

Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape

NEIL HAMMERSCHLAG,^{1,2,12} ANNETTE C. BRODERICK,³ JOHN W. COKER,⁴ MICHAEL S. COYNE,⁵ MARK DODD,⁶ MICHAEL G. FRICK,⁷ MATTHEW H. GODFREY,⁸ BRENDAN J. GODLEY,³ DUBOSE B. GRIFFIN,⁹ KYRA HARTOG,¹ SALLY R. MURPHY,⁹ THOMAS M. MURPHY,⁴ EMILY ROSE NELSON,¹ KRISTINA L. WILLIAMS,¹⁰ MATTHEW J. WITT,¹¹ AND LUCY A. HAWKES³

¹Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149 USA

²Leonard and Jayne Abess Center for Ecosystem Science and Policy, P.O. Box 248203, University of Miami, Coral Gables, Florida 33124 USA

³Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall TR10 9FE United Kingdom

⁴South Carolina Department of Natural Resources, Wildlife and Freshwater Fisheries Division, 585 Donnelley Drive, Green Pond, South Carolina 29446 USA

⁵SeaTurtle.org, 1 Southampton Place, Durham, North Carolina 27705 USA

⁶Georgia Department of Natural Resources, 1 Conservation Way, Brunswick, Georgia 31520 USA

⁷Archie Carr Center for Sea Turtle Research, Department of Biology, University of Florida, Gainesville, Florida 32611 USA

⁸North Carolina Wildlife Resources Commission, 1507 Ann Street, Beaufort, North Carolina 28516 USA

⁹South Carolina Department of Natural Resources, Wildlife and Freshwater Fisheries Division, 217 Fort Johnson Road, Charleston, South Carolina 29422 USA

¹⁰Savannah Science Museum, Caretta Research Project, P.O. Box 9841, Savannah, Georgia 31412 USA

¹¹Environment and Sustainability Institute, University of Exeter, Penryn Campus, Cornwall TR10 9FE United Kingdom

Abstract. The “landscape of fear” model has been proposed as a unifying concept in ecology, describing, in part, how animals behave and move about in their environment. The basic model predicts that as an animal’s landscape changes from low to high risk of predation, prey species will alter their behavior to risk avoidance. However, studies investigating and evaluating the landscape of fear model across large spatial scales (tens to hundreds of thousands of square kilometers) in dynamic, open, aquatic systems involving apex predators and highly mobile prey are lacking. To address this knowledge gap, we investigated predator–prey relationships between tiger sharks (*Galeocerdo cuvier*) and loggerhead turtles (*Caretta caretta*) in the North Atlantic Ocean. This included the use of satellite tracking to examine shark and turtle distributions as well as their surfacing behaviors under varying levels of home range overlap. Our findings revealed patterns that deviated from our a priori predictions based on the landscape of fear model. Specifically, turtles did not alter their surfacing behaviors to risk avoidance when overlap in shark–turtle core home range was high. However, in areas of high overlap with turtles, sharks exhibited modified surfacing behaviors that may enhance predation opportunity. We suggest that turtles may be an important factor in determining shark distribution, whereas for turtles, other life history trade-offs may play a larger role in defining their habitat use. We propose that these findings are a result of both biotic and physically driven factors that independently or synergistically affect predator–prey interactions in this system. These results have implications for evolutionary biology, community ecology, and wildlife conservation. Further, given the difficulty in studying highly migratory marine species, our approach and conclusions may be applied to the study of other predator–prey systems.

Key words: biotelemetry; *Caretta caretta*; ecology of fear; ecosystem; *Galeocerdo cuvier*; landscape of fear; predation risk; predator–prey interactions; satellite tagging; sharks; trophic cascades; turtles.

INTRODUCTION

The “landscape of fear” model has recently been proposed as a possible unifying concept in ecology, to explain in large part how animals move and interact

within their landscape (Brown et al. 1999, Brown and Kotler 2004, Laundré et al. 2010). The model has been expanded to explain the drivers of animal population dynamics (Laundré et al. 2014). Central to the model is that prey must forage and survive in both their home range and that of their predators; thus, an animal’s knowledge of safe and risky areas within its home range is paramount for survival (Laundré et al. 2010). By contrast, predators that can adapt their behavior to

Manuscript received 10 November 2014; revised 27 January 2015; accepted 17 February 2015. Corresponding Editor: J. F. Bruno.

¹² E-mail: nhammerschlag@rsmas.miami.edu

target vulnerable prey within their home ranges will have increased feeding success and fitness advantages (Bergman et al. 2006). The basic landscape of fear model predicts that as an animal's landscape changes from low to high risk of predation, it will alter its behavior to risk avoidance. Understanding the landscape of fear for key species is important because it may also impact ecosystem structure and function through trophic cascades (Creel and Christianson 2008, Ritchie and Johnson 2009, Hammerschlag and Trussell 2011). For example, experiments have revealed that in the presence of sit-and-wait predatory spiders, grasshoppers will shift their foraging from high-quality grasses (high-risk habitats) to low-quality herbs (low-risk habitat) to reduce predation risk (Schmitz et al. 1998). This behavioral change by the grasshoppers has a positive indirect impact on the grasses by reducing herbivory, but a negative indirect impact on the herbs. Moreover, this shift in grasshopper habitat use correlates with reduced nutrition and elevated stress and metabolic needs (Schmitz et al. 1998).

