DIVING BEHAVIOR AND INTERNESTING MOVEMENTS OF LEATHERBACK SEA TURTLES IN U.S. VIRGIN ISLANDS

A Dissertation

by

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ABSTRACT

The leatherback sea turtle (hereafter referred to as LB), which is monotypic in the family Dermochelyidae, is morphologically and physiologically distinct from the other six extant sea turtle species. Despite its worldwide distribution and ancient lineage, it is one of the least understood marine turtles because of its pelagic life. The goal of this study was to use miniature, animal-borne video and data recorders and satellite telemetry to monitor the diving performance, foraging behavior and movements of LB during the internesting interval on St. Croix in the U.S. Virgin Islands. I tested two hypotheses: 1) foraging is rare and opportunistic during the internesting interval, and 2) the offshore movements during the internesting interval is an antipredator strategy. The results show that LB make two types of dives: Shallow Transit (ST) and Deep Transit (DT) dives. ST dives were short, shallow and associated with slow subsurface swimming to reduce drag. DT dives involved gliding and were moderately deeper than ST dives with a longer distance traveled at the same slow speed. LB spent 94% time at sea making ST and DT dives with short surface resting periods, but there was no indication of prolonged periods of resting or sleep. Six species of gelatinous prey were identified. Reduced foraging effort indicated fasting during nesting season (i.e., capital breeding strategy). There was no indication of behavioral thermoregulation. Assuming LB fast during the nesting season, the energy expended while at sea for the entire internesting interval would be equivalent to the catabolism of 26.3 kg of fat (39 kg fat including egg production). LB are at risk of predation from sharks once they leave the beach, most likely from tiger sharks based on scars, wounds, and missing flippers. When attacked, their response was instantaneous, robust, and involved evasive swimming at an elevated speed with rapid rotation, steep descent and ascent, and lateral inversion. Most shark encounters were short (< 5 min), which indicates that defensive behavior is effective, although this behavior cannot eliminate injury and death. Shark attacks were most frequent (3-fold) when LB were < 6 km from St. Croix compared to > 6 km offshore. If LB had remained < 6 km from shore for the entire interesting interval, they potentially would have experienced 48% more shark attacks. Therefore, offshore internesting trips appear to be a strategy to reduce shark encounters (i.e., avoidance behavior) while the next clutch of eggs develops.

DEDICATION

To Mr. Raul Teran and the worldwide Kosen-rufu.

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NOMENCLATURE

3D	three-dimensional
BM	body mass
CCL	curved carapace length
CCW	curved carapace width
CRW	correlated random walk
CVA	canonical variates analysis
cm	centimeters
DEM	digital elevation model
DT	deep transit
Eq	equation
FDR	false discovery rate
GB	gigabytes
GEBCO	General Bathymetric Chart of the Oceans
GIS	Geographic Information System
GMT	Greenwich Mean Time
GPS	Global Positioning System
hr	hours
Hz	hertz
kg	kilograms
kJ	kilojoules

LC	location class
LT	leatherback sea turtle(s)
m	meters
min	minutes
NOAA	National Oceanic and Atmospheric Administration
QDR	quadratic discriminant analysis
RMR	resting metabolic rate
s	seconds
SD	standard deviation
SPNWR	Sandy Point Natural Wildlife Refuge
spp.	species
SR	surface resting
ST	shallow transit
USGS	United States Geological Survey
USVI	United States Virgin Islands
VDR	video-data recorder
VHF	very high frequency
viz	videlicet
W	watts

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1. INTRODUCTION

1.1 Taxonomy and Demography

The leatherback sea turtle (*Dermochelys coriacea*; hereafter referred to as LB) is the only species in the family Dermochelyidae and the fourth largest extant reptile behind three species of crocodilians. (Fig. 1.1a). Compared with the other six species of extant sea turtles (Family Cheloniidae), it is the only one with a leathery integument instead of keratinous scutes covering a bony carapace. Ancestors of LB evolved over 110 million years and survived the Cretaceous–Paleogene extinction when most other marine reptiles (e.g., plesiosaurs, mosasaurs) became extinct (Wood et al. 1996; Parham and Pyenson 2010; Cadena and Parham 2015).

LB are wide-ranging and occur in all oceans except for the Arctic and Southern Oceans (Willgohs 1957; Martof et al. 1980; Goff and Lien 1988; Spotila 2004; Hamann et al. 2006). The current limit of the northern and southern migratory range is Finnmark, Norway and Foveaux Strait, New Zealand (Fig. 1.2, Eggleston 1971; Carriol and Vader 2002). However, nesting beaches occur on tropical and subtropical islands or along the continental coastlines (Eckert et. al. 2012). Post-nesting females in the western Atlantic generally migrate to the North Atlantic Ocean for foraging each winter, and the maximum distance recorded was 13,793 km. In contrast, internesting females tend to stay within 160 km of nesting beaches and often remain on the continental shelf (James et al. 2005; Eckert 2006; Eckert et al. 2006a; Benson et al. 2007; Fossette et al. 2007, 2008a; Witt et al. 2009; Stewart et al. 2013).

LB are cosmopolitan in their distribution with three genetic haplogroups identified in the Atlantic, Indian, and Pacific Oceans (Dutton et al. 1999; Bowen and Karl 2007; Dutton et al. 2007; Dutton et al. 2013b; Dutton and Shanker 2015). The last world population estimate was made in 1996 and ranged from 26,000-43,000 adult females. Today, seven regional management units (RMU) are recognized based on genetics, nesting and tagging studies, and satellite tracking. These units include the Northwest (NW) Atlantic, Southwest (SW) Atlantic, Southeast (SE) Atlantic Oceans, SW Indian, NE Indian Oceans, West Pacific and East Pacific Oceans (Wallace et al. 2010). Many populations are experiencing a decline in nesting colonies, especially the Pacific populations (Spotila et al. 1996; Spotila et al 2000). A total of 467 nesting sites are currently identified in the Wider Caribbean Region, which includes the NW Atlantic Leatherback RMU (Wallace et al. 2010). Regional trends in annual LB nesting counts have declined significantly in this area since the 1990s, and only French Guiana, Panama and Trinidad and a few other sites still have more than 1,000 nests per year. Smaller colonies, including the Northern Caribbean population of Puerto Rico and St. Croix in the U.S. Virgin Islands, are distributed throughout Caribbean island nesting beaches (Eckert et al. 1986; Girondot et al. 2007; Eckert and Eckert, 2019). Globally, LB are listed as Vulnerable according to the International Union for the Conservation of Nature (IUCN), but many subpopulations (such as in the Pacific and Southwest Atlantic) are Critically Endangered. In the United States, LB are listed as Endangered under the Endangered Species Act of 1973.

1.2 Morphology

Adult LB are large, with a curved carapace length (CCL) of 140-170 cm and a body mass of 250-500 kg (Eckert et al. 1989; Boulon et al. 1996; Leslie et al. 1996; James et al. 2007; Eckert et al. 2012). The largest recorded LB was a male, which stranded in Wales in 1988, had a CCL of 260 cm and a body mass of 916 kg. There is no apparent size sexual dimorphism except for tail length at sexual maturity. Adult males have a longer tail than that of the female similar to other marine turtles, and the cloaca extends further beyond the posterior tip of the carapace (Davenport 1990; Wyneken 2001; James 2004; James et al. 2007).

As with other sea turtles, LB are hydrodynamically shaped. The back tapers from the shoulders to the caudal tip with dorsal-ventral compression (i.e., an oval shape in the transverse plane). The forelimbs are modified into elongated, clawless flippers for cost-efficient locomotion (Davenport 1987; Renous and Bels 1993; Wyneken 1996). Unlike other sea turtles, the integument of LB is smooth and elastic, with no keratinous scutes. The leathery skin forms a dermal carapace that is 3-4 cm thick and covers a mosaic of thousands of small polygonal osteoderms (small bony plates) with interlocking sutures, which makes them flexible (Chen et al. 2015; Wyneken 2015). Below the osteoderms is a layer of adipose tissue (Goff and Stenson 1988; Harris et al. 2016). Seven distinct ridges extend from the cranial to caudal margin of the back, which enhance hydrodynamic performance (Bang et al. 2016). The dorsal surface is black with mottling, especially the head, but the ventral surface is mostly white, although there is much variation. A pink spot on the top of the head is associated with the pineal gland, which regulates biorhythms (Davenport et al. 2014).

LB use pectoral oscillation for locomotion. The enlarged fore flippers act as both lift-based hydrofoils and drag-based paddles similar to sea lions (Davenport 1987; Feldkamp 1987b; Davis 2019). The oscillating fore flippers generate lift-based thrust during the upstroke and drag-based thrust during the downstroke. The hind flippers generate no thrust but contribute to maneuvering. When on land, LB use protraction of all four flippers to crawl across the sand on nesting beaches, which is called "swing-and-stance" movement pattern as if using a crutch to move forward (Wyneken 1996). The main use of the spade-shaped hind flippers for nesting females is to dig the egg chamber (Davenport 1987; Renous and Bels 1993; Wyneken 1996).

The head of LB is oval with dorsally directed nares and a pair of large, posteriorly-pointed cusps along the anterior edge of the upper jaw but no rhamphotheca (i.e., keratinous beak) like other sea turtles (Fig. 1.3a). LB feed on gelatinous plankton (i.e., Cnidaria, Ctenophora, and Urochordata) using suction feeding, which is made possible by expansion of the buccal and pharyngeal cavities (Doyle et al. 2007; Fraher et al. 2010; Heaslip et al 2012; Bardet et al. 2013). The mouth and throat are lined with sharply pointed, keratinized buccopharyngeal papillae that point posteriorly and become more numerous at the back of the buccopharyngeal cavity (Fig. 1.3b). The highly distensible oesophagus entraps prey until closure of the mouth, expulsion of water, and swallowing. The papillae may prevent the ingestion of excessive amounts of seawater (Wyneken 2001; Wallace and Jones 2015; Wyneken 2015).

1.3 Physiology

1.3.1 Metabolism and Thermoregulation

Sea turtles are ectotherms, which means they have a reduced mass-specific resting metabolic rate (RMR) and a labile core body temperature compared to endothermic mammals and birds. For example, green sea turtles have a mass-specific RMR (0.13 W kg^{-1}; BM 135 kg), which is 17% of the allometric prediction (0.76 W kg^{-1}) for a eutherian mammal of the same mass (McNab 2008; Davis 2019). Instead of endothermy, ectotherms rely on ambient sources of heat to regulate their core body temperature. Most marine turtles rely on behavioral thermoregulation to maintain core body temperature by balancing the amount of time they spend in water of different temperatures (Southwood et al. 2005). However, LB have a mass-specific RMR (0.36 W kg^{-1}; BM 334 kg) that is 3.5-fold higher than that in green sea turtles and 61% of the allometric prediction (0.59 W kg^{-1}) for a eutherian mammal of the same mass (Lutcavage et al. 1992; McNab 2008; Davis 2019). The elevated RMR of LB indicates an endothermic capacity not present in green sea turtles, although it is less than that in mammals of the same body mass. The source of this increased thermogenic capacity may occur in all LB tissues through enhanced mitochondrial proton leak (i.e., futile cycles). However, LB have a layer of adipose tissue, composed of two layers, which is located below the osteoderms (Goff and Stenson 1988; Harris et al. 2016). The superficial layer is firm and composed of a white adipose tissue that provides thermal insulation but also serves as an energy reserve. The inner layer, which is tan in color and vascularized, resembles thermogenic brown adipose tissue in mammals and may be an important source of heat to maintain an elevated core body temperature, especially in cold water. The slow swimming speed (~0.7 m sec^{-1}) further increases metabolic rate (i.e., 2-fold higher above the RMR) and heat production, but only modestly (Eckert 2002).

In addition to enhanced thermogenesis, LB have a vascular anatomy in the fore flippers that acts as a counter-current heat exchanger to reduce heat loss and maintain core body temperature, which can be up to 18° C higher than ambient water temperature (Frair et al. 1972; Greer et al. 1973; Davenport et al. 2015). The large size of LB provides thermal inertia (i.e., gigantothermy), which prevents rapid changes in core body temperature, especially in cold (e.g., 8° C) water. However, if LB need to dissipate heat, the large fore flippers can act at thermal windows (i.e., circumventing the counter-current vascular system), although this may be a problem only on land (Davenport et al. 2015).

1.3.2 Energy Balance

LB feed on low energy-density gelatinous plankton, but have an elevated mass-specific RMR that is 3.5-fold higher than that in green sea turtles and 61% of the allometric prediction for a eutherian mammal of the same mass (see Section 1.3.1). As a result, they must consume large quantities of prey. The mean wet mass for the compass jellyfish (*Chrysaora hysoscella*), lion’s mane jellyfish (*Cyanea capillata*), and barrel jellyfish (*Rhizostoma octopus*) is 1,558 g, of which 1,496 g (96%) is water (Doyle et al. 2007). The mean energy density for these three species is 0.13 kJ g wet mass^{-1} (Heaslip et al 2012). The estimated at-sea metabolic rate of adult female LB is 19,219 kJ day^{-1}, which would require ~148 kg day^{-1} of gelatinous prey (*viz*. 19,219 kJ day^{-1} ÷ 0.13 kJ g wet mass^{-1} ÷ 1000 g kg^{-1}) or 44% of body mass for a 334 kg LB (see Chapter 2). This prey intake does not include the additional prey consumption for growth, egg production, or to acquire fat reserves before the nesting fast.

1.3.3 Diving

LB are capable of deep (> 1,000 m), long (> 60 min) dives. (Eckert et al. 1986, 1989, 2012; Hays et al. 2004). Nevertheless, mean maximum dive depth is shallower (< 100 m) with a duration of < 25 min, and this appears to be true during internesting interval and post-nesting migration (Hays et al. 2004). The estimated aerobic dive limit (ADL) is ~17 min with most of the oxygen stores in the blood and muscle (Eckert 1989). During the internesting interval, LB swim almost continuously at a mean speed of 0.6 m sec^{-1}, with extensive shallow, subsurface swimming (Eckert 2002).

1.3.4 Osmoregulation

Reptilian kidneys cannot produce urine that is hyperosmotic to plasma. To supplement renal function, LB rely on lachrymal glands to excrete salt ingested in the diet. The paired lachrymal glands are large (0.4% of body mass) and produce salt secretions with a concentration of up to 1,650 mOs kg^{-1}, 2-fold more concentrated than that in loggerhead sea turtles (*Caretta caretta*) and more concentrated that seawater (~1,200 mOs kg^{-1}) (Hudson and Lutz 1986; Davenport 2017). A daily consumption of 148 kg of gelatinous prey (see 1.3.2 above), which is 96% water and isosmotic with seawater (35 g NaCl kg^{-1} seawater), results in the ingestion of 143 kg of water and 4.97 kg of salt daily (*viz*. 148 kg prey day^{-1} x 0.96 x 35 g NaCl kg^{-1} ÷ 1,000 g kg^{-1}). As a result, LB produce a continuous flow of lachrymal secretions with a high osmolality (Davenport 2017). The kidneys excrete the remainder of the ingested water and NaCl.

1.4 Sensory Systems

Sensory systems in LB have not been studied extensively. Based on ocular morphology and corneal electroretinogram, their vision is not well adapted to dim light despite their deep diving ability (Crognale 2007, 2008; Brudenall et al. 2008). There is no evidence for low-light vision or a blue shift in the wavelengths of peak sensitivity as occurs in deep diving Pinnipedia (Eckert et al. 2012; Davis 2019). There are not data for underwater acuity, olfaction, audition or vocalizations for LB. Although LB make wide ranging migrations, there is no experimental evidence for a geomagnetic navigational ability. A pink spot on the top of the head is associated with the pineal gland, which regulates biorhythms and seasonal migration (Davenport et al. 2014).

1.5 Life History and Reproductive Strategy

Age at maturity for LB is uncertain and has been estimated to be 6-29 years (Zug and Parham 1996; Avens et al. 2009; Eckert et al. 2012). The recruitment of female neophytes into the breeding population is also uncertain. There are few descriptions of courtship, and the time and location of mating is uncertain. In one observation of courtship, the male lunged at the female followed by mounting attempts to position the penis for intromission (Carr and Carr 1986). Females may avoid aggressive males by descending to the seafloor and remaining motionless (Reina et al. 2005). Males may travel among nesting beaches, perhaps looking for sexually receptive females. Single paternity is the most prevalent mating strategy, indicating that females store sperm during the reproductive season (Crim et al. 2002).

LB produce 5-6 clutches during a 3-6 months season, which varies geographically (Boulon 1996; Eckert et al. 2012). Nesting is nocturnal on sandy beaches with course-grained sand. Nest sites must be above the high tide line for successful incubation of the eggs, and adjacent seawater temperatures of 26-32°C may be important for hatchlings. Nesting behavior is stereotypic and consists of: 1) emergence from the sea onto the nesting beach;, 2) overland traverse to and selection of a suitable nest site;, 3) excavation of a body pit;, 4) excavation of the nest chamber;, 5) oviposition (egg-laying);, 6) filling of the nest chamber;, 7) covering and concealing the nest site;, and 8) returning to the sea (Miller 1997; Garner and Garner 2009; Eckert et al. 2012). The entire process requires about two hours. The eggs are large (~80 g) with a pliable shell, and each clutch consists of 60-100 eggs. A ~10 day internesting interval occurs between each clutch, during which time the female goes to sea. At the end of the nesting season, LB travel to higher latitudes to feed. Remigration (i.e., nesting in subsequent years) may occur on a 2-4 year interval and reflects the time necessary to require fat stores, which depend on habitat quality and prey availability (Boulon 1996; Dutton et al. 2005; Garner et al. 2017). These data indicate that LB are capital breeders: that is, to forage and obtain energy in one area and fast during the reproductive period. (Jönsson 1997; Bonnet et al. 1998; Perrault et al. 2014; Okuyama et al. 2016; Robinson et al. 2017).

1.6 Research Goals

We have much to learn about life history, foraging/diving behavior, and physiology of LB, in part because they are the most pelagic of the marine turtles. As with other marine vertebrates, tracking their movements at sea and recording their life while submerged is challenging. The development of animal-borne telemetry and recorders has offered new insight into the life of marine animals. The first use of time-depth recorders on LB did not occur until 1985, and it revealed a remarkable capacity for deep, long dives (Eckert 1986). However, time-depth records provide little information about the behavior of marine animals while at depth, swimming performance, or habitat associations. Animal-borne instruments that record video and additional channels of data on performance (e.g., speed and flipper or fluke stroke frequency) and environmental data (e.g., temperature and salinity), which became available in the late 1990s, have revised our understanding of marine animals (Davis 2019). In this study, I used miniature video and data recorders (VDRs) in combination with satellite tracking to provide new information on the behavior of female LB during the internesting interval. My hypotheses for this study were: 1) female LB feed infrequently and opportunistically, based on results of Eckert (1989) and Casey et al. (2010) for Chapter 2, and 2) gravid LB may use the offshore movements during the internesting interval to avoid predation for Chapter 3. Using animal-borne video and high-resolution data on dive characteristics, swimming performance, and long-distance movements, I confirmed that feeding was rare and opportunistic and not likely the reason for exhibited dive patterns (see Chapter 2). Instead, I found that LB use the internesting trip to offshore as an antipredator strategy combined with elaborate defensive behaviors when attacked by sharks (Chapter 3). Hence, this study provides new information on the behavior of LB and the purpose of the internesting interval at sea.

2. DIVING AND FORAGING BEHAVIORS OF GRAVID LEATHERBACK SEA TURTLES (*Dermochelys coriacea*)

2.1 Introduction

Leatherback sea turtles (hereafter referred to as LB) are the most widely distributed and deep diving marine reptile. They are the largest of the seven extant species of sea turtles and one of the most ancient reptiles whose ancestors survived the Cretaceous–Paleogene extinction (Wood et al. 1996; Parham and Pyenson 2010; Cadena and Parham 2015). Their migratory range covers all oceans except for the Arctic and Southern Oceans, but they can occur as far north as 61°N lat, which ~500 km south of the Arctic Circle (Willgohs 1957; Martof et al. 1980; Spotila 2004; Hamann et al. 2006). Although LB are a monotypic genus with a shallow phylogeny, they are cosmopolitan in distribution with three genetic haplogroups identified in the Atlantic, Indian, and Pacific Oceans (Dutton et al. 1999; Bowen and Karl 2007; Dutton et al. 2007; Dutton et al. 2013b; Dutton and Shanker 2015). Nesting beaches occur on tropical and subtropical islands or along continental coastlines.

A total of 467 nesting sites are currently identified in the Wider Caribbean Region, which comprises the Northwest Atlantic (NWA) leatherback regional management unit (Wallace et al. 2010). The regional trends of annual LB nest counts have declined significantly since the 1990s, and only French Guiana, Panama and Trinidad and a few other sites still have more than 1,000 nests per year. Smaller colonies, including the Northern Caribbean population of Puerto Rico and St. Croix in the U.S. Virgin Islands, are distributed throughout Caribbean island nesting beaches (Eckert et al. 1986; Girondot et al. 2007; Eckert and Eckert, 2019). Post-nesting females from these regions generally migrate into the North Atlantic Ocean to forage each winter, and the maximum distance recorded in this migration is 13,793 km. In contrast, gravid females generally remain within 160 km of nesting beaches during the nesting season in the spring, often on the continental shelf (James et al. 2005; Eckert 2006; Eckert et al. 2006; Benson et al. 2007, 2011; Fossette et al. 2007, 2008a; Witt et al. 2009; Stewart et al. 2013).

Prior to the mid-1980s, researchers speculated that LB were deep divers because, unlike most sea turtles, they lack a heavily calcified bony anatomy (Rhodin et al. 1981). From 1985-88, the first data were collected on their diving behavior using animal-borne recorders attached to adult females on the Caribbean island of St. Croix, the same nesting population used in this study (Eckert et al. 1986, 1989). These studies revealed the ability of LB to make deep (> 1,000 m), long (37 min) dives, although most were more modest (< 125 m deep, < 15 min in duration). A subsequent study using female LB from St. Croix recorded a routine swim speed of ~0.7 m sec^{-1} (Eckert et al. 2002). Diving behavior also was recorded for LB during the internesting interval in the shallow coastal waters near Rantau Abang, Malaysia (Eckert et al. 1996). Together, these studies described the basic diving behavior and swimming performance of LB during the internesting interval.

LB nesting on St. Croix lay 5-6 clutches every 2-3 years, with an ~10-day interesting interval at sea between clutches. Females swim almost continuously at a speed of ~0.7 m s^{-1}, so they travel about the same distance each day (Eckert et al. 2002). Much of the time, LB swim just below the surface (~2 m depth) to reduce hydrodynamic drag and the cost of transport (Eckert et al. 2002). When they dive deeper, the time-depth profile is symmetrical (V- or U-shaped) and usually to moderate depths (< 120 m). The function of these dives was unknown, but foraging was the favored hypothesis (Eckert 1989).

Although LB feed on gelatinous zooplankton during the winter, foraging during the internesting interval has remained speculative (Wallace et al. 2005). Results from animal-borne instruments that recorded cloacal temperature, jaw movement, and 3-axis acceleration to identify prey captures were inconclusive, as was the use of short-duration video recording using animal-borne cameras (Reina et al. 2005; Myers and Hays 2006; Fossette et al. 2008). In contrast, recording the gastrointestinal tract temperature using animal-borne instruments on females from St. Croix during the internesting interval indicated when a cold bolus entered the stomach, which may have been associated with the consumption of gelatinous prey. However, prey size and species could not be determined, and mariposa (seawater drinking) could not be ruled out. Nevertheless, the results indicated a mean capture rate of 0.11 prey hr^{-1}, which would have provided < 1% of the energy needed for reproduction (Casey et al. 2010). As a result, foraging appeared to be rare and opportunistic, possibly because gelatinous prey in oceanic waters of the Eastern Caribbean Sea are sparse (Hargraves et al. 1970; Marshall 1973). Conclusive evidence through the use of video-recorded prey capture and detailed dive analysis is needed to validate foraging during the interesting interval.

