) at the end of summer/beginning of autumn before heading

south at the end of autumn. Then, leatherbacks spent the winter and the beginning of spring between 10°N and 25°N before heading north again to spend the summer at high latitudes. Five leatherbacks adopted this strategy in the eastern Atlantic and seven in the western Atlantic. The second strategy (hereafter called the "northern" strategy, six individuals), consisted in heading northeast to 30–40°N, 25–30°W but instead of moving south at the end of the autumn, leatherbacks remained in the area throughout the winter before moving to the Irish sea and the bay of Biscay in spring. After summering in this area, leatherbacks moved south and reached the latitudes 5–15°N in winter. Then, leatherbacks either stayed in the tropical Atlantic or headed back to the northwest Atlantic. The last strategy (hereafter called the "equatorial" strategy) concerned three females that spent
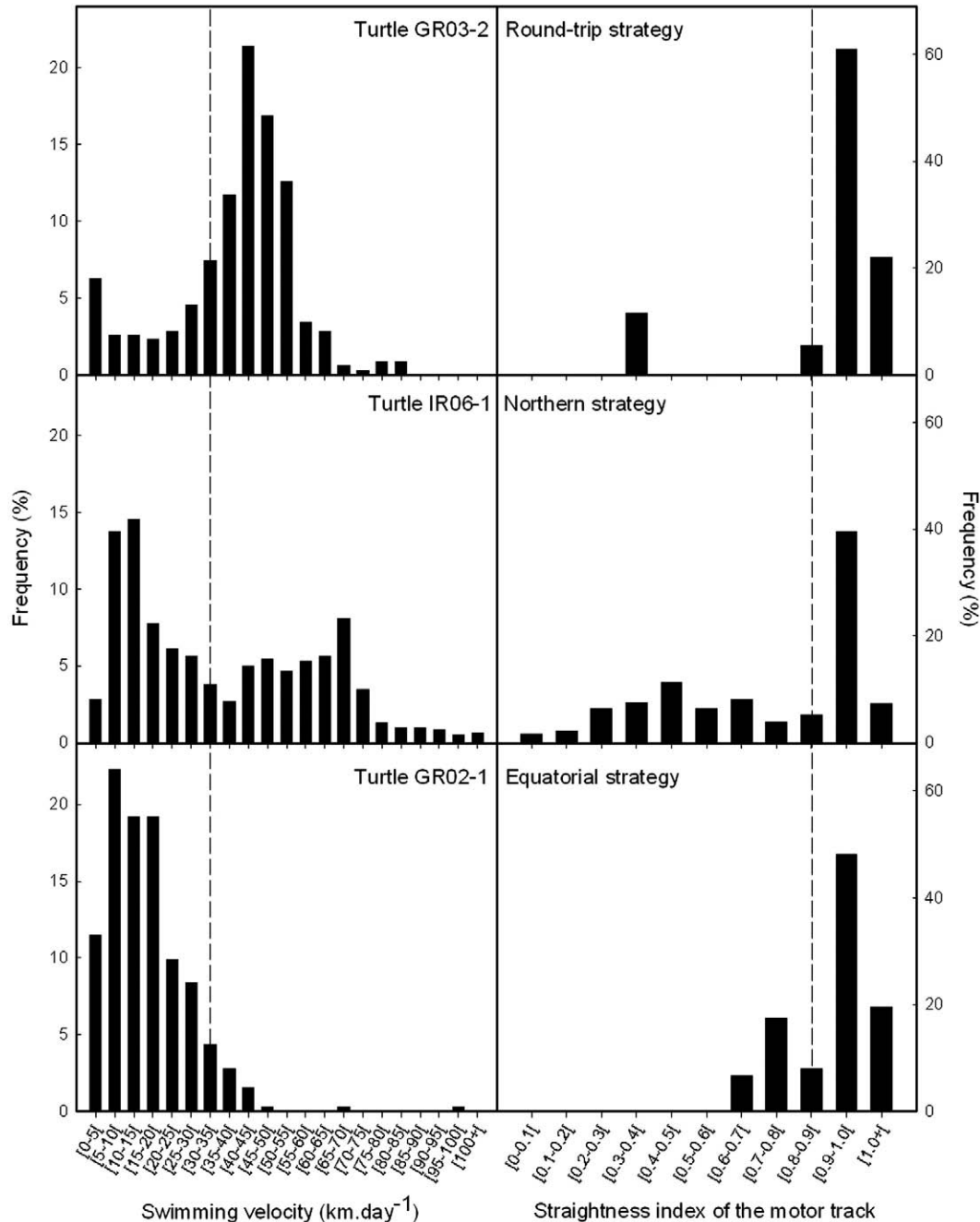

