Hydrobiologia (2006) 569:449–455

J.C. Trexler, E.E. Gaiser & D.L. Childers (eds), Interaction of Hydrology and Nutrients in Controlling Ecosystem Function in Oligotrophic Coastal Environments of South Florida
DOI 10.1007/s10750-006-0148-6

Influence of teleost abundance on the distribution and abundance of sharks in Florida Bay, USA

Leigh G. Torres[1,]*, Michael R. Heithaus[2] & Bryan Delius[2]
[1]*Duke University Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA*
[2]*Marine Biology Program Department of Biological Sciences, Florida International University, 3000 NE 151 St, North Miami, FL 33181, USA*
*(*Author for correspondence: E-mail: lgt3@duke.edu)*

Key words: sharks, habitat use, spatial scale, predator–prey interactions

Abstract

Understanding the factors that influence the distribution and abundance of predators, including sharks, is important for predicting the impacts of human changes to the environment. Such studies are particularly important in Florida Bay, USA where there are planned large-scale changes to patterns of freshwater input from the Everglades ecosystem. Studies of many marine predators suggest that links between predator and prey habitat use may vary with spatial scale, but there have been few studies of the role of prey distribution in shaping habitat use and abundance of sharks. We used longline catches of sharks and trawls for potential teleost prey to determine the influence of teleost abundance on shark abundance at the scale of regions and habitats in Florida Bay. We found that shark catch per unit effort (CPUE) was not linked to CPUE of teleosts at the scale of sampling sites, but shark CPUE was positively correlated with the mean CPUE for teleosts within a region. Although there does not appear to be a strong match between the abundance of teleosts and sharks at small spatial scales, regional shark abundance is likely driven, at least partially, by the availability of prey. Management strategies that influence teleost abundance will have cascading effects to higher trophic levels in Florida Bay.

Introduction

Understanding the factors influencing the distribution of animals is important for predicting the likely impacts of anthropogenic changes to the environment. Such studies are particularly important in Florida Bay, a large semi-enclosed body of water between south Florida and the Florida Keys. Once considered an estuary, many parts of Florida Bay now experience hypersalinity because up to 70% of the natural freshwater flow through the Florida Everglades is diverted by upstream management to support agriculture, control floods, and provide water to the growing population of South Florida (Light & Dineen, 1994; McPherson & Halley, 1996). These large-scale anthropogenic changes to the natural freshwater flow throughout south Florida have disturbed the greater Everglades ecosystem, including Florida Bay. The Comprehensive Everglades Restoration Project (CERP), which aims to restore more natural water flow to the Everglades ecosystem, will modify the quality, quantity, and timing of freshwater inputs into this system (Ogden et al., 1999). As anthropogenic alterations to this ecosystem continue, understanding factors influencing habitat use and abundance of species at high trophic levels will allow managers to apply effective management schemes and monitor the results.

Previous studies have shown that alterations of habitats within Florida Bay, such as increased salinity and elevated nutrient levels, have stimulated algal blooms, resulting in large-scale dieoffs of seagrasses, sponges and mangroves (Robblee et al., 1991; Butler et al., 1995; Rudnick et al., 1999). This habitat degradation has resulted in reductions in the abundance and diversity of teleosts and changes in the composition of their communities (Matheson et al., 1999). However, there is currently no information on the effects of these changes on large predators like sharks.

The distribution and abundance of predators may be driven primarily by the abundance of prey resources, with predators distributed across habitats proportional to prey availability (e.g. ideal free distribution; Fretwell & Lucas, 1970). While the distribution of large marine predators often coincides with that of their prey at large spatial scales, there is often a mismatch between the distribution of predators and prey at small spatial scales in marine environments (e.g. Sih, 1984; Fauchald et al., 2000; Guinet et al., 2001). A lack of covariation in predator and prey distributions may be caused by a number of factors including anti-predator behavior of prey (e.g. Sih, 1984), physical attributes of the habitat that influence prey-capture probability (Hugie & Dill, 1994), and a lack of predictability of prey resources.

Florida Bay supports a diverse community of sharks that are relatively large-bodied predators and may have important influences on the distribution of fishes and other species in Florida Bay through predator-prey interactions (e.g. Heithaus, 2004). However, no studies have specifically investigated the possible links between shark distributions and the distribution of their prey. Due to large variation in the physical habitats of Florida Bay and spatial variation in potential prey abundance (Sogard et al., 1989; Thayer & Chester, 1989; Matheson et al., 1999; Thayer et al., 1999), shark abundances likely are spatially variable as well.

Previous studies have shown variable support for the hypothesis that sharks match the distribution of their prey. In open ocean habitats, basking sharks forage in frontal regions with high zooplankton densities (Sims & Quayle, 1998), while in coastal seagrass habitats of Australia tiger sharks show a preference for habitats with the highest prey density (Heithaus et al., 2002). In contrast, juvenile blacktip sharks within a coastal nursery do not spend the majority of their time in areas where fish trap catches of teleosts were highest (Heupel & Hueter, 2002). Thus, it is unclear to what extent the distribution of sharks is impacted by prey resources, or vice versa, at both regional and habitat spatial scales.