The goal of this study was to use miniature, animal-borne video and data recorders (VDRs) to monitor the diving and foraging behavior of LB during the internesting interval on St. Croix. In addition, we used satellite telemetry to track their movements while at sea. My hypothesis was that the females feed infrequently and opportunistically based on the results of Eckert et al. (1989) and Casey et al. (2010). Unlike previous studies using animal-borne recorders, VDRs provide extended video and high-resolution data on dive characteristics, swimming performance, and long-distance movements. Using high-resolution data with simultaneous video recording of prey capture, the results from this study advanced our understanding of the at-sea behavior, foraging strategies, prey preference, predator interactions, and habitat-associations of LB.

2.2 Methods

2.2.1 Animals and Instrumentation

We studied nine gravid female LB (mean body mass ~334 kg; Eckert et al. 1989) that were nesting at the Sandy Point National Wildlife Refuge (Lat 17.67 N, Long 64.92 W), St. Croix, U.S. Virgin Islands from 2015-18 (Fig.2.1). This refuge, which was designated as Critical Habitat in 1978 and a National Wildlife Refuge in 1984 under the U.S. Endangered Species Act (ESA) of 1973, is the principal nesting location for the western Atlantic population. Females nesting in the refuge have been tagged and monitored annually since 1981 (Eckert et al. 1982, 1984; Eckert and Eckert 1983). As a result, the Sandy Point refuge has one of the longest histories of known nesting female LB. The nesting season extends between February and August, peaking in May. We conducted this study from April-May to have the largest selection of suitable females for instrumentation.

The VDR (12 cm long, 5.7 cm wide and 4.6 cm high; weight in water is ca. 60 g) is encased in polyurethane and depth rated to 2,000 m (Fig. 2.2a-c). It has a low-light sensitive monochrome video camera and six near-infrared (γ_{max} = 850nm) Light Emitting Diodes (LEDs), which provide illumination in total darkness up to a distance of 70 cm without disturbing the LB (near-infrared light is invisible to marine vertebrates; Levenson et al. 2006; Crognale et al. 2008). Compressed video (MPEG4) was stored on a digital video recorder with 32 GB of memory, and data were stored on an 8 GB Flash memory card. The VDR contains a three-axis accelerometer, a three-axis magnetometer, and sensors for depth, speed, light level, temperature, and sound (50 Hz-16 kHz). Sensor data were recorded at 1 Hz except speed (4 Hz) and the 3-axis accelerometer (16 Hz). Power was provided by two lithium-ion batteries (10 cm L, 3 cm W, 3 cm H; mass = 270 g in water each). The batteries enabled 27 hr of programmable video and continuous data while the females were at sea. Data were recorded as soon as the female entered the water, but video recording occurred after an initial delay of two days and below a depth of 50 m (in 2015-2017) or 30 m (in 2018). All sensors were calibrated prior to deployment.

Females with numbered flipper tags and passive radio-frequency identification (RFID or Pit) tags were identified when they came ashore to determine their suitability based on: 1) size (curved carapace length [CCL] > 140 cm), 2) a prominent ridge on the carapace for attaching instruments, 3) nesting history (past and recent), 4) had completed two or three nesting activities that season. I waited until oviposition (i.e., egg laying) before taking morphological measurements (i.e., CCL, curved carapace width [CCW], and maximum head width) and attaching instruments. I attached a VDR (Pisces Design, San Diego, CA), a satellite transmitter (Spot 6; 120 g; Wildlife Computer, Redmond, WA), a VHF transmitter (87 g; Advanced Telemetry System, Isanti, MN), and two lithium-ion batteries to the central ridge of the carapace (Fig. 2.2d). The VDR was mounted mid-dorsally overlooking the head, and the batteries and transmitters were mounted on a plastic plate behind the VDR. Both the VDR and plastic plate were secured to the carapace with steel wire that was passed through nylon tubes inserted in small drilled holes though the dorsal ridge. Before drilling the holes, the carapace was sterilized. This attachment method is widely used in leatherback research and approved by the Herpetological Animal Care Committee (HACC) of the American Society of Ichthyologists and Herpetologists, the U.S. Fish and Wildlife Service, and the Texas A&M Institutional Animal Use Committee (IACUC) (Jones et al. 2011). The attachment procedure required ~20 min, after which the female departed for sea. Each female was tracked while at sea using satellite telemetry. After returning to shore to lay another clutch of eggs, females were relocated using radio telemetry and the instruments quickly recovered.

2.2.2 Data Analysis

VDRs were recovered from five females with complete data during the internesting interval at sea. A total of 10,472 dives were analyzed using a custom Matlab program and R version 3.6.1 for calculation and statistical modeling (R Core Team 2013). Dive descent commenced when the seawater sensor on the VDR was submerged, dive depth increased for > 3 sec, and swim speed was > 0.2 m s^{-1}. Ascent occurred when dive depth decreased for > 3 sec and ended when the seawater sensor was no longer submerged. A bottom phase occurred when a female was no longer descending for > 3 sec and ascent had not commenced. No bottom phase was recorded if ascent commenced < 3 sec after the end of descent. Flipper stroke rate (strokes min^{-1}) was determined from the sine wave of the x-axis accelerometer using peak detection function in R. Gliding occurred when flipper stroking ceased for > 10 sec. Resting at the surface occurred when the seawater sensor was dry and swim speed was < 0.1 m s^{-1}. Distance swum was calculated by summing the 1-sec instantaneous speeds for each dive.

2.2.3 Video Analysis

We recorded 108 hr of video during 674 dives for four females (one VDR failed to record video). The video was scanned for prey encounters and simultaneous dive variables, which could be used to identify prey encounters in the data without video (Fig. 2.3). Speed, pitch, and X- and Y-axis accelerometry data provided the best indication of prey encounters using a rule-based detection protocol, which was validated for dives with video-recorded prey captures (Fig. 2.4). The criteria included: 1) speed < 0.1 m sec^{-1} for at least two sec, 2) rapid change in pitch, 3) sine wave on the Y-axis accelerometer reflecting head movement during prey ingestion, and 4) X-axis accelerometer indicating a rapid change in motion.

2.2.4 Statistical Analysis

Thirty dive variables and five environmental variables were extracted from the data and compiled into a matrix/data frame in R to classify 10,472 dives (Table 2.1). Elbow and Silhouette methods and the R package NbClust, which contained a total of 30 indices of clustering algorithms, were used to determine the optimal number of clusters (ONC) (Charrad et al. 2015). With the ONC, we used K-means cluster analysis and principal component analysis (PCA) to separate the dives into two clusters and identify explanatory variables (i.e. dive characteristics) (Yang and Yang 2003). Two discriminant analysis methods were used to identify the descriptors for two clusters. First, quadratic discriminant analysis (QDA) in R package MASS was used to determine the predictors of the clusters with 80% and 20% random partitioning for training and testing groups (Ripley et al. 2013). To examine the model accuracy with the predictors, the QDA model was fit into a predictor model with the testing group to generate a confusion matrix at the end. Canonical variates analysis (CVA) with Monte Carlo simulation tests for significance was conducted using Canoco version 5.0 to verify the results from QRD (ter Braak and Smilauer 2012). False Discovery Rate (FDR), an approach implemented in Canoco for the proportion of type I errors among all significant results, was used to adjust the raw *p*-values to account for false negatives in the results (Benjamini and Hochberg 1995). FDR is well suited for forward selection, although slightly conservative (Benjamini and Gavrilov 2009). Environmental variables (i.e., mean and maximum light level, mean and maximum temperature, and time of day) also were examined for correlations with dive classification using redundancy analysis (RDA). Time of day was defined as day (0900-1459), dusk (1500-2059), night (2100-0259), and dawn (0300-0859) local time (GMT-4). Variance Inflation Factors (VIF) were computed to indicate multicollinearity among explanatory variables (R package car), Shapiro-Wilks Test for normality (R package rstatix), and Box's M Test function in R package haplots for homoscedasticity of the dataset (Fox et. Al 2012; Kassambara 2017). The significance levels of spatial and temporal parameters (i.e., diel and daily occurrences) associated with the dive and resting periods were computed using Wilcoxon Rank Sum test, Kruskal-Wallis test, and Chi-square (all $\alpha = 0.05$) in R package dplyr (Wickham et al. 2020). Mean values are shown with standard deviation.

2.2.5 Movement Analysis

Locations for females were downloaded from the ARGOS satellite system (https://www.argos-system.org/). Departure and return locations on the nesting beach were determined with a handheld Global Positioning System (GPS). Location Class (LC), which a measure of accuracy, is ranked from the best (most accurate) to worst as 3, 2, 1, 0, A, B, and Z (invalid) respectively. Location classes B and Z were excluded from the analysis (Hays et al. 2001; Vincent et al. 2002; James et al. 2005). Locations were filtered in ArcGIS using a combination of error radius, the crawl package in R, and vmask function in the argosfilter package in R (Jonsen et al. 2005; Freitas et al. 2008; Johnson et al. 2008; Freitas 2010; Fleming et al. 2016; Johnson et al. 2018). Speed for vmask function was based on the maximum speed recorded for each female. Turning angle for the sdafilter was 20° (Jonsen et al. 2007; Freitas 2010). Feeding and shark interaction locations were estimated from the closet Argos locations and measured speed if more exact locations were not available. Dead reckoning was applied using a R package animalTrack to correct set and drift for constructing three-dimensional dive paths (Farrell and Fuiman 2014). Bathymetry maps were based on the General

Bathymetric Chart of the Oceans (GEBCO) and USGS Digital elevation models (DEMs).

2.3 Results

2.3.1 Classification of Dives

Of the 10,472 dives used in the dive classification analysis, 70% was assigned to Shallow Transit (ST) dives and 30% to Deep Transit (DT) dives (Fig. 2.5). Of the 30 variables used in the statistical analysis, 13 were significant (*p*-value 0.002) as explanatory variables accounting for 92.1 % of the variation, and in identifying the two dive types (Table 2.2). The most influential variables in separating the two dive types were: 1) total number of strokes, total gliding (% of dive), and glide duration (sec). The six environmental variables did not contribute significantly to separating the two dive types.

2.3.2 ST Dives

ST dives were shallow (3 ± 6.8 m) and short in duration (1.14 ± 1.24 min) with a speed of 0.6 ± 0.3 m s^{-1} and flipper stroke rate of 13.6 ± 2.93 stroke min^{-1} (Fig. 2.6a; Table 2.3). The total (not straight-line) distance swum during a ST dive was 45 ± 57 m. Most dives were associated with descent (38%) and ascent (48%) with a small percentage (14%) associated, with horizontal swimming at the bottom of the dive. Descent and ascent angles (-14 ± 7° and 4 ± 9°, respectively) were gradual with no gliding. The mean temperature for ST dives was 24.7 ± 0.8° C (range 23.5-26.1° C).

ST dives were more frequent in occurrence (69%) than DT dives, but they represented only 31% of the time at sea because of their short duration (Fig. 2.7). Their occurrence was not significantly different among four diel periods (i.e. day, dusk, night, dawn), and the daily percent occurrence (33 ± 5.8%) of ST dives did not change significantly throughout the internesting interval (Fig. 2.8). There were no prey encounters during ST dives.

2.3.3 DT Dives

Compared to ST dives, DT dives were deeper (84 ± 51.8 m; maximum 531 m) and longer in duration (13.42 ± 4.29 min; maximum 28.85 min) but had a similar swim speed of 0.6 ± 0.2 m s^{-1} (maximum 3.4 m s^{-1}) and flipper stroke rate of 14.07 ± 2.32 stroke min^{-1} (Fig. 2.5b; Table 2.3). Seventy-nine percent of DT dives were < 100 m, 96% < 200 m, and 99% < 300 m in depth (Fig. 2.9a). Sixty-seven percent of DT dives were < 15 min, 91% < 20 min, and 99% < 25 min in duration (Fig. 2.9b). The total (not straight-line) distance swum was 446 ± 168 m (maximum 1,676 m). Most of DT dives was associated with descent (46%) and ascent (53%) with < 1% associated with horizontal swimming at the bottom of the dive. Descent and ascent angles (-24 ± 9° and 9 ± 13°, respectively) were steeper, and 7.4% of the dive duration was spent in gliding, primarily during descent. The mean temperature during DT dives was 24.3 ± 1.1° C (range 12.4-26.1° C).

DT dives were less frequent (16%) in occurrence than ST dives, but they represented the highest percentage (63%) of the time at sea because they were 12.2-fold longer in duration than ST dives (Fig. 2.7). Their daily percent occurrence was not significantly different among four diel periods (i.e. day, dusk, night, dawn), and the daily percent occurrence (based on time) of DT dives did not change significantly throughout the internesting interval (Fig. 2.8).

The deepest and longest duration DT dive was 531 m and 28.9 min, respectively, with a minimum water temperature of 12.4° C. It was preceded by 8 ST dives and an 8 min SR. After the dive, there was a 10.2 min SR followed by 9 ST dives and a 3 min SR. The next DT dive was shallower (68 m).

2.3.4 Surface Resting (SR)

The average duration of SR was 1.71 ± 1.15 min, and 92% were < 3 min. SR was less frequent (15%) in occurrence than ST and DT dives and represented the lowest percentage (6%) of the time at sea (Fig. 7). Its occurrence was significantly different among four diel periods (day > night > dawn > dusk; Kruskal-Wallis test, $\chi^2 = 17.6$, $p = 0.0005$), but the daily percent occurrence (5 ± 1.2%) of SR (based on time) did not change significantly throughout the internesting interval (Fig. 2.8). The mean temperature during SR was 25.1 ± 0.7° C.

2.3.5 Sequence of ST Dives, DT Dives, and SR

On average, females made 5.7 ± 5.16 ST dives between DT dives, and SR occurred immediately before 71% of DT dives. In some cases, a SR without ST dives preceded a DT, and some DT dives had an SR immediately after surfacing. On average, the ratio of SR to DT dives was 0.78 ± 0.59, and 67% of intervals between DT dives was a combination of ST and SR.

2.3.6 Movements

When females departed the nesting beach, they generally swam north into the Virgin Islands Trough or southwest towards the Muertos Trough before returning to Sandy Point (Fig. 2.10). The mean transit distance (based on satellite-based locations at the surface) was 421 ± 76 km (range 303-498 km) during 9.5 ± 0.8 days, or 43.7 km day^{-1}. This transit distance is similar to the estimated total distance 417 km based on the percentage of ST and DT dives (85%) and the mean swim speed of 0.6 m sec^{-1} (*viz*. 9.5 days x 0.85 x 0.6 m sec^{-1} x 86,400 sec day^{-1}) (Fig. 2.7 and Table 2.3).

2.3.7 Foraging

During the combined 47.6 days at sea for the five females, 18 prey captures by three females (11, 4, 3 captures, respectively) were recorded on video and five encounters (likely captures) by two females (2 and 3 encounters, respectively) were identified during dives without video. Prey were captured or encountered primarily during ascent (74%) and during dawn (39%), day (43%), and dusk (17%), but not at night. All prey captures and encounters occurred during DT dives. The mean depth and water temperature for prey encounters was 79 ± 75 m (range 17-296 m) and 24.4 ± 2.4° C (range 18.8-26.1° C), respectively. In addition to 23 prey captures or encounters, 15 potential prey were observed in the video but not pursued by the females.

Six species of gelatinous prey were identified including: (a) Atlantic sea nettle (5: *Chrysaora quinquecirrha*), (b) Comb jelly (1: Family *Bathocyroidae*), (c) Crystal jelly (2: *Aequorea spp*.), (d) Giant fire salp (1: *Pyrosoma spp*.), (e) Moon jelly (2: *Aurelia aurita*), and (f) Pelagic salp (1: *Salpa aspera*) (Figs. 2.3 and 2.11). The average duration of feeding was 18 ± 5.4 sec. One female fed on a Pelagic salp for 91 sec, but departed without consuming the remainder of this very long prey (Fig. 2.3b). Most prey encounters occurred over deep waters of the continental slope and basin of the Virgin Island Trough (Fig. 2.12). Three prey encounters occurred along the northern edge of the Muertos Trough.

2.4 Discussion

We deployed VDRs and satellite transmitters on five female LB for a combined duration of 47.6 days during the internesting interval. After nesting, female LB spent 9.5 ± 0.8 days swimming north into the Virgin Islands Trough or southeast into the Muertos Trough before returning to nest. They spent 85% of the time at sea making ST and DT dives, with the remaining time spent at the surface, consistent with previous studies (Eckert et al., 1986, 1989, 2002). Prey captures or encounters were rare and opportunistic as they swam over deep water while the next clutches of eggs matured.

ST dives accounted for 31% of the time as sea and averaged 3 ± 6.8 m in depth and 1.14 ± 1.24 min in duration. These dives covered a short distance (45 ± 57 m) at modest speed (0.6 ± 0.3 m s^{-1}) (Fig. 2.5a; Table 2.3). ST dives were subsurface swimming at a depth (2-3 m or three body diameters) that minimizes hydrodynamic drag, which would be 4-fold greater at the surface because of wave generation (Eckert 2002; Davis 2019). Hence, ST dives were optimized for long distance travel at a reduced energetic cost, which conserves energy reserves (i.e., fat). The daily and diel percent occurrence (based on time) of ST dives did not change, so they were unaffected by trip duration and ambient light, respectively (Fig. 2.8).

DT dives were moderately deep (84 ± 51.8 m) and longer in duration (13.42 ± 4.29 min) than ST dives but with the same modest swim speed (0.6 ± 0.3 m s^{-1}) (Fig. 2.5a; Table 2.3). Because of their longer duration, DT dives accounted for 63% of the time as sea. The mean total distance swum during a single DT dive was 446 ± 168 m, which was 9.9-fold greater than for ST dives. Because DT dives were deeper, descent and ascent angles were greater, and 7.4% of the dive duration was spent in gliding descent (i.e., no flipper stroking) as the females transitioned from neutral to negative buoyancy at a depth of 34 ± 15 m. Functionally, we classified these dives as deep transit because there were very few (23) prey captures or encounters over the combined 47.6 days at sea. Compared to ST dives, there is no energetic advantage for females to make DT dives when traveling long distances, which suggests another explanation (Davis and Weihs 2007; Davis 2019). Deep transit dives in northern elephant seals (*Mirounga angustirostris*) in the eastern Pacific Ocean may be associated with avoiding predators such as white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*) (Davis et al. 2001; Davis and Weihs 2007). Swimming near the surface makes marine animals vulnerable to attack by predators that silhouette their prey from below. We know that LB are vulnerable to tiger shark (*Galeocerdo cuvier*) attack, so DT dives may be a strategy to decrease this risk while awaiting the development of the next clutch of eggs (Eckert et al. 1986; Keinath and Musick 1993; DeLand 2017; Stewart and Lombard 2017).

The mean depth of DT dives was 84 m, and only 4% and 1% were greater than 200 m and 300 m, respectively. The mean depth for prey captures and encounters was 76 ± 82 m, so deeper dives were not associated with enhanced foraging success. The deepest and longest dive recorded (531 m in depth, 28.9 min in duration) did not have prey captures or encounters, so its purpose is uncertain. Ninety-one percent of DT dives were < 20 min, which is consistent with the estimated aerobic dive limit (ADL) of ~17 min. (Fig. 2.9; Eckert 1986). As a result, the 28.9 min duration dive probably exceeded the ADL (Kooyman 1989; Davis 2019). The post-dive recovery from this dive included a 10.2 min SR, which is five-fold greater than the average SR, followed by nine ST dives and another 3 min SR. The next DT dive was 68 m, which was less than the average depth. Hence, dives that exceed the ADL may require an extended SR and a series of shallow ST dives to metabolize lactate and restore muscle pH before regular DT dives resume.

Only 23 prey were captured or encountered during 47.6 days at sea, but six species of gelatinous prey were identified (Fig. 2.11). These prey occurred in warm water (24.4 ± 2.4° C) at a shallow depth (79 ± 75 m), primarily along the continental slope of the Virgin Islands Trough (Fig. 2.12). Prey were usually captured during ascent (74%) and from dawn to dusk (99%), suggesting that LB use vision to detect and silhouette their prey in relatively shallow water, similar to the foraging behavior of LB in Nova Scotia, Canada (Wallace et al. 2015). When prey were captured, feeding duration was short (18 ± 5.4 sec). The longest duration feeding event (91 sec) occurred with a long Pelagic salp, although it stopped feeding before consuming it entirely (Figs. 2.3b and 2.11). An additional 15 potential prey were observed in the video but not pursued by the females, which indicates that active foraging does not occur during the interesting interval.

Sea turtles are ectotherms, which means that they have a reduced resting metabolic rate (RMR) and a labile core body temperature compared to endothermic mammals and birds. Instead of endothermy, ectotherms rely on ambient sources of heat to regulate their core body temperature. Marine turtles rely on behavioral thermoregulation to maintain core body temperature by balancing the amount of time they spend in water of different temperatures (Southwood et al. 2005). However, LB have a mass-specific RMR (0.36 W kg^{-1}; BM 334 kg) that is 3.5-fold higher than green sea turtles and 61% of the allometric prediction (0.59 W kg^{-1}) for a eutherian mammal of the same mass (Lutcavage et al. 1992; McNab 2008; Davis 2019). The elevated RMR of LB indicates an endothermic capacity not present in green sea turtles, although it is less than that in mammals of the same mass. Once the core body temperature of LB has equilibrated with the ambient water temperature, the large size of the LB provides thermal inertia (i.e., gigantothermy), which prevents rapid changes in core body temperature. In this study, the mean water temperature was 24.7 ± 0.8° C for ST dives, 24.3 ± 1.1° C for DT dives, 25.1 ± 0.7° C for SR. Taking into account the percentage of time that the females spent at these water temperatures, the overall mean temperature while at sea was 24.5° C (Fig. 2.7). During DT dives, the ambient temperature at the mean depth of 84 m was 24.1° C, not much different from the overall mean temperature. Hence, the thermal regime experienced by the females while at sea varied little, which would have produced a stable core body temperature of ~24° C or a few degrees warmer (Mrosovsky 1980; Standora et al. 1982). The slow swimming speed and flipper stroke frequency of the females during ST and DT dives would have increased metabolic rate modestly, so the primary influence on core body temperature would have been the mean water temperature. When one female made a rare dive to a depth 531 m, it experienced a minimum water temperature of 12.4° C for three minutes. The thermal inertia of the female's body (~326 kg) would have prevented a significant decrease in core body temperature. Hence, the females in this study probably had a high (~24° C) and stable core body temperature while at sea. There was no indication of behavioral thermoregulation associated with diving.

For some vertebrates, strategic fasting is a part of their life history, often in response to reduced food availability. As a result, they eat as much as possible and build body fat reserves when food is available. In some marine mammals, strategic fasting is associated with lactation in capital breeders such as Mysticeti (baleen whales) and Phocidae (seals) (Davis 2019). Capital breeding marine mammals provision their young using stored energy and nutrients accumulated at an earlier time and fast during lactation (Drent and Daan 1980; Houston et al. 2007). In these species, fasting is a strategic use of optimum feeding and nursing locations, which are separated temporally and geographically and often involve migration. Some large Mysticeti feed for half the year at high latitudes in the summer and fast during the winter while giving birth and nursing a calf in lower latitude, warmer waters. Phocidae fast (completely or partially) on shore or on ice during lactation, which can range from 4-45 days. Although they do not lactate or care for their offspring, female LB are capital breeders that acquire fat reserves while foraging in more productive, high latitude habitats (similar to Mysticeti) and nest at lower latitudes, which are warmer and more conducive to embryonic development and survival of hatchlings.