Despite a large body of theoretical and empirical work in support of the landscape of fear model, the majority of field studies have primarily been conducted at relatively small spatial scales (tens to hundreds of square kilometers) and/or on terrestrial species (e.g., ungulates, wolves, rodents), in relatively pristine or restored systems, and/or across discrete habitat types that differ in high or low predation risk (e.g., vegetated vs. open areas, shallow vs. deep). It has recently been argued that highly mobile predators may not induce prey behavioral alterations because wide-ranging predators probably do not produce consistent and predictable predation risk cues at large spatial or temporal scales (Kauffman et al. 2010). This especially may be the case in large, fluid systems, such as the open ocean. Here, prey may not modify their foraging or habitat use at levels necessary to initiate behaviorally mediated trophic cascades (Kauffman et al. 2010). In addition to making behavioral decisions based on perceived foraging and predation risk, animals must also balance other factors, such as biological requirements (e.g., somatic growth and reproduction), abiotic factors (e.g., temperature), as well as other anthropogenic stressors. For example, roe deer (*Capreolus capreolus*) in southern Norway do not shift habitat use in response to predation risk during winter because they are constrained by other factors such as thermoregulation and starvation due to food limitation (Ratikainen et al. 2007, Lone et al. 2014). Determining optimal strategies in light of different trade-offs can be particularly challenging for highly mobile species that move across dynamic landscapes (Herfindal et al. 2009, Beauchesne et al. 2013). However, there is a general paucity of studies that have tested the landscape of fear model across dynamic environments involving highly migratory species at large spatial scales (tens to hundreds of thousands of square kilometers), probably due to logistical and technological

challenges of working in such systems, particularly in open aquatic systems.

Tiger sharks (*Galeocerdo cuvier*; see Plate 1) are large (up to 600 kg), mobile apex predators that are distributed across temperate and tropical seas (Compagno et al. 2005). Despite having relatively low daily energy requirements (Hammerschlag et al. 2013), tiger sharks have a diverse diet and commonly feed on sea turtles (e.g., Heithaus 2001, Simpfendorfer et al. 2001). In addition to possessing specialized teeth morphology permitting them to prey on sea turtles (Witzell 1987), tiger shark eyesight may be adapted for surface capture of prey such as sea turtles. Specifically, their visual streak (the area of highest acuity in the retina) is located on the ventral surface of the retina, giving the tiger shark highest visual acuity and spatial resolution in the upper visual field (Bonazzo and Collin 2000, Hart et al. 2006), which probably enhances their ability to distinguish turtles at the surface when sharks are hunting from below. In the Northwest Atlantic Ocean, loggerhead sea turtles (*Caretta caretta*) are a common prey item of tiger sharks (Castro 2011). The eastern coastline of the United States represents the world's second largest nesting assemblage of loggerhead turtles, composed of genetically distinct groups (Ehrhart et al. 2003). Adult loggerhead turtles from the northern group exhibit seasonal latitudinal and longitudinal movements between northerly/nearshore summer foraging grounds and southerly/offshore winter foraging areas, while some individuals also exhibit pelagic excursions associated with entrainment in the Gulf Stream in the north Atlantic (Hawkes et al. 2011, Griffin et al. 2013). These movement patterns may render loggerhead turtles vulnerable to tiger shark predation where their distributions overlap. For example, Williams and Frick (2008) received a tag return from a loggerhead turtle originally tagged in Georgia that was found in the stomach of a tiger shark that was landed in North Carolina. Work in other systems has found tiger sharks can use cognitive maps to precisely synchronize their migrations with prey availability (Meyer et al. 2010, Fitzpatrick et al. 2012). As such, loggerheads may trade off between predator avoidance and feeding/nesting when their home ranges overlap with tiger sharks (Robinson and Merrill 2013).

In the present study, we bring together extensive, long-term satellite-tracking data sets of both tiger sharks and adult female loggerhead turtles from the Northwest Atlantic Ocean to determine their seasonal spatial overlap and evaluate whether loggerhead turtles modify their behavior according to a basic landscape of fear. The surfacing behaviors of both loggerhead turtles and tiger sharks make them a model group to investigate such predator-prey relationships. As obligate air-breathers, loggerhead turtles face mutually exclusive constraints between the need for ventilation at the surface and predator avoidance (Heithaus and

