Limnol. Oceanogr., 54(2), 2009, 472–482
© 2009, by the American Society of Limnology and Oceanography, Inc.

Physical factors influencing the distribution of a top predator in a subtropical oligotrophic estuary

Michael R. Heithaus[1] *and Bryan K. Delius*
Department of Biological Sciences, Florida International University, 3000 NE 151 St., North Miami, Florida 33181

Aaron J. Wirsing
Department of Biological Sciences, Florida International University, 3000 NE 151 St., North Miami, Florida 33181; College of Forest Resources, University of Washington, Box 3052100, Seattle, Washington 98195

Meagan M. Dunphy-Daly
Department of Biological Sciences, Florida International University, 3000 NE 151 St., North Miami, Florida 33181

Abstract

We used longline fishing to determine the effects of distance from the ocean, season, and short-term variation in abiotic conditions on the abundance of juvenile bull sharks (*Carcharhinus leucas*) in an estuary of the Florida Everglades, U.S.A. Logistic regression revealed that young-of-the-year sharks were concentrated at a protected site 20 km upstream and were present in greater abundance when dissolved oxygen (DO) levels were high. For older juvenile sharks (age 1+), DO levels had the greatest influence on catch probabilities followed by distance from the ocean; they were most likely to be caught at sites with >3.5 mg L^{-1} DO and on the main branch of the river 20 km upstream. Salinity had a relatively small effect on catch rates and there were no seasonal shifts in shark distribution. Our results highlight the importance of considering DO as a possible driver of top predator distributions in estuaries, even in the absence of hypoxia. In Everglades estuaries hydrological drivers that affect DO levels (e.g., groundwater discharge, modification of primary productivity through nutrient fluxes) will be important in determining shark distributions, and the effects of planned ecosystem restoration efforts on bull sharks will not simply be mediated by changing salinity regimes and the location of the oligohaline zone. More generally, variation in DO levels could structure the nature and spatiotemporal pattern of top predator effects in the coastal Everglades, and other tropical and subtropical estuaries, because of interspecific variation in reliance on DO within the top predator guild.

Estuarine systems are vulnerable to human effects including eutrophication, habitat alteration and destruction, degradation of water quality, increased hypoxia, and changes to freshwater inputs (Kennish 2002). In order to predict the consequences of anthropogenic modifications for estuaries and to assess the likely effects of management alternatives, it is necessary to understand how variation in physical factors affects the distribution and abundance of organisms within them. Of particular interest is how large predators will respond to variation in physical conditions because these species can help to structure communities (Heithaus et al. 2008) and are often of commercial or recreational importance.

Studies of the movements and distribution of predators in estuarine systems have focused primarily on the most obvious changes in physical factors—salinity and water temperature. More recently, however, the role of chronic and/or acute hypoxic events that lead to mass movements or mortality of individuals have received greater attention (Eby and Crowder 2002; Baird et al. 2004; Altieri and Witman 2006). Most of these studies on the role of dissolved oxygen levels in driving consumer distributions and mortality patterns have been conducted in temperate areas where enhanced primary productivity due to eutrophication combined with stratification of the water column can lead to hypoxia that can persist for considerable periods. For example, in the Neuse River Estuary of North Carolina, U.S.A., small mobile consumers (e.g., crabs, small teleosts) vary considerably in their responses to chronic and episodic hypoxia and prolonged hypoxic events may lead to enhanced interspecific competition or predator–prey interactions in shallow oxygenated waters (Eby and Crowder 2002; Bell and Eggleston 2005) and ultimately to a reduction in energy transfer to higher trophic levels (Baird et al. 2004). However, species that can tolerate low levels of dissolved oxygen may experience reduced predation risk from more oxygen-sensitive predators (Eby and Crowder 2002; Altieri and Witman 2006). Less appreciated is the potential for variation in dissolved oxygen levels over short temporal and small spatial scales

[1] Corresponding author (heithaus@fiu.edu).

Acknowledgments

Funding for this project was provided by National Science Foundation Grants DBI0620409 and DEB9910514 and Florida International University's Marine Sciences Program. We thank the many volunteers who assisted with shark fishing, especially Derek Burkholder and Richard Chang. Thanks also to Joel Trexler and Dan Childers who provided an introduction to the Everglades estuaries, funding, and logistical support for this project. Research was conducted under Everglades National Park permits EVER-2007-SCI-0025 and EVER-2005-SCI-0030 and Florida International University Institutional Animal Care and Use Committee authorizations.

to structure the distribution of large consumers, especially in subtropical and tropical estuaries that are less prone to the seasonal hypoxia characteristic of temperate estuaries.

The subtropical estuaries of the coastal Everglades, Florida, U.S.A., which constitute the largest mangrove ecosystem in the Western Hemisphere, are human-dominated systems that exhibit marked temporal and spatial variation in physical factors including dissolved oxygen levels. Most obviously, there is distinct seasonal variation in precipitation and freshwater delivery to these estuaries. Although the timing and magnitude of wet and dry seasons within the Everglades vary interannually, salinities tend to be lowest from December to May and highest from June to November (Childers et al. 2006). The overall delivery of freshwater to the estuaries, however, is low compared to historical levels due to the construction of water management canals and levees over the past 100 yr and the diversion of much of the freshwater that historically flowed to the Everglades (Davis et al. 2005). This modification to the system's hydrology has almost certainly had major effects on mobile predators in the coastal estuaries of the Everglades, as will the planned attempts to restore water flow to a more natural level (Comprehensive Everglades Restoration Plan [CERP] 1999). Therefore, studies of the factors influencing the distribution and abundance of top estuarine predators are important for predicting how ecosystem engineering will influence their use of the Everglades estuaries.

Juvenile bull sharks (*Carcharhinus leucas*) are a euryhaline upper trophic-level predator in many estuaries of the subtropics including those of the Everglades (Pillans and Franklin 2004; Pillans et al. 2005; Wiley and Simpfendorfer 2007). Thus, studies of the factors influencing the distribution and abundance of bull sharks are potentially important for understanding the dynamics of Everglades estuaries and predicting the consequences of proposed ecosystem management strategies. The objective of this study was to determine the factors influencing the distribution and abundance of juvenile bull sharks in the estuary of the Shark River Slough of Everglades National Park, and in particular to evaluate the influence of temporal and spatial variation in abiotic factors (water temperature, salinity, dissolved oxygen, distance from the Gulf of Mexico).

Methods

Study site—Juvenile bull sharks are one of the largest bodied predators in the Shark River Estuary (Loftus 2000; Wiley and Simpfendorfer 2007), but other large predators including American alligators (*Alligator mississippiensis*), tarpon (*Megalops atlanticus*), snook (*Centropomus undecimalis*), and goliath grouper (*Epinephelus itajara*) also are present in portions of the estuary (Loftus 2000; Wiley and Simpfendorfer 2007). Large sharks that could be a predation threat to juvenile bull sharks are present in the Gulf of Mexico and may move short distances into the river (Torres et al. 2006; Wiley and Simpfendorfer 2007).

We defined six study sites along the Shark River, Everglades National Park, Florida, U.S.A. (Fig. 1) to represent a gradient of environmental conditions and distances from the Gulf of Mexico (Table 1). Sampling at the three sites farthest downstream (mouth, SRS4, and SRS5) occurred near long-term environmental sampling platforms maintained by the Florida Coastal Everglades long-term ecological research program (www.fcelter.fiu.edu). Sampling near the mouth of the estuary and at SRS5 occurred in broad ($\sim$50–100 m wide) mangrove-lined channels with water depths of $\sim$1.2–3.0 m. SRS4 and Otter Creek were located at upstream portions of a broad open area, Tarpon Bay (Fig. 1). Sampling in Tarpon Bay occurred where water depths ranged between 1.5 m and 2.5 m in both channels (Otter Creek and SRS4) and more open waters where several branches of the slough converge (SRS4). Sampling in upstream sites occurred in channels similar to those of SRS5 and the mouth, but these channels often were narrower ($\sim$20–50-m wide) and rarely exceeded 2 m depth, but were at least 1.2 m deep.