Fig. 2. Three examples of the frequency distribution of (i) swimming velocity (left panels) and (ii) straightness index of the motor track (right panels) of leatherback turtles during their migration in the North Atlantic Ocean. The dashed line indicates the threshold separating higher foraging success areas (swimming velocity < 30 km day^{-1} and/or straightness index < 0.8) from traveling/lower foraging success areas (swimming velocity > 35 km day^{-1} and/or straightness index > 0.9). Top panel: Turtle GR03-2 following the round-trip strategy, middle panel: turtle IR06-1 following the northern strategy, bottom panel: turtle GR02-1 following the equatorial strategy.

the first year after the nesting season in the tropical Atlantic before heading north at the beginning of the summer to reach high latitudes in autumn. The winter and the following spring were then spent between 40 and 50°N in the eastern Atlantic.

3.2. Foraging behavior

For highlighting higher foraging success areas from lower foraging success areas, we fixed threshold values for the swimming velocity and the straightness index (S) based on the assumption that decreasing velocity and/or motor track straightness indicate increasing foraging success. It has not been proven yet that a turtle may be able to detect a current and its direction when traveling in open sea (which is almost impossible for a moving animal without any stationary reference points) and thus adjust its swimming behavior accordingly to take advantage of this current. Therefore we assume that a turtle will decrease its own swimming velocity and/or motor track straightness under a certain threshold when foraging only. We based our definition of the thresholds on the analysis of the individual frequency distributions for each parameter. Individual frequency distributions of the swimming velocity were of three types: (1) swimming velocities mostly distributed between 5 to 30 km day^{-1}, (2) swimming velocities mostly distributed between 35 and 70 km day^{-1} and (3) swimming velocities showing both distributions (Fig. 2). A similar threshold value around 30–35 km day^{-1} has also been highlighted by Fossette et al. (submitted for publication). Similarly, the frequency distributions of the straightness index of the 21 motor tracks showed a threshold value of 0.8 separating two distinct patterns (Fig. 2). A similar threshold value has been previously highlighted by Gaspar et al. (2006). Accordingly, we decided to classify as "high-success foraging", animal positions where the velocity was below 30 km day^{-1} and S < 0.8. Positions with velocities above 35 km.day^{-1} and S > 0.8 were classified as "low success foraging". To remain in a given restricted area, animals may either reduce their swimming velocity or modify their trajectory straightness or do both concurrently. Conse-

quently, areas where swimming velocity and straightness index gave a contradictory classification were still considered as high foraging success areas. After having identified the "high-success foraging" positions along the motor tracks, these positions were converted back from the current-corrected positions to the actual geopositions. The subsequent analyses, computing and mapping the percentage of high and low success foraging positions in 2° × 2° boxes (Fig. 3), were carried out on the apparent tracks.

As a general rule, areas of high foraging success were located at high latitudes (between 35°N and 50°N: along the North American coasts, in Nova Scotia waters, in the Gulf of Saint-Laurent, in the western and northern part of the Gulf Stream, in the Northeast Atlantic, along the Azores front and northeast of the Azores Islands, north of the Canary Islands) and in the sub-Equatorial region (between 5°N and 15°N: in the region of the Mauritania upwelling, south of the Cape Verde islands, in the Guinea Dome area, in the westward flow of the North Atlantic Equatorial Current, off the coasts of Venezuela, Guyana and Suriname) and were almost absent in the North Atlantic Gyre and the Sargasso Sea (Fig. 3).