A gravid female that nests at Sandy Point typically lays six clutches of eggs separated by a ~10-day internesting period at sea. This period presumably allows the next clutch of eggs to mature before returning to the nesting beach. Females return to sea because remaining onshore during the internesting period is dangerous (i.e., terrestrial predators) and physiologically challenging (e.g., thermoregulation). However, females face predation from tiger sharks, which aggregate near nesting beaches (see Chapter 3). To avoid predators, females meander within ~160 km radius around the nesting beach to avoid predators, especially tiger sharks, which aggregate along nesting beaches. There are no data on tiger shark distribution and abundance around St. Croix. However, tiger sharks generally prefer near-shore habitats, and most of the females nesting at Sandy Point have scars, wounds or missing flippers from shark attacks (Heithaus et al. 2002, 2007; DeLand 2007; Stewart and Lombard 20017). In addition to LB, green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) sea turtles also nest at Sandy Point, which is an additional attraction for sharks. Thus, LB may avoid shark attack by moving away from nesting beaches while at sea. Although this strategy does not eliminate encounters with predators, it does reduce them (see Chapter 3). However, leaving nearshore waters and continually swimming has an energetic cost, which can be estimated for a 334 kg LB assuming that 85% of the time at sea is associated with swimming and 15% associated with resting (Fig. 2.7). Assuming that the energetic cost of swimming at 0.6 m s^{-1} is 2-fold higher than resting metabolism (*viz*. 0.36 W kg^{-1} x 2 = 0.72 W kg^{-1}; Lutcavage et al.1992; Wallace et. al. 2005; Bostrom and Jones 2007), the energy expenditure (E_{Trip}) for a 9.5 day (228 hr) internesting interval based on resting metabolic rate (RMR) and swimming metabolic rate (SMR) would be the sum of resting (E_{Rest}) and swimming (E_{Swim}) energy expenditure:

Eq. 1. E_{Rest} = 334 kg x 0.36 W kg^{-1} x 228 hr x 0.15 x 3,600 sec hr^{-1} ÷ 1,000 J kJ^{-1}= 14,804 kJ

Eq. 2. E_{Swim} = 334 kg x 0.72 W kg^{-1} x 228 hr x 0.85 x 3,600 sec hr^{-1} ÷ 1,000 J kJ^{-1}= 167,778 kJ

Eq. 3. E_{Trip} = 14,804 kJ + 167,778 kJ = 182,582 kJ (19,219 kJ day^{-1})

If the energy expended (E_{Trip}) during an internesting period (not including egg production, see below) came from stored fat while the female was fasting, then the amount of fat catabolized would be:

Eq. 4. 182,582 kJ ÷ 37.66 kJ g^{-1} lipid ÷ 0.9 g lipid g^{-1} fat ÷ 1,000 g kg^{-1} = 5.4 kg fat

This equation assumes that fat is 90% lipid and 10% water. If females (BM = 334 kg) in this study made five internesting trips to sea, then the total energetic cost at sea would be 912,910 kJ (*viz*. 5 x 182,582 kJ) and require the catabolism of 26.3 kg of fat (*viz*. 912,910 kJ ÷ 37.66 kJ g^{-1} lipid ÷ 0.9 g lipid g^{-1} fat ÷ 1,000 g kg^{-1}), which is 8% of body mass.

Females could offset this cost be foraging, but that does not appear to occur. Instead, they use cost-efficient of locomotion (i.e., hybrid lift and drag-based pectoral oscillation) during subsurface swimming to conserve body energy reserves (i.e., fat) throughout the nesting season (Davenport 1987; Renous and Bels 1993; Wyneken 1996). Although we recorded a few prey captures and encounters, they were rare. Why females do not forage more is uncertain. It may result from the low density of prey in oligotrophic waters around St. Croix (Hargraves et al. 1970; Marshall 1973). Perhaps foraging efficiency is so low in this area that females do not actively search for prey. However, even when prey were encountered, the females did not appear motivated to feed. Whether this behavior is hormonally-linked to breeding is uncertain, but female LB behave like capital-breeding marine mammals, which stop feeding during lactation (Perrault et al. 2014).

Lactation is the most energetically costly part of reproduction in mammals, and in ungulates it comprises 75-80% of the total energetic cost of reproduction (Clutton-Brock et al. 1989; Oftedal et al. 1987). In capital breeding northern elephant seal females, which lose 31% of the initial body mass during their two-month lactation fast, 72% is from the loss of fat and only 18% from protein, a remarkable conservation of lean tissue mass (Costa et al. 1986a). Female blue whales (*Balaenoptera musculus*) may lose half of the energy stored as blubber over a six-month lactation period (Oftedal 1997). LB do not have lactation costs, but they produce multiple clutches of eggs during a 6-week nesting period. There are no data on the energetic cost of egg production (E_{egg}) in LB, but it can be estimated based on the energetic cost for egg production in domestic chickens (10.1 kJ g^{-1} egg mass; Brainer et al. 2016). Assuming that LB produce six clutches of 80 eggs and that each egg has a mass of 84 g (Leslie et al. 1996), then the energetic cost of egg production would be:

Eq. 5. E_{egg} = 10.1 kJ g^{-1} egg x 84 g egg^{-1} x 80 eggs $clutch^{-1}$ x 6 clutches = 407,232 kJ

If the energy to produce these eggs came from stored fat, which is 90% lipid, the amount of fat catabolized would be:

Eq 6. 407,232 J ÷ 37.66 kJ g^{-1} lipid ÷ 0.9 g lipid g^{-1} fat = 12 kg fat

Combining the energetic cost of the five internesting trips and egg production, the estimated total energetic cost (E_{Total}) during the 6-week nesting period would be:

Eq. 7. E_{Total} = 912,910 kJ + 407,232 kJ = 1,320,142 kJ

This amount of energy would require the catabolism of ~39 kg of fat (*viz*. 1,320,142 kJ ÷ 37.66 kJ g^{-1} lipid ÷ 0.9 g lipid g^{-1} fat), which is ~12% of the estimated mean body mass. The lower metabolic rates for ectotherms and the absence of lactation costs reduces the overall cost of reproduction in LB compared to marine mammals (Davis 2019). Nevertheless, females must store enough energy to make the round trip to nesting areas and avoid predators that wait for their arrival. Their principal strategy is to conserve energy and avoid predators, then return to more productive areas to forage and replenish energy reserves until the next breeding season.

2.5 Conclusions

LB make two types of dives: Shallow Transit (ST) and Deep Transit (DT) dives. ST dives were short, shallow and associated with slow, subsurface swimming to reduce drag with no periods of gliding descent. DT were moderately deeper than ST dives, involved gliding descent, and covered a longer distance (10-fold) at the same slow speed. LB spent 94% time at sea making ST and DT dives with short surface resting periods, but there was no indication of prolonged surface or subsurface resting or sleep. The diving behavior of LB was consistent throughout the internesting interval with no significant difference in ST and DT dive occurrence (based on time) among the four diel periods, but SR more frequent during the day. Only 4% and 1% of DT dives were deeper than 200 m and 300 m, respectively. The deepest and longest DT dive was 531 m in depth, 28.9 min in duration. Feeding was rare and opportunistic but generally occurred during ascent from dawn to dusk indicating visual prey detection. Six species of gelatinous prey were identified. Reduced foraging effort indicated fasting during nesting season (i.e., capital breeding strategy). The mean temperature while at sea was 24.5° C with little variation, and there was no indication of behavioral thermoregulation. Assuming LB fast during the nesting season, the energy expended while at sea for five internesting trips over six weeks would be equivalent to the catabolism of 26.3 kg of fat (39 kg fat including egg production). My results indicate that the purpose of the internesting interval is not associated with feeding, but the purpose of infrequent deep dives (> 300 m) remains uncertain.

3. MOVEMENTS AND ANTIPREDATOR BEHAVIOR DURING THE INTERNESITNG INTERVAL OF LEATHERBACK SEA TURTLES (*Dermochelys coriacea*)

3.1 Introduction

Large predators affect prey through mortality but also by altering their behavior. Prey treat predation risk as an activity cost and respond accordingly. In fact, changes in prey behavior can be more influential on population dynamics and fitness than mortality (Brown et al. 1999). Avoiding high-risk areas creates the ecology of fear in which fear-mediated behavior in response to a powerful and lethal predator can shape a species' distribution (Lima and Dill 1990; Schmitz et al. 1997; Brown et al. 1999; Heithaus et al. 2007; Wirsing et al. 2008; Srinivasan et al. 2010, Srinivasan 2019). By avoiding some areas, prey may exchange safety for resources or pay an energetic cost, which would not occur in the absence of predators.

Leatherback sea turtles (hereafter referred to as LB) are the fourth largest extant reptile behind three species of crocodilians. However, unlike carnivorous crocodilians, LB feed on gelatinous plankton (i.e., Cnidaria, Ctenophora, and Urochordata) using suction feeding (James and Herman 2001; Houghton et al. 2006; Fraher et al. 2010; Eckert et al. 2012; Bardet et al. 2013). As with other marine turtles, they are prey for upper trophic level predators like sharks, especially tiger sharks (*Galeocerdo cuvier*) (Witzell 1987; Simpfendorfer et al. 2001; Heithaus et al. 2008; Heithaus 2013). Unlike other sea turtles, LB lack the defensive morphological feature of hard carapace. In addition, LB lack a rhamphothecae (i.e., keratinous beak) and have bicuspid tomiodonts on the anterior maxillary bones, which are associated with feeding on soft-bodied prey (Fig. 1.3; Pritchard 1971; Wyneken 2001; Moldowan et al. 2016). Wounds on LB nesting on St. Croix in the U.S. Virgin Island have been attributed to tiger sharks based on the asymmetrical serrations and broad tip angle of the bite marks (Eckert et al. 1986; Keinath and Musick 1994; DeLand 2007). Tiger sharks are the only large shark species around St. Croix that feeds on sea turtles and has the dentition to cause such distinctive wounds and scars. Because LB lay between 5-6 clutches of eggs with 10 days between each nesting event, they remain in tropical waters during the six month nesting season (Eckert et al. 1996, 2006, Eckert and Eckert 1988, Eckert 2002). This residency and the necessity of returning regularly to the same nesting beach increases the potential risk of predation by tiger sharks. Evidence for increased predation risk is based on the high percentage (~55%) of female LB with shark wounds and scars, especially to the head, neck, shoulders, carapace, and flippers (DeLand 2007; Stewart and Lombard 2017; K. Stewart, pers. comm.). Although there are a few accounts of LB and other sea turtles responding vigorously to threats, their antipredator strategies and tactics are not well understood (Cropp 1979; Engbring et al. 1992; Heithaus 2013). Defensive behavior includes erratic diving, inverted swimming, somersaulting, and thrashing all four flippers on the surface.

The goal of this study was to use miniature, animal-borne video and data recorders (VDRs) to monitor diving and foraging behavior of LB during the internesting interval on St. Croix. In addition, I used satellite telemetry to track their movements while at sea.

I found that feeding during the interesting interval is rare and opportunistic (see Chapter 2) and not likely the reason for internesting trips. Instead, I found that LB use the offshore internesting trip as an antipredator strategy combined with elaborate defensive behaviors when attacked by sharks.

3.2 Methods

3.2.1 Animals and Instrumentation

I studied nine gravid female LB (mean body mass 323 ± 36 kg) that were nesting at the Sandy Point National Wildlife Refuge (Lat 17.67 N, Long 64.92 W), St. Croix, U.S. Virgin Islands (USVI) from 2015-18 (Fig.3.1 and Table 3.1). This refuge, which was designated as Critical Habitat in 1978 and a National Wildlife Refuge in 1984 under the U.S. Endangered Species Act (ESA) of 1973, is a small but well studied nesting location for the western Atlantic population. Females nesting in the refuge have been tagged and monitored annually since 1981 (Eckert et al. 1982, 1984; Eckert and Eckert 1983). As a result, the Sandy Point refuge has one of the longest histories of known nesting female LB. The nesting season extends between February and August, peaking in May. I conducted this study from April-May to have the largest selection of suitable females for instrumentation.

The VDR (12 cm long, 5.7 cm wide and 4.6 cm high; weight in water is ca. 60 g) is encased in polyurethane and depth rated to 2,000 m (Fig. 3.2a-c). It has a low-light sensitive monochrome video camera and six near-infrared (γ_{max} = 850nm) Light Emitting Diodes (LEDs), which provide illumination in total darkness up to a distance of 70 cm without disturbing the LB (near-infrared light is invisible to marine vertebrates;

Levenson et al. 2006; Crognale et al. 2008). Compressed video (MPEG4) was stored on a digital video recorder with 32 GB of memory, and data were stored on an 8 GB Flash memory card. The VDR contains a three-axis accelerometer, a three-axis magnetometer, and sensors for depth, speed, light level, temperature, and sound (50 Hz-16 kHz). Sensor data were recorded at 1 Hz except speed (4 Hz) and the 3-axis accelerometer (16 Hz). Power was provided by two lithium-ion batteries (10 cm L, 3 cm W, 3 cm H; mass = 270 g in water each). The batteries enabled 27 hr of programmable video and continuous data while the females were at sea. Data were recorded as soon as the female entered the water, but video recording occurred after an initial delay of two days and below a depth of 50 m (in 2015-2017) or 30 m (in 2018). All sensors were calibrated prior to deployment.

Females with numbered flipper tags and passive radio-frequency identification (RFID or Pit) tags were identified when they came ashore to determine their suitability based on: 1) size (curved carapace length [CCL] > 140 cm), 2) a prominent ridge on the carapace for attaching instruments, 3) nesting history (past and recent), 4) had completed two or three nesting activities that season. I waited until oviposition (i.e., egg laying) before taking morphological measurements (i.e., CCL, curved carapace width [CCW], and maximum head width) and attaching instruments. I attached a VDR (Pisces Design, San Diego, CA), a satellite transmitter (Spot 6; 120 g; Wildlife Computer, Redmond, WA), a VHF transmitter (87 g; Advanced Telemetry System, Isanti, MN), and two lithium-ion batteries to the central ridge of the carapace (Fig. 2d). The VDR was mounted mid-dorsally overlooking the head, and the batteries and transmitters were mounted on a plastic plate behind the VDR. Both the VDR and plastic plate were secured to the carapace with steel wire that was passed through nylon tubes inserted in small drilled holes though the dorsal ridge. Before drilling the holes, the carapace was sterilized. This attachment method was widely used in leatherback research and approved by the Herpetological Animal Care Committee (HACC) of the American Society of Ichthyologists and Herpetologists, the Texas A&M Institutional Animal Use Committee (IACUC), and the U.S. Fish and Wildlife Service (Jones et al. 2011). The attachment procedure required ~20 min, after which the female departed for sea. Each female was tracked while at sea using satellite telemetry. After returning to shore to lay another clutch of eggs, females were relocated using radio telemetry, and the instruments were quickly recovered.

3.2.2 Movements at Sea

I tracked movements of eight LB using satellite telemetry for the complete internesting interval (10 ± 1.9 days; Table 3.1). The ninth female (LB1) was tracked for six days before satellite locations ceased because the satellite telemeter had been removed, presumably by a shark attack as rake wounds were present. Locations for females were downloaded from the ARGOS satellite system (https://www.argos-system.org/). Departure and return locations on the nesting beach were determined with a handheld Global Positioning System (GPS). Location Class (LC), which is a measure of accuracy, is ranked from the best (most accurate) to worst as 3, 2, 1, 0, A, B, and Z (invalid) respectively. Location classes B and Z were excluded from analysis (Hays et al. 2001; Vincent et al. 2002; James et al. 2005). Locations were filtered in ArcGIS (v

10.7.1, Esri) using a combination of error radius, and vmask function in the argosfilter package in R (Freitas et al. 2008; Johnson et al. 2008; Freitas 2010; Fleming et al. 2016; Johnson et al. 2018). Speed for vmask function was based on the maximum speed recorded for each female. Turning angle for the sdafilter was 20° (Jonsen et al. 2007; Freitas 2010). A Continuous-time correlated random walk (CRW) model within the Correlated Random Walk Library (crawl package) for R was used to reconstruct movements based on the raw Argos satellite locations, mean swam speed, and estimated drift caused by currents. This model predicts missing locations by estimating the trajectory of raw data with known travel speed and by incorporating the estimated effect of currents (Jonsen et al. 2005, 2007; Johnson et al. 2008; Fleming et al. 2016; Johnson et al. 2018). The U.S. Virgin Islands is located in the WSG 84/UTM zone 20N, and EPSG 3262 was set for the special reference (specialreference.org) in the model. Shark encounter locations were calculated based on the two closest Argos locations if the exact locations were not available. Dead reckoning was applied using a R package animalTrack to correct set and drift for constructing three-dimensional dive paths (Farrell and Fuiman 2014). Bathymetry maps were based on the General Bathymetric Chart of the Oceans (GEBCO) and USGS Digital elevation models (DEMs). Spatial Analysis toolbox was used to calculate surface distance, nearest distance (from St. Croix and Sandy Point), and zoning radius for temporal and spatial analysis for shark and LB interactions.

3.2.3 Dive Behavior

3.2.3.1 Data Analysis

VDRs with complete data were recovered from five females during the internesting interval at sea. A total of 10,472 dives were analyzed using a custom Matlab program and R version 3.6.1 (R Core Team 2013). Dive descent commenced when the seawater sensor on the VDR was submerged, dive depth increased for > 3 sec, and swim speed was > 0.2 m s^{-1}. Ascent occurred when dive depth decreased for > 3 sec and ended when the seawater sensor was no longer submerged. A bottom phase occurred when a female was no longer descending for > 3 sec and ascent had not commenced. No bottom phase was recorded if ascent commenced < 3 sec after the end of descent. Flipper stroke rate (strokes min^{-1}) was determined from the sine wave of the x-axis accelerometer using peak detection function in R. Gliding occurred when flipper stroking ceased for > 10 sec. Resting at the surface occurred when the seawater sensor was dry and swim speed was < 0.1 m s^{-1}. Distance swum was calculated by summing the 1-sec instantaneous speeds for each dive.

A total of 102 episodes of defensive behavior were identified in the data using a custom Matlab program and R version 3.6.1 for calculation and statistical analyses (ODR 5.4 and 7.1; R Core Team 2013). Defensive behavior was identified by fluctuations in heading (rotation), pitch (summersault), and roll (inversion) (Figs 3.3). These events were validated and visualized with three-dimensional dive plots and, when available, video recordings. Although no sharks appeared in the video, the wounds and loss of animal-borne instruments indicated that this defensive behavior was directed towards sharks. This assumption is supported by the asymmetrical serrations and broad tip angle of the recent bite marks and the fact that tiger sharks are the only large shark near St. Croix that feeds on sea turtles.

Diel periods were defined as day (0900-1459), dusk (1500-2059), night (2100-0259 h), and dawn (0300-0859) local time (GMT-4). Shapiro-Wilks Test was used for testing normality (R package rstatix) of the dataset (Fox et al. 2012). The significance levels of spatial and temporal parameters (i.e., diel and daily occurrences) associated with shark encounters were computed using Wilcoxon Rank Sum test, Kruskal-Wallis test, and Chi-square (all $\alpha = 0.05$) in R package dplyr (Wickham et al. 2020). Pearson's correlation test was used to determine the correlation between shark encounters and time duration.

3.2.3.2 Video Analysis

I recorded 108 hr of video during 674 dives for four females (one VDR failed to record video). The video was scanned for defensive behaviors and simultaneous dive variables, which could be used to infer and validate defensive behavior in the data without video (Figs 3.3). Eight of the defensive behaviors were recorded on video.

3.3 Results

3.3.1 Movements at Sea

The mean internesting interval for seven LB (not including LB1 and LB6) was 10.19 ± 1.73 days with a mean transit distance of 466 ± 106 km (Table 3.1). After they departed the nesting beach, females either swam north into the Virgin Islands Trough (LB1-4 and LB7) or west and south into the Muertos Trough (LB5, 6, 8, 9), and all females were over deep water (> 500 m) within four hours. (Fig 3.4). One female swam along the southeastern edge of Puerto Rico, where LB from St. Croix occasionally switch nesting locations. The farthest distance from the nesting beach was 160 km.

3.3.2 Shark Encounters and Defensive Behavior

In total, 102 shark encounters with defensive behavior were identified. These events were associated with rapid fluctuations in heading (rotation; 180° in 1.3 sec), pitch (rapid descent and ascent; somersaulting; 360° in 17 sec), and roll (lateral inversion; 360° in 5.5 sec) (Figs. 3.3). Eight of the encounters had simultaneous video, but no sharks were imaged. The mean number of shark encounters experienced by each female during the internesting interval was 20.4 ± 10.8, which is equivalent to 2.1 encounters day^{-1} (*viz*. 102 encounters ÷ 47.55 days) or 0.05 encounters km^{-1} (*viz*. 102 encounters ÷ 2106 km) (Table 3.2). One-half (51) of the shark encounters occurred > 6 km from the St. Croix, which is equivalent to 1.4 encounters day^{-1} (*viz*. 51 encounters ÷ 36.27 days). The other one-half (51) of the shark encounters occurred < 6 km from the St. Croix, which is equivalent to 4.4 encounters day^{-1} (*viz*. 51 encounters ÷ 11.28 days). The mean depth at the start of shark encounters was 22 ± 30.9 m (maximum 173 m) with a mean encounter duration of 2.52 ± 4.36 min (maximum 30.0 min) and a mean water temperature of 24.3 ± 1.73°C (maximum 26.4°C). Of 102 shark encounters, 41% began at the surface, 23% during descent and 36% during ascent.

One female (LB8) had a shark encounter 3.2 km from St. Croix while returning to the nesting beach. The encounter began at a depth of 25 m while the female was ascending from a Deep Transit (DT) at night (2221 local time) (Fig, 3.5a and 3.6a; see Chapter 2). The female continued to ascend throughout the attack with occasional shallow (~5 m) descents associated with circling and rolling inversions (Fig, 3.5b and 3.6b). The mean swim speed was 1.3 ± 0.3 m sec^{-1}, which was 2-fold faster than the routine speed but less than the burst speed of 3.4 m sec^{-1} recorded during an earlier shark encounter. The defensive behavior continued for 2.4 min, after which the battery cables to the VDR were severed by the shark and recording ended. No video was recorded for this dive because the 27-hr limit had occurred earlier in the trip. This female remained offshore for another 25 hr before nesting, at which point the instruments were recovered. Fresh rake wounds were observed on the back, especially around the VDR attachment, and damage to the VDR (Fig. 3.7c, f).

A 30-min shark attack (the longest in this study) was recorded for LB4, which started at the surface (Figs. 3.8a and 3.9a). During the encounter, the female made more than 40 shallow, looping dives (~20 m deep) with steep descents and ascents, somersaulting, and rolling inversions at a mean swim speed of 1.3 ± 0.4 m sec^{-1} (Figs. 3.8b and 3.9b). The shark severed one battery cable, but the VDR continued to record data until the female came ashore, at which point we recovered all instruments. Fresh bite injuries were observed where the cable was severed.

Shark encounters with defensive behavior occurred throughout the internesting interval in the Virgin Islands Trough and Muertos Trough (Fig. 3.10a). However, the highest concentration of encounters occurred < 6 km from St. Croix (Figs. 3.10b and 3.11). Of the 102 shark encounters, 51 (50%) occurred < 6 km from the island, of which 45 (44%) occurred while inbound. The other 50% of shark encounters were distributed at varying distances up to 160 km from St. Croix.

The daily occurrence of shark encounters did not differ throughout the internesting interval except for the 9th day, which was significantly greater than other days as females approached the nesting beach (Fig. 3.12a). Two females (LB4 and LB8) returned early to St. Croix and remained near the coast (< 6 km) for three days, which accounted for shark encounters starting on day 5 of the interesting interval. The diel occurrence of shark encounters < 6 km from St. Croix was significantly greater at night and dawn than during the day (Fig. 3.12b). There were no significant differences among dawn, day, and dusk or among any diel period > 6 km from St. Croix. Hence, 76% of shark encounters occurred at night and dawn < 6 km from St. Croix as the females prepared to come ashore.

When the females returned to St. Croix, they spent 2.03 ± 1.83 days < 6 km from the island before coming ashore to nest. A total of 45 shark encounters occurred inbound, which is equivalent to 4.4 encounters day^{-1} (*viz*. 45 encounters ÷ 10.13 days) (Table 3.2). Three females (LB4, LB5, LB9) spent less than one day (0.79 ± 0.80 days) within 6 km of St. Croix before coming ashore and had a total of 8 shark encounters, which is equivalent to 3.4 encounters day^{-1} (*viz*. 8 encounters ÷ 2.38 days) (Fig. 3.13b, c, e). In contrast, LB3 returned to St. Croix after 4.54 days of a 9.00-day internesting trip and swam along the coast < 6 km from shore for 4.46 days. This female had 18 shark encounters before coming ashore (Fig. 3.13a; Table 3.2). Similarly, LB8 returned to St. Croix after 5.63 days of an 8.91-day internesting trip, made a series of zigzag movements between the southwest tip of the island (i.e., Sandy Point) and offshore (up to 8 km) for 3.28 days, and had 19 shark encounters (Fig. 3.13d; Table 3.2). Combined, LB3 and LB8 experienced 82% of all inbound shark encounters, which is equivalent to 4.8 encounters day^{-1} (*viz*. 37 encounters ÷ 7.74 days) (Fig. 3.13a, d).