Field methods—From May 2005 to February 2008 we sampled bull sharks using a $\sim$500-m longline fitted with 42 $\pm$ 6.7 SE gangions. Each gangion consisted of a heavy-duty clip with swivel attached to $\sim$2 m of 400-kg monofilament line. A second swivel was positioned in the middle of the line, which terminated in a 12/0–15/0 Mustad tuna circle hook with offset point that was baited with mullet (*Mugil* sp.). Pilot fishing efforts found no effect of hook size on size of sharks captured or shark catch probabilities. Lines were set between dawn and dusk and were allowed to soak for 1 h after the last gangion was deployed before being retrieved. After the longline was set, we recorded environmental conditions including water temperature, salinity, and dissolved oxygen using a YSI85 at depth of 1–1.5 m.

Upon retrieval, we recorded the presence or absence of bait at every hook. Sharks were brought alongside the boat, sexed based on the presence or absence of claspers, measured (precaudal, fork, total, and stretched total lengths) to the nearest centimeter, tagged using a plastic roto tag affixed through the first dorsal fin, freed from the hook, and then released.

Data analysis—Because shark responses to environmental conditions may vary with age (e.g., Simpfendorfer et al. 2005) we analyzed data for individuals $<$1 yr old (young of the year [YOY]) and sharks $>$1 yr old (juveniles) separately. Consistent with previous studies (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008), we considered all individuals $<$96 cm stretched total length (STL) as young of the year. For both age classes, we used logistic regression to determine the factors influencing the probability of capturing at least one bull shark on a longline set and the probability of capturing a bull shark on an individual hook. By analyzing these two response variables, we were able to elucidate the factors influencing the presence (or absence) of sharks (per longline analysis) and the abundance of sharks (per hook analysis). Using only the per hook analysis was not appropriate because each hook does not represent a truly independent sample of shark abundance. Note also that we could not use catch rates of sharks per longline set as a dependent variable because they could not be transformed to meet the assumptions of available analytical procedures.

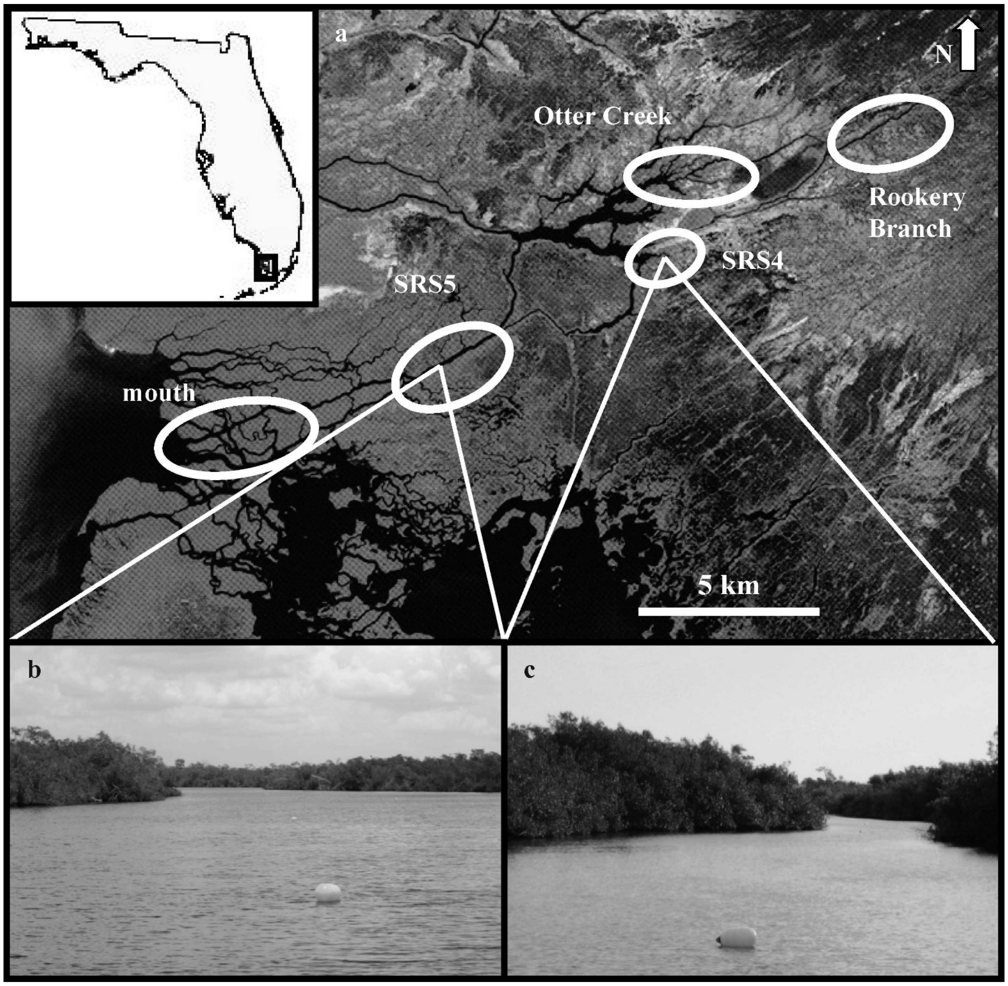

Fig. 1. The study was conducted in the Shark River Estuary of Everglades National Park, U.S.A. Longlines were set within spatially distinct sites (ovals) from the mouth of the estuary to 30 km upstream. (b) Sampling occurred in broad channels at the mouth and SRS5 and in slightly more open waters of Tarpon Bay. (c) Channels feeding into Tarpon Bay and in Rookery Branch generally were narrower than those located further downstream.

For both sets of logistic regressions (per longline and per hook) we created two models. The first model tested the effects of season (wet: Jun–Nov, dry: Dec–May), site, and their interaction to determine whether bull shark presence and abundance fluctuated with correlated seasonal changes in mean environmental factors (Fig. 2) and whether this led to seasonal changes in the distribution of sharks (site × season interaction). For example, if sharks were shifting their use of the estuary to stay within optimal mean salinity ranges or responding to seasonally available prey at particular sites, then an interaction of site and season would be expected. Site was used in all analyses, rather than the continuous variable of distance from the Gulf of Mexico, for ease of data presentation. Exploratory analyses showed a significant nonlinear effect of distance from the estuary mouth on catch rates. Treating distance as a continuous variable with a polynomial function in full models did not affect the results of analyses or the relative

Table 1. Physical characteristics and shark captures during sampling at five sites along the Shark River Estuary. Data presented are means ± SE (min–max).

Site	Sets	Sharks	Distance upstream (km)	Temperature (°C)	Salinity	Dissolved oxygen (mg L^{-1})
Mouth	20	6	2.3±0.2(1.0–3.9)	26.9±0.8(20.8–32.1)	27.2±1.4(15.9–35.2)	3.5±0.2(2.0–4.9)
SRS5	40	16	9.0±0.3(5.6–11.8)	25.7±0.6(17.3–32.4)	12.5±1.2(1.6–27.7)	3.9±0.2(1.8–6.7)
SRS4	45	32	18.5±0.08(17.6–20.6)	25.9±0.6(18.1–32.8)	6.1±0.9(0.3–20.8)	4.2±0.2(1.3–7.0)
Otter Creek	28	22	20.8±0.07(20.2–21.8)	25.6±0.4(19.8–28.9)	3.2±0.9(0.3–16.1)	3.6±0.3(1.9–6.8)
RB*	36	8	26.0±0.3(23.4–29.6)	26.4±0.5(19.3–29.6)	1.6±0.4(0.2–10.4)	3.2±0.2(1.1–8.2)

* RB = Rookery Branch.