The time spent achieving high foraging success by the 21 individuals varied from 5.6% to 91.4% during the tracking period (Table 1). Since these percentages depended on both the duration of the different tracks and the specific period of the post-nesting migration, we calculated monthly percentages of time spent achieving high foraging success throughout the migration for each individual. By using these individual monthly values, we then looked at the evolution of the percentage of time spent achieving high foraging success throughout the migration for the three strategies (Fig. 4). For the "round-trip" strategy, the mean monthly percentage of time spent achieving high foraging success was 39.8 ± 22.01% (mean ± SD, n = 24 values, 12 turtles considered) varying between 37.3 ± 21.2% (mean ± SD, n = 12 values, 10 turtles considered) the first year after the nesting season to 44.1 ± 24.4% (mean ± SD, n = 7 values, 4 turtles considered) the following years (Fig. 4). Leatherbacks following this strategy showed relatively high foraging success at high latitudes (35–
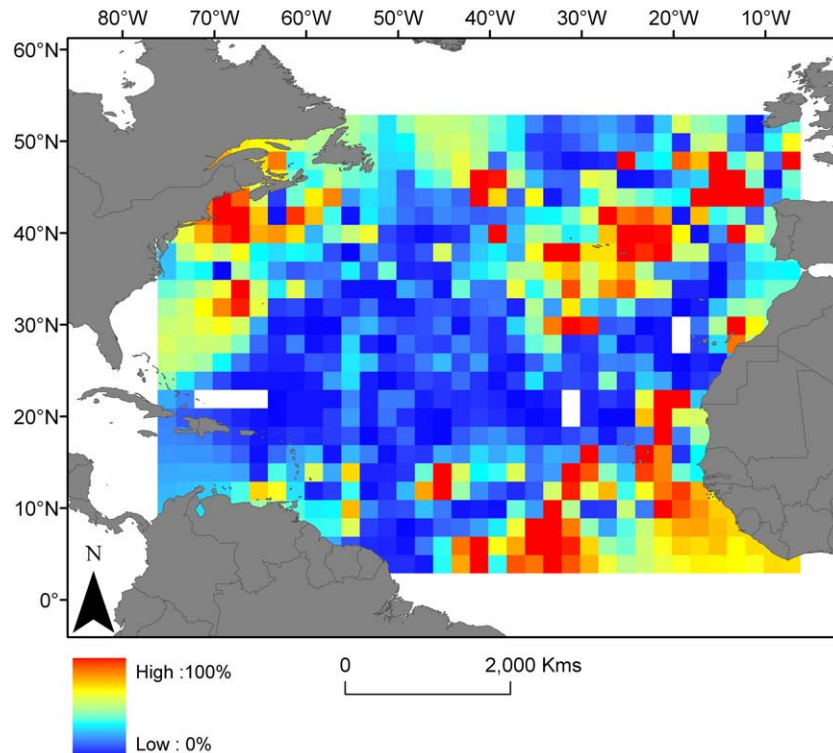