Materials and methods

Study site

Florida Bay is a large (2200 km^2) and complex estuarine system that lies between the southern tip of the Florida peninsula and the Florida Keys. For this study, Florida Bay was divided into five environmentally distinct regions based on salinity, water clarity, productivity, water depth, and bottom sediment types (Fig. 1). Within regions, benthic habitats are spatially heterogeneous and may include seagrass, mud, hardbottom, and sand in varying levels and combinations. However, regions were selected to be as homogeneous as possible. The Eastern region is most influenced by freshwater discharge through the canals and freshwater sheet flow through the Everglades. The Eastern region is characterized by low productivity, low to moderate salinity, moderate depth (1.5–2.5 m), high water clarity, and the bottom substrate is dominated by seagrass (*Thalassia testudinum*). The Central region is very shallow with an average depth of 1 m and experiences limited water circulation due to extensive mudbanks. The Central region has relatively high salinity (up to 50 ppt), benthic habitats dominated by mud and mudbanks, low water clarity, and high productivity. The Atlantic region is heavily influenced by water flow from the Atlantic Ocean through various passes between the middle Florida Keys. This region has oceanic salinity (~35 ppt), high water clarity, moderate to deep waters (1.5–3 m), is composed of hardbottom and sparse seagrass benthic habitats, and has moderate productivity levels. The Gulf region is open to the Gulf of Mexico on its western and southwestern sides. It is characterized by oceanic salinities (~35 ppt) with moderate to high productivity rates, relatively low water clarity, and is the deepest region of our

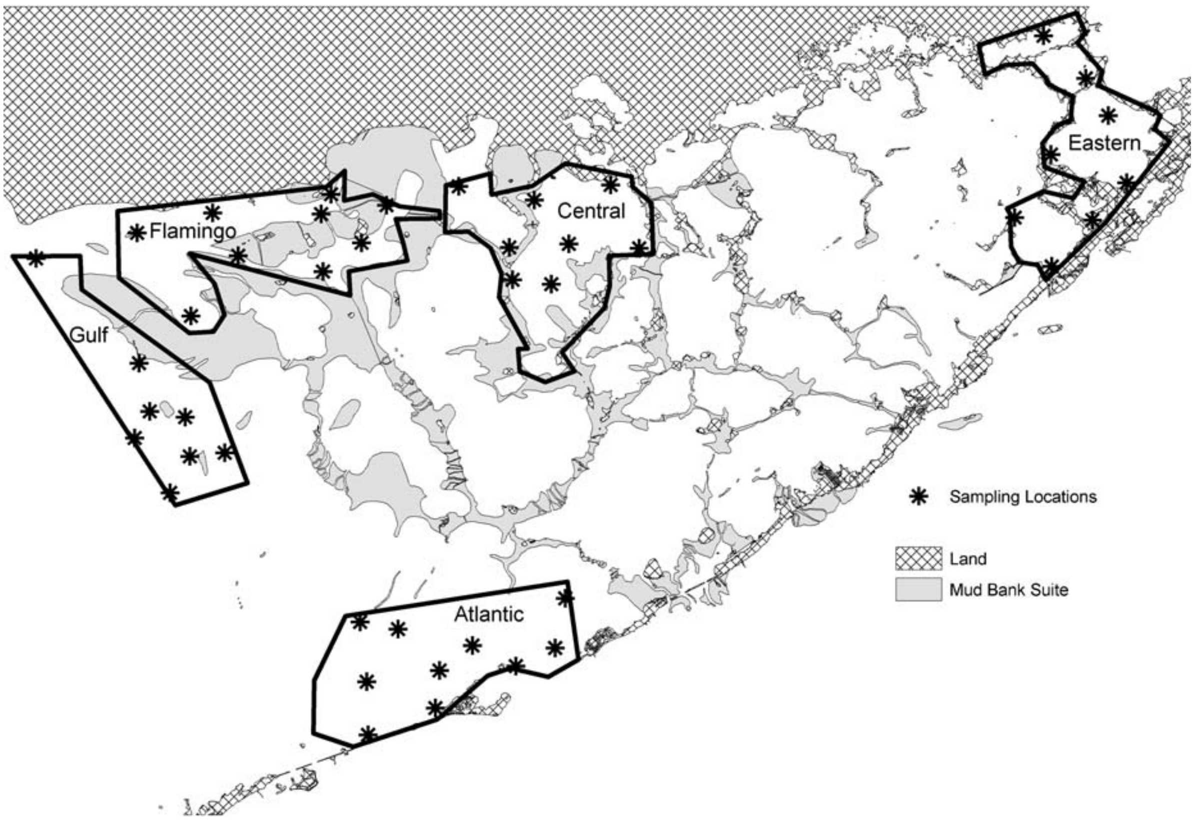

Figure 1. Location of sampling sites (*) within five regions of Florida Bay, USA.

study (1.5–3.5 m). The substrates are dominated by mixed seagrass (*Thalassia testudinum* and *Syringodium filform*), mud or sand. The Flamingo region lies between the Central and Gulf regions of Florida Bay and, therefore, is influenced to some degree by oceanic waters of the Gulf of Mexico. The Flamingo region is a shallow area dominated by mudbanks and seagrass (*Thalassia testudinum* and *Halodule wrightii*) with numerous channels that connect basins. The Flamingo region is typically very turbid, has moderate productivity, and normal to high salinity levels.