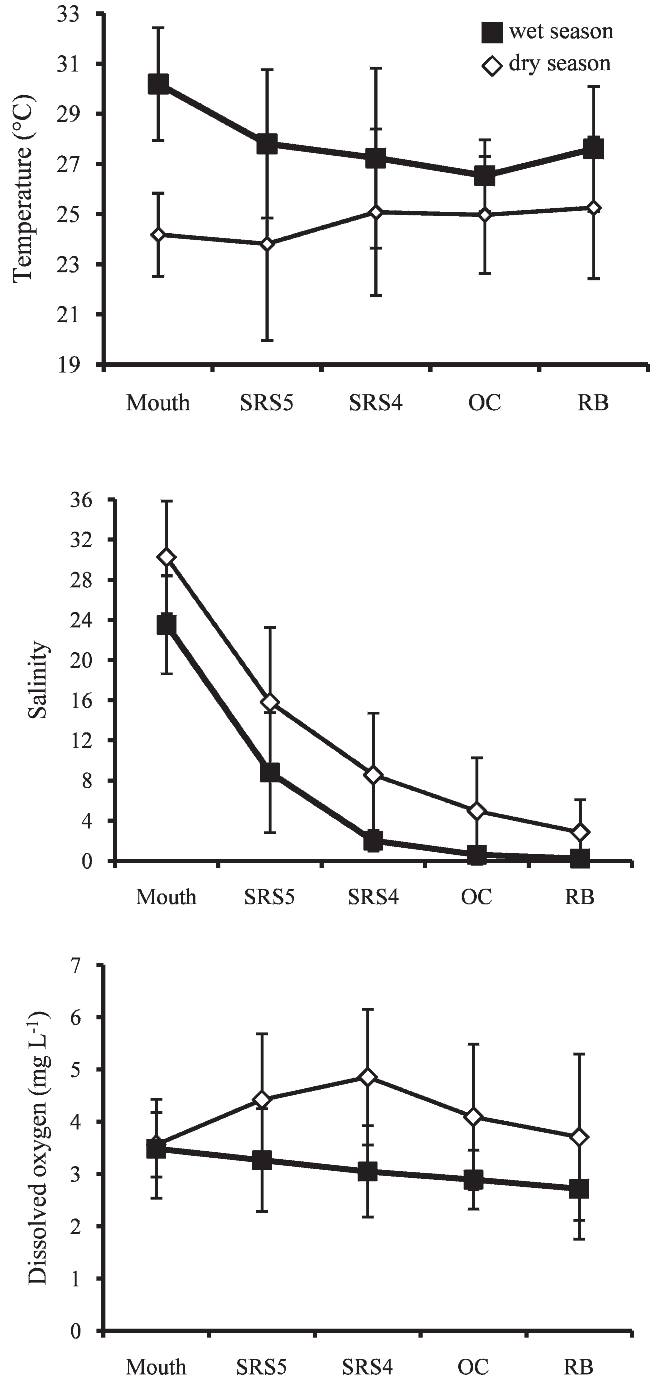

Fig. 2. Spatial and seasonal variation in physical factors measured during longline sampling. Open diamonds are the dry season (Dec–May) and filled squares are the wet season (Jun–Nov). Error bars are SD. *See* Table 1 for ranges of observations at each site.

effect sizes of individual factors. We also included number of hooks, probability of bait loss, and time of day in analyses. Nonsignificant interactions and main effects ($p >$ 0.10) were removed through backwards-stepping. Relative effect sizes were calculated as likelihood ratios (i.e., twice the difference between the log likelihood of the final full model and that of the reduced model excluding the factor of interest; Haining 1990).

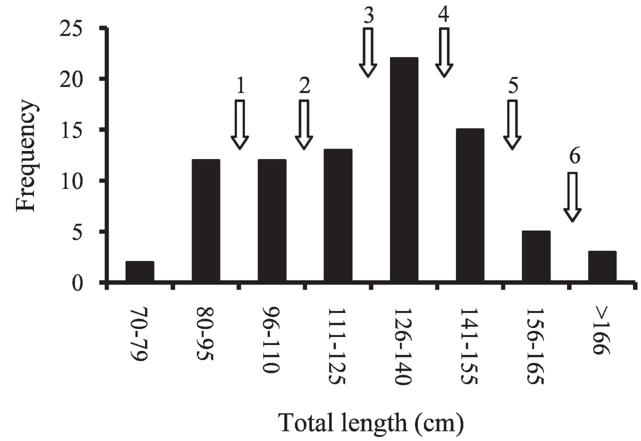

Fig. 3. Size distribution of bull sharks captured in the Shark River Estuary, Everglades National Park, U.S.A. Numbered arrows indicate the approximate total length at which sharks reach a given age. Length-at-age data estimates are based on size at age 1 data for bull sharks in southwestern Florida nurseries (Heupel and Simpfendorfer 2008) and growth rates of bull sharks in the Gulf of Mexico (Branstetter and Stiles 1987).

The second set of logistic regressions tested the effects of season and site as well as environmental conditions (water temperature, salinity, dissolved oxygen level) at the time of a longline set, and all plausible interactions. This set of models allowed us to ask whether catches of sharks were influenced by the conditions at the time of sets, rather than average seasonal conditions that were tested by the first set of models described above. Also, we included the factors time of day and probability of bait loss and models were backwards-stepped as above. To further explore relationships between environmental factors and shark presence we conducted a post hoc classification tree analysis in JMP_IN 6.0.0 using a maximize split significance criterion for tree-building.

Spatial variation in shark sizes was investigated using analysis of variance. Shark lengths were log-transformed to normalize data.

Results

We captured 84 bull sharks on 7177 hooks set on 169 longlines. Sharks were captured from the mouth of the Shark River to more than 26 km upstream, during all months of sampling, in salinities from 0.2 to 33.4, and in water temperatures between 17.3°C and 31.3°C. Sharks ranged from 72 cm to 190 cm total length (mean = 124 ± 24.8 cm SD; Fig. 3). Fourteen individuals were estimated to be <1 yr old and 70 individuals were older. Based on the absence of calcified claspers in males and size at maturity of female sharks in the Gulf of Mexico (Clark and von Schmidt 1965), all sharks were juveniles. The sex ratio was ~1 : 1 (χ^2 = 0.60, p = 0.44). There was significant spatial variation in the sizes of bull sharks ($F_{4,82}$ =11.8, $p <$ 0.0001), with the smallest sharks found at SRS4 (Fig. 4). Three sharks were recaptured over the course of the study. Two neonates (determined by the presence of an umbilical scar) were captured, and subsequently recaptured, at SRS4

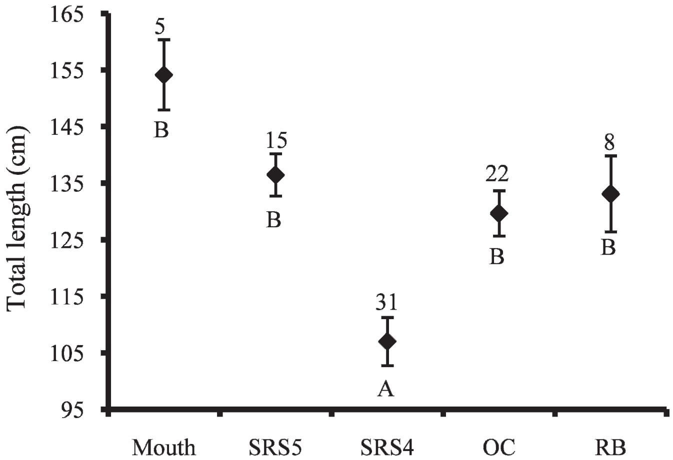

Fig. 4. Spatial variation in bull shark total lengths. Numbers above bars indicate sample sizes. Letters below bars indicate sites that differ significantly based on post hoc Tukey's tests.

after 7 days and 378 days. The third individual was captured as a 1-yr-old at SRS4, recaptured 748 days later in Rookery Branch, and then recaptured after another 253 days back at SRS4.