Fig. 3. High-success foraging areas of 21 Argos-tracked leatherback turtles during their migration in the North Atlantic Ocean (the scale indicates the mean percentage of time spent achieving high foraging success per pixel of 2° × 2°, see methods for details).
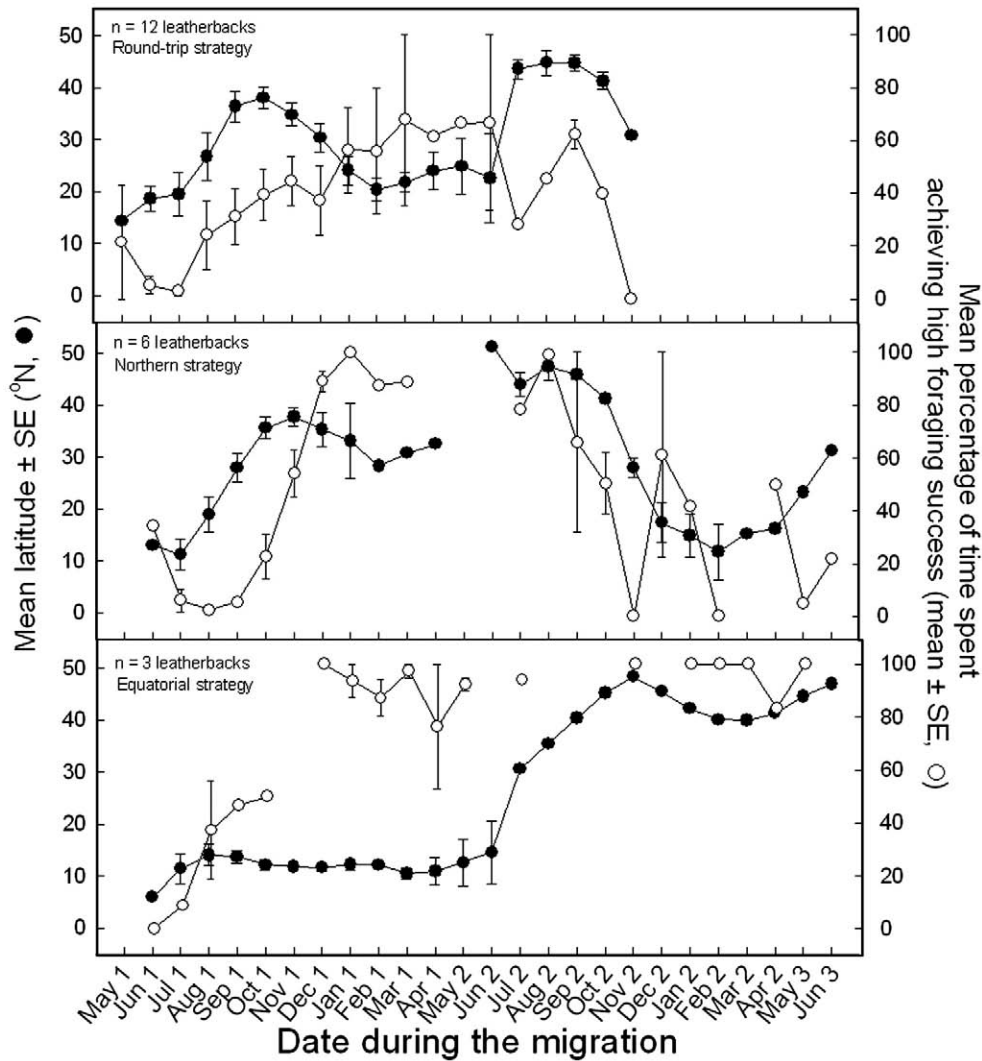
Fig. 4. Mean monthly latitudinal dispersion (black dots) and mean monthly percentage of time spent achieving high foraging success (white dots) of 21 Argos-tracked leatherback turtles (top panel: 12 individuals, "round-trip" strategy, middle panel: 6 individuals, "northern" strategy, low panel: 3 individuals, "equatorial" strategy) during their migration in the North Atlantic Ocean. May 1 to April 1, May 2 to April 2 and May 3 to July 3: first, second and third years of the migration, respectively (see Results for details).

50°N) during the summer and autumn (mean ~35%) but also at latitudes 15–25°N during the winter (mean ~60%). For the "northern" strategy, the mean percentage of time spent achieving high foraging success was $45.9 \pm 35.5\%$ (mean $\pm$ SD, $n = 21$ values, 6 turtles considered) varying between $49.0 \pm 39.6\%$ (mean $\pm$ SD, $n = 10$ values, 4 turtles considered) the first year after the nesting season to $43.0 \pm 33.1\%$ (mean $\pm$ SD, $n = 11$ values, 2 turtles considered) the following years (Fig. 4). Leatherbacks following this strategy showed relatively high foraging success at latitudes 30–40°N during the summer and autumn (mean ~30%) and particularly during the winter (mean ~90%) of the first year of migration. The second year, they then foraged at latitudes 40–50°N during the summer (mean ~80%) and at latitudes 5–15°N during the winter (mean ~35%). For the "equatorial" strategy, the mean percentage of time spent achieving high foraging success was $76.0 \pm 32.8\%$ (mean $\pm$ SD, $n = 18$ values, 3 turtles considered) varying between $59.8 \pm 36.8\%$ (mean $\pm$ SD, n = 10 values, 3 turtles considered) the first year after the nesting season to $96.2 \pm 6.1\%$ (mean $\pm$ SD, $n = 8$ values, 3 turtles considered) the following years (Fig. 4). Individuals following this strategy showed a high foraging success at latitude ~10°N during the winter and spring (mean ~90%) of the first year of migration. The second year, they then foraged at high latitudes (40–50°N) from autumn to spring (mean ~95%). The time spent achieving high foraging success was however

highly uncertain for the "equatorial" strategy due to the low number of individuals following this strategy and long periods of missing data (up to several months for SU05-1).