Frid 2003). Tiger sharks are ambush predators, primarily attacking turtles at the surface where turtles have limited options for escape and their ability to detect the darkly pigmented dorsum of a tiger shark stalking from below is compromised, and where turtles are backlit against the surface, providing sharks with both a visual and tactical advantage (Heithaus and Frid 2003). Thus, loggerhead turtles should reduce their exposure at the surface to reduce the probability of being attacked by tiger sharks, while tiger sharks should increase subsurface movements in areas of overlap with turtles to maximize cryptic and enable ambush attacks (Heithaus and Frid 2003). Accordingly, we evaluated tiger shark and loggerhead turtle surfacing behavior under varying levels of home range overlap (a high-risk scenario for turtles, but high foraging opportunity for sharks). Taken together, we used these data to map the turtles' landscape of fear and evaluate the following three a priori predictions: (1) overlap in turtle–shark home ranges will be highest during the summer, when turtle activity (foraging and nesting) is highest; (2) in areas of core home range overlap, tiger sharks will spend more time subsurface to enable ambush on turtles from below; and (3) likewise, loggerhead turtles will spend less time at the surface to reduce their predation risk from tiger sharks in areas of high home range overlap.

Generally, the landscape of fear is portrayed as having regions with peaks and valleys of predation risk, usually due to stark differences in habitat structure (e.g., vegetation or elevation) that affect prey escape and refuge and/or predator hunting efficiency (Laundré et al. 2010). It is possible that in an open marine system involving migratory species, there are no discrete predation risk landscape features on which to map fear effects for both predator and prey. The Northwest Atlantic Ocean is characterized by variation in biological, environmental, and anthropogenic factors (Christensen et al. 2003, Minobe et al. 2008), thus providing a great opportunity to study potential predator–prey interactions across a dynamic, open environment involving highly migratory species.

MATERIALS AND METHODS

Satellite tracking

Tiger sharks.—From January 2010 to August 2013, satellite tags were attached to 31 tiger sharks captured in Florida and the western Bahamas (for exact tagging locations, see Hammerschlag et al. 2012a). Sharks ranged in size from 184 to 403 cm total length (283 ± 58 cm, mean \pm SD). Sharks in this size range are known to consume turtles; unlike other sharks, tiger sharks are not gape limited (Heithaus 2001, Simpfendorfer et al. 2001). Their specialized teeth allow them to cut and take chunks out of large adult turtles (Witzell 1987). A subset of the tiger shark tracking data used in this study, including tag type and tagging methodology, was published in Hammerschlag et al. (2012a).

Loggerhead turtles.—From 1998 to 2008, satellite tags were attached to 68 female loggerhead turtles that were encountered nesting on beaches along the U.S. eastern seaboard in North Carolina, South Carolina, and Georgia during standard nighttime nesting beach surveys. Turtles ranged in size from 81 to 112 cm curved carapace length (CCL, 99.2 ± 6.7 cm, mean \pm SD). Data from these turtles, including tag type and tagging methodology, have previously been published elsewhere (Hawkes et al. 2011, Griffin et al. 2013). Although the shark and turtle data sets did not overlap temporally, the use of multiyear data (35 558 tracking days combined) from a large number of tagged animals permits adequate determination of core home range for each species that we subsequently compared. Such an approach has previously been used by Hammerschlag et al. (2012b). Moreover, home ranges for turtles and sharks are consistent between years (Hawkes et al. 2011, Hammerschlag et al. 2012a).

Movement data

The geographic locations of satellite-tagged sharks and turtles were determined by Doppler-shift calculations made by the Argos Data Collection and Location Service (Argos CLS, *available online*).¹³ Argos location data for both sharks and turtles were filtered following Witt et al. (2010), retaining the best daily location, defined as the first received highest quality location per day, and mapped in ArcGIS 10.1 (ESRI, Redlands, California, USA).

Areas of core habitat use (home range) were determined for turtles and sharks separately using kernel density estimates, KDE (quartic kernel; 0.5 degree smoothing parameter and a 0.1 degree [<10 km²] grid cell), for all filtered location data. A few sharks ($n = 7$) and turtles ($n = 4$) undertook pelagic excursions into the Gulf Stream, making looping movements over deep water offshore. However, because these existed for the minority of animals and for a small proportion of time in the animals that exhibited it, we excluded these positions (i.e., those outside 20–45° N and 85–70° W) from home range analysis to ensure that we captured majority behavior (99% of all location data) and to avoid skewing home range calculations. We generated 25%, 50%, 75%, 90%, and 95% density volume contours from the KDEs and then calculated the 90% KDE delineating the spatial extent (area in km²) in which shark and turtle core habitat use was likely to occur 90% of the time (i.e., hereafter core home range). We then calculated the spatial overlap of these core home ranges, representing high-risk areas for turtles, but high-predation opportunities for sharks. Movement data for turtles and sharks were analyzed for the winter (December–February) vs. the summer (June–August).