Although the outbound time spent < 6 km from shore was only 18% of the total, the rate of shark encounter was 5.2 day^{-1} (*viz*. 6 encounters ÷ 1.15 days) (Table 3.2). Hence, the rate of shark encounters < 6 km from St. Croix, including both inbound and outbound legs for the five females, was 4.5 encounters day^{-1} (*viz*. 51 encounters ÷ 11.28 days) (Table 3.2). The two females (LB3 and LB8) that returned early spent 4.9-fold longer < 6 km from shore (i.e., mean 3.87 days) and had 4.6-fold more shark encounters than the three females that spent only 0.79 days near shore. Hence, the number of encounters experienced by LB increased as they spent more time < 6 km from shore before nesting (Fig. 3.14). Overall, LB had 1.5 shark encounters day^{-1} offshore (> 6 km) and 4.5 encounters day^{-1} nearshore (< 6 km). Hence, the only way to minimize shark encounters is to avoid or minimize time near shore. Why some LB return early and spend more time < 6 km from shore than others is unknown.

3.4 Discussion

LB have an obligate ~10-day internesting interval between clutches of eggs, so they go to sea until the next nesting period. Other than waiting for the next clutch of eggs to develop, the purpose of these journeys has been uncertain, but foraging and predator avoidance have been hypothesized. I now know that feeding is rare and opportunistic, so feeding is not the best explanation. (see Chapter 2). My results indicate that predator avoidance is the likely explanation. Females spend the internesting interval at sea because remaining onshore for 10 days would be dangerous (e.g., predators) and physiologically challenging (i.e., thermoregulation). However, LB face predation from sharks once they leave the beach. This is apparent from the high percentage (~50%) of LB at Sandy Point that have shark wounds and scars, especially to the head, shoulders, neck, carapace, and fore flippers (Figs, 3.7 and 3.15; DeLand 2007; Stewart and Lombard 2017; K. Stewart, pers. comm.). The asymmetrical serrations and broad tip angle indicate tiger shark attacks (Eckert et al. 1986; Keinath and Musick 1994; Carrier et al. 2012). In addition, LB remains have been found in the stomach of tiger sharks captured by local fishermen on St. Croix (Fig. 15.a).

During this study, I recorded 102 episodes of defensive behavior that were consistent with previous observations of LB responding to threats (Engbring et al. 1992). The defensive behavior differs from courtship behavior, which includes idling on the seafloor until the male departs (Reina et. al. 2005). The wounds and damage or loss of instruments indicate that the defensive behavior was associated with shark encounters. Three females whose VDRs were either damaged or removed had rake wounds on the edge of left anterior carapace (i.e., above shoulder) and adjacent to the VDR attachment (Fig 3.7d). It is likely that these attacks were from tiger sharks, the only species of large shark that occurs around St. Croix that regularly feeds on sea turtles (Pickard et al. 2016; Casselberry et al. 2020).

There are three antipredator strategies that LB could use in response to sharks: avoidance (seeking a location that is inaccessible to predators), crypsis (the ability to avoid observation or detection), and vigilance (detection of danger). Avoidance and crypsis may reduce the probability of a predatory confrontation, but at an energetic cost.

After they departed the nesting beach, females swam north into the Virgin Islands Trough or west and south into the Muertos Trough within ~160 km radius around St. Croix. The mean transit distance during 10.19 days at sea was 434 km. On average, the females had 2.1 shark encounters day^{-1} (*viz*. 102 encounters ÷ 47.55 days) while offshore (Table 3.2). In contrast, they had 4.4 encounters day^{-1} when they were < 6 km of St. Croix. Hence, moving away from St. Croix to reduce the probability of shark encounters appears to be predator avoidance behavior while waiting for the next clutch of eggs to develop. However, the mean energetic cost for each female during the internesting interval was 182,582 kJ, which is 2-fold higher than resting metabolism (see Chapter 2). Assuming that the females were fasting during the internesting interval, this energetic cost is equivalent to 5.4 kg fat. This type of behavioral adaptation to predation risk is commonly observed in aquatic prey (Lima and Bednekoff 1999; Heithaus et al. 2007; Wirsing et al. 2008). Some reef fishes in the Caribbean move between reef habitats based on time of a day (i.e., diel horizontal migration) because of predatory barracuda (*Sphyraena barracuda*) (Rooker et al. 2018). Bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, seek deep water, which has a lower risk of tiger shark predation even if it reduces food availability (Heithaus and Dill 2002).

LB were submerged 63% of the time during the internesting interval while making Deep Transit (DT) dives and 31% for Shallow Transit dives (ST) with nearly continuous swimming (see Chapter 2). In contrast, surface resting (SR) occurs only 5% of the time, usually before or after DT dives. Hence, it appears that LB do not rest or sleep while at depth or the surface. Whether DT dives are an example of cryptic behavior to avoid predators is uncertain. Southern elephant seals (*Mirounga leonina*) use this antipredator strategy while sleeping/resting at depths of 300-500 m (i.e., drift dives) (McGovern et al. 2019). In essence, they hide in the deep sea rather than rest at the surface to reduce detection by predators. The plastron (ventral surface) of LB is white and mottled, which might be cryptic coloration that camouflages LB from sharks attacking from below, but it would not prevent silhouetting (Bustard 1970; Salmon et al. 2016; Smith and Salmon 2009).

Vigilance (detection of danger) is another antipredator strategy. Prey must select their optimal level of vigilance in response to the perceived threat. The density of prey and their vigilance will influence the behavior of the predator (FitzGibbon 1989; Brown et al. 1999; Heithaus et al. 2002; Pickard et al. 2016). Although group behavior may increase detection by a predator, it enables group vigilance as an antipredator strategy (Foster 1981; Delm 1990; Connor 2002; Heithaus and Dill 2002). For example, Hawaiian spinner dolphins (*Stenella longirostris*) often swim in a tightly spaced carpet formation just above the seafloor at a depth of 10-20 m during periods of rest sleep (Würsig et al. 1994). During these periods of unihemispheric slow wave sleep (USWS), the dolphins group more tightly and swim over open, sandy areas to enhance visual vigilance, probably against potential shark attack from below. The transition between USWS and wakefulness appears to be rapid, so a response would be almost immediate, which is essential if vigilance is to be successful.

LB are solitary except during mating. The success of vigilance as an antipredator strategy depends on the ability of LB to confront the threat. The mean depth at the beginning of a shark encounter was 22 m, but it occurred anywhere from the surface to a depth of 173 m. Forty-one percent of shark attacks occurred while the LB were at the surface, suggesting that sharks were silhouetting them. Tiger sharks are ambush predators (Carrier et al. 2012; Hammerschlag et al. 2015). Hence, these encounters were likely an ambush attack rather than prolonged pursuit. The response of LB to sharks was instantaneous, robust, and involved pursuit at an elevated speed (1.3 ± 0.3 m sec^{-1}), which was 2-fold faster than routine swimming speed (0.6 m sec^{-1}; see Chapter 2). During shark encounters, LB engaged in rapid rotation, steep descent and ascent, and lateral inversion (Figs. 3.5, 3.6, 3.8. 3.9), behaviors that have been described previously in response to a threat (i.e., flight-or-fight response; Engbring et al. 1992). The mean duration of shark encounters was 2.52 ± 4.36 min (maximum duration was ~30 min), which indicates that the defensive behavior was generally effective. Although antipredator behavior may reduce injury (bite wounds, loss of an appendage) or death, it cannot eliminate them (Figs. 3.7 and 3.17). Of the nine LB that were tracked in this study, eight ultimately returned to the nesting beach, albeit two (LB1 and LB7) lost their instruments < 6 km of St. Croix. However, satellite contact was lost with one female (LB6) < 6 km from the island, which was never seen again that season or the following year. Hence, the attack on LB6 may have been lethal.

When the females departed the nesting beach at the beginning of the internesting interval, they experienced fewer shark attacks because they moved immediately offshore and then spent very little (0.23 ± 0.10 days) time < 6 km from the island. Although the mean internesting interval for the five LB with VDRs was 9.51 days, two returned early and spent 4.46 and 3.28 days, respectively, < 6 km from St. Croix until the internesting interval was complete. As a result, these two LB experienced the majority (82%) of shark encounters at a rate of 4.8 encounters day^{-1} (*viz*. 37 encounters ÷ 7.74 days) (Table 3.2). In contrast, the other three LB remained > 6 km from St. Croix until the day before nesting. They spent less than one day (0.79 ± 0.80 day) within 6 km of the island and had 18% of shark encounters at a rate of 3.4 encounters day^{-1} (*viz*. 8 encounters ÷ 2.38 days). Therefore, LB that spent more time nearshore (i.e., < 6 km from St. Croix) experienced more shark encounters (Fig 3.14).

Tiger sharks are nomadic, but may concentrate near nesting beaches around St. Croix (Holland et al. 1999; Heithaus et al. 2002, 2007; Mayer et al. 2009; Pickard et al. 2016). The five females in this study spent 24% of internesting interval < 6 km from St. Croix and the remainder > 6 km offshore. Hypothetically, if they had spent 100% of the internesting interval < 6 km from St. Croix with 4.5 encounters day^{-1}, they would have experienced 214 shark attacks (*viz*. 4.5 encounters day^{-1} x 47.55 days) instead of 102, a 2.1-fold increase. It appears that the offshore internesting trip is a predator avoidance strategy, which reduces but does not eliminate shark encounters. Why some LB return to St. Croix early is uncertain. Whatever the explanation, returning early can have severe consequences resulting in injury or death.

3.5 Conclusions

LB risk predation from sharks once they leave the beach, most likely from tiger sharks. DT dives may be a way for LB to detect sharks swimming near the surface, but they would not prevent sharks from silhouetting them from below. When attacked, their response was instantaneous, robust, and involved evasive swimming at an elevated speed with rapid rotation, steep descent and ascent, and lateral inversion. Most shark encounters were short (< 5 min), which indicates that defensive behavior is effective, although this behavior cannot completely eliminate injury and death. Shark attacks were most frequent (3-fold) when LB were < 6 km from St. Croix compared to > 6 km offshore. If LB had remained < 6 km from shore for the entire interesting interval, they potentially would have experienced 48% more shark attacks. Therefore, offshore internesting trips appear to be a strategy to reduce shark encounters (i.e., avoidance behavior) while the next clutch of eggs develops.

4. SUMMARY AND CONCLUSIONS

4.1. Previous Research and Basis for This Study

In this study, I focused on two aspects of leatherback sea turtle (hereafter referred to as LB) behavior during the internesting interval: foraging and predator avoidance. As an evolutionary strategy, separating foraging from nesting enables LB to optimize the location for both. Capital breeders forage and acquire energy reserves (fat) in one area, and fast during reproduction in another area, which is more conducive to the successful production of offspring (Jönsson 1997; Bonnet et al. 1998; Shertzer and Elliner 2002; Houston et al. 2007; Stephens et al. 2009). This separation of foraging and reproduction often involves a long-distance migration. LB appear to be capital breeders because they forage in cool temperate waters on gelatinous zooplankton and nest on beaches in tropical and subtropical areas such as St. Croix (Plot et al. 2013; Perrault et al. 2014). Although the foraging behavior of LB in cool temperate waters along the coast of Nova Scotia, Canada, has been studied, less is known about their behavior including foraging during their migration to the Caribbean and during the nesting season (James and Herman 2001; Hays et al. 2006; Houghton et al. 2006; Myers and Hays 2006; Jonsen et al. 2007; Casey et al. 2010; Heaslip et al. 2012; Wallace et al. 2015).

LB nesting on St. Croix lay 5-6 clutches, have an obligate internesting interval of ~10 days between each nesting event (i.e., clutch). This period presumably allows the next clutch of eggs to mature before returning to the nesting beach. Females go to sea between each clutch because remaining onshore during the internesting period would be too dangerous (i.e., predators) and physiologically challenging (e.g., thermoregulation). While at sea, LB swim almost continuously with routine dives < 100 m but occasional dives > 1,000 m (Eckert et al. 1989). This diving behavior led to the hypothesis that LB feed during the interesting interval. However, gastrointestinal tract temperature recording using animal-borne instruments on LB from St. Croix during the internesting interval indicated that foraging was rare, possibly because gelatinous prey in oceanic waters of the Eastern Caribbean Sea are sparse (Hargraves et al. 1970; Marshall 1973; Casey et al. 2010).

When LB at St. Croix go to sea, they are vulnerable to shark predation. Evidence for increased predation risk is based on the high percentage (~55%) of female LB with shark wounds and scars, especially to the head, neck, shoulder, carapace and fore flippers (DeLand 2007; Stewart and Lombard 20017; K. Stewart, pers. comm.). Wounds on LB nesting on St. Croix in the U.S. Virgin Island have been attributed to tiger sharks based on the asymmetrical serrations and broad tip angle of the bite marks (Eckert et al. 1986; Keinath and Musick 1994; DeLand 2007). Tiger sharks are upper trophic predators of marine turtles, but information on defensive behavior is scarce with no quantitative data (Witzell 1987; Engbring et al. 1992; Simpfendorfer et al. 2001; Heithaus et al. 2002; Heithaus et al. 2007; Heithaus 2013; Hammerschlag et al. 2015; Archibald and James 2018). At my study site on St. Croix, the only large shark species that feeds on sea turtles is tiger shark, which has dentition that can cause such distinctive wounds and scars (Carrier et al. 2012; Pickard et al. 2016; Casselberry et al. 2020).

Based on previous research, I tested two hypotheses:

1. Foraging by LB is rare and opportunistic during the internesting interval
2. The offshore movements during the internesting interval is an antipredator strategy

To test these hypotheses, I attached miniature, animal-borne video and data recorders (VDRs) to monitor the diving and foraging behavior of LB during the internesting interval. In addition, I used satellite telemetry to track their movements while at sea. Unlike previous studies using animal-borne recorders, VDRs provide extended video and high-resolution data on dive characteristics, foraging behavior, prey preference, and swimming performance, including three-dimensional movements based on speed, heading and depth.

4.2. Diving and Foraging Behavior

I identified two dive types: Shallow Transit (ST) dives and Deep Transit (DT) dives. ST dives were short, shallow and associated with slow (0.6 m s^{-1}) subsurface swimming to reduce drag, but no gliding during descent. DT dives involved gliding and were moderately deeper than ST dives with a longer horizontal distance (10-fold) at the same slow speed. LB spent 94% time at sea making ST and DT dives with short surface resting periods, but there was no indication of prolonged resting or sleep at the surface or during DT dives. The diving behavior of LB was consistent throughout the internesting interval with no significant difference in ST and DT dive occurrence (based on time) among the four diel periods, but SR more frequent during the day and less frequent during dusk. Only 4% and 1% of DT dives were deeper than 200 m and 300 m, respectively. The deepest and longest DT dive was 531 m in depth, 28.9 min in duration.

Feeding was rare and opportunistic but generally occurred during ascent from dawn to dusk indicating visual prey detection. Six species of gelatinous prey were identified. Reduced foraging effort indicated fasting during nesting season (i.e., capital breeding strategy). The mean temperature while at sea was 24.5° C with little variation, and there was no indication of behavioral thermoregulation. Assuming LB fast during the nesting season, the energy expended while at sea for five internesting trips over six weeks would be equivalent to the catabolism of 26.3 kg of fat (39 kg fat including egg production).

4.3. Movements and Antipredator Behavior

LB face predation from sharks once they leave the beach, most likely from tiger sharks in this area. Shark predation on sea turtles is common and indicated by scars and partially missing flippers (Witzell 1987; Simpfendorfer et al. 2001; Heithaus et al. 2002; Heithaus et al. 2007). Antipredator strategies that LB could use include avoidance, crypsis, and vigilance. Internesting trips with DT dives may be associated avoidance and crypsis, but are energetically costly and require the use of energy stores (fat) because feeding is rare. LB are vigilant against the risk of shark attack. DT dives may be a way for LB to detect sharks swimming near the surface, but they would not prevent sharks from silhouetting them from below. When attacked, their response was instantaneous, robust, and involved evasive swimming at an elevated speed with rapid rotation, steep descent and ascent, and lateral inversion. Most shark encounters were short (< 5 min), which indicates that defensive behavior is generally successful, although this behavior cannot completely eliminate injury and death. Shark attacks were most frequent (3-fold) when LB were < 6 km from St. Croix compared to > 6 km offshore. If LB had remained

< 6 km from shore for the entire interesting interval, they potentially would have experienced 48% more shark attacks. Therefore, offshore internesting trips appear to be a strategy to reduce shark encounters (i.e., avoidance behavior) while the next clutch of eggs develops.

4.4. Final Thoughts

LB are the fourth largest extant reptile behind three species of crocodilians. Despite their large size, they have no defensive morphological features such as a hard carapace or keratinous beak and only bicuspid tomiodonts on their upper jaw. Their only defense against large predators such as tiger sharks is avoidance and vigilance with robust defensive behavior to avoid serious injury and death. Overall, this strategy appears to work, although not completely. Nevertheless, the ancestors of LB survived the Cretaceous–Paleogene extinction, so this predatory-prey interaction with sharks probably has evolved over a long period (Wood et al. 1996; Shimada and HOOKS III 2004; Cadena and Parham 2015; Amalfitano et al. 2017).

Although there are no data on tiger shark distribution around Sandy Point, it would be interesting to track the movements of LB and tiger sharks simultaneously during the nesting season. In the future, it may be possible to deploy VDRs on tiger sharks to obtain a better understanding of their behavior when interacting with LB. Whether shark attack has contributed to the recent decline in LB on St. Croix is uncertain (Garner et al. 2017; Stewart and Lombard 2017; Northwest Atlantic leatherback working group 2018). Regardless, anthropogenic effects have been a greater threat to LB on St. Croix and populations throughout the world during the past 200 years.

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APPENDIX A

TABLES

Table 2.1. Thirty dive variables and six environmental variables for dive classification and correlation test.

Variables	R Code name
Dive characteristics	
Mean depth (m)	DepthMn
Max depth (m)	DepthMx
Depth SD (m)	DepthSD
Descent duration (min)	TimeDsc
Bottom duration (min)	TimeBtm
Ascent duration (min)	TimeAsc
Total dive duration (min)	TimeTot
Mean speed (m s^{-1})	SpeedMn
Max speed (m s^{-1})	SpeedMx
Speed SD (m s^{-1})	SpeedSD
Total dove distance (m)	DistTot
Number of descent strokes	StrNDsc
Descent stroke rate (stroke min^{-1})	StrRDsc
Number of bottom strokes	StrNBtm
Bottom stroke rate (stroke min^{-1})	StrRBtm
Number of ascent strokes	StrNAsc
Ascent stroke rate (stroke min^{-1})	StrRAsc
Total Number of stokes	StrNTot
Total stroke rate (stroke min^{-1})	StrRTot
Mean stroke rate (stroke min^{-1})	StrRMn
Max stroke rate (stroke min^{-1})	StrRMx
Stroke rate SD (stroke min-1)	StrSD
Glide duration during descent (sec)	GlidDsc

Table 2.1. Continued

Variables	R Code name
Glide duration during ascent (sec)	GlidAsc
Total glide duration (sec)	GlidTot
Descent glide (% of dive)	GlidDscPct
Ascent glide (% of dive)	GlidAscPct
Total glide (% of dive)	GlidTotPct
Mean decent angle (°)	AngDscMn
Mean ascent angle (°)	AngAscMn
Environmental variables	
Interval Day	IntvlDay
Time of Day	TimeDDND
Mean water temperature (°C)	TempMn
Max water temperature (°C)	TempMx
Mean light level (Lux)	LitMn
Max light level (Lux)	LitMx

Table 2.2. Significant variables identified by Forward Selection in canonical variate analysis (CVA) based on 30 dive variables with adjusted p-values of False discovery rate (FDR) at the α = 0.05 level. All 13 variables scored raw p-value of 0.002 and Bonferroni Holm's correction (BH) adj. p-value of 0.06 accounting for the 92.1% of the variation. Variables in bold account for the top three influential explanatory dive characteristics.

Variables		Explains %	Contribution %	Pseudo-*F*	FDR adj. *p*-value
Total number of strokes	**StrNTot**	84.17	91.18	55660	0.012
Total glide (% of dive)	**GlidTotPct**	4.13	4.48	3697	0.01
Total glide duration (sec)	**GlidTot**	2.12	2.3	2318	0.009
Mean ascent angle (°)	AngAscMn	0.69	0.74	809	0.008
Descent glide (% of dive)	GlidDscPct	0.23	0.25	287	0.006
Mean depth (m)	DepthMn	0.17	0.19	223	0.005
Descent duration (min)	TimeDsc	0.16	0.17	193	0.007
Total dove distance (m)	DistTot	0.14	0.15	174	0.005
Number of bottom strokes	StrNBtm	0.11	0.12	139	0.005

Table 2.2. Continued

Variables		Explains %	Contribution %	Pseudo-*F*	FDR adj. *p*-value
Total stroke rate (stroke min^{-1})	StrRTot	0.08	0.08	100	0.004
Number of descent strokes	StrNDsc	0.04	0.04	51.3	0.004
Max stroke rate (stroke min^{-1})	StrRMx	0.02	0.02	27	0.004
Mean speed (m s^{-1})	SpeedMn	0.01	0.02	19.7	0.005

Table 2.3. Summary statistics (mean ± SD) for Shallow Transit (ST) dives and Deep Transit (DT) dives. All variables except for Bottom duration (min) are significantly different between ST and DT dives at the $\alpha = 0.05$ level (Kruskal-Wallis test). N indicates the number of dives of each type. Maximum values shown in parentheses.

	Dive types		
	ST	DT	
Variable			*p*-value
Position			
Mean maximum depth (m)	3 ± 6.8	84 ± 51.8 (531)	< 0.01
Duration			
Dive duration (min)	1.14 ± 1.24	13.42 ± 4.29 (28.85)	< 0.01
Descent duration (min)	0.43 ± 0.58	6.19 ± 2.40	< 0.01
Bottom duration (min)	0.16 ± 0.30	0.09 ± 0.11	0.097
Ascent duration (min)	0.55 ± 0.77	7.14 ± 3.39	< 0.01
Displacement			
Distance swum (m)	45 ± 57	446 ± 168 (1676)	< 0.01
Speed			
Mean speed (m s^{-1})	0.6 ± 0.3	0.6 ± 0.2 (3.4)	0.014
Angle			
Descent angle (°)	-14 ± 7	-24 ± 9 (-60)	< 0.01
Ascent angle (°)	4 ± 9	9 ± 13 (68)	< 0.01
Stroking			
Mean stroke rate (stroke min^{-1})	13.6 ± 2.93	14.07 ± 2.32 (44.4)	< 0.01
Descent stroke rate (stroke min^{-1})	15.0 ± 3.40	13.43 ± 2.95	< 0.01
Bottom stroke rate (stroke min^{-1})	7.8 ± 7.94	3.67 ± 6.03	< 0.01
Ascent stroke rate (stroke min^{-1})	11.4 ± 5.02	14.95 ± 2.50	< 0.01

Table 2.3. Continued

	Dive types		
	ST	DT	
Variable			*p*-value
Gliding			
Glide (% of dive)	0 ± 0	7.4 ± 7.5 (37)	< 0.01
Descent glide (% of dive)	0 ± 0.9	15.4 ± 14.7 (69)	< 0.01
Ascent glide (% of dive)	0 ± 0	0 ± 1 (14)	< 0.01
No. prey encounters/captures	0	23	
N	7280 (70%)	3192 (30%)	

Table 3.1. Deployment data with morphometrics for nine leatherback females. Abbreviations: carapace curved length (CCL), carapace curved width (CCW), and body mass (BM), which was estimated based on the equation $BM = 5.3346 \times (CCL - 500.67)$ (Eckert et al. 1989). Transit distances were estimated from satellite locations.