3.3. Dive behavior

Slow periods of swimming and low straightness index were often associated with changes in dive behavior. For instance, the swimming velocity and the straightness of the motor track of turtle IR06-1 dropped to below 30 km day^{-1} and 0.8, respectively, from the 7th until the 100th day after tag deployment (Fig. 5). During this time dives became very short (mean 8 min) and shallow (mean 48 m, Fig. 5). As a general rule, individuals performed deeper dives in traveling (81.8 ± 56.2 m, mean $\pm$ SD) than in higher foraging success (53.6 ± 33.1 m, mean $\pm$ SD) areas (Mann–Whitney test, $W_{1085, 2183} = 1359172.0$, $p < 0.001$). Accordingly, leatherbacks dived deeper in the North Atlantic Gyre and the Sargasso Sea than at high latitudes and in the Equatorial region (Fig. 6).

4. Discussion

In this study, an analytical approach based on both the swimming velocity and the straightness of the animal's own track (Gaspar et al.,
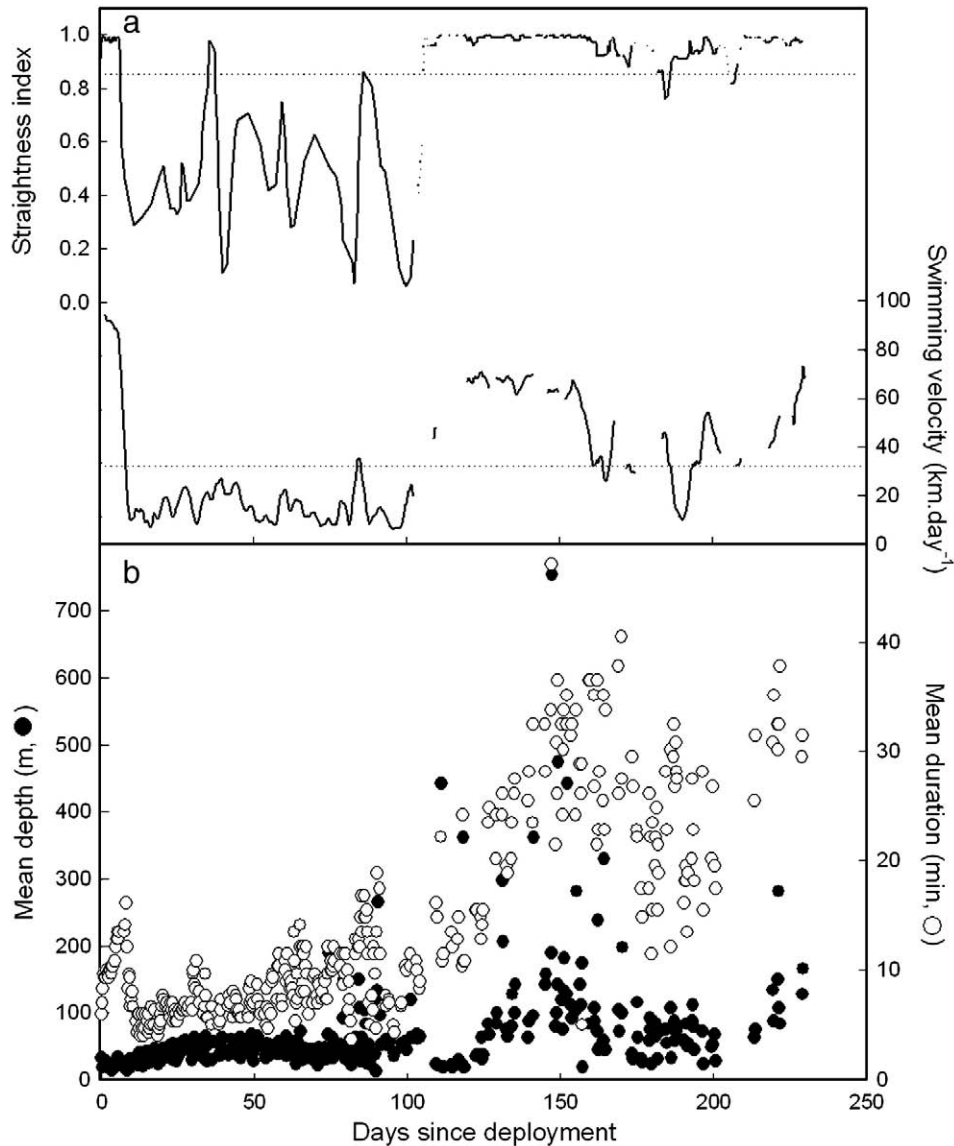
Fig. 5. a — Straightness (S) index (top panel) computed along the motor track and swimming velocity (bottom panel) during the migration of the turtle IR06-1. The dashed line indicates the threshold separating higher foraging success areas (swimming velocity < 30 kmday^{-1} and/or straightness index < 0.8) from traveling/lower foraging success areas (swimming velocity > 35 kmday^{-1} and/or straightness index > 0.9). b — Mean depth (black dots) and mean duration (white dots) of dives recorded in individual 6 h-intervals during the migration of the turtle IR06-1.