¹³ www.argos-system.org

Surfacing behavior

To analyze surfacing behavior for sharks and turtles, we took advantage of the fact that satellite tags only transmit to Argos receivers when a tag's salt water switch circuit breaks the water surface. The proportion of transmission being received by overpassing satellites should thus be an indicator of (1) the duration of time the animals are at the surface, (2) the frequency of surfacing, and/or (3) a combination of surfacing duration and frequency. Therefore, we extracted the total number of transmissions received per day from location data as an indicator of time at the surface (hereafter referred to as surfacing behavior). We analyzed our data separately in two regions, the North Region (North Carolina to South Carolina) and the South Region (Georgia to Florida) to account for potential differences in latitudinal satellite coverage. To gain further insight into our proxy of surfacing behavior based on Argos transmissions, we compared recorded surfacing data from two turtles (ID# 29349 and #52199) tagged with Satellite Relayed Data Loggers (SRDL 9000X, Sea Mammal Research Unit, St. Andrews University, Aberdeen, UK) which recorded diving behavior) against the corresponding number of transmissions received by the Argos satellites. Specifically, we conducted two separate analyses. First, we used Pearson's product-moment correlation coefficient to evaluate the relationship between recorded surface duration (total time at surface in hours) per day against total number of Argos transmissions received per day. Second, we compared the mean recorded duration at the surface per day against the mean number of Argos messages per day for the two turtles.

Shark–turtle interactions

For each position data point, we determined the total number of messages received by Argos satellites per day. We then used GIS to determine if that position occurred in or out of the 90% KDE turtle–shark overlap area. This permitted us to test for differences in both turtle and shark surfacing behavior in and out of home range overlap areas. Surfacing data were not normally distributed and therefore were analyzed using nonparametric statistics. Kruskal-Wallis tests were used to examine for statistical differences in turtle surfacing and shark surfacing in overlap vs. no-overlap areas (seasonally and regionally). We also plotted mean turtle and shark surfacing (mean number of Argos messages per day) against kernel density overlap (km^2) in turtle–shark home range by season and region to further explore the relationship between the degree of turtle–shark habitat overlap and surfacing behavior.

RESULTS

Argos transmitters attached to tiger sharks operated for 8 to 844 days (204 ± 225 days, mean \pm SD) for a total of 6736 tracking days. Core habitat use (home

ranges) for all filtered tiger shark locations combined (KDE) was $437\,397 \text{ km}^2$ (90%; Fig. 1).

Argos transmitters attached to loggerhead turtles transmitted between 57 and 1374 days (443 ± 247 days) for a total of 28 822 tracking days. Core habitat use for all filtered loggerhead turtle locations combined (KDE) was $178\,716 \text{ km}^2$ (90%; Fig. 1).

Turtle–shark overlap

Core overlap (using KDE) was higher in the summer than winter (Fig. 2). Specifically, overlap (KDE) values were $22\,652 \text{ km}^2$ (summer, North Region), followed by $18\,903 \text{ km}^2$ (summer, South Region), $13\,852 \text{ km}^2$ (winter, South Region), and 1555 km^2 (winter, North Region).

Argos messages as a proxy for surfacing behavior

Comparison of recorded surfacing data and received Argos transmissions for the two turtles with SRDL tags revealed a positive relationship between the sum surface duration (hours) per day and the sum Argos messages received per day (Pearson's $r = 5.11$, $df = 1$, 124 , $P < 0.01$ and $r = 12.7$, $df = 1$, 247 , $P < 0.01$, respectively, for the two turtles). Similarly, we found a positive relationship between the recorded mean surface duration and mean number of Argos messages received per day for both turtles (although only statistically significant for turtle ID #29349; Pearson's $r = 3.09$, $df = 1$, 247 , $P < 0.01$). These data suggest that the daily number of Argos locations should be a useful indicator of time spent at the surface, with the caveat that this was only tested using two turtles.

Seasonal and regional patterns in surfacing vs. overlap

Turtle surfacing was significantly higher in the summer vs. the winter (Kruskal-Wallis, $P < 0.0001$; summer median 16.0 messages per day, IQR = 9.0–27.0; winter median 7.0, IQR = 4.0–12.0). Conversely, shark surfacing was significantly lower in the summer vs. the winter (Kruskal-Wallis, $P < 0.0001$; summer median 8.0 messages per day, IQR = 4.0–15.0; winter median 14.0, IQR = 9.0–24.0). During winter, there were no significant differences in turtle and shark surfacing between areas of home range overlap and nonoverlap (Table 1). During the summer in both the North and South Regions, turtle surfacing was higher in overlapping areas (Table 1), whereas shark surfacing was lower (Table 1). Mean turtle surfacing was positively related with home range overlap (KDE) by region and season, whereas shark surfacing was negatively related to home range overlap by region and season (Fig. 2).