Analysis of the effect of season and site on the probability of capturing at least one shark revealed a significant effect only of site (Wald $\chi^2 = 30.5$, $p = 0.0001$) for young of the year (YOY). Predicted capture probabilities were highest at SRS4 (0.2 per longline set) and extremely low at all other sites. Only one YOY was captured outside of SRS4, at Otter Creek. The probability of capturing an older juvenile (age 1+) was influenced by site (Wald $\chi^2 = 10.6$, $p = 0.03$). Capture probabilities were highest at Otter Creek (0.5) and lowest upstream (0.13). There also was a trend toward higher estimated capture probabilities in the dry season (0.33) than the wet season (0.21; Wald $\chi^2 = 3.4$, $p = 0.06$). There was not a seasonal shift in the distributions of sharks of either age class (i.e., the interaction was eliminated from final models).

Analysis of all factors showed that the probability of catching at least one YOY on a longline was influenced by site and dissolved oxygen level (Table 2). Despite wide fluctuations in salinity within and among seasons at SRS4 (Table 1; Fig. 2), salinity was not a significant predictor of catches (Wald $\chi^2 = 0.07$, $p = 0.78$). Relative effect sizes show that dissolved oxygen had a strong effect on captures of YOY at SRS4, with no sharks captured below 2.9 mg L^{-1} and high catch probabilities above 5.95 mg L^{-1} (Fig. 5). The probability of catching an age 1+ shark on a longline was influenced by site, salinity, and dissolved oxygen (Table 2). In general, capture probabilities increased with increasing salinity, were highest at Otter Creek, and increased with increasing dissolved oxygen concentration. Relative effect sizes show that salinity had the lowest effect on catch probabilities and dissolved oxygen the highest (Table 2; Fig. 6). Indeed, classification tree analysis based on site, salinity, and dissolved oxygen (Fig. 7) revealed no splits in the top 10 based on salinity. The primary split in capture probabilities occurred at dissolved oxygen concentrations of 3.5 mg L^{-1}, with 40%

Table 2. Summary of logistic regression for predicting the probability of capturing at least one bull shark on a longline set ($n = 169$ for final models). Only factors with $p < 0.10$ are included.

Factor	df	Wald χ^2	P	Relative effect size
<1 yr old*				
Site	4	18.4	0.001	2.3
Dissolved oxygen	1	4.1	0.04	9.1
>1 yr old†				
Site	4	15.1	0.004	7.6
Salinity	1	4.8	0.03	2.4
Dissolved oxygen	1	10.6	0.001	13.1

* Whole model (<1 yr) − log likelihood = 24.5; Wald $\chi^2 = 25.8$, $p < 0.0001$; $R^2 = 0.34$, df = 5.
† Whole model (>1 yr) − log likelihood = 79.9; Wald $\chi^2 = 26.4$, $p = 0.0002$; $R^2 = 0.14$, df = 6.

of longline sets made above 3.5 mg L^{-1} capturing age 1+ sharks compared to 16% of those deployed when below 3.5 mg L^{-1}. The next two splits occurred within these dissolved oxygen concentration categories and showed higher catch rates at Otter Creek than all other sites. Other splits within the higher dissolved oxygen category differentiated SRS5 from the Mouth, SRS4, and Rookery Branch, then catches within SRS5 into groups based on dissolved oxygen levels above 4.32 mg L^{-1} (57% capture rate) and between 3.5 mg L^{-1} and 4.32 mg L^{-1} (25% capture rate). Also, captures at sites other than Otter Creek in <3.5 mg L^{-1} DO split into sets in 2.2–3.5 mg L^{-1} (15% capture rate) and those below 2.2 mg L^{-1} (0%).

In the analysis of seasonal and spatial variation in the probability of capturing a shark on an individual hook, the probability of capturing YOY was only influenced by site with a peak at SRS4 (Wald $\chi^2 = 30.5$, $p < 0.0001$). There was no seasonal shift in the distribution of YOY. For age 1+ sharks, the probability of capturing a shark on an individual hook was influenced by both season (Wald $\chi^2 = 6.3$, $p = 0.01$) and site (Wald $\chi^2 = 10.1$, $p = 0.04$), but there were no seasonal shifts in distribution. Predicted capture probabilities per hook were higher in the dry season than the wet season and were highest at Otter Creek and lowest at Rookery Branch (Fig. 8).

In the full model, the catch probability of YOY bull sharks per hook was influenced significantly only by site. There was a nonsignificant trend towards higher catches with higher dissolved oxygen (Table 3). The probability of catching an age 1+ shark on an individual hook was influenced by site, salinity, and dissolved oxygen (Table 3), with dissolved oxygen having the greatest effect (highest relative effect size) followed by site and then salinity. Sharks were more likely to be captured at Otter Creek and predicted capture probabilities within all sites were positively correlated with increasing dissolved oxygen concentration and higher salinities (Fig. 9).

Discussion

Based on our recapture rates, the size structure of the population we assessed, the size at birth for bull sharks in

