Progress in Oceanography 142 (2016) 58–71

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

The influence of oceanographic features on the foraging behavior of the olive ridley sea turtle *Lepidochelys olivacea* along the Guiana coast

Philippine Chambault [a,*], Benoît de Thoisy [b], Karine Heerah [c], Anna Conchon [d], Sébastien Barrioz [b], Virginie Dos Reis [b], Rachel Berzins [e], Laurent Kelle [f], Baptiste Picard [g], Fabien Roquet [h], Yvon Le Maho [a], Damien Chevallier [a]

[a] DEPE-IPHC, UMR 7178, CNRS-UdS, 23 rue Becquerel, F-67087 Strasbourg cedex 2, France
[b] Association Kwata, 16 avenue Pasteur, BP 672, F-97335 Cayenne cedex, France
[c] LOCEAN-UMR 7159, 4 place Jussieu, 75252 Paris cedex 05, France
[d] Collecte Localisation Satellites, Direction Océanographie Spatiale, 8-10 rue Hermès, 31520 Ramonville, France
[e] Office National de la Chasse et de la Faune Sauvage – Cellule technique Guyane, Campus agronomique, BP 316, 97379 Kourou cedex, France
[f] WWF Guyane, N°5 Lotissement Katoury, F-97300 Cayenne, France
[g] Centre d'Études Biologiques de Chizé, UMR 7372 CNRS – Université de La Rochelle, 79360 Villiers-en-Bois, France
[h] Stockholm University, Department of Meteorology (MISU), Sweden

ARTICLE INFO

Article history:
Received 13 August 2015
Received in revised form 28 January 2016
Accepted 28 January 2016
Available online 4 February 2016

ABSTRACT

The circulation in the Western Equatorial Atlantic is characterized by a highly dynamic mesoscale activity that shapes the Guiana continental shelf. Olive ridley sea turtles (*Lepidochelys olivacea*) nesting in French Guiana cross this turbulent environment during their post-nesting migration. We studied how oceanographic and biological conditions drove the foraging behavior of 18 adult females, using satellite telemetry, remote sensing data (sea surface temperature, sea surface height, current velocity and euphotic depth), simulations of micronekton biomass (pelagic organisms) and *in situ* records (water temperature and salinity). The occurrence of foraging events throughout migration was located using Residence Time analysis, while an innovative proxy of the hunting time within a dive was used to identify and quantify foraging events during dives. Olive ridleys migrated northwestwards using the Guiana current and remained on the continental shelf at the edge of eddies formed by the North Brazil retroflection, an area characterized by low turbulence and high micronekton biomass. They performed mainly pelagic dives, hunting for an average 77% of their time. Hunting time within a dive increased with shallower euphotic depth and with lower water temperatures, and mean hunting depth increased with deeper thermocline. This is the first study to quantify foraging activity within dives in olive ridleys, and reveals the crucial role played by the thermocline on the foraging behavior of this carnivorous species. This study also provides novel and detailed data describing how turtles actively use oceanographic structures during post-nesting migration.

1. Introduction

The circulation in the Western Equatorial Atlantic is characterized by a highly dynamic mesoscale activity driven by the North Brazil Current (NBC) and the North Equatorial Countercurrent (NECC) (Pauluhn and Chao, 1999; Froidefond et al., 2002; Fratantoni and Richardson, 2006) – see Appendix A. The NBC originates from the South Equatorial Current, and carries upper-ocean waters northwards to the equator. During the boreal fall season, a large part of the NBC at approximately 7°N–48°W retroflects eastwards, feeding the NECC (Lumpkin and Garzoli, 2005). This retroflection generates anticyclonic eddies with radii up to 200 km, which then move toward the Caribbean for several months every year (Didden and Schott, 1993).

These mesoscale features transport and disperse nutrient-rich waters originating from the Amazon River, further east (Baklouti et al., 2007). The Amazon is the largest river in the world, and discharges large amounts of sediment as well as particulates and chromophoric dissolved organic materials ($115 \cdot 10^7$ tons per year) into the Equatorial Atlantic Ocean (DeMaster et al., 1996; Meade, 1996). In this context, the Amazon plume strongly influences the oceanographic and biochemical conditions in the north-eastern part of the South American continental shelf, stretching from the

* Corresponding author.
E-mail address: philippine.chambault@gmail.com (P. Chambault).

http://dx.doi.org/10.1016/j.pocean.2016.01.006

North Brazilian coast to the Caribbean, making it a highly productive area (Muller-Karger et al., 1988; DeMaster et al., 1996).

The French Guiana continental shelf reaches from the Amazon River to the Trinidad Island sector and hosts three sea turtles species, namely the green turtle *Chelonia mydas* (Baudouin et al., 2015; Chambault et al., 2015), the leatherback *Dermochelys coriacea* (Fossette et al., 2006, 2010a,b) and the olive ridley *Lepidochelys olivacea* (Kelle et al., 2009; Plot et al., 2015). Although all three species remain on the continental shelf throughout the breeding and nesting seasons (Fossette et al., 2006; Georges et al., 2007), they exhibit different dispersal strategies during their post-nesting migration (Fossette et al., 2010b; Chambault et al., 2015; Plot et al., 2015; Baudouin et al., 2015). Only the olive riley sea turtles remain on the French Guiana continental shelf after the nesting season (Plot et al., 2015).

The olive ridley population that nests in French Guiana remains within the neritic domain during its northwestward post-nesting migration, which is an unusual habitat, confirming that this species can occupy different habitats according to the population (Polovina et al., 2004). Olive ridleys also exhibit behavioral plasticity in terms of dispersal and diving behavior through the use of different habitats according to the individual, i.e. the continental shelf, the continental slope or deep waters (Plot et al., 2015). This post-nesting migration, over the Guiana basin, occurs in the equatorial waters of the Atlantic, making this site unique as it is on the very periphery of the species range (Grinnell, 1917). Furthermore, nothing is known to date about how this population uses mesoscale features to forage at its range boundaries.