DISCUSSION

Trade-offs often exist between fitness-enhancing activities (feeding/mating) and risk avoidance, because prey movements and behaviors are often conspicuous and targeted by predators (Brown et al. 1999, Bergman et al. 2006). As an animal's landscape of fear changes

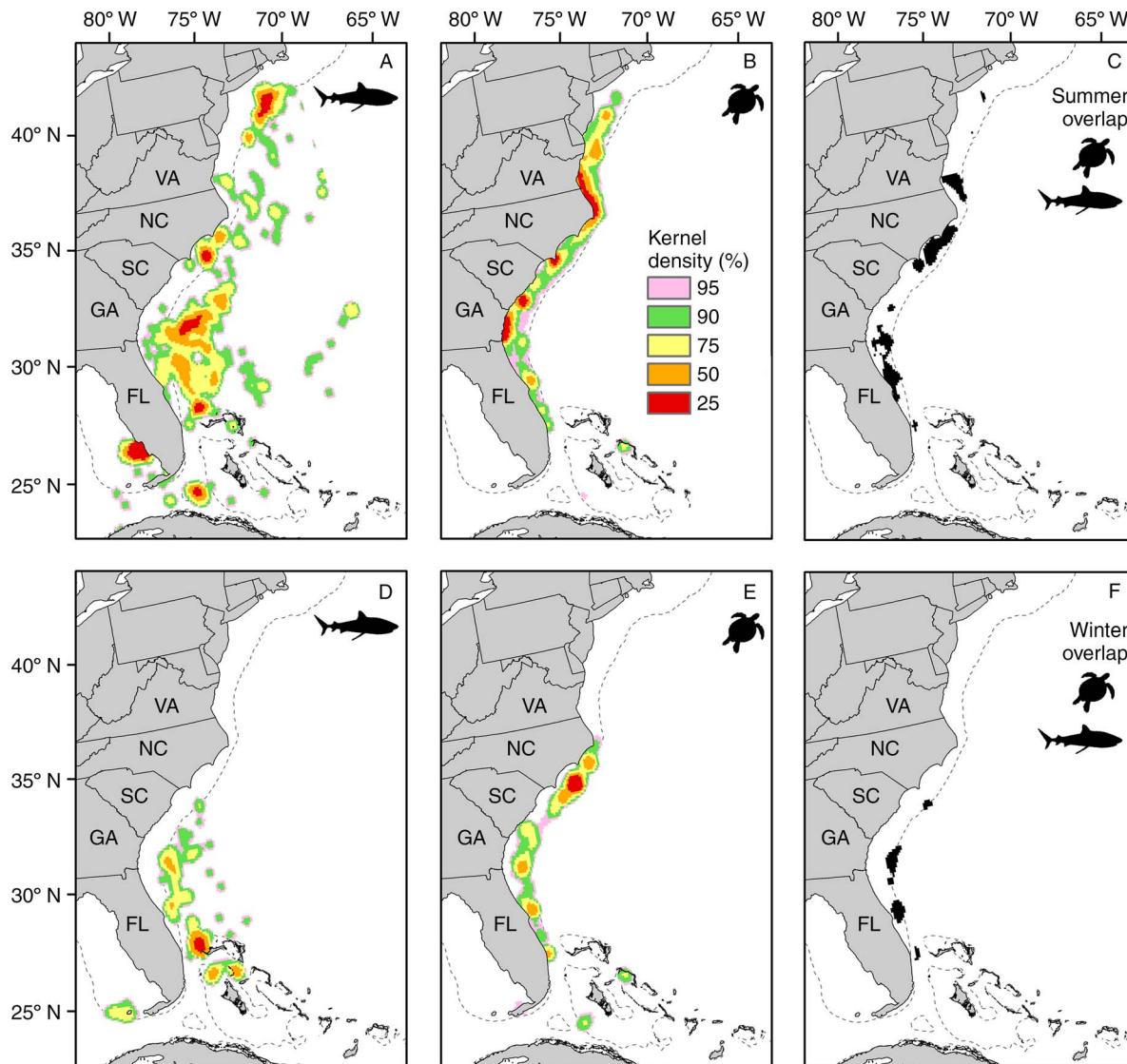


FIG. 1. Plot of kernel densities for (A, D) tiger sharks (*Galeocerdo cuvier*) and (B, E) loggerhead turtles (*Caretta caretta*), as well as (C, F) their overlap in home range (90% kernel density) for the North Atlantic Ocean in (A–C) summer and (D–F) winter. Home range overlap represents high-risk areas for turtles, but high potential predation areas for sharks.

from low to high risk of predation, prey species should alter their behavior to risk avoidance (Brown and Kotler 2004, Laundré et al. 2010). However, determining optimal strategies in light of different trade-offs may be particularly challenging for highly mobile species moving over large and dynamic spatial scales that are exposed to fluxes in predator encounter rates, physiochemical environmental conditions, and anthropogenic disturbances.

Our investigation of predator–prey relationships between an apex predator (tiger sharks) and a highly mobile prey (loggerhead turtles) across a large, dynamic seascape (Northwest Atlantic Ocean) revealed patterns that deviated from our a priori predictions based on the basic landscape of fear model. Specifically, loggerhead

turtles did not appear to exhibit shark risk avoidance behaviors by reducing surfacing under high-risk conditions (overlap in shark–turtle core home range). In contrast, tiger sharks spent more time subsurface in areas of high overlap, which might have enabled them to ambush loggerhead turtles from below and might have enhanced predation opportunity. This may be supported by the documented higher frequency of stranded loggerheads with apparent tiger shark bite wounds during the summer months in the study region, when turtle–shark core habitat overlap is highest (Foley et al. 2007).