2006) has provided a tool for objectively defining three main spatio-temporal foraging strategies of a key bio-indicator, the zooplanktivore leatherback turtle, in the North Atlantic. Estimating foraging patterns through the use of Argos tracking data, whatever the analytical approach used, can only provide a gross picture of the actual foraging behavior of the concerned species. Indeed all the methods are constrained by the raw frequency and the initial error of the Argos locations. Our method presents however the main advantage to be intuitive and relatively easy to implement, compared to other statistical models such as the State Space Model (SSM), and yet provides reliable results. Our approach took also into account two important issues in the analysis of marine animal's behavior. First, all tracks of our study had prolonged periods with few or no recorded satellite positions which may be due to biofouling or tag defects such as salt-water switch failure (Hays et al., 2007). In these situations, linear interpolation is usually used to compensate for the lack of data although this may be unrealistic when the interval between locations is long (Tremblay et al., 2006). Accordingly, in our study, linearly interpolated track segments longer than 3 days were not analyzed

resulting in less but more reliable data. Similarly there are various other approaches for objectively identifying changes in behavior from tracking data including techniques such as first passage time analysis and state space models (Hamer et al., 2009; Patterson et al., 2009). These approaches might have utility for further refining estimates of where leatherbacks spend more time successfully foraging but, as our approach, they are also sensitive to long periods with missing data (e.g. Bailey et al., 2008). Secondly, as animals move through complex dynamic oceanographic systems it has been recommended to consider the drifting impact of oceanic currents on an animals' movement when analyzing tracks (Luschi et al., 2003; Girard et al., 2006; Bailey et al., 2008). To date however, other approaches such as SSMs have not dealt with oceanic currents in the definition of behavioral modes (e.g. Jonsen et al., 2005, 2007; Bailey et al., 2008) which however may be achievable. Here, we applied a correction by the currents along the tracks before defining two behavioral modes. It should be noted that although the delineation of the threshold between the two modes (higher foraging vs lower foraging success) was subjective which impacts the calculated absolute percentage of
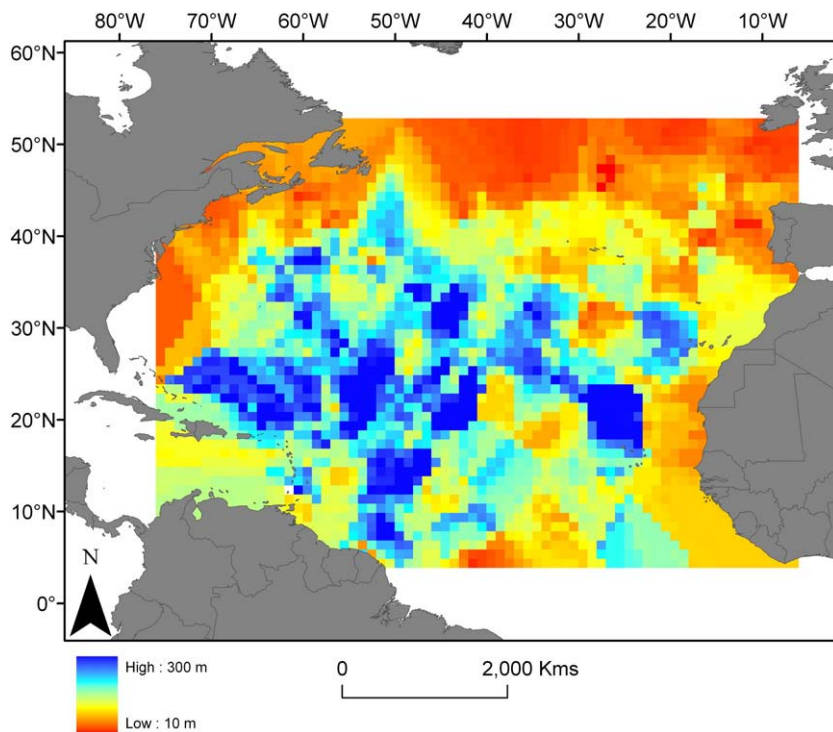
Fig. 6. Mean depth of dives recorded in individual 6 h-intervals for 20 Argos-tracked leatherback turtles during their migration in the North Atlantic Ocean. No summary dive data was received for the turtle NS05-2. The scale indicates the mean depth of the dives performed in each pixel of $1° \times 1°$.