This study is the first to investigate the role of mesoscale features in the foraging behavior of olive ridley sea turtles. Mesoscale features such as eddies, fronts and upwelling/downwelling are highly variable in size and duration, covering from 100 km to 500 km and lasting anywhere between 10 and 100 days (Croxall, 1987). They are expected to strongly influence the foraging strategies of pelagic organisms, especially marine megafauna (Bailleul et al., 2010). Indeed, these oceanic structures contribute to ocean mixing, enhancing primary productivity at low trophic levels and concentrating prey for megafauna organisms, thereby affecting the entire food chain through bottom-up processes (Lévy, 2008). Recent studies in two different populations of elephant seals have demonstrated links between foraging behavior and eddies – fronts (Campagna et al., 2006; Bailleul et al., 2010; Dragon et al., 2010). Similar results have been obtained in cetaceans (Davis et al., 2002), seabirds (Weimerskirch et al., 2004; Pinaud and Weimerskirch, 2005; Cotté et al., 2007; Tew-Kai and Marsac, 2009) and sea turtles (Polovina et al., 2006; Lambardi et al., 2008), indicating that areas of high productivity provide feeding grounds for a broad range of marine megafauna species.

To date, the identification of eddies and fronts has mainly been based on remote sensing data such as Sea Surface Temperature (SST), Sea Surface Height (SSH), primary production and oceanic circulation (current velocity). However, an innovative modeling approach based on the distribution of pelagic preys has emerged over the last decade: the Spatial Ecosystem And Population Dynamics Model (SEAPODYM) (Lehodey et al., 2008). This model of mid-trophic organisms is based on several types of prey that are vertically distributed within the water column, i.e. the micronekton. The technique has been initially used to predict tuna population dynamics (Lehodey et al., 2010a,b; Lehodey et al., 2012; Sibert et al., 2012) and recently cetacean distribution (Lambert et al., 2014), and also to simulate turtle movements (Abecassis et al., 2013).

Several techniques have been developed to detect foraging events. In the horizontal dimension, the identification of Areas of Restricted Search (ARS) was based on the detection of decrease in travel speed and increase in turning angles (Kareiva and Odell, 1987; Robinson et al., 2007; Dragon et al., 2012). The detection of ARS has helped to identify foraging activity in numerous species via a wide range of techniques (Fauchald and Tveraa, 2003; Weimerskirch et al., 2004; Jonsen et al., 2005, 2006, 2007; Gaspar et al., 2006; Pinaud, 2008; Bailey et al., 2008; Barraquand and Benhamou, 2008; Dragon et al., 2012; Plot et al., 2015). There is a significant depth structure to foraging behavior within the water column in particular areas of prey aggregation (Fuiman et al., 2002; Watanabe et al., 2003; Mitani et al., 2003), making it essential to take the vertical dimension into account as well (Bailleul et al., 2008). New techniques using acceleration data from data loggers placed on pinnipeds (Viviant et al., 2014; Labrousse et al., 2015) and sea turtles (Okuyama et al., 2009; Fossette et al., 2010a,b, 2012a,b) have made it possible to identify prey capture attempts during the dives. However, such techniques were mostly inapplicable to low resolution datasets, which require tag retrieval after tracking (Heerah et al., 2014, 2015). Consequently, vertical foraging activity is often identified and quantified using foraging indices such as bottom time, dive shape (Fedak et al., 2001; Dragon et al., 2012) or, more recently, hunting time (Heerah et al., 2015). This study applies the hunting time index to olive ridley sea turtles for the first time, making it possible to estimate the time spent foraging within-dives.

In 2013 and 2014, satellite tags were deployed on 20 adult female olive ridley sea turtles to assess the influence of oceanographic and biological features on their foraging behavior in horizontal and vertical dimensions during their post-nesting migration from French Guiana. This study aims to (1) analyze horizontal movements in relation to remote sensing data and micronekton biomass, then to (2) quantify and link foraging events within dives to *in situ* data directly recorded within the water column.

2. Materials and methods

2.1. Ethics statements

This study met the legal requirements of the country in which the work was carried out, and followed all institutional guidelines. The protocol was approved by the "Conseil National de la Protection de la Nature" (CNPN, http://www.conservation-nature.fr/acteurs2.php?id=11), which is under the authority of the French Ministry for ecology, sustainable development and energy (permit number: 09/618), and acts as the ethics committee for French Guiana. The fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of Cayenne, French Guiana, France, in order to minimize any disturbance of the animals.

2.2. Study area and tag deployment

During the 2013 and 2014 nesting seasons, 20 adult female olive ridleys were equipped with satellite tags on the beaches of Remire-Montjoly (4.53°N–52.16°W, Cayenne, French Guiana). Eight Argos-linked Fastloc GPS tags (MK10, Wildlife Computers Redmond, WA, USA) were deployed from July to August 2013. Twelve Conductivity Temperature Depth Fluorometer-Satellite Relayed Data Loggers (CTD-SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland) were fitted during the same period in 2013 ($n = 2$) and 2014 ($n = 10$).

Using a red light to minimize disturbance, the satellite tags were attached during night-time egg laying, i.e. at the only moment when individuals are static – for details see Baudouin et al., 2015. The carapace was cleaned with scrapers, water and acetone, then the tags were fixed to the carapace as close as possible to the head using an epoxy resin, with the antenna facing