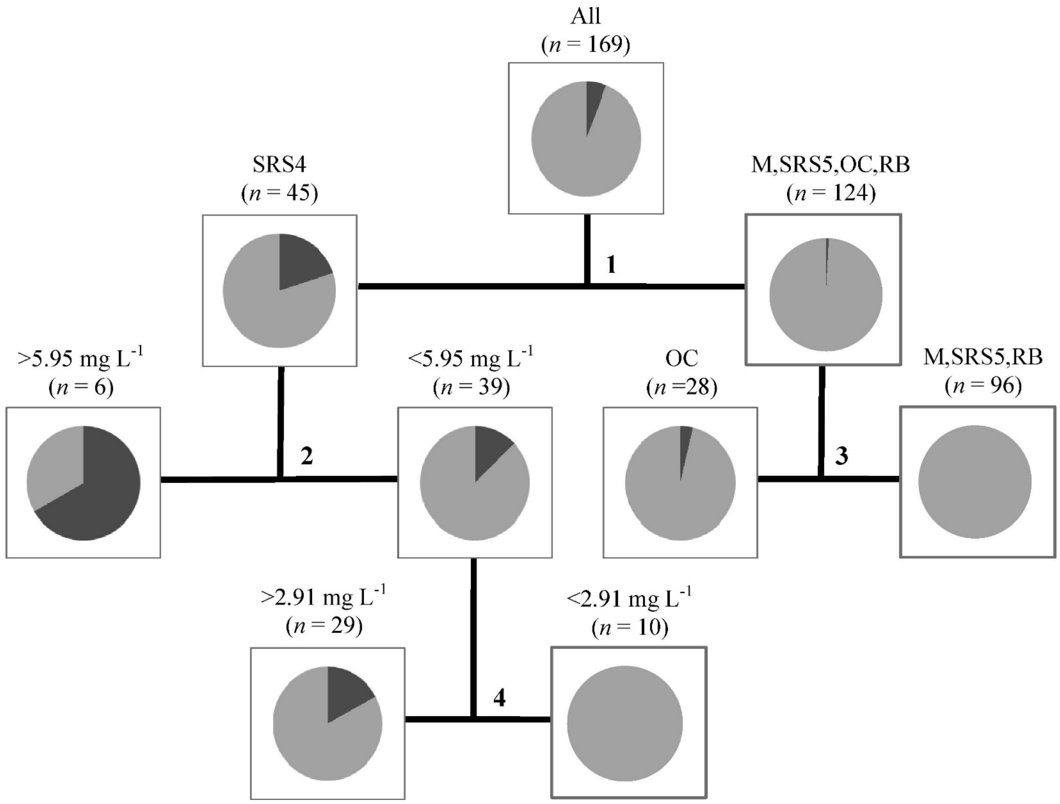

Fig. 5. Classification tree for the probability of capturing at least one young of the year (YOY) bull shark on a longline set based on the factors site, salinity, and dissolved oxygen level. M = mouth, RB = Rookery Branch. Dark shading indicates the proportion of sets that captured at least one shark and light shading indicates sets where no sharks were captured. Numbers beside vertical lines indicate the order of splitting.

Southern Florida (e.g., Simpfendorfer et al. 2005), and published growth rates of bull sharks in the Gulf of Mexico (Branstetter and Stiles 1987), it appears that bull sharks use the Shark River Estuary for at least their first three or four years. The residence times of individual sharks, however, are unclear. The low recapture rate of sharks tagged and recaptured within the estuary (3 of 80 individuals) could be indicative of a large population size within the Shark River Estuary and/or high rates of dispersal to and from the coastal waters of Everglades National Park and beyond (Wiley and Simfendorfer 2007).

Bull shark use of the Shark River Estuary varies with body size and physical characteristics of the environment. As has been found in other nurseries (e.g., the Caloosahatchee River, Florida; Simpfendorfer et al. 2005), the smallest sharks were concentrated at one location. In the case of the Shark River Estuary this occurs at SRS4. Indeed, only one YOY was captured away from SRS4 despite similar salinity, temperature, and dissolved oxygen conditions being present at other locations at least seasonally. In contrast, age 1+ bull shark catch rates were relatively low at SRS4 and peaked at Otter Creek. Such size segregation within immature animals could be driven by neonates avoiding potentially cannibalistic older juveniles (Simpendorfer et al. 2005). Alternatively, younger sharks may congregate in the broad shallow waters at SRS4 to avoid higher velocity currents that occur at sites within main channels (Heupel and Simpfendorfer 2008).

Catch probabilities of age 1+ bull sharks were influenced by site, dissolved oxygen, and salinity. Relative effect sizes suggest that dissolved oxygen is a greater predictor of shark abundance than either site or salinity. The probability of capturing age 1+ sharks peaked at Otter Creek and increased equally at all sites in the dry season when salinities are higher (i.e., more sharks were in the system but the relative abundance of sharks remained similar among sites). On shorter time scales, sharks appear to respond heavily to dissolved oxygen levels. Indeed, the primary spilt in our classification tree occurred at 3.5 mg L^{-1} with further splits based on dissolved oxygen levels occurring after splits based on sites.

Previous studies of juvenile bull sharks suggest that they move up- and downstream to remain within optimal salinity and temperature ranges and that YOY are more heavily influenced by salinity than older juveniles (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008). For example, in the Caloosahatchee River of southwest Florida catch rates of YOY were highest between 7.05‰ and 17.45‰. In contrast, we found that the abundance of both YOY and older (age 1+) juvenile bull sharks was more heavily influenced by site and dissolved oxygen levels and that salinity was not a significant predictor of YOY catches. Indeed, half of the YOY captures at SRS4 occurred outside of conditions between 7.05‰ and 17.45‰. If bull sharks in the Shark River Estuary were moving to stay within an optimal temperature and salinity

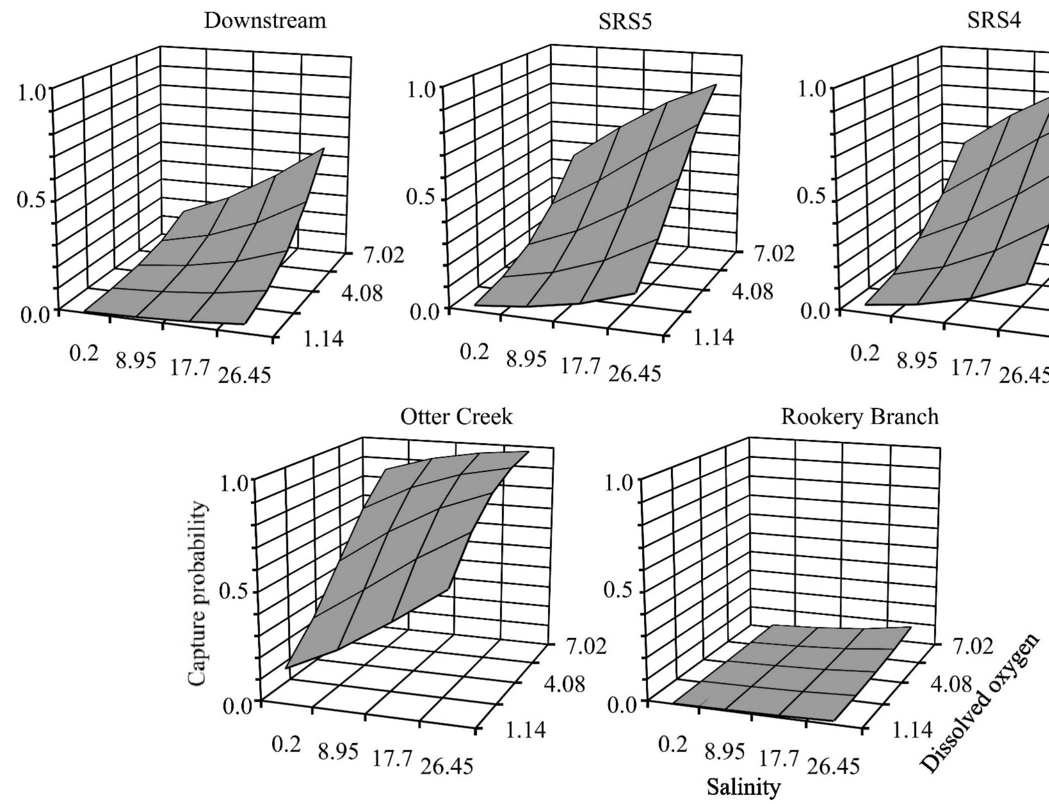

Fig. 6. Effects of site, dissolved oxygen, and salinity on the predicted probability of capturing at least one juvenile (>1 yr old) bull shark on a longline set. Note that predicted capture probabilities are displayed for conditions that are beyond those actually measured within some sites.

range over short or long temporal periods we would have expected an interaction between season and site; such an interaction was not observed for either age class. Although salinity was a significant factor for catches of older juvenile sharks, there did not appear to be an optimal salinity range because catches were predicted to be higher as salinity increased at all sites. This result may, in fact, be driven more by seasonal increases in older juvenile sharks in the system than by salinity fluctuations.