In False Bay, South Africa, white sharks (*Carcharodon carcharias*) actively hunt Cape fur seals (*Arctocephalus pusillus pusillus*) at their rookeries (Hammerschlag

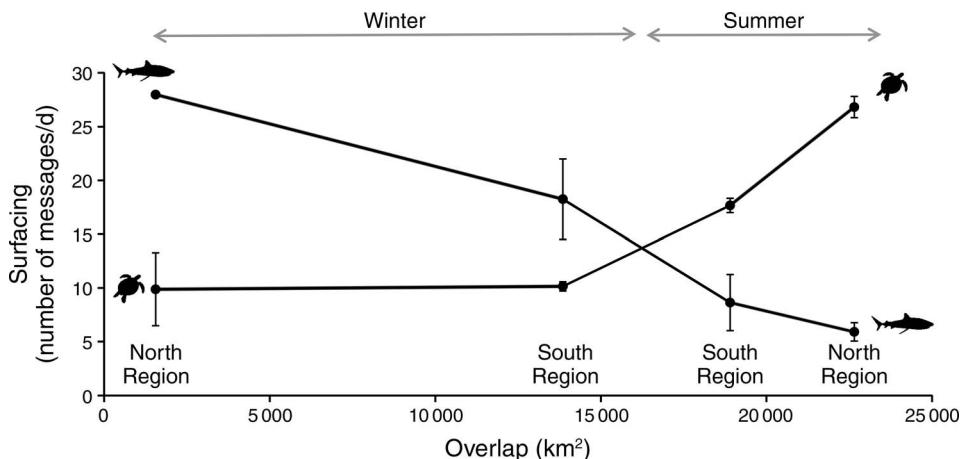


FIG. 2. Turtle and shark surfacing behavior (number of Argos messages per day, mean \pm SE) vs. turtle–shark home range overlap (90% KDE) by region and season. Values are indicated with a black circle; lines show relationships, but are not a fitted model. The winter season is December–February; the summer season is June–August.

et al. 2006). As obligate surface breathers, seals are most vulnerable to ambush attack from below when silhouetted against the surface during low-light conditions (Martin and Hammerschlag 2012). Here, white sharks increase their hunting efficiency by utilizing the bottom topography and taking advantage of differences in seal surfacing behavior to station themselves at specific locations that increase their predatory success rate, a behavior that appears to be learned (Martin et al. 2009). Spatiotemporal risk to seals from white sharks is highly predictable and seals exhibit risk avoidance, such as employing group swimming, reducing surface movements, increasing vigilance, and alternating the time and duration of foraging forays that effectively reduce frequency and the success rates of white shark attack (Martin and Hammerschlag 2012). In contrast, loggerhead turtles in the present study may not display similar risk avoidance surfacing behaviors due to a combination of both biotic and physically driven factors, to be discussed.

Temperature has a large effect on loggerhead turtle regional distribution and activity (Spotila et al. 1997).

During winter months, loggerhead turtles exhibit offshore/southerly distributions and colder temperatures may induce metabolic suppression and reduced surfacing activity (Spotila 1997, Hawkes et al. 2011). Reduced surfacing by loggerhead turtles during the winter may also, in part, lower their risk to predation from tiger sharks while they are relatively inactive. Tiger sharks are also ectothermic and the observed winter movements during this study may be driven in large part by behavioral thermoregulation. We found that tiger sharks spent more time at the surface during winter, potentially to enhance thermoregulation in warmer surface waters (Holland et al. 1992). Moreover, during the winter, tiger shark core use areas were in the Bahamas, south of loggerhead turtle core use areas, probably such that tiger sharks could take advantage of warmer waters (Hammerschlag et al. 2012a). Thus, the low turtle–shark overlap in winter could be a result of temperature primarily limiting their interactions.

During summer months, loggerhead turtles exhibit nearshore/northerly movements and increased surfacing activity during foraging and nesting (Spotila et al. 1997,

TABLE 1. Turtle surfacing and shark surfacing per day by season and region, for tiger sharks (*Galeocerdo cuvier*) and loggerhead turtles (*Caretta caretta*) in the North Atlantic Ocean.

Season	Region	Variable	Overlap	Nonoverlap	Significance
Summer	North	turtle msgs	24.0 (12.0–38.0)	18.0 (9.0–29.0)	****
		shark msgs	4.0 (2.0–9.5)	10.0 (3.0–16.0)	**
	South	turtle msgs	15.5 (8.0–25.0)	12.0 (7.0–20.0)	***
		shark msgs	4.0 (2.0–14.0)	9.0 (5.0–16.0)	ns
Winter	North	turtle msgs	7.5 (3.5–14.5)	7.0 (4.0–11.0)	ns
		shark msgs	28.0 (28.0–28.0)	15.5 (5.0–25.5)	ns
	South	turtle msgs	8.0 (5.0–13.0)	8.0 (4.0–12.0)	ns
		shark msgs	14.0 (8.0–28.0)	13.5 (9.0–23.0)	ns

Notes: Values are the median number of total messages (msgs) received by Argos per day based on location data, with interquartile range in parenthesis. Kruskal-Wallis tests were used to explore statistical differences in turtle surfacing and shark surfacing in overlapping vs. nonoverlapping home range areas. The statistical significance level between variables in overlap vs. nonoverlap areas indicated as ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; ns, nonsignificant.