Turtle	USFWS ID	CCL (cm)	CCW (cm)	Body mass (kg)	Tagging date	Recovery date	Internesting Interval (day)	Transit distance (km)	Number of shark encounters
LB1[b]	SPP296	154	110	321	5/22/2015	5/31/2015	8.89[a]	185	
LB2[c]	SPP081	148	109	289	5/6/2016	5/21/2016	13.79	692	
LB3[d]	SPP001	154	112	321	5/25/2016	6/4/2016	9.97	303	29
LB4[e]	AAV935/SPP008	164	118	376	4/29/2017	5/8/2017	9.00	367	10
LB5[f]	SPP061	143	107	263	5/5/2017	5/14/2017	8.96	494	16
LB6[g]	MJ43/SPP405	153	110	315	5/17/2017	n/a	10.66[a]	465	
LB7[h]	AAR287/SPP297	153	110	315	5/18/2017	5/28/2017	9.96	461	
LB8[i]	3064	155	119	326	5/2/2018	5/12/2018	8.91	444	37
LB9[j]	AAC270/SPP345	166	116	385	5/1/2018	5/12/2018	10.71	498	10
Mean		***154***	***112***	***323***			***10.19***	***434***	***20.4***
s.d.		***6.7***	***4***	***35.8***			***1.73***	***133.2***	***10.8***

[a] Not included in the mean and s.d. because they lost their satellite tag and/or did not return to the nesting beach

[b] LB1. Satellite locations ceased after six days at sea. When the female returned to the nesting beach, one battery and the satellite telemeter had been removed, presumably by a shark encounter (Fig. 3.7e). Rake wounds were present.

Table 3.1. Continued

[c] LB2. Satellite and radio telemeters only

[d] LB3. Complete deployment and recovery of all instruments

[e] LB4. Complete deployment and recovery of all instruments. One battery cable was during a shark encounter. Rake wounds on head and right fore flipper (Fig. 3.7a). This shark encounter is shown in Figs. 3.8 and 3.9

[f] LB5. Complete deployment and recovery of all instruments. However, the VDR did not record video

[g] LB6. We tracked this female for nine days. The female was near the nesting beach on the day 10, but satellite locations ceased, presumably because of shark encounter. This female was not seen again, and no instruments were recovered

[h] LB7. This female was tracked at sea, but all instruments were removed at sea, presumably because of shark encounter. Rake wounds were present around the VDR attachment area and on the left shoulder (Fig. 3.7d)

[i] LB8. Complete deployment and recovery of all instruments. However, both battery cables were severed during a shark encounter. The female came ashore 25 hr later with rake wounds and VDR damage (Fig. 3.7c, f). This shark encounter is shown in Figs. 3.5 and 3.6

[j] LB9. Complete deployment and recovery of all instruments

Table 3.2. Summary of shark encounters. Mean with s.d. and maximum (*Max.*) values with range in parentheses.

	Shark encounters			Time at sea (day)		Shark encounters <6 km from shore		Inbound time at sea < 6 km from shore (days)
Turtle	Total	< 6 km from shore	> 6 km from shore	< 6 km from shore	> 6 km from shore	Outbound	Inbound	
LB3	29	21	8	4.82	5.15	3	18	4.46
LB4	10	5	5	2.00	7.00	2	3	1.71
LB5	16	6	10	0.55	8.42	1	5	0.44
LB8	37	19	18	3.50	5.41	0	19	3.28
LB9	10	0	10	0.42	10.29	0	0	0.23
Sum	***102***	***51***	***51***	***11.28***	***36.27***	***6***	***45***	***10.13***
Mean	***20.4 ± 10.8***	***10.2 ± 9.3***	***10.2 ± 4.2***	***2.26 ± 1.90***	***7.25 ± 2.15***	***1.2 ± 1.3***	***9.0 ± 8.9***	***2.03 ± 1.83***
Max.	***37***	***21***	***18***	***4.82***	***10.29***	***3***	***19***	***4.46***

APPENDIX B

FIGURES

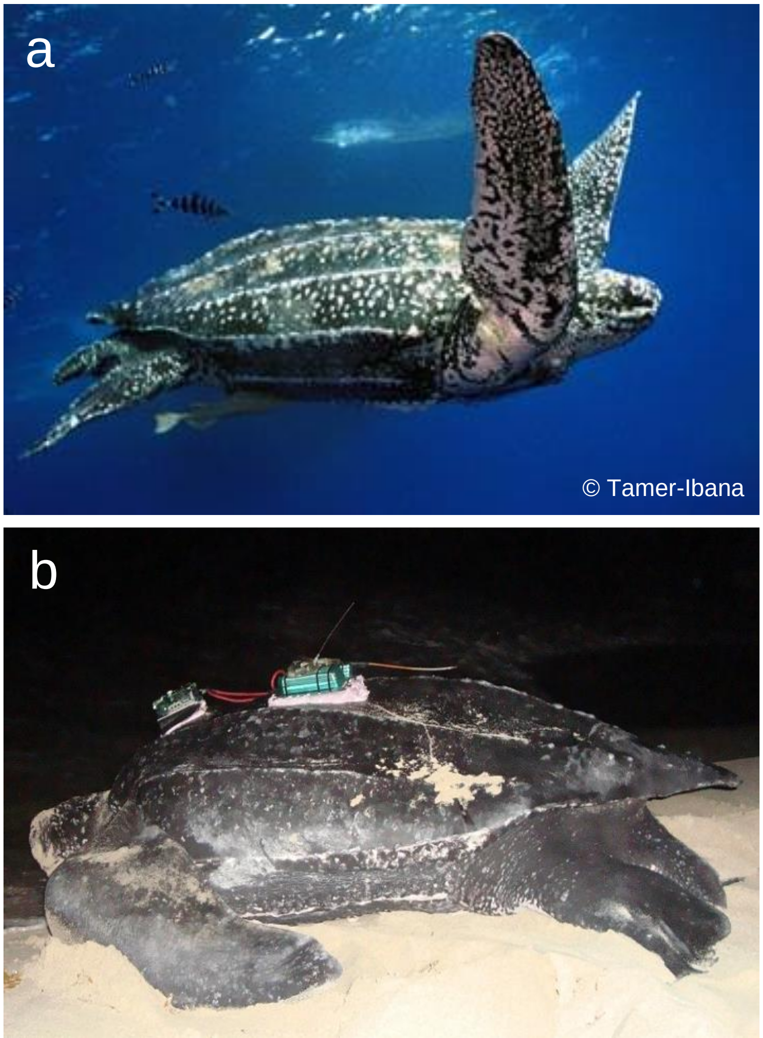
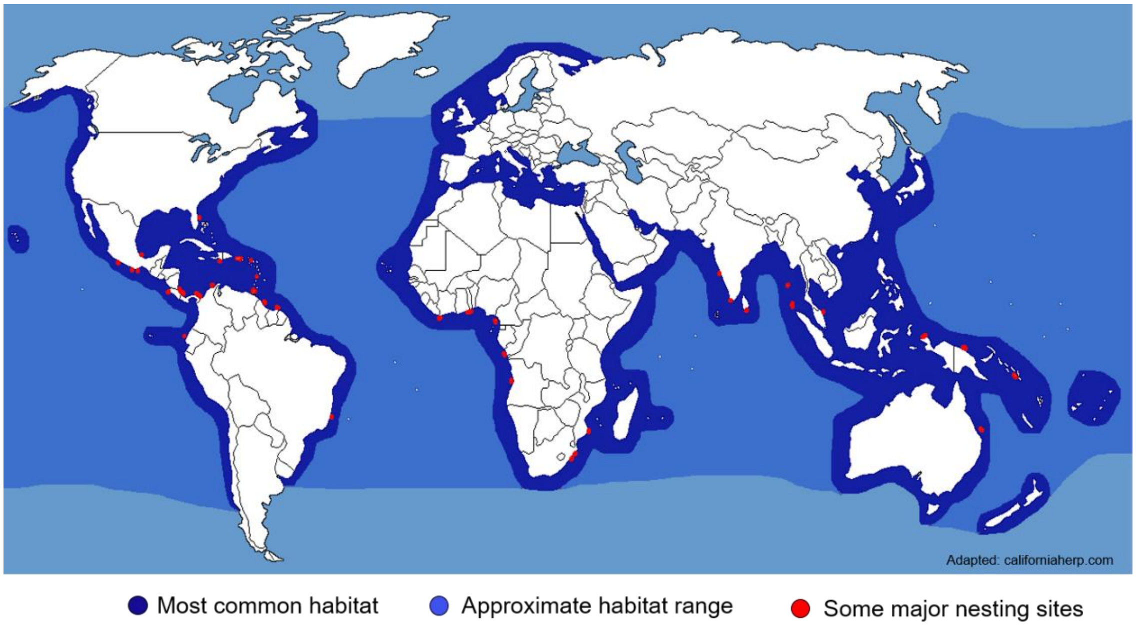


Fig. 1.1 (a) Leatherback sea turtle at sea. (b) Leatherback nesting with instruments for tracking movements, video recording behavior, and recording data on performance and environmental variables



Adapted: californiaherp.com

Fig. 1.2. World-wide range and nesting sites of the leatherback sea turtle

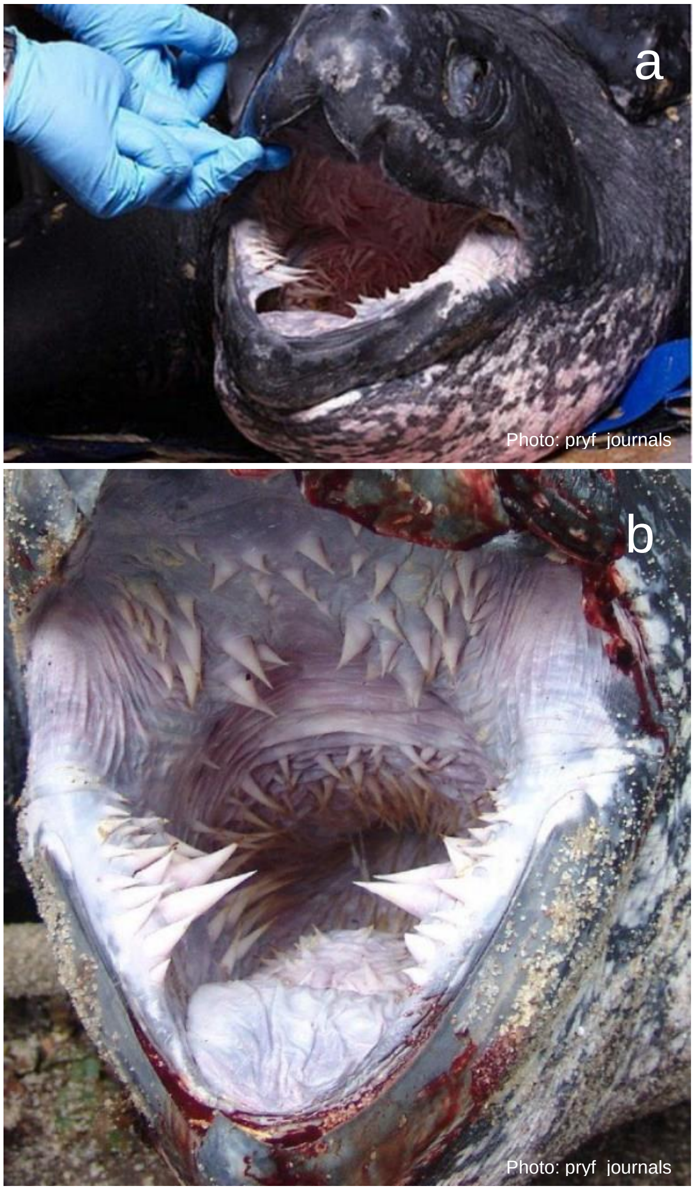


Fig. 1.3. (a) Head of a leatherback showing the pair of large, posteriorly-pointed bicusps along the anterior edge of the upper jaw but no rhamphotheca (i.e., keratinous beak). (b) The mouth and throat lined with sharply pointed, keratinized buccopharyngeal papillae that point posteriorly

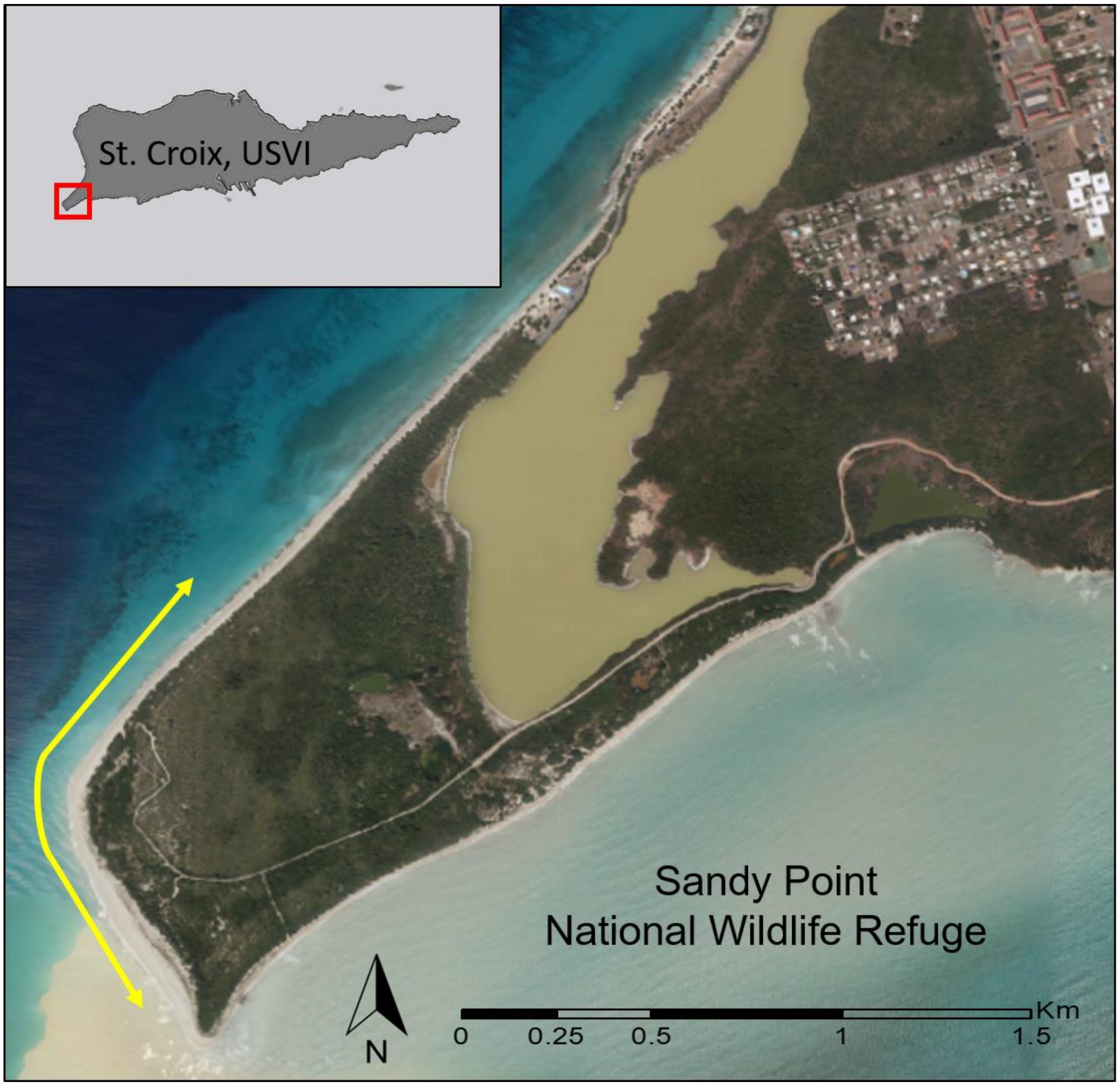


Fig. 2.1. The study site at the Sandy Point National Wildlife Refuge (SPNWR) with the primary nesting beach (yellow arrow) located Southwest of St. Croix, U.S. Virgin Islands (USVI)

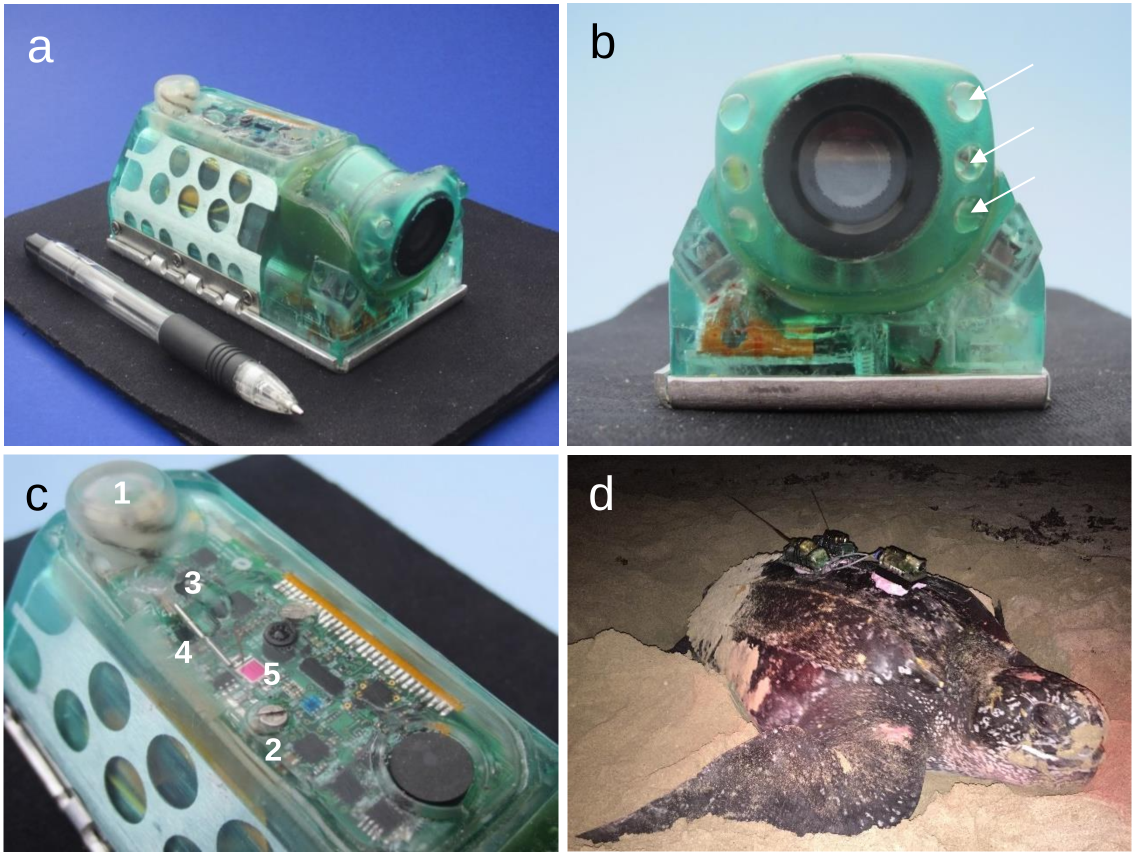


Fig. 2.2. Video and data recorder (VDR) showing: (a) size, (b) six near-infrared LEDs (three on either side, arrows) for illumination and two speed sensors (circles), (c) sensors (1) GPS antenna, (2) seawater sensor, (3) pressure, (4) temperature, (5) light, and (d) attachment of the VDR, axillary battery pack, satellite transmitter, and VHF radio transmitter to a female leatherback sea turtle. Image of leatherback sea turtle courtesy of G. Carvajal

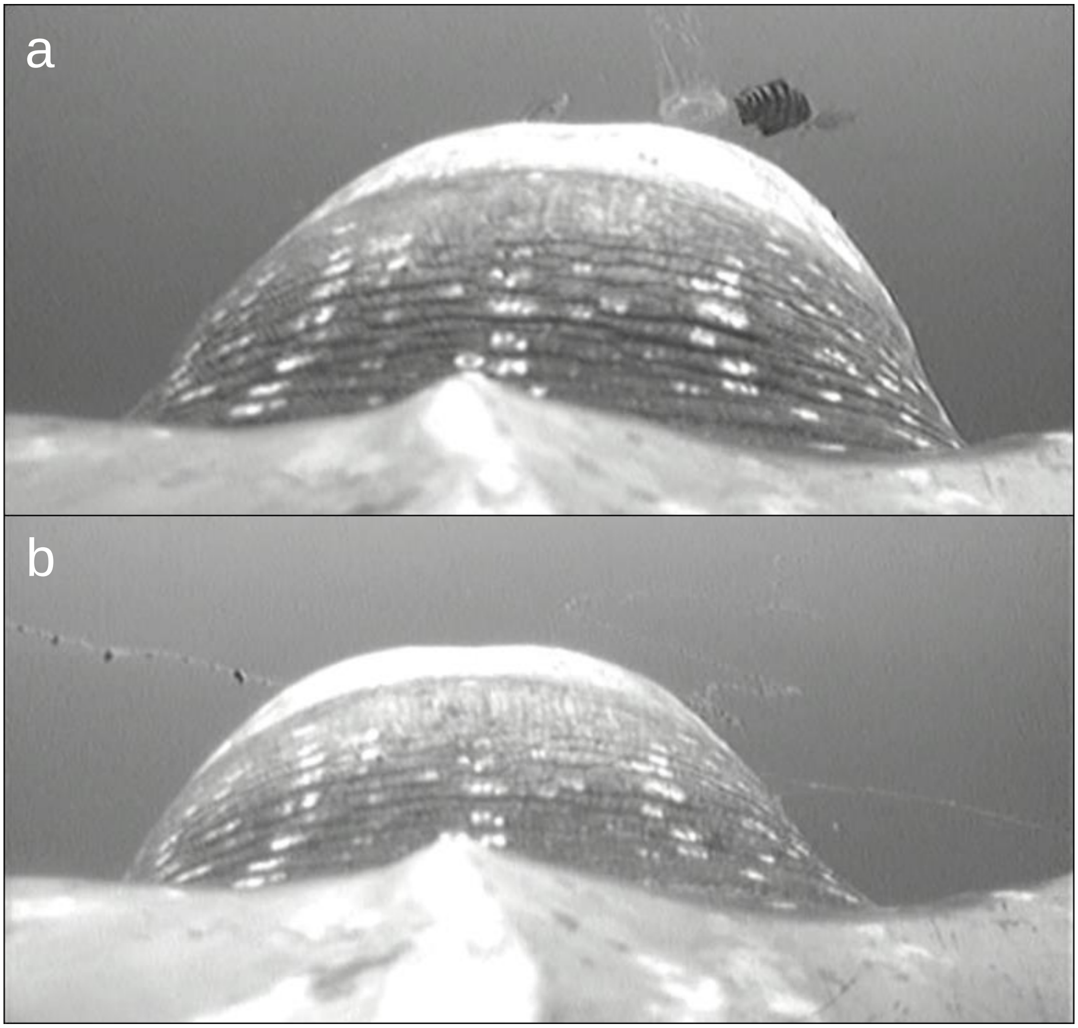


Fig. 2.3. Feeding on (a) Atlantic sea nettle (*Chrysaora quinquecirrha*) and (b) pelagic salp (*Salpa aspera*)