Because previous studies of bull sharks did not measure dissolved oxygen levels, which co-vary to some degree with temperature and salinity, it is possible that bull shark movements in other estuaries are influenced by dissolved oxygen levels as well. More likely, there is real spatial variation in the physical factors influencing shark abundance that is driven by major differences in the physical structure and hydrological dynamics of the estuaries. For example, unlike the Shark River Estuary, the estuarine zone of the Caloosahatchee River consists of one channel that is very wide (often >1 km) and is characterized by extreme coastal development. Also, water management practices have greatly increased freshwater delivery to the Caloosahatchee Estuary that causes acute high-volume inputs of freshwater during the wet season. Therefore, bull sharks in this estuary may have to move to avoid the physiological costs of rapid change in salinities (Pillans et al. 2006; Heupel and Simpfendorfer 2008). In contrast, the Shark River Estuary receives less extreme pulses of freshwater and sharks are unlikely to experience such rapid changes in salinity or water temperature.

Food resources appear to play a minor role in determining fine-scale bull shark distributions in the Shark River Estuary. During the dry season there is an influx of potential bull shark prey (both large and small freshwater fishes) into the narrow mangrove-lined creeks in upstream regions (e.g., our Rookery Branch site) due to dry-down in the upstream marshes and resulting loss of available habitat (Rehage and Loftus 2007). Although there is an increase in the abundance of older juvenile bull sharks in the estuary during the dry season, the distribution of sharks differs from that predicted by temporal and spatial variation in potential prey. If bull sharks were distributing themselves relative to prey availability, there should have been an upstream increase in catch probabilities of bull sharks during the dry season when freshwater prey is most available. Shark distributions were, however, temporally stable and, during the dry season, sharks did not make great use of Rookery Branch where prey abundance would have been highest. Furthermore, analyses of stable isotopic signatures of bull sharks captured in the estuary do not suggest heavy reliance on freshwater prey (Delius 2007). Why bull sharks do not take greater advantage of potential prey upstream, especially during dry-down events, is still unclear, especially because dissolved oxygen levels are relatively high upstream at this time of year and salinities are well within the physiological tolerances of bull sharks (Pillans et al. 2005). Fine-scale measurement of

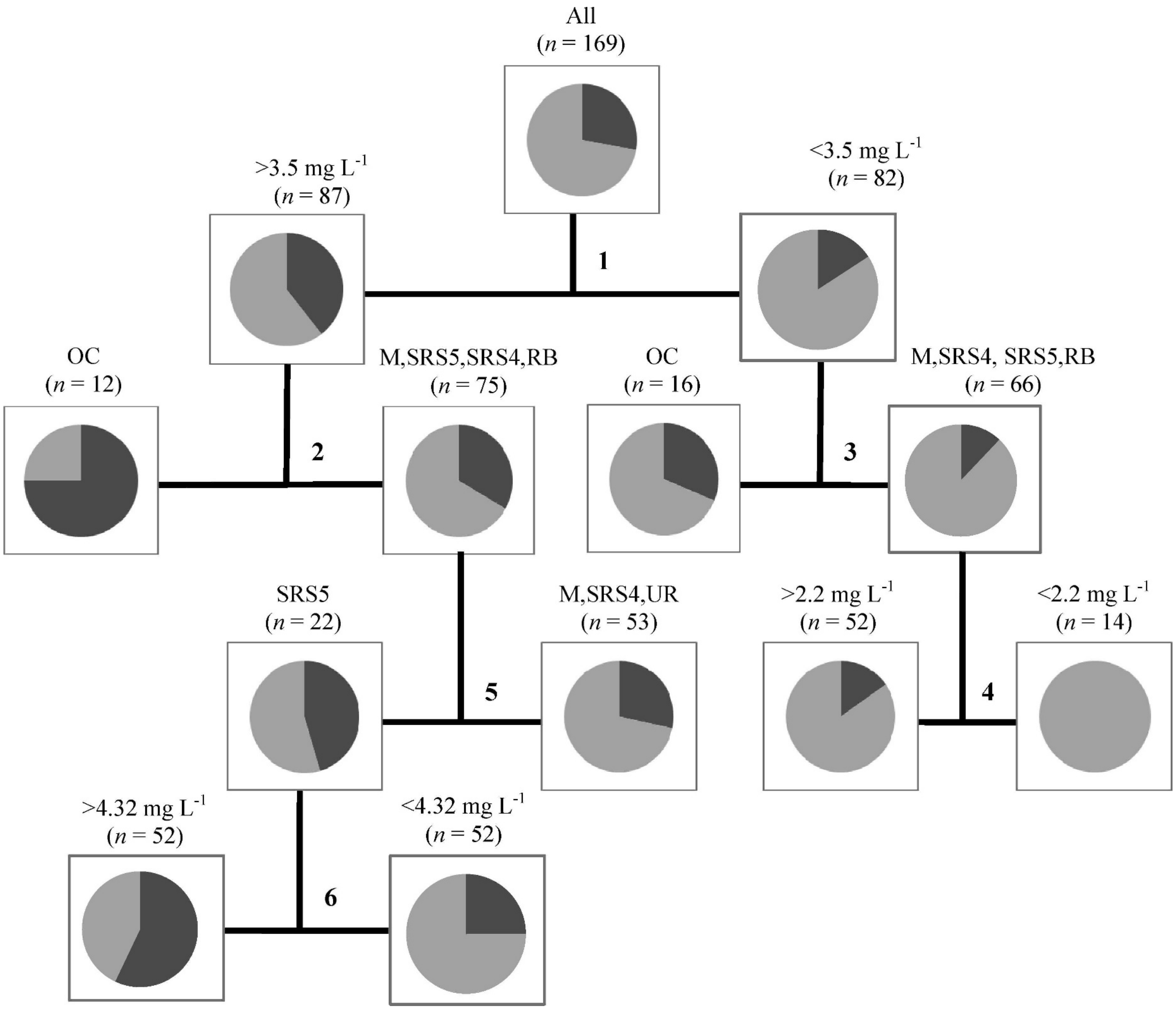

Fig. 7. Classification tree for the probability of capturing a juvenile shark (age 1+) on a longline set based on the factors site, salinity, and dissolved oxygen level. M = mouth, RB = Rookery Branch. Dark shading indicates the proportion of sets that captured at least one shark and light shading indicates sets where no sharks were captured. Numbers beside vertical lines indicate the order of splitting.

prey distribution relative to movements of bull sharks should allow for a more detailed analysis of the effects of prey availability on shark abundance and distribution in the estuary.

Bull sharks likely use the upper regions of the estuary (i.e., SRS4, Otter Creek, and Rookery Branch) because they provide a refuge from predation. Indeed, use of nursery areas by many species of coastal sharks likely is driven largely by the need to avoid predators rather than access to food resources (Heithaus 2007; Heupel et al. 2007). Although downstream areas of the Shark River Estuary and surrounding coastal waters likely offer bull sharks abundant prey resources, they also support populations of several large shark species that are potential predators of juvenile bull sharks (Torres et al. 2006; Wiley and Simpfendorfer 2007). During our study, large sharks that could prey upon juvenile bull sharks were captured on longlines at the mouth of the river and SRS5. Thus, the abundance and distribution of juvenile bull sharks likely is influenced by various factors at different scales. The use of the estuary as a nursery and the general sites where and seasons when sharks are abundant likely are influenced by both biotic factors (i.e., presence of food resources and scarcity of predators) and generally favorable abiotic conditions. In contrast, the probability of sharks being present over shorter time periods or at smaller spatial scales (i.e., during a longline set or location within a site) apparently is driven by the presence of favorable abiotic conditions. For bull sharks in the Shark River Estuary, fine-scale variation in movements within the estuary appear to be driven largely by dissolved oxygen levels in a manner similar to some predators in temperate estuaries (e.g., striped bass [*Morone saxatilis*]; Tupper and Able 2000).