PLATE 1. The tiger shark (*Galeocerdo cuvier*) is a wide-ranging apex predator distributed across temperate and tropical seas. Tiger sharks possess behavioral and anatomical specializations for hunting sea turtles. The top surface of the shark is darkly pigmented which also allows them to maintain camouflage when hunting turtles resting at the water surface. This study used long-term satellite tagging data from large tiger sharks and adult female loggerhead sea turtles (*Caretta caretta*) to examine their movements relative to one another and evaluate if turtles modify their behaviors to reduce their chances of shark attack. The results show that turtles do not alter surfacing behavior to risk avoidance but that sharks may modify their behavior in an effort to increase their chance to prey on surfacing turtles. Photo credit: N. Hammerschlag.

Hawkes et al. 2011). Increased foraging activity may lead to higher daily activity costs and thus to an increased need to surface to breathe. Increased surfacing during the summer may be further related to migration using landmarks or even a solar compass for navigation (e.g., Avens and Lohmann 2003, 2004). Turtles could also be surfacing more in the summer to enhance foraging opportunities by detecting food availability through odor cues (Endres et al. 2009). Thus, summer behaviors probably render the loggerhead turtles more vulnerable to tiger sharks due to their conspicuous activity and because neither species is constrained by temperature (Brown et al. 1999). In a similar manner, predatory water pythons (*Liasis fuscus*) migrate seasonally to feed on dusky rats (*Rattus colletti*) in Northern Australia (Madsen and Shine 1996). During the dry season, the rats live in soil crevices in the floodplain, where conditions allow them to co-occur and snakes

target the rats, but when wet-season flooding forces rats to higher ground, snakes migrate away from the area (Madsen and Shine 1996).

The absence of documented modifications in surfacing behavior during the summer by loggerhead turtles in response to shark predation risk may be due to a dilution of predator effects occurring over large spatial scales. This hypothesis is compatible with the proposition by Kauffman et al. (2010) that wide-ranging predators may not induce fear-driven behavioral alterations by prey due to a lack of consistent and predictable predation risk cues at any given spatial or temporal location. In combination, loggerhead turtle behaviors may be driven primarily by other physical (environmental conditions), biological (foraging, nesting), or anthropogenic factors (e.g., boat avoidance) that outweigh predation risk responses. Indeed, stranded loggerhead turtles with shark bites make up a small amount of

overall turtle standings (<5%) in parts of the region, with other factors, such as trauma due to propeller wounds and entanglement in fishing gear, being a far greater threat (Foley et al. 2007). Other studies have also found that influences of human disturbances on animal behavior may exceed those from natural predators. For example, a recent study by Ciuti et al. (2012) measured elk behavior in response to predators, environmental factors, and human activities (land use type, traffic, roads) in Alberta, Canada. They found that effects of human disturbance on elk behavior exceeded those of natural predators (Ciuti et al. 2012).

Another, non-mutually exclusive, hypothesis explaining our results is that the historical exploitation of both loggerhead turtles and tiger sharks in the North Atlantic over the past several decades (Lotze and Worm 2009) may have reduced their populations below ecologically functional densities that would otherwise elicit turtle antipredator behaviors in pristine areas (Heithaus et al. 2008). Such a situation appears to have occurred with wolves (*Canis lupus*) and moose (*Alces alces*) in Sweden, where human removals of wolves since the 1800s have rendered them functionally extinct (Nicholson et al. 2014). Following wolf recolonization in the 1980s, moose now face a high threat of wolf predation. However, recent satellite tracking of both species has revealed little evidence of wolf avoidance behavior by moose. This lack of antipredatory response by moose was attributed to extensive hunting pressure and only recent exposure to wolves (Nicholson et al. 2014). Such a situation may be occurring in the case of tiger sharks and turtles in the North Atlantic. This hypothesis is important from an evolutionary standpoint, given that these two species have coevolved as predators and prey for millions of years. Tiger sharks have evolved unique teeth among all elasmobranchs that permit them to specialize on turtles (Witzell 1987). The shape and structure of fossilized *Galeocerdo* sp. teeth, similar in form to those from extant tiger sharks, infers that members of this genus have been well-suited for the preferential consumption of sea turtles. Additionally, fossilized sea turtles from the Late Cretaceous period (100–66 million years ago) and Miocene deposits (23.03–5.332 mya) have been collected with the teeth of extinct tiger sharks embedded within them (Applegate 1965, Druckenmiller et al. 1993), further suggesting that the life histories of sea turtles and tiger sharks have been intertwined for some time now.