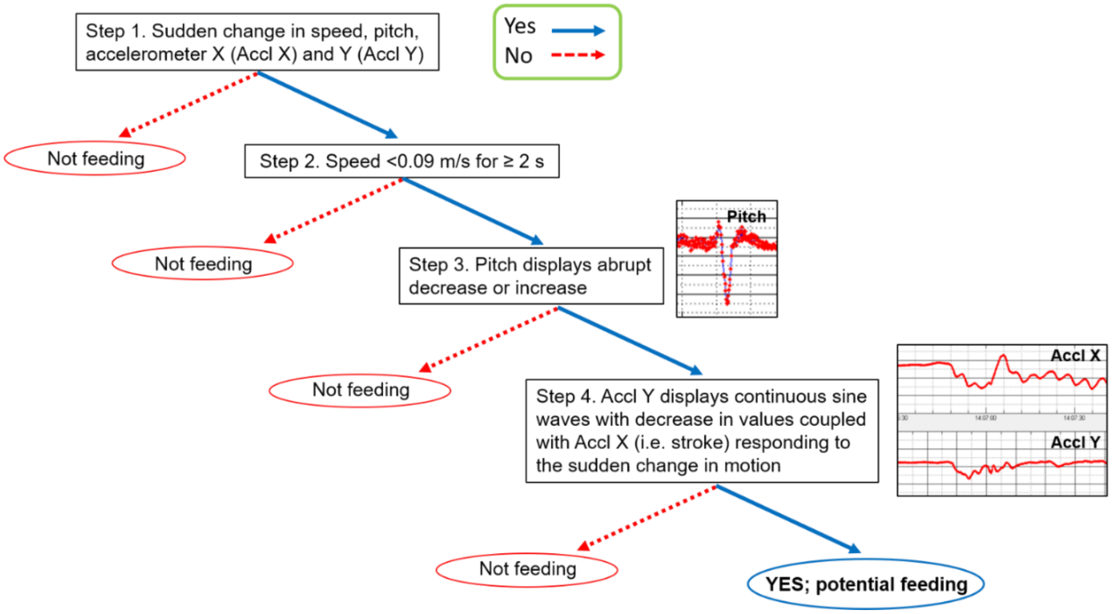


Fig. 2.4. Yes-No feeding detection diagram to identify prey encounters for dives without video recordings. Each step was validated for prey captures with video

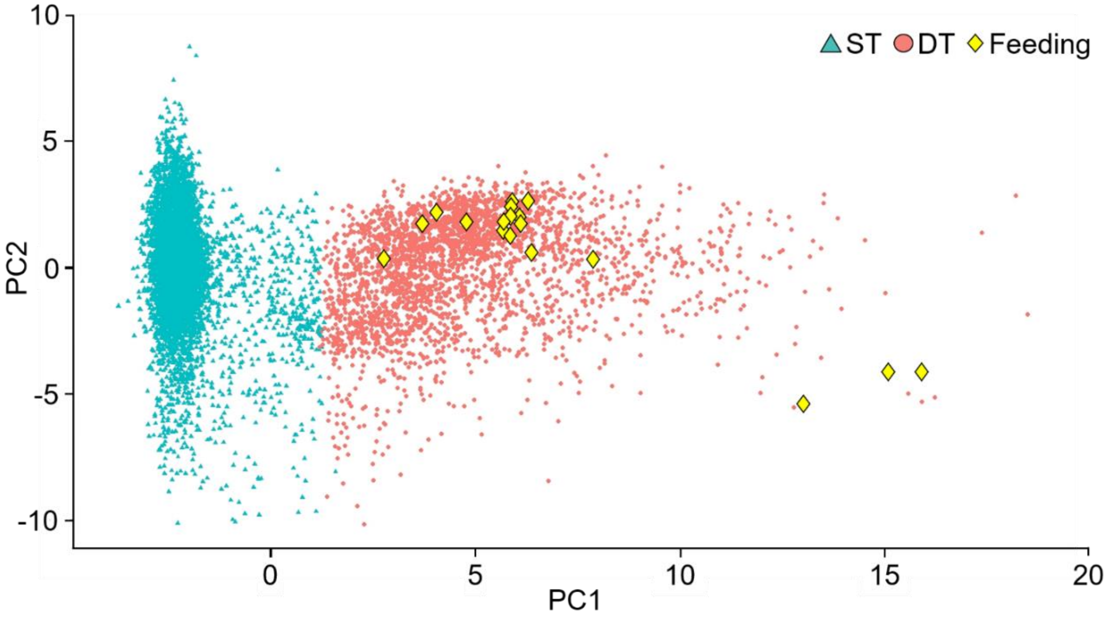


Fig. 2.5. Results of Principal Component Analysis (PCA) derived from *k-means* cluster analysis identifying two dive types: Shallow Transit (ST) dives and Deep Transit (DT) dives. Yellow diamonds are dives (18) with prey encounters or captures. PC1 accounted for 39.8% of the variation and PC2 accounted for an additional 14.9%

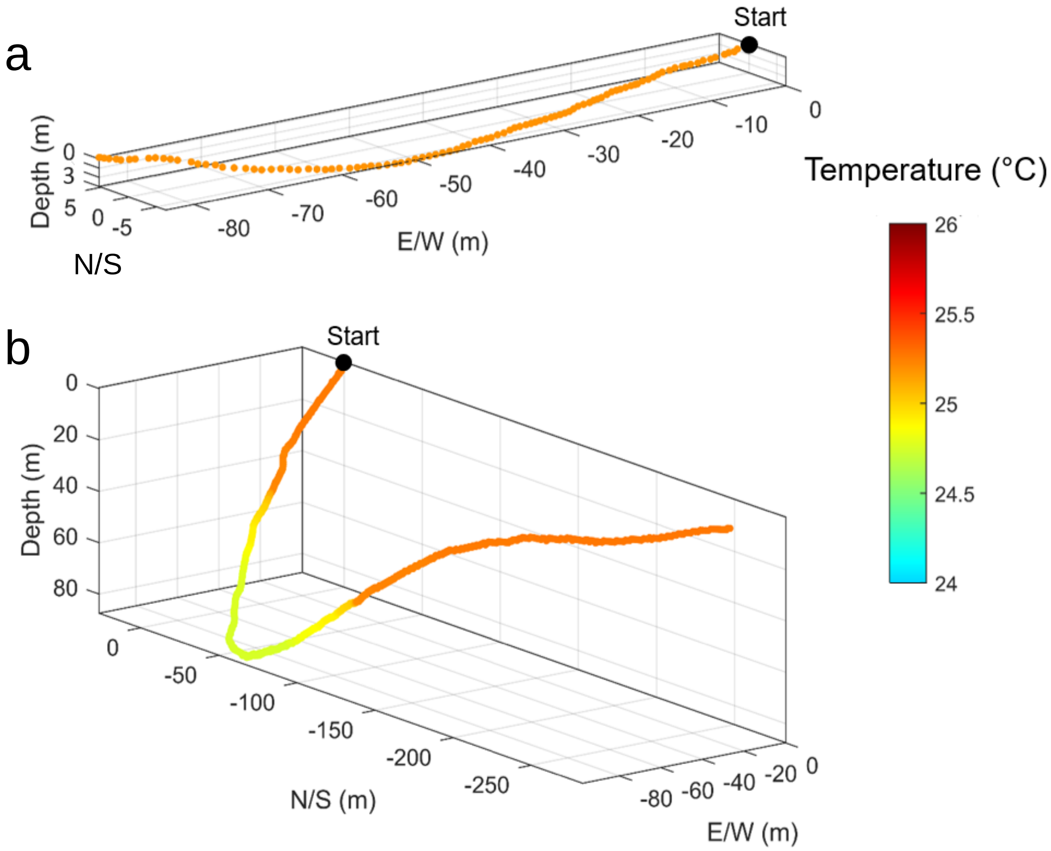


Fig. 2.6. (a) Shallow Transit Dive (STD) and (b) Deep Transit Dive. The mean maximum depth and duration of STD was 3 m and 1.2 min, respectively. The mean maximum depth and duration of DTD was 85 m and 13 min, respectively. Scale is in meters (m) for depth, displacement north-south (N/S), and displacement east-west (E/W)

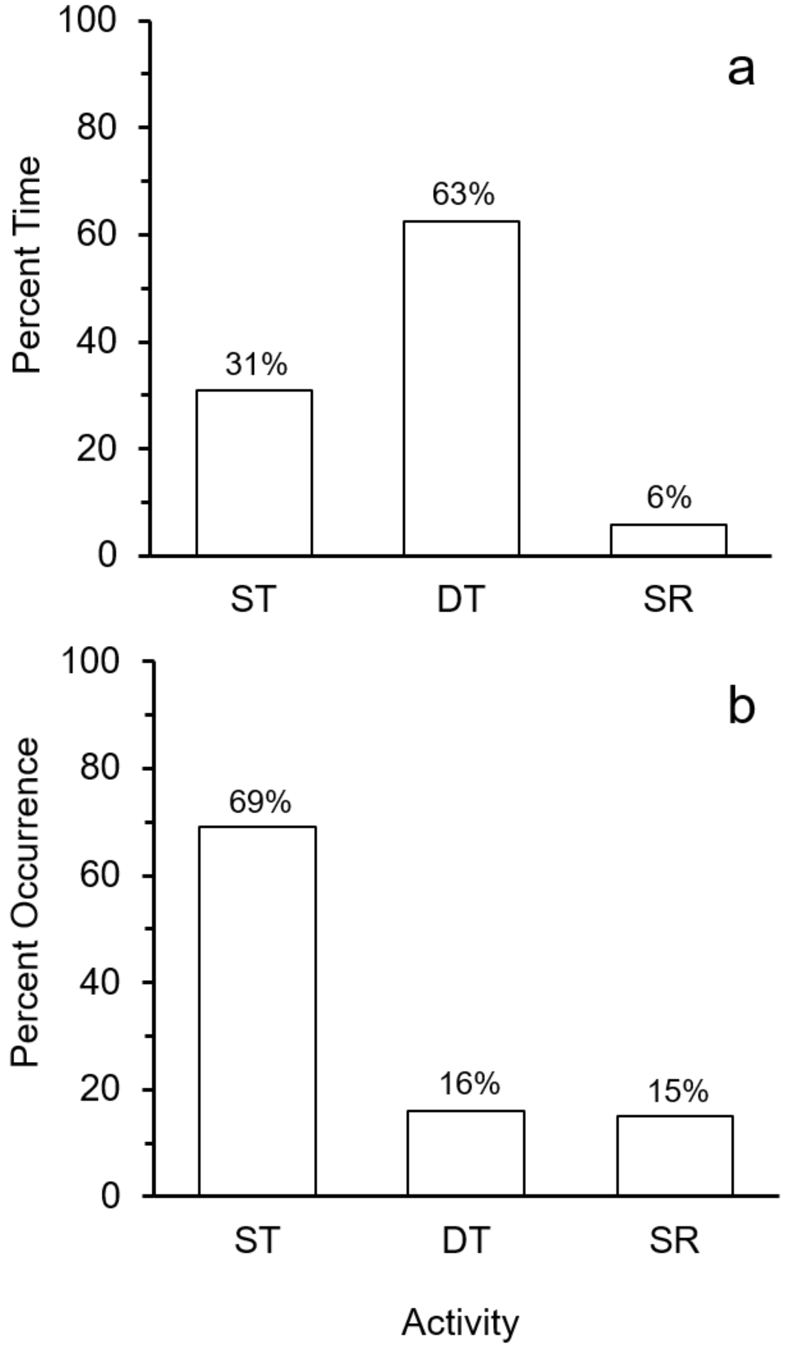


Fig. 2.7. Distribution of Shallow Transit (ST) dives, Deep Transit (DT) dives, and surface resting (SR) based on (a) percent occurrence and (b) percent time at sea during the internesting interval

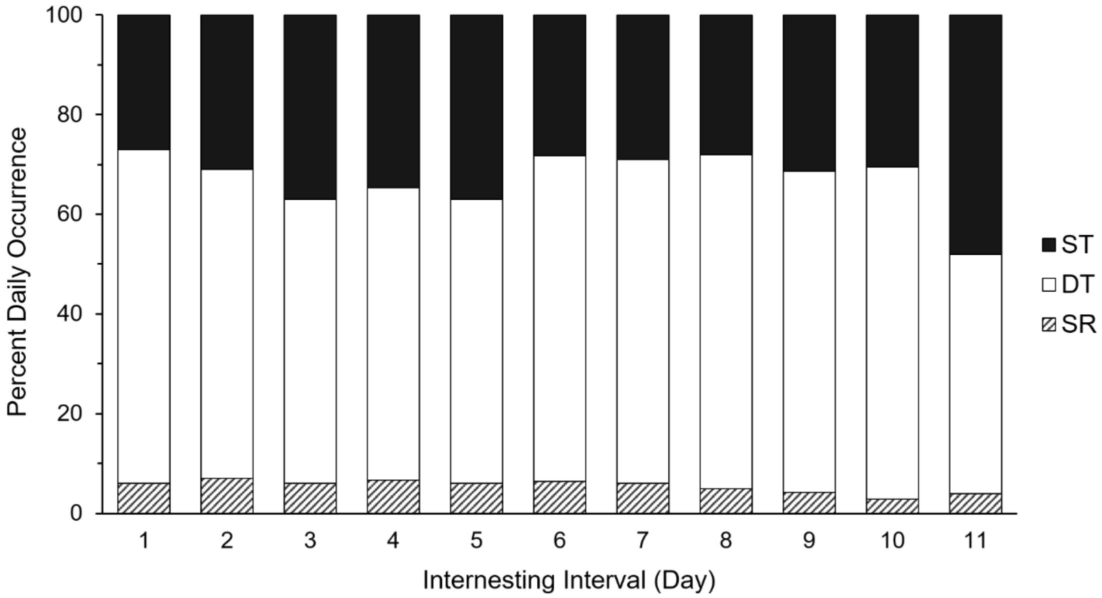


Fig. 2.8. Percent daily occurrence (based on time) of Shallow Transit (ST) dives, Deep Transit (DT) dives, and Surface Resting (SR) during the 11-day internesting interval. The mean daily percent occurrence was 33 ± 5.8% for ST dives, 62 ± 5.7% for DT dives, and 5 ± 1.2% for SR, and there were no significant differences throughout the interesting interval (Kruskal-Wallis Test, *p*>0.05)

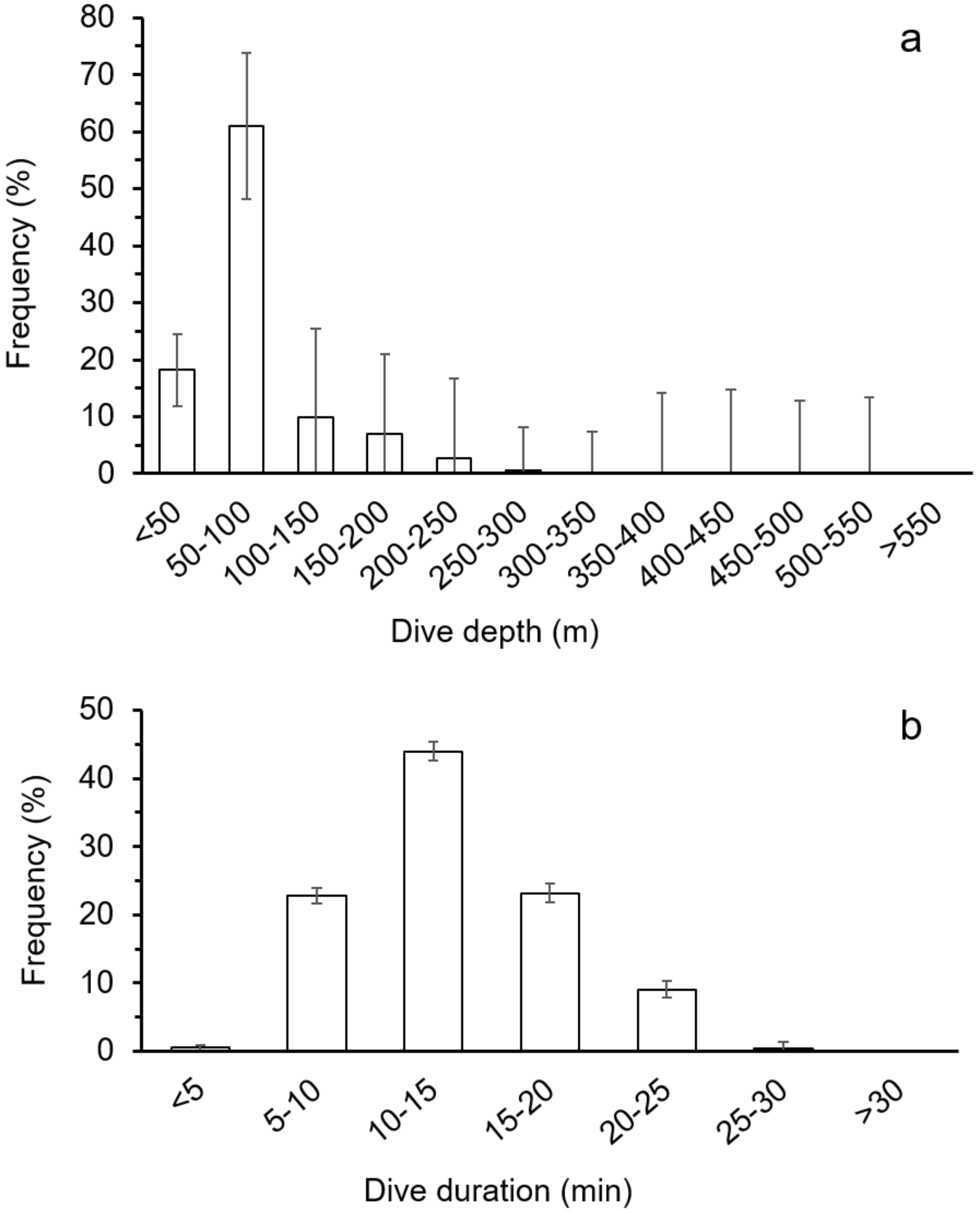


Fig. 2.9. Frequency distribution of (a) dive depth and (b) dive duration for DT dives

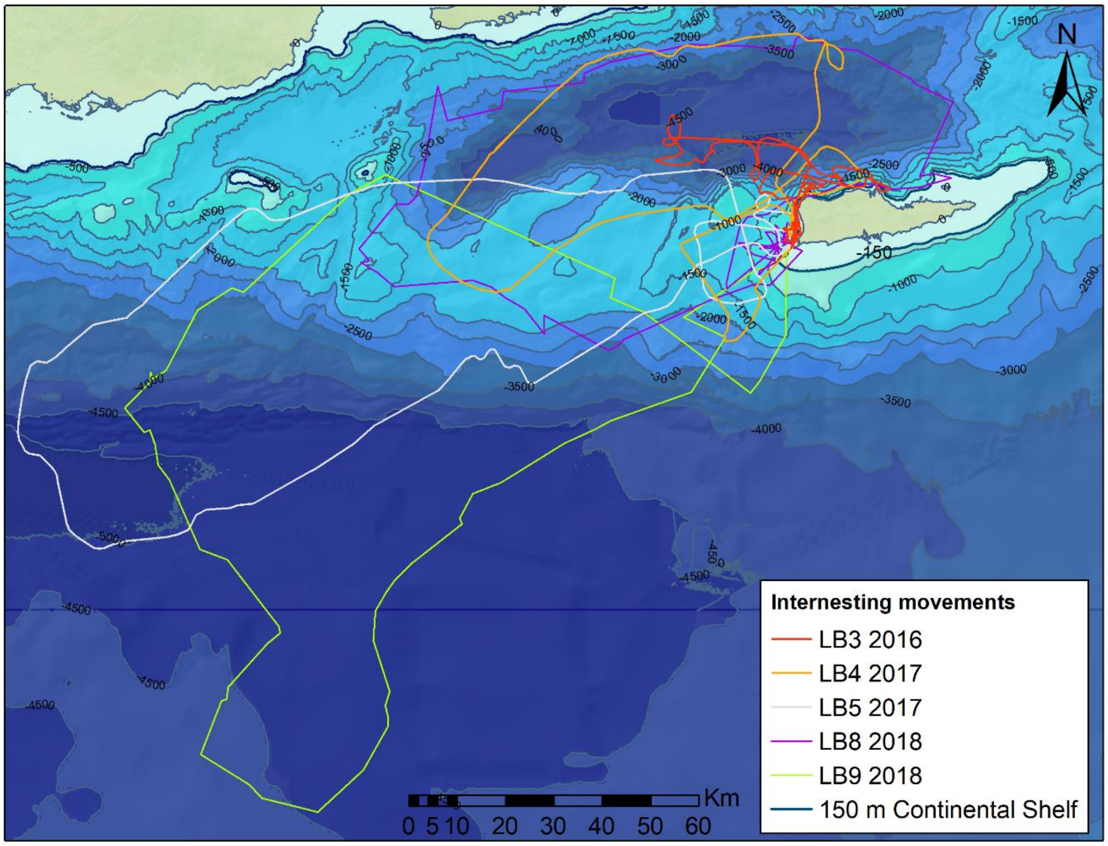


Fig. 2.10. Movements based on satellite tracking of five female leatherback turtles during their internesting interval

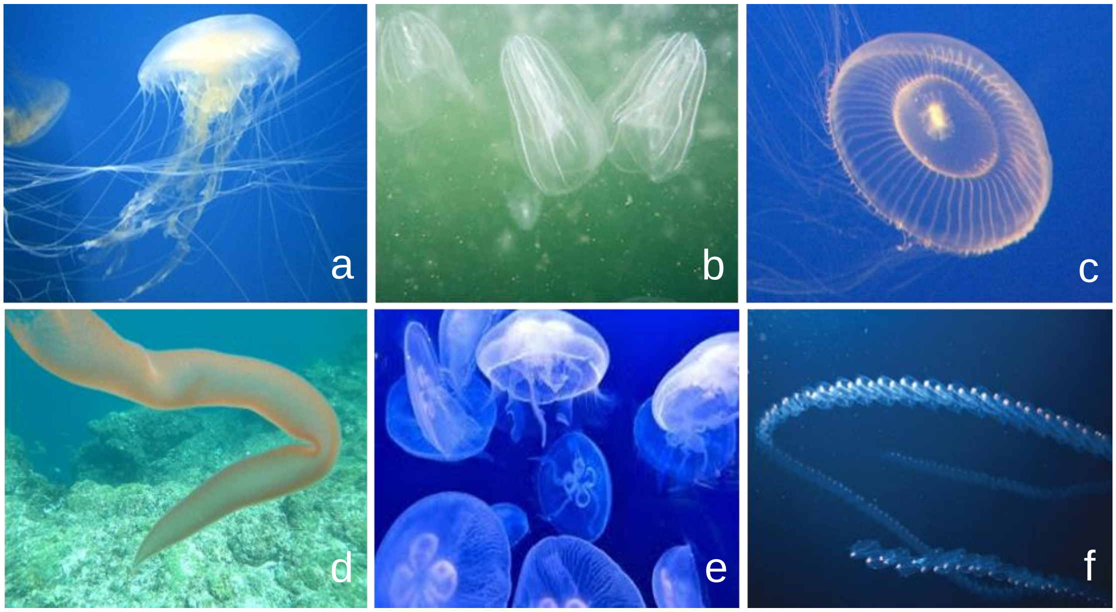


Fig. 2.11. Images (not from the VDR) of prey consumed by the female leatherback sea turtles: (a) Atlantic sea nettle (*Chrysaora quinquecirrha*), (b) Comb jelly (*F: Bathocyroidae*), (c) Crystal jelly (*Aequorea spp*.), (d) Giant fire salp (*Pyrosoma spp*.), (e) Moon jelly (*Aurelia aurita*), and (f) Pelagic salp (*Salpa aspera*)