We found that hypoxic conditions were relatively rare in the Shark River Estuary with the exception of Rookery Branch, where 6 of 36 sets occurred in dissolved oxygen levels below 2 mg L^{-1} (compared to 6 of 132 sets elsewhere in the system). Therefore, bull sharks do not regularly have to move to avoid extremely low dissolved oxygen levels but still are highly responsive to this factor.

Dissolved oxygen levels can vary within the Shark River Estuary over small spatial and temporal scales—up to

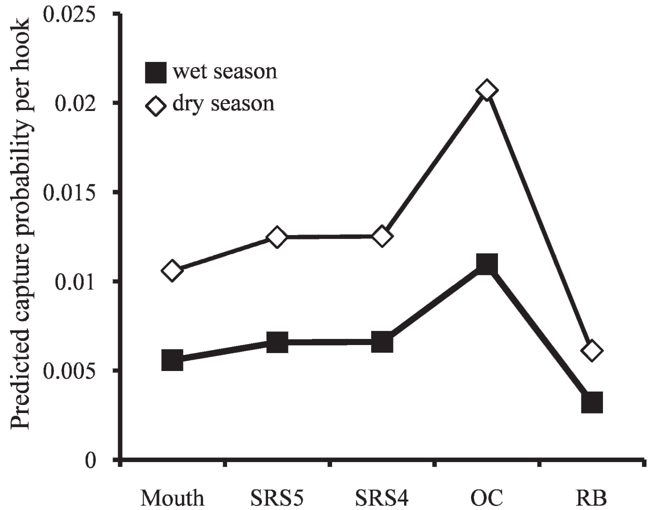

Fig. 8. Seasonal and spatial variation in the predicted probability of capturing an age 1+ bull shark on an individual hook. Note that although capture probabilities are higher in the dry season there is *not* a seasonal shift in the distribution of bull sharks upstream to take advantage of seasonally abundant prey in the upper estuary.

Table 3. Summary of logistic regression for predicting the probability of capturing a bull shark on an individual hook (n = 7177 for final models). Only factors with $p < 0.15$ are included.

Factor	df	Wald χ^2	p	Relative effect size
<1 yr old*				
Site	4	25.2	0.0001	3.8
Dissolved oxygen	1	3.08	0.08	25.0
>1 yr old†				
Site	4	16.4	0.002	8.2
Salinity	1	12.6	0.0004	6.3
Dissolved oxygen	1	5.5	0.02	35.3

* Whole model (<1 yr) − log likelihood = 348.8; Wald χ^2 = 32.7, p = 0.0001; R^2 = 0.16, df = 6.

† Whole model (>1 yr) − log likelihood = 348.8; Wald χ^2 = 26.2, p = 0.0002; R^2 = 0.04, df = 6.

almost 3 mg L^{-1} among sites on the same day and up to 2 mg L^{-1} within a site during a day. Thus, bull sharks could make short-term movements to stay within optimal dissolved oxygen conditions and, in such a situation, prey of bull sharks that are more tolerant of relatively low oxygen levels would experience lower predation risk from sharks. Bull sharks, however, are not the only large predator in Everglades estuaries. Rather, their distribution overlaps with those of large-bodied predators that are air-breathers (American alligators and American crocodiles [*Crocodylus acutus*]) facultative air breathers (e.g., tarpon), and those dependent on dissolved oxygen (e.g., Goliath grouper, snook). Because of variation in the dissolved oxygen tolerances of these predators and available prey (Schofield et al. 2007), dissolved oxygen could play an important role in structuring top predator effects and predator–prey interactions through behavioral changes in mobile consumers. In temperate estuaries, prey resistant to low dissolved oxygen levels experience a refuge from predation during periods of hypoxia (Eby and Crowder 2002; Bell and Eggleston 2005). Such a refuge may be less likely in tropical and subtropical estuaries where some predators that are less dependent on oxygen in the water column are abundant. Instead, dissolved oxygen in these estuaries is more likely to mediate the predator type in a particular location and shifts in the abundance of some predators, like bull sharks, may occur well above hypoxic conditions. Further studies of the effect of dissolved oxygen levels on habitat use patterns of the large predator guild and prey species, including when oxygen levels are far from hypoxic, will help to elucidate the role of this physical factor in structuring community dynamics of estuaries in the tropics and subtropics. Telemetry studies that can reveal links between short-term movements and variation in physical factors including dissolved oxygen levels would be particularly useful.

Everglades estuaries, especially those inside Everglades National Park, provide some of the only undeveloped nursery areas for bull sharks in the southeast United States (Wiley and Simpfendorfer 2007), yet the planned modification of freshwater flow during restoration of the Everglades is predicted to cause substantial changes to temporal and spatial variation in physical factors including a downstream shift in the oligohaline zone (CERP 1999; Davis et al. 2005). The drivers of dissolved oxygen levels in Everglades estuaries are complex and still not completely understood. Upwelling of anoxic groundwater, high primary productivity, and increases in water temperature will tend to decrease dissolved oxygen levels. The large-scale modification of freshwater flow that will occur with the restoration of the Everglades will have an effect on all of these factors, as will sea level rise predicted with climate change. Although dissolved oxygen levels alone do not appear to control the distribution and abundance of bull sharks, our studies show that they can be an important predictor of bull shark habitat use. Thus, an understanding of how various factors (e.g., freshwater inputs, sea level rise) interact to control dissolved oxygen content is important for predicting the effects that restoration and future management strategies will have on bull sharks, their role in the estuaries, and possibly the spatiotemporal pattern of top estuarine predator effects in general. More generally, our results suggest that studies of the factors influencing the distribution and abundance of large predators should not be limited to a small subset of physical factors (e.g., salinity and temperature) and instead should strive to include data on as many parameters, both biotic and abiotic, as possible.

Finally, anthropogenic changes to dissolved oxygen levels in the Everglades estuaries may have cascading consequences beyond the estuary that are mediated by bull sharks. Many shark populations are thought to be limited at the juvenile life-history stage (Castro 1987; see Heithaus 2007 for a review), and thus changes in their nurseries are likely to affect adult bull shark abundance, which in turn may alter the dynamics of nearby costal oceans where bull sharks are one of the largest predators (Heithaus et al. 2008). Thus, further studies of the physical factors influencing the suitability and use of estuaries by top