time spent achieving high foraging success, the relative occurrence of these two modes remained however objective. Furthermore, even though foraging success may be considered as a continuous variable, with some feeding occurring outside high use areas (Weimerskirch, 2007; Horsburgh et al., 2008; Kuhn et al., 2009), we are confident that our method provides a reliable proxy to objectively identify spatial and temporal differences in leatherback foraging success.

Little is known about the basin-wide distribution of gelatinous zooplankton (Houghton et al., 2006; Richardson et al., 2009) and consequently people have tended to use satellite-derived chlorophyll levels as a proxy for the prey availability for leatherbacks (Saba et al., 2008). Yet the links between chlorophyll levels and gelatinous zooplankton abundance are unknown. A closer link to gelatinous zooplankton abundance might be expected to be provided by measures of integrated zooplankton abundance. However, datasets which allow mapping the distribution of marine biota, and notably zooplankton, are indeed sparse. A recent study however has managed to combine satellite data with in-situ datasets from the COPEPOD and the Continuous Plankton Recorder (CPR) databases, to generate a map of the annual meso-zooplankton biomass in the North Atlantic (Strömberg et al., 2009). Even though this map does not directly reflect the jellyfish distribution, it may be assumed that gelatinous macro-zooplankton is likely to be situated in the same areas as meso-zooplankton. If we consider leatherback's high-success foraging areas as a proxy for jellyfish occurrence, then this assumption seems to be supported by our results. Indeed, the spatio-temporal foraging patterns of leatherbacks described in this study seem to relatively closely match the main features about zooplankton distribution (Fig. 7) described in Strömberg et al. (2009). First, a relatively high zooplankton biomass in the Atlantic Westerlies Domain and the Northwest and Northeast Atlantic continental shelves was observed (Strömberg et al., 2009). It is well known indeed that the progressive shoaling of the deep winter mixed layer in response to increasing radiation and decreasing wind stress results in algal spring blooms and a subsequent increase of secondary productivity in summer and autumn in these areas (Longhurst et al., 1995; Sathyendranath et al.,