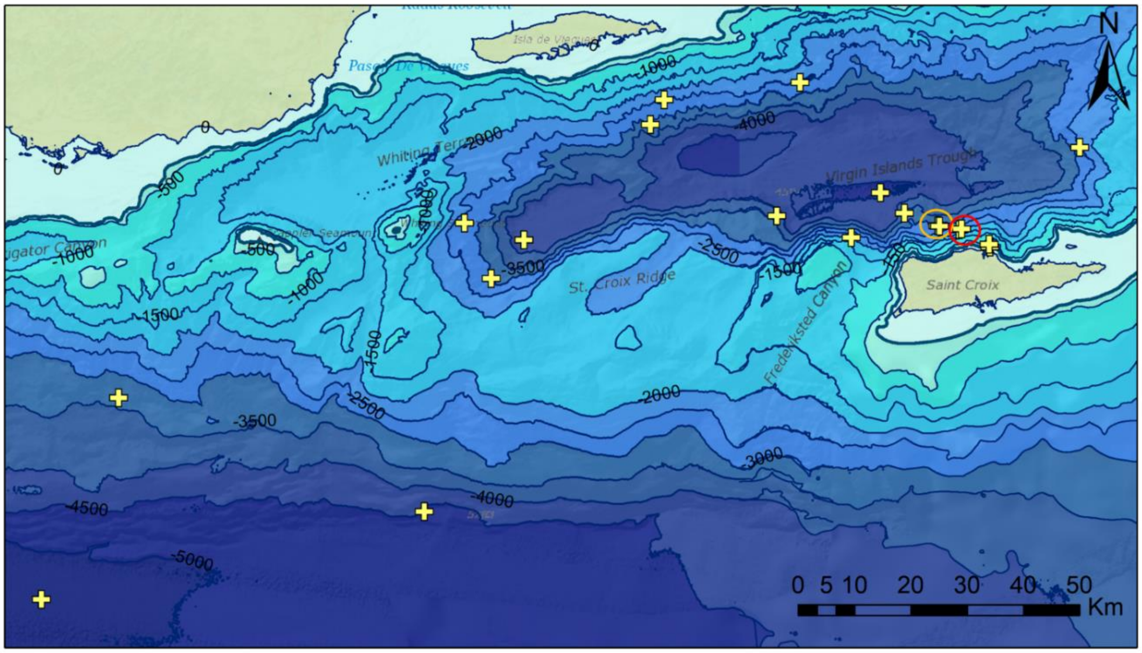


Fig. 2.12. The location of 23 prey captures/encounters (yellow crosses) during the internesting interval. Two prey encounters (orange circle) occurred during one dive and four prey encounters (red circle) occurred in another dive

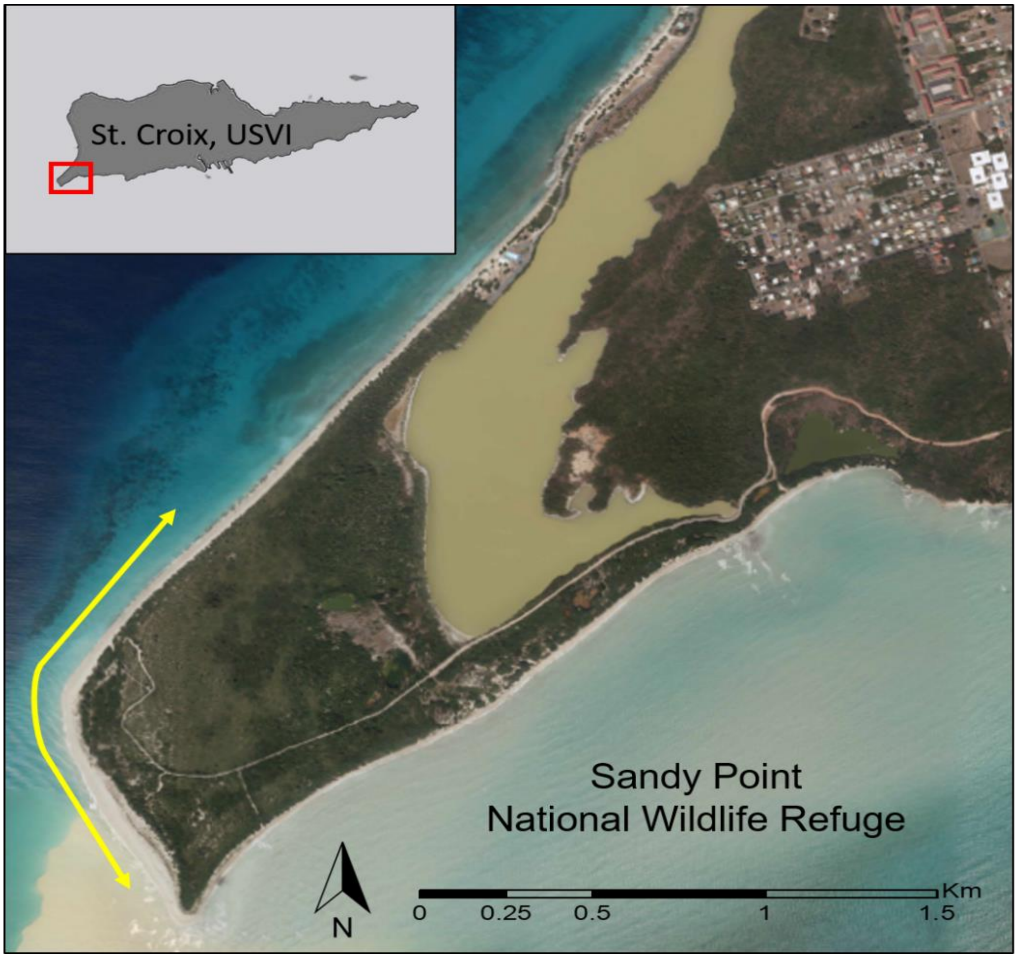


Fig. 3.1. The leatherback sea turtle nesting beach (yellow arrow) at the Sandy Point National Wildlife Refuge (SPNWR), St. Croix, U.S. Virgin Islands (USVI)

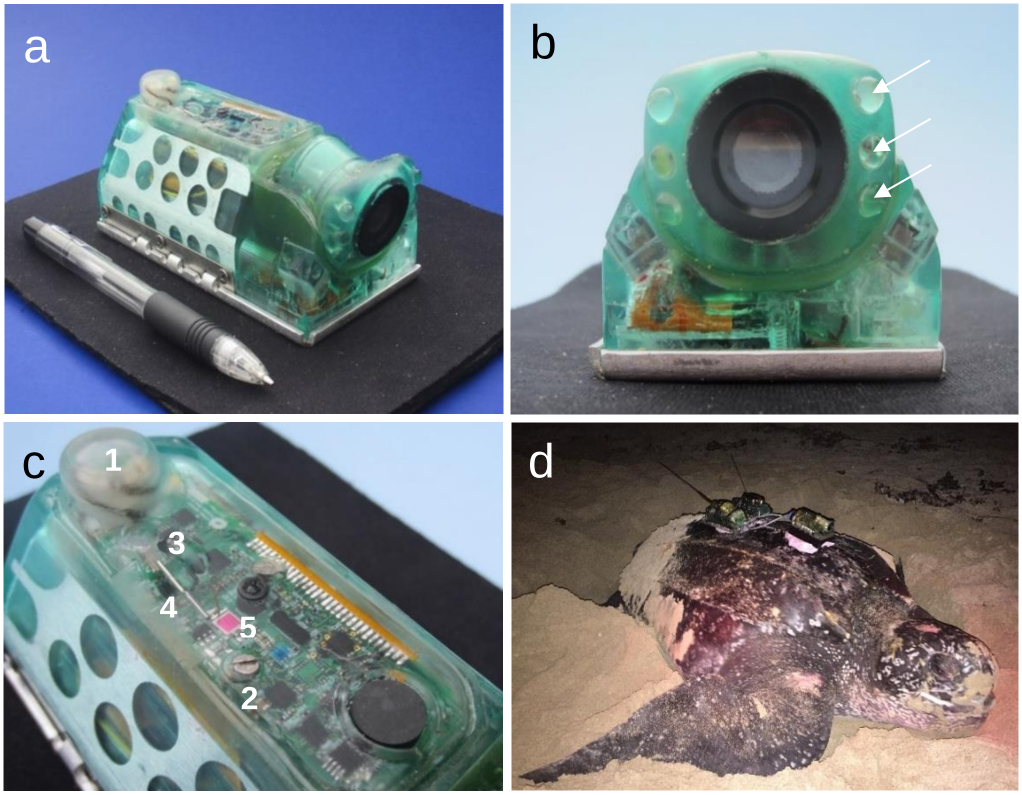


Fig. 3.2. Video and data recorder (VDR) showing: (a) size, (b) six near-infrared LEDs (three on either side, arrows) for illumination and two speed sensors (circles), (c) sensors (1) GPS antenna, (2) seawater sensor, (3) pressure, (4) temperature, (5) light, and (d) attachment of the VDR, axillary battery pack, satellite transmitter, and VHF radio transmitter to a female leatherback sea turtle. Image of leatherback sea turtle courtesy of G. Carvajal

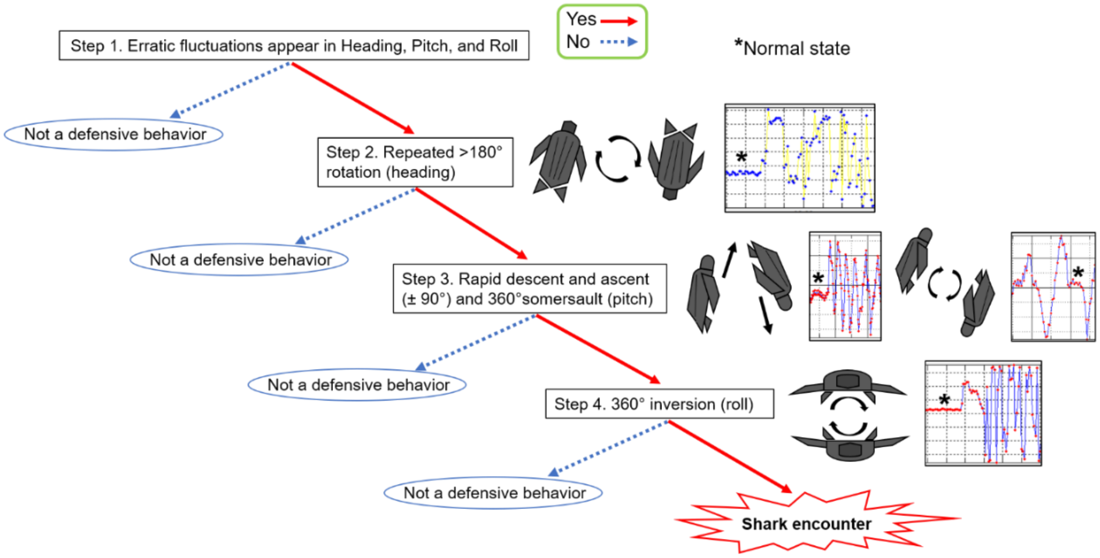


Fig. 3.3. Yes-No decision tree to identify shark encounters with defensive behavior in dive data, When available, shark encounters were validated with video from the VDR

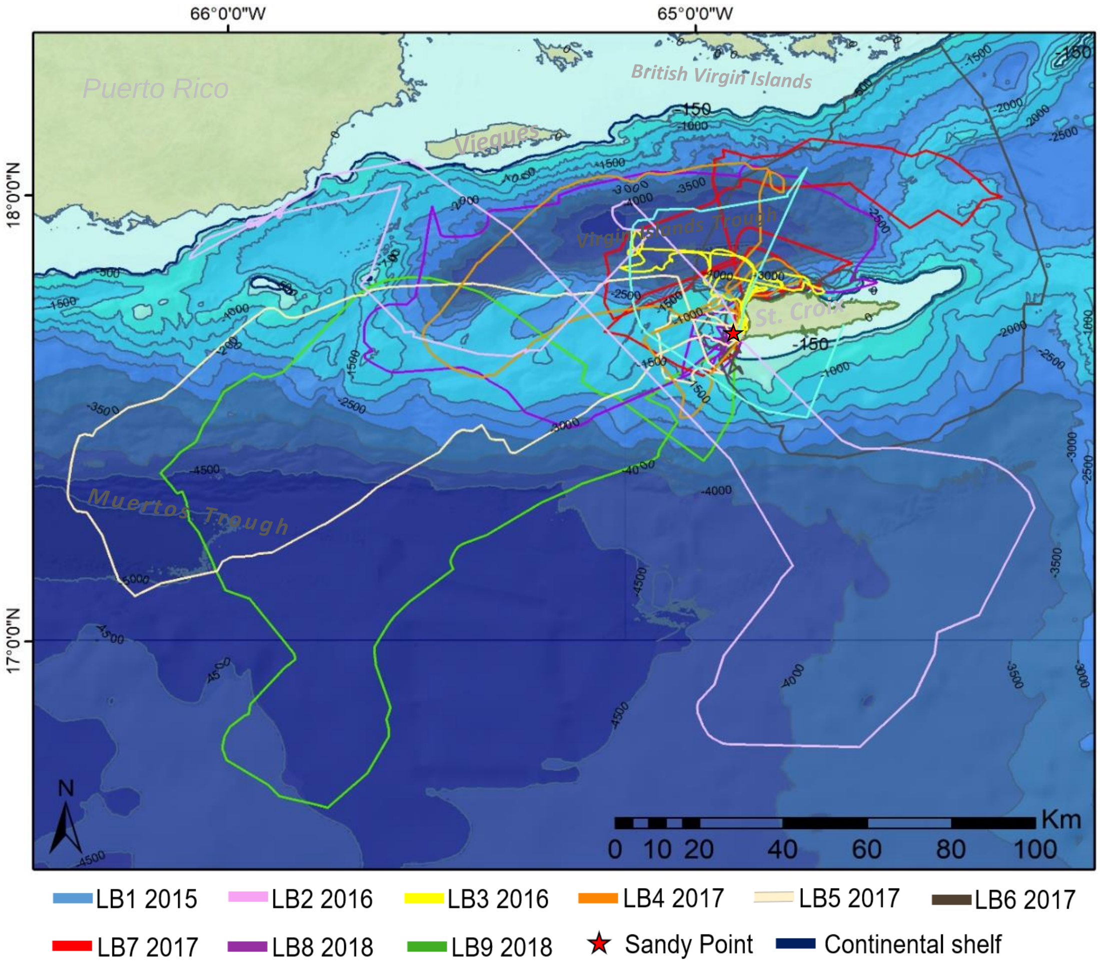


Fig. 3.4. Movements of all nine deployed gravid leatherbacks. The mean internesting interval for seven LB (not including LB1 and LB6) was 10.19 ± 1.73 days with a mean transit distance of 466 ± 106 km

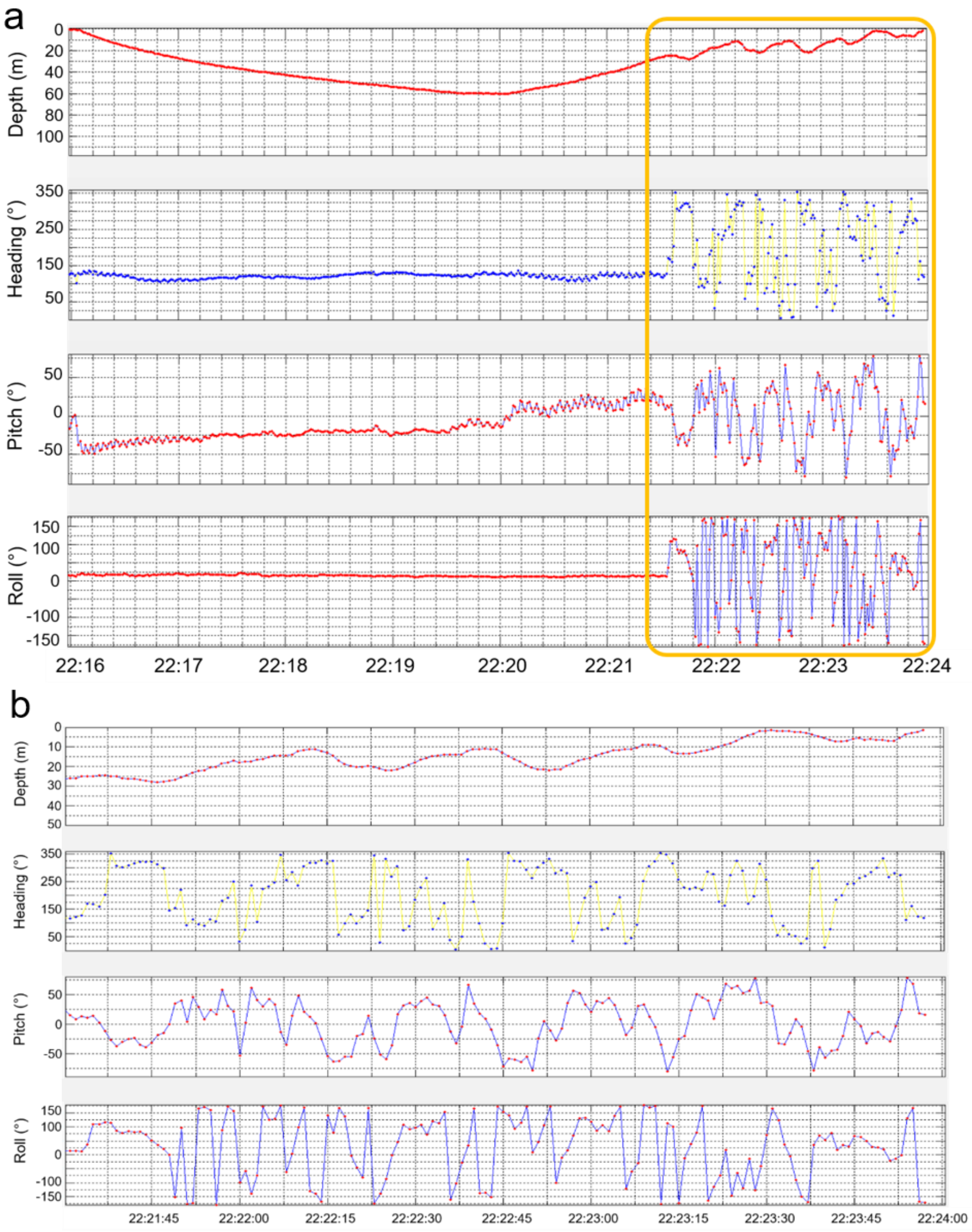


Fig. 3.5. (a) Data for depth, heading, pitch and roll during a shark with defensive behavior (orange rectangle) at the end of a deep transit (DT) dive. (b) Enlargement of the area in the orange rectangle. The mean swim speed during the shark encounter was 1.3 ± 0.34 m sec^{-1}

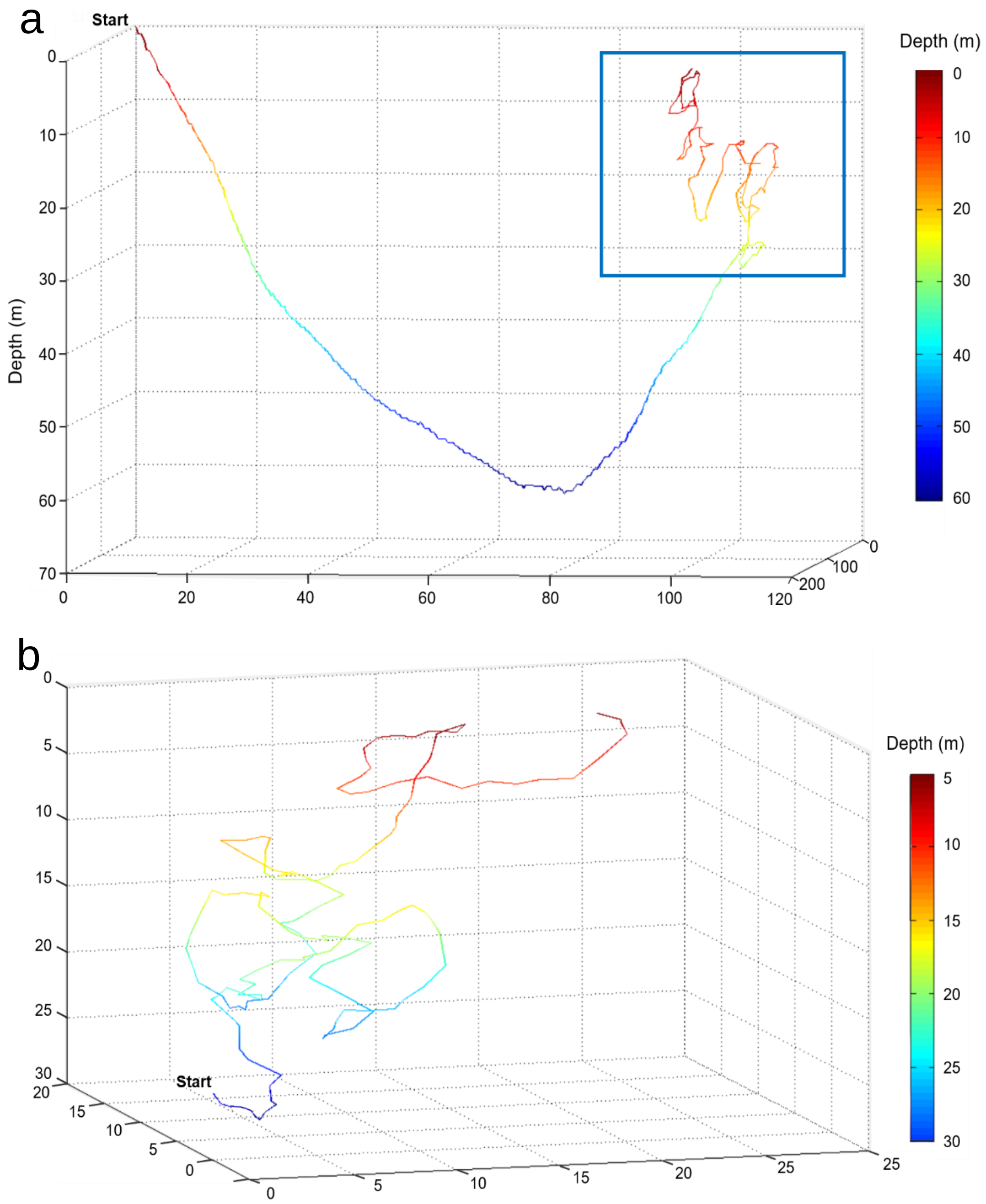


Fig. 3.6. (a) Three-dimensional view of shark encounter and defensive behavior (blue box) during a DT dive. (b) Enlargement of the area in the blue box

Fig. 3.7. Images of LB wounds and instrument damage from shark attack: (a) head wounds, (b, c, and d); penetrating rake wounds on carapace, (e) missing battery and severed battery cables to the VDR, and (f) damaged speed sensor and base. Images b and c courtesy of the U.S. Fish and Wildlife Sandy Point National Wildlife Refuge Leatherback Project

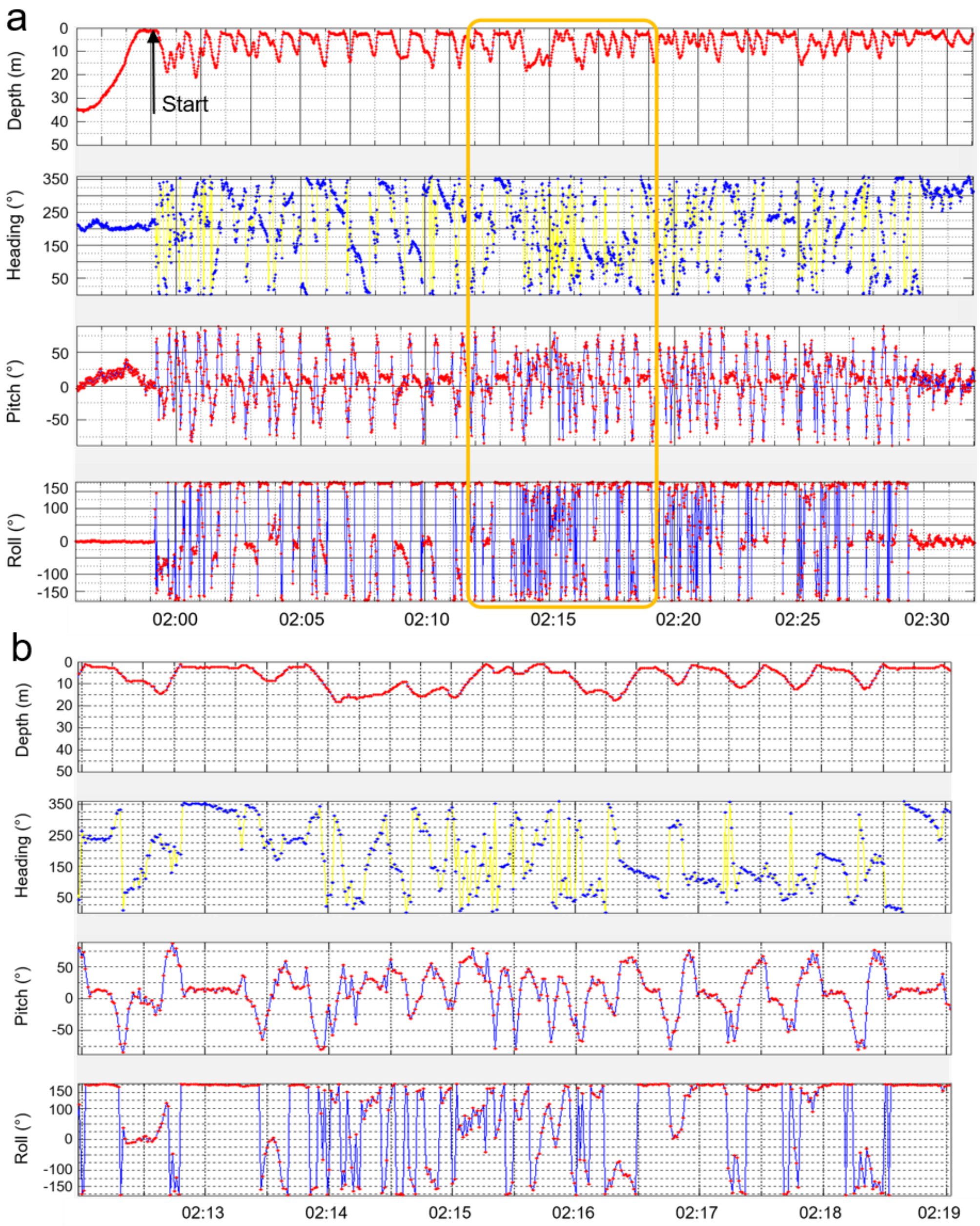


Fig. 3.8. (a) Data for depth, heading, pitch and roll during a 30 min shark encounter with defensive behavior that began during a deep transit (DT) dive. (b) Enlargement of the area in the orange rectangle. The mean swim speed during the shark encounter was 1.3 ± 0.43 m sec^{-1}