The observed inverse relationship between loggerhead turtle and tiger shark surfacing with increasing home range overlap might suggest that, for loggerhead turtles, predation risk from tiger sharks may not be a large factor in determining their distribution and behavior. However, for tiger sharks, loggerhead turtles may be important factor in driving shark movement patterns because of the tiger shark's capacity to predict and time their migration with the seasonal pulse of nesting and foraging loggerhead turtles, which represent a landscape

of opportunity for tiger sharks (Laundré et al. 2010). Indeed, studies of tiger shark movements in Hawaii have shown that they undertake long-term, reciprocal migrations between distant foraging locations indicative of using detailed cognitive maps of resource availability, such as fledgling albatross (*Phoebastria* spp.) prey (Meyer et al. 2010).

There are numerous predictions that could be derived using the landscape of fear framework that we did not investigate. For instance, exposure to predation may lead to increased vigilance by prey species and to higher levels of stress. These may necessitate higher resting metabolic rates, which may require higher rates of energy intake (Brown and Kotler 2004) and longer surface intervals due to an increased demand for oxygen. In this study, we were also unable to determine the depth that tiger sharks and loggerhead turtles were occupying within the water column when subsurface. However, loggerhead turtles should avoid being near the surface (even if underwater) in high-risk areas to reduce vulnerability to tiger shark attack from below and increase escape probability (Heithaus and Frid 2003, Heithaus et al. 2008). Based on Snell's Law, the higher the loggerhead turtle is in the water column (and the deeper the tiger shark), the more distinctly the loggerhead turtles are backlit at the surface (discussed in Martin and Hammerschlag 2012). In contrast, downwelling light is dimmed and scattered, rendering the tiger shark's dark dorsum difficult to discriminate by the turtle when sharks are hunting at depth below the turtle. It is also worth noting that loggerhead turtles probably employ antipredatory strategies when they are confronted by a tiger shark. Such responses could include rapid dives or tight circling to outmaneuver sharks and/or positioning their carapace toward the shark to prevent being grasped (Heithaus et al. 2002).

It is unfeasible to experimentally test our predictions through manipulations, given the nature of our system and the conservation status and highly migratory behavior of the animals involved. Accordingly, our conclusions are based on correlation, not causation. Other studies involving large, mobile, marine species have tested predation risk effects on prey habitat use by undertaking empirical observations in the wild when predators are present or absent (e.g., Heithaus and Dill 2002). We also combined our approach with satellite tagging that has recently been used as a tool to assess predation risk effects of marine predatory sharks on behaviors of mobile prey fishes (e.g., Fitzpatrick et al. 2012, Hammerschlag et al. 2012b). We believe that combining the former two methodologies provides a useful approach to evaluate predator–prey interactions involving marine species across large spatial scales. Given the inherent challenges of studying and testing ecological theories involving highly migratory marine species, our approach and conclusions may be applicable to the study and understanding of other predator–prey systems sharing common features.

In summary, the landscape of fear model has recently been proposed as a possible unifying theme in ecology, also providing a “missing link” in understanding the population dynamics of species from a wide variety of taxa and ecosystems (Laundré et al. 2014). The present study is among the first to empirically evaluate the landscape of fear model across large (tens to hundreds of thousands of square kilometers) and dynamic seascapes involving highly mobile predators and prey. These results are important, given that it is generally accepted and ubiquitously cited that large predators are ecologically important and capable of indirectly driving trophic cascades through predation risk effects on prey.

Predation by tiger sharks on loggerhead turtles may play an important role in regulating turtle populations (Simpfendorfer et al. 2001); risk from tiger sharks can alter the foraging behaviors of other populations of sea turtles in pristine systems (Burkholder et al. 2013), and both may independently and synergistically impact ecosystem function through trophic cascades (Heithaus et al. 2008). Therefore, our results have conservation, ecological, or evolutionary implications if human-induced tiger shark or turtle population declines and/or habitat disturbances have altered predator–prey interactions between loggerhead turtles and sharks in our study system. Accordingly, we suggest that further studies of this kind are warranted, given increased rapid habitat modifications, biodiversity loss, widespread declines of top predators and consumers, and increased climate change impacts on marine megafauna (Worm et al. 2006, Halpern et al. 2008, Estes et al. 2011). Our approach and findings may provide a mechanism for contextualizing and investigating other predator–prey systems across wide spatial scales involving highly mobile species.

ACKNOWLEDGMENTS

Turtle tracking was funded by: the Bald Head Island Conservancy, the British Chelonia Group, Juanita Roushdy, Natural Environmental Research Council, WAVE Foundation/Newport Aquarium Cincinnati, PADI project AWARE, SEATURTLE.ORG, and the Whitener Foundation (NC); an Endangered Species Act Section 6 Cooperative Agreement with NOAA Fisheries and the Grays Reef National Marine Sanctuary (South Carolina and Georgia). Shark work was funded by the Batchelor Foundation and the Dinsey Conservation Fund. We are grateful to A. Gallagher, D. Shiffman, and the interns and staff of the University of Miami's Marine Conservation Program for assistance. B. J. Godley and M. J. Witt received funding from NERC. We thank J. F. Bruno and anonymous reviewers for valuable feedback that greatly strengthened the manuscript.

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