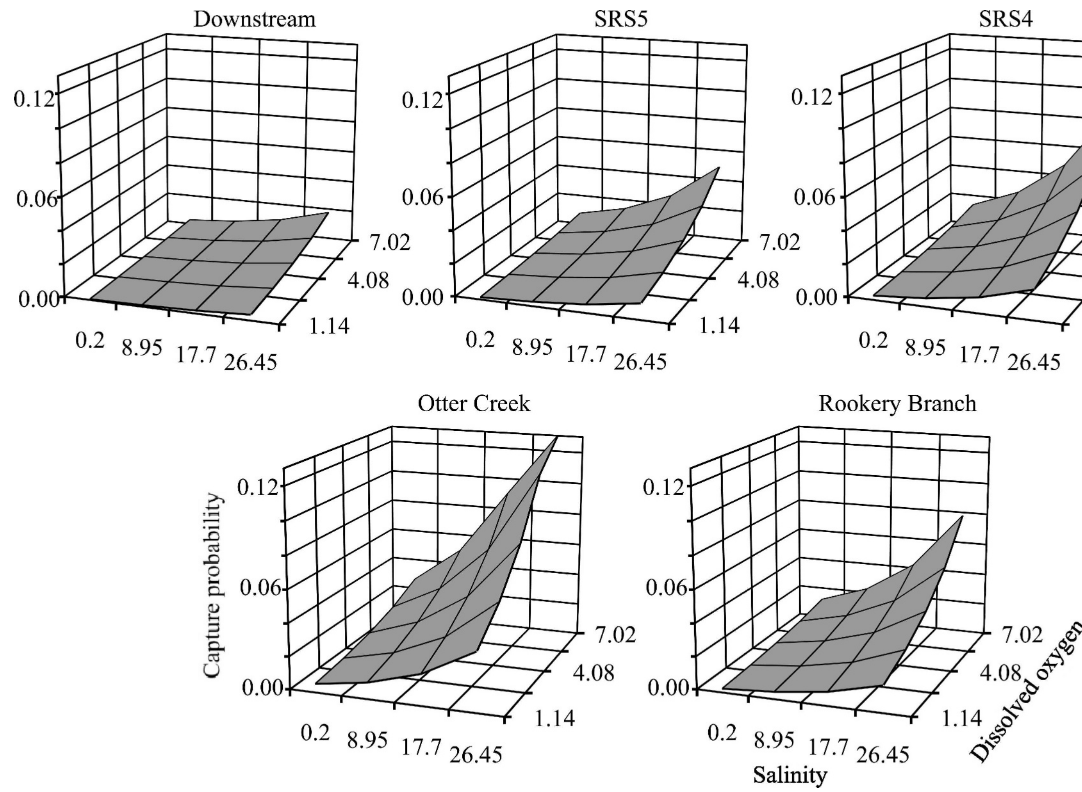

Fig. 9. Effects of site, dissolved oxygen, and salinity on the predicted probability of capturing a juvenile (age 1+) bull shark on a longline hook. Note that predicted capture probabilities are displayed for conditions that are beyond those actually measured within some sites.

predators, and especially those that increase our understanding of the potential for geographic variation in the relative importance of particular environmental factors, are important for predicting the consequences of continued anthropogenic modifications for both estuarine and adjacent marine systems.

References

ALTIERI, A. H., AND J. D. WITMAN. 2006. Local extinction of a foundation species in a hypoxic estuary: Integrating individuals to ecosystem. Ecology **87:** 717–730.

BAIRD, D., R. R. CHRISTIAN, C. H. PETERSON, AND G. A. JOHNSON. 2004. Consequences of hypoxia on estuarine ecosystem function: Energy diversion from consumers to microbes. Ecol. Appl. **14:** 805–822.

BELL, G. W., AND D. B. EGGLESTON. 2005. Species-specific avoidance responses by blue crabs and fish to chronic and episodic hypoxia. Mar. Biol. **146:** 761–770.

BRANSTETTER, S., AND R. STILES. 1987. Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. Environ. Biol. Fishes **20:** 169–181.

CASTRO, J. I. 1987. The position of sharks in marine biological communities: An overview, p. 11–17. *In* S. Cook [ed.], Sharks, an inquiry into biology, behavior, fisheries, and use. Oregon State Univ. Extension Service.

CHILDERS, D. L., J. N. BOYER, S. E. DAVIS, C. J. MADDEN, D. T. RUDNICK, AND F. H. SKLAR. 2006. Relating precipitation and water management to nutrient concentrations in the oligotrophic "upside-down" estuaries of the Florida Everglades. Limnol. Oceanogr. **51:** 602–616.

CLARK, E., AND K. VON SCHMIDT. 1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. **15:** 13–83.

COMPREHENSIVE EVERGLADES RESTORATION PLAN (CERP). 1999. U.S. Army Corps of Engineers and South Florida Water Management District, Jacksonville, FL. Available from http://www.evergladesplan.org/pub/restudy_eis.aspx

DAVIS, S. M., D. L. CHILDERS, J. J. LORENZ, H. R. WANLESS, AND T. E. HOPKINS. 2005. A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. Wetlands **25:** 832–842.

DELIUS, B. K. 2007. Distribution and trophic position of juvenile bull sharks in an oligotrophic estuary. M.S. thesis, Florida International Univ.

EBY, L. A., AND L. B. CROWDER. 2002. Hypoxia-based habitat compression in the Neuse River Estuary: Context-dependent shifts in behavioral avoidance thresholds. Can. J. Fish. Aquat. Sci. **59:** 952–965.

HAINING, R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge Univ. Press.

HEITHAUS, M. R. 2007. Nursery areas as essential shark habitat: A theoretical perspective, p. 3–13. *In* C. T. McCandless, N. E. Kohler and H. L. Pratt, Jr. [eds.], Shark nursery grounds of the Gulf of Mexico and the East Coast Waters of the United States. Amer. Fish. Soc. Symp. 50.

———, A. FRID, A. J. WIRSING, AND B. WORM. 2008. Predicting the ecological consequences of marine top predator declines. Trends Ecol. Evol. **23:** 202–210.

HEUPEL, M. R., J. K. CARLSON, AND C. A. SIMPFENDORFER. 2007. Shark nursery areas: Concepts, definition, characterization and assumptions. Mar. Ecol. Prog. Ser. **337:** 287–297.

———, AND C. A. SIMPFENDORFER. 2008. Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. Aquat. Biol. **1:** 277–289.

KENNISH, M. J. 2002. Environmental threats and environmental future of estuaries. Environ. Conserv. **29:** 78–107.

Loftus, W. F. 2000. Inventory of fishes of Everglades National Park. Fla. Sci. **63:** 27–47.

Pillans, R. D., W. G. Anderson, J. P. Good, S. Hyodo, Y. Takei, N. Hazon, and C. E. Franklin. 2006. Plasma and erythrocyte solute properties of juvenile bull sharks, *Carcharhinus leucas*, acutely exposed to increasing environmental salinity. J. Exp. Mar. Biol. Ecol. **331:** 145–157.

———, and C. E. Franklin. 2004. Plasma osmolyte concentrations and rectal gland mass of bull sharks *Carcharhinus leucas*, captured along a salinity gradient. J. Comp. Physiol. A: Molec. Integrat. Physiol. **138:** 363–371.

———, J. P. Good, W. G. Anderson, N. Hazon, and C. E. Franklin. 2005. Freshwater to seawater acclimation of juvenile bull sharks (*Carcharhinus leucas*): Plasma osmolytes and $Na^+/K^+ -$ ATPase activity in gill, rectal gland, kidney and intestine. J. Comp. Physiol. B: Biocem. Syst. Environ. Physiol. **175:** 37–44.

Rehage, J. S., and W. F. Loftus. 2007. Seasonal fish community variation in headwater mangrove creeks in the southwestern Everglades: An examination of their role as dry-down refuges. Bull. Mar. Sci. **80:** 625–645.

Schofield, P. J., W. F. Loftus, and M. E. Brown. 2007. Hypoxia tolerance of two centrarchid sunfishes and an introduced cichlid from karstic Everglades wetlands of southern Florida. J. Fish. Biol. **71:** 87–99.

Simpfendorfer, C. A., G. G. Freitas, T. R. Wiley, and M. R. Heupel. 2005. Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida estuary. Estuaries **28:** 78–85.

Torres, L. G., M. R. Heithaus, and B. Delius. 2006. Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA. Hydrobiologia **569:** 449–455.

Tupper, M., and K. W. Able. 2000. Movements and food habits of striped bass (*Morone saxatilius*) in Deleware Bay (USA) salt marshes: Comparison of a restored and reference marsh. Mar. Biol. **137:** 1049–1058.

Wiley, T. R., and C. A. Simpfendorfer. 2007. The ecology of elasmobranchs occurring in the Everglades National Park, Florida: Implications for conservation and management. Bull. Mar. Sci. **80:** 171–189.

Edited by: Luc De Meester

Received: 18 June 2008
Accepted: 12 November 2008
Amended: 9 December 2008