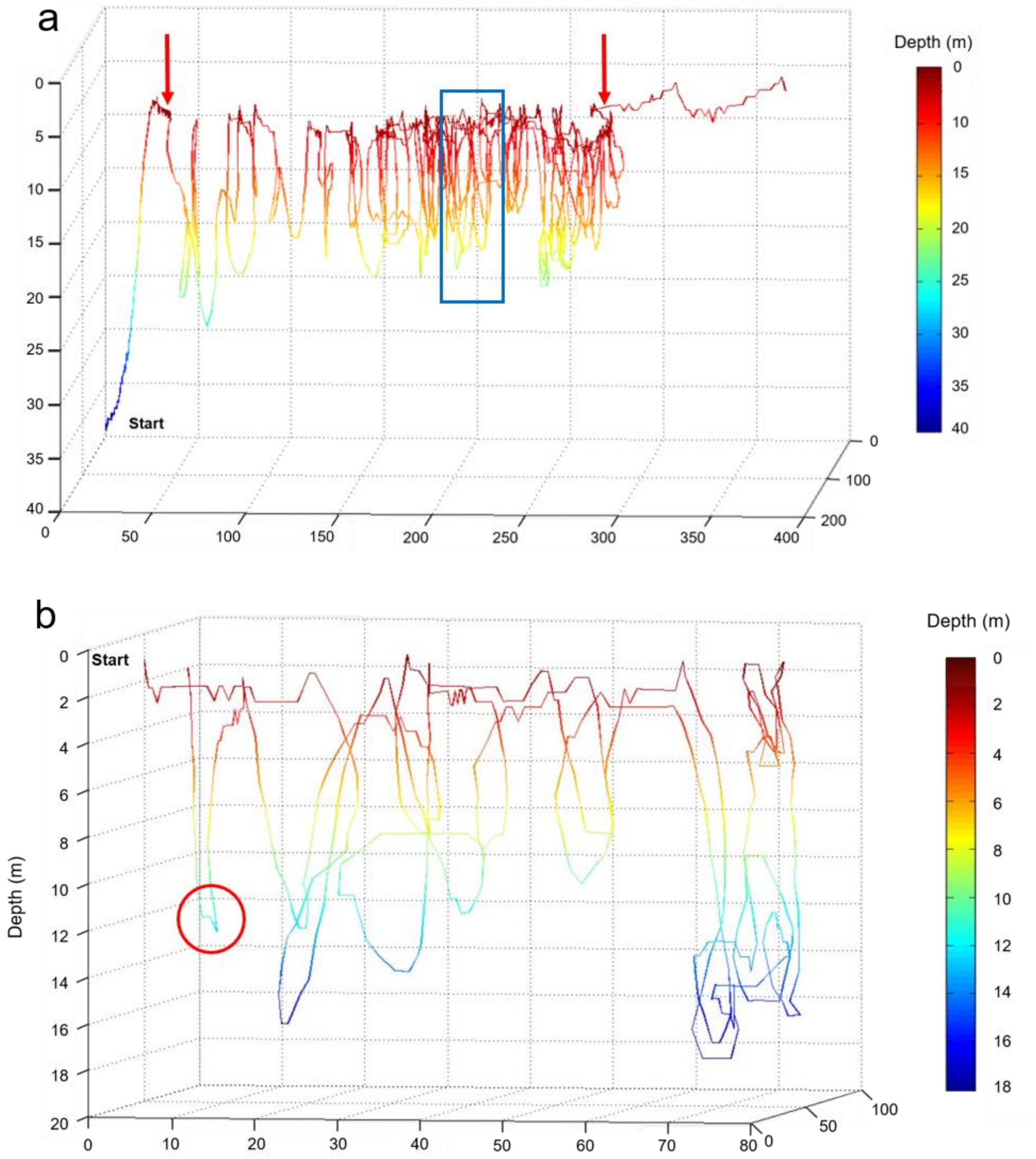


Fig. 3.9. (a) Three-dimensional view of shark encounter and defensive behavior that began at the surface. Red arrows indicate the beginning and end of the encounter, (b) Enlargement of the area in the blue rectangle. Red circle indicates where a forward somersault occurred

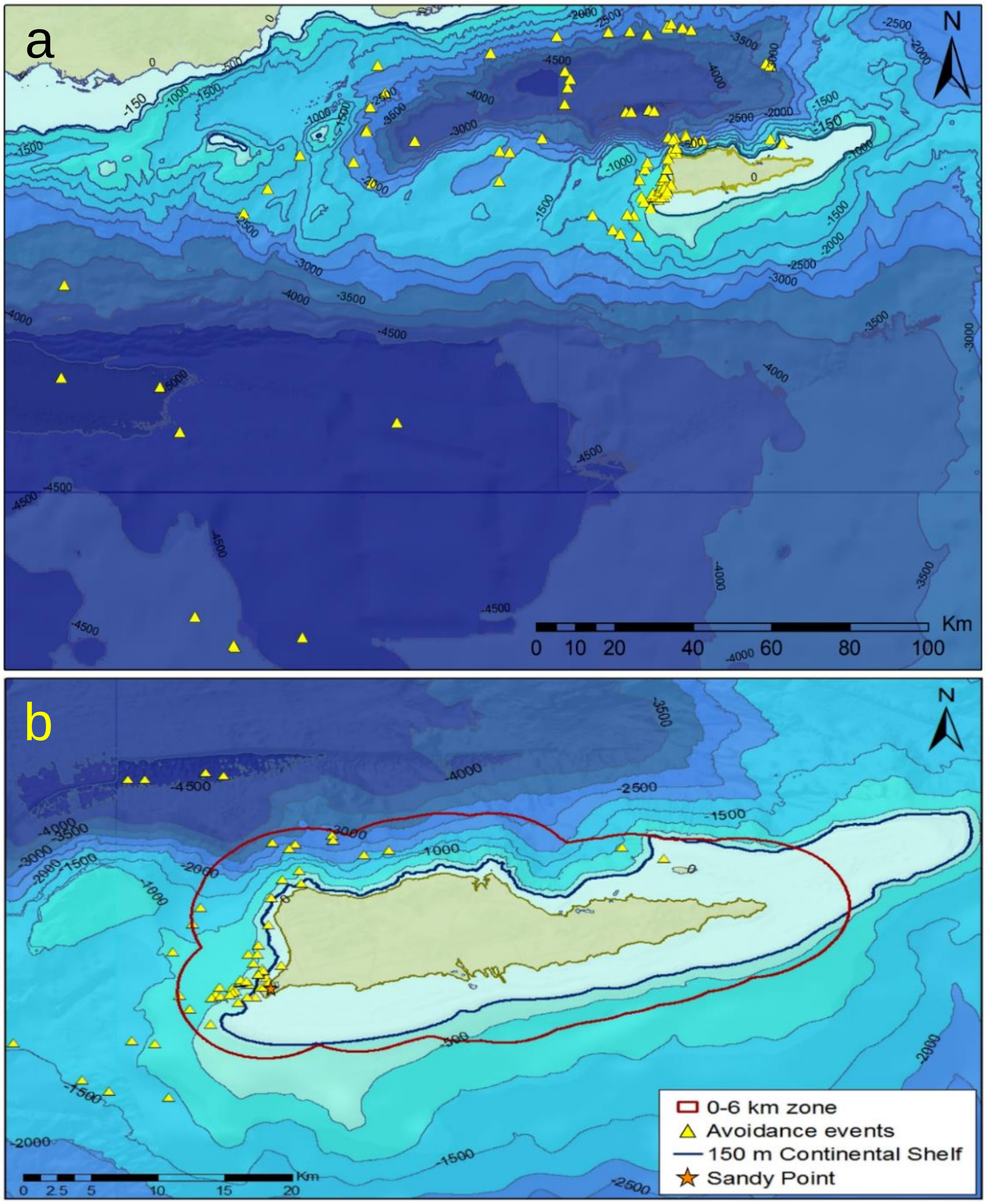


Fig. 3.10. (a) Locations for 102 shark encounters around St. Croix Island and in the Virgin Islands Trough and Muertos Trough and (b) shark encounters < 6 km from St. Croix. Of the 102 shark encounters, 51 (50%) occurred within a 6 km radius of which 45 (88%) occurred while the females were returning to the nesting beach

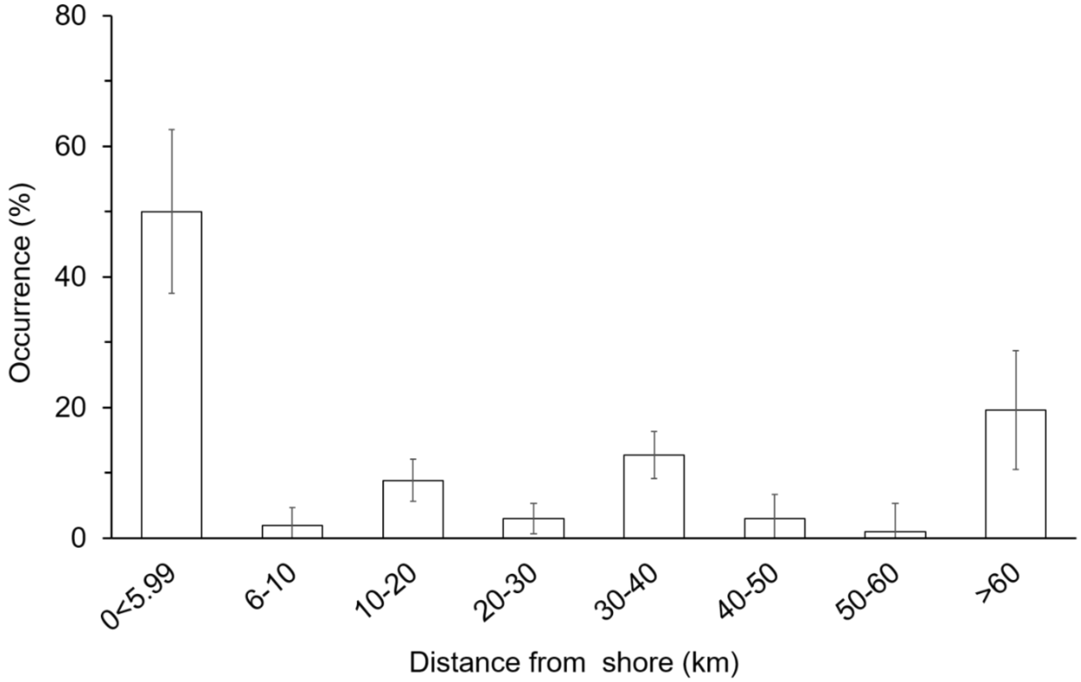


Fig. 3.11. Percent occurrence of the shark encounters and defensive behavior as a function of distance from St. Croix

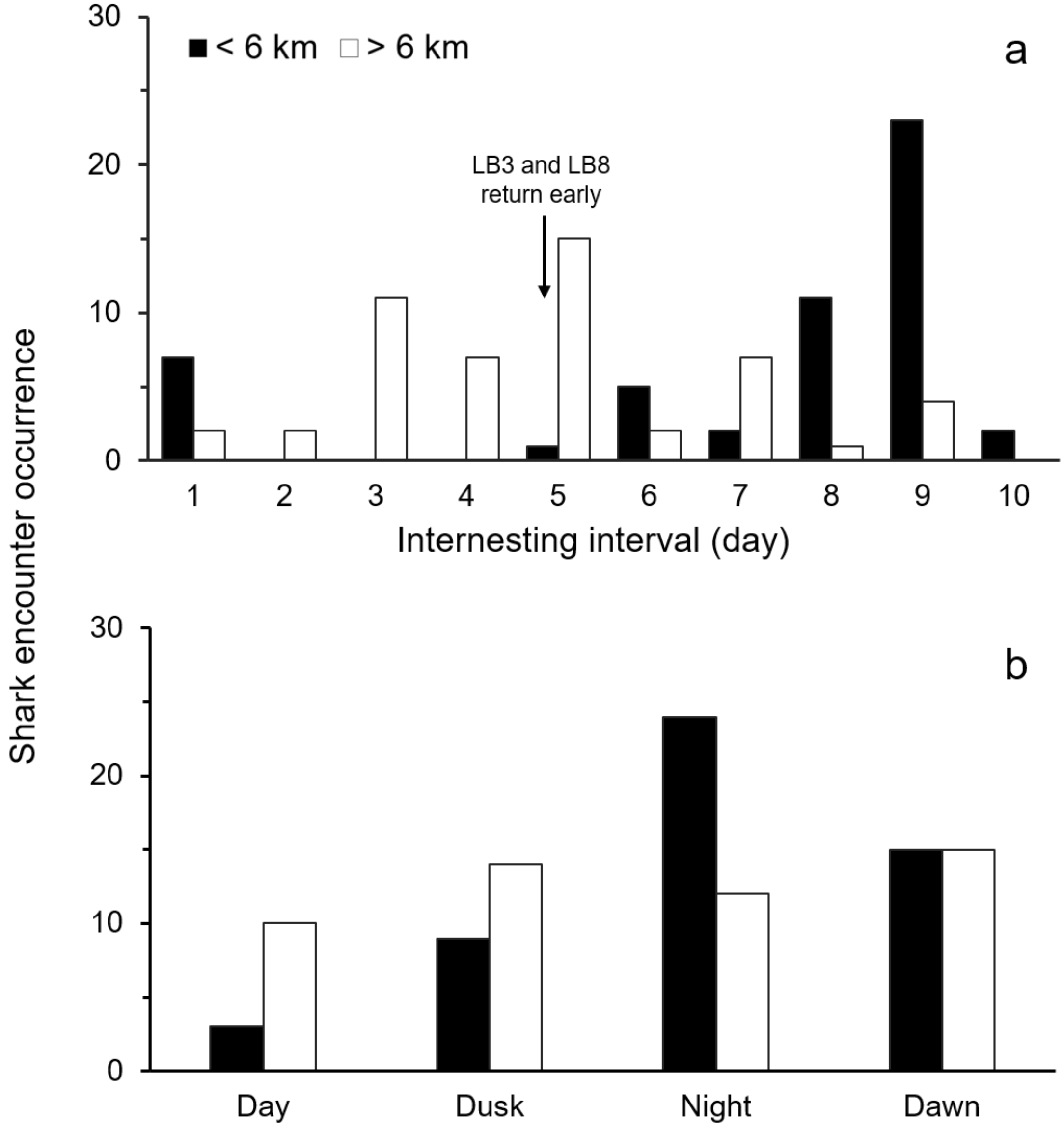


Fig. 3.12. (a) Daily occurrence of shark encounters > or < 6 km from St. Croix during the interesting interval (9.51 days ± 0.8). (b) Diel occurrence of shark encounters > or < 6 km from St. Croix during the interesting interval. Diel periods are defined as day (0900-1459), dusk (1500-2059), night (2100-0259), and dawn (0300-0859) Local Time (GMT-4)

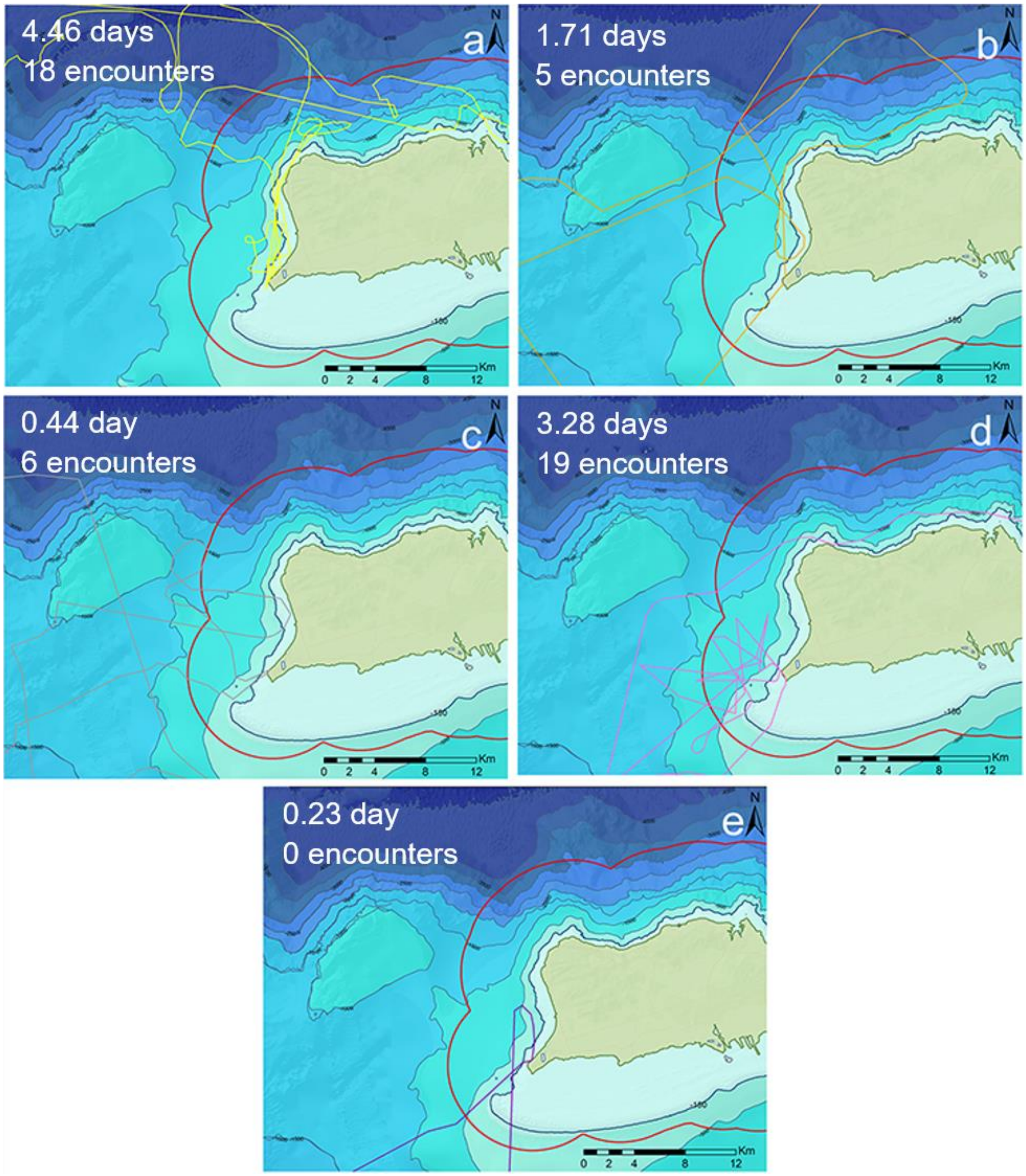


Fig. 3.13. Inbound tracks for (a) LB3, (b) LB4, (c) LB5, (d) LB8 and (e) LB9. The red line indicates 6 km from shore. Insert: Time spent within 6 km of St. Croix and number of shark encounters before coming ashore to nest. The mean time spent within 6 km of St, Croix was 2.26 ± 1.90 days

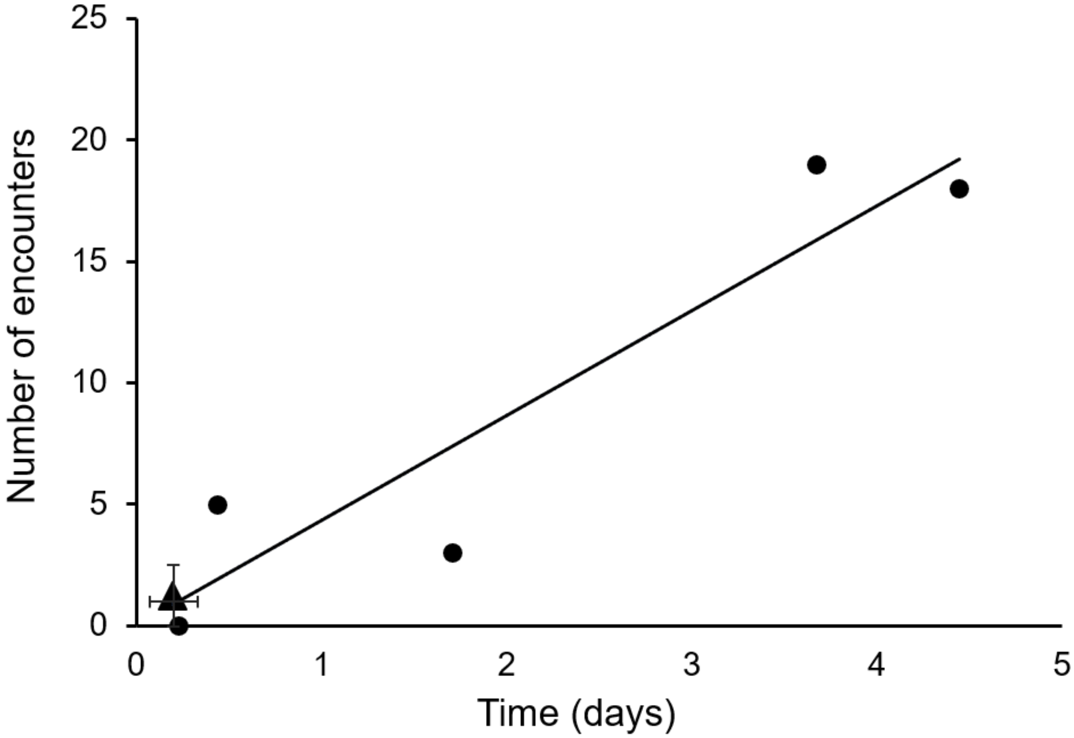


Fig. 3.14. Relationship between the number of shark encounters and the time (days) spent < 6 km from St. Croix when returning from an interesting interval (y = 4.3266 x - 0.0303, R^2 = 0.8869; Pearson's test, $p < 0.05$). The triangle shows the mean number of shark encounters (1.2 ± 1.3 encounters) and the mean time (0.23 ± 0.10 days) spent < 6 km from St. Croix when departing the nesting beach

Fig. 3.15. LB injuries, likely from tiger shark attacks: (a) the head of leatherback in the stomach of a tiger shark captured by local fishermen in St. Croix, (b and c) rake wounds on head, (d and e) rake wounds on carapace and shoulder, and (f) severed fore flipper. Image (a) courtesy of Shark Defenders. Images b-f from St. Croix courtesy of the U.S. Fish and Wildlife Sandy Point National Wildlife Refuge Leatherback Project