1995; Pérez et al., 2005). This matches the leatherback's foraging patterns described in this study which suggests that gelatinous prey may thus be abundant from early summer in the northwestern Atlantic (see also James and Herman, 2001; Lucas, 2001) until autumn in the northeastern Atlantic (see also Houghton et al., 2006). More surprisingly, some leatherbacks over-wintered along the Azores front, north of the Azores and off the Portuguese coasts, and seemed to achieve relatively high foraging success during this period. Presumably gelatinous plankton is abundant off these areas in winter, although empirical evidence is lacking. This strategy seems at least to enable leatherbacks increasing their north-eastward extent (i.e. notably to the Irish Sea and the Bay of Biscay) in the second year of migration, perhaps as a result of increased fat stores. Secondly, high zooplankton biomass was highlighted in the Western Tropical Atlantic, the northern part of the Eastern Tropical Atlantic and the southern boundary of the North Atlantic Tropical Gyre (i.e. in the Guinea Dome area and in the westward flow of the North Equatorial Current), notably on continental shelves and in upwelling regions (Strömberg et al., 2009). These areas have been compared in terms of primary production to the North Atlantic spring bloom (Platt et al., 1991; Longhurst, 1993). These highly productive oceanic regions (e.g. Signorini et al., 1999; Marañón et al., 2000; Hu et al., 2004) match the high foraging success areas that leatherbacks used all year round (this study). Lastly, low zooplankton biomass characterized the North Atlantic Gyre and the Sargasso Sea (Strömberg et al., 2009) which are indeed considered as oceanic deserts due to the low levels of nutrients in these areas (Marañón et al., 2000). In these oligotrophic areas, leatherbacks had low foraging success suggesting a low concentration of gelatinous zooplankton. They also dived deeper than in their temperate and equatorial key foraging grounds. The pattern of diving therefore provided independent verification of the patterns of foraging success provided by the analyses swimming velocity and track straightness. When in key foraging areas, they seem indeed to concentrate their foraging effort in the upper part of the water column, with more than half of the time spent at very shallow depths. This has also been observed in another planktivore species: the
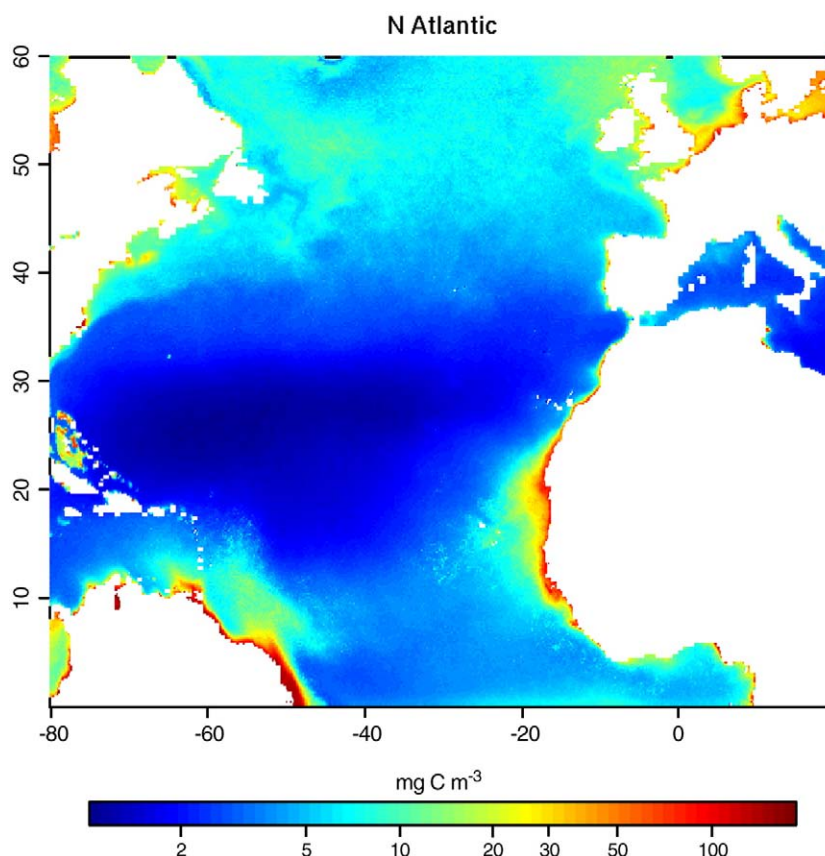
Fig. 7. Annual (1998–2005) zooplankton biomass [mg C m^{-3}] from the model developed by Strömberg et al., 2009 based on the COPEPOD and the Continuous Plankton Recorder databases.

basking shark *Cetorhinus maximus* (Sims et al., 2005) and likely reflects the distribution of their prey in the water column. Shallow foraging by leatherbacks will help reduce the transit costs of traveling from the surface (where they breathe) to foraging depths and hence may provide an efficient solution for maximizing energy gain while foraging. Little is known however about the diving behavior of gelatinous zooplankton although a recent study by deploying time–depth recorders on free-living jellyfish has shown a range of vertical movements (from the surface down to a maximum of about 30 m) during the tracking period (Hays et al., 2008).

Most of the migrating tracks previously described for leatherbacks in the North Atlantic (Ferraroli et al., 2004; James et al., 2005; Eckert, 2006) can be classified in one of the three strategies we defined in this study. Individual variations in the foraging route-choice behavior have previously been reported in several marine species (e.g. Antarctic fur seals: Bonadonna et al., 2001, grey seals: Austin et al., 2004) and were linked with sex, season of tag deployment, or individual experience. In this study, neither the season of tag deployment (i.e. at the beginning or the end of the nesting season), nor the nesting site of departure or the body size seems to have influenced the migration strategy. Thus, other hypotheses such as the role of individual experience or of body condition in driving these individual variations in migration strategies need to be investigated.

In summary we show strong evidence for distinct patterns in leatherback turtle foraging success in the North Atlantic, with these patterns of foraging being linked to patterns of secondary production. Our results highlight a large area in the centre of the North Atlantic gyre, where leatherback foraging success is low. This area is traversed at high speed by leatherbacks on their way to more productive areas at higher latitudes. Wider application of our methodology may reveal whether these links between leatherback foraging success and secondary production occur in other ocean basins.

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