Field methods

From 29 June to 23 July 2005, we sampled teleosts, sharks, and environmental conditions at 43 sites (Fig. 1). Sample sites were chosen to represent the diversity of habitats present within each region so a range of habitats and fish communities would be sampled while also obtaining adequate spatial coverage of each region. At each site, we collected environmental data (temperature, salinity, turbidity, percent dissolved oxygen, and chlorophyll *a*) using a YSI 6600 Sonde. At a minimum of two sites in each region, water samples were obtained and filtered to calibrate the chlorophyll *a* readings produced by the YSI. These filters were later extracted in the lab and a linear regression model was developed to convert the YSI chlorophyll *a* readings into accurate chlorophyll *a* values. The depth and bottom habitat type were also recorded at each sampling site. A trawl was then conducted to sample the teleost community and a longline was set approximately 100 m from the trawled area to sample the shark community. Trawls were conducted at each sampling location immediately before the longline was set. The relatively short duration of trawls relative to longline soak times and the distance between trawls and longlines minimized potential impacts of trawls on catch rates of sharks. A total of 43 trawls and 43 longline sets were conducted.

The trawl sample used a 3-m research otter trawl towed at approximately 4 km/h for 3 min. All captured fish were identified and their total length (TL) measured and recorded, before being released alive. GPS position was recorded at the start and end of each trawl in order to calculate the exact distance trawled using GIS (ArcGIS; Version 8.2). Catch per unit effort (CPUE) was calculated as fish captured per meter of trawling.

Sharks were captured on a 600 m longline baited with 35–50 hooks spaced approximately 10–15 m apart. Each hook (size 13/0–15/0 Mustad tuna circles) was baited with mullet or squid (bait types were distributed randomly across regions) and attached to an approximately 3 m long individual clip line made of 900 lb monofilament. The longline was allowed to soak for approximately 1 h. Upon retrieval, the presence or absence of bait on each hook was noted. All captured sharks were identified, measured, tagged, and released alive. Shark CPUE is expressed as the number of sharks captured per hour of bait soaking. To account for variation in the number of hooks deployed on the longline, we expressed soak time for a set as the sum of soak times for each hook where hooks that captured a shark or lost bait were considered to have lost the bait half way through the soak time (see Heithaus, 2001).

Analysis

We determined the influence of teleost abundance and physical features of the environment on shark CPUE using ANOVA on log $(x+1)$ transformed data. To determine whether sharks responded to teleost abundance at large (regional) and small (the sampling site) spatial scales, we included teleost CPUE at the site and mean CPUE for the region in the analysis. Because not all fishes that were captured are likely to be consumed by sharks we present analyses that include only fishes over 2.0 cm TL. Also, we eliminated six groups of fish from the analysis that are unlikely to be prey items of sharks: rainwater killifish (*Lucania parva*), blenny sp. (*Blenniidae* spp.), seahorse sp. (*Hippocamous* spp.), goby sp. (*Gobiidae* spp.), sheepshead minnow (*Cyprinodon variegatus variegatus*), and pipefish sp. (*Syngnathidae* spp.). Results were similar for analyses that included all species of all sizes, all species of fishes over 2.0 cm TL, and all fishes over 5.0 cm TL. We did not attempt to analyze only fish species that are known prey of sharks because of a lack of data on shark diets in the region and the likelihood of considerable geographic variation in shark diets (see Simpfendorer et al., 2001; Weatherbee & Cortes, 2004). Furthermore, teleost data from trawls serve as an index of secondary production within habitats and regions rather than precise measures of food available to sharks.

Results

We captured 7 shark species and 45 species of teleosts (Appendix 1 & 2, see electronic supplemental materials). The Gulf region had the greatest diversity of shark species and the highest shark CPUE, followed closely by the Flamingo region (See Electronic Supplemental Materials[1]). The most commonly captured shark species were bonnethead (*Sphyrna tiburo*), lemon (*Negaprion brevirostris*) and nurse sharks (*Ginglyostoma cirratum*). The most frequently captured teleosts were gulf killifish (*Fundulus grandis grandis)*, mojarra sp. (*Eucinostomus* spp.), and pinfish (*Lagodon rhomboids*). The Flamingo and Gulf regions also had the highest teleost CPUE.

Shark CPUE was not influenced by any of the physical features of the environment that we sampled, nor was it correlated with chlorophyll *a* levels (Table 1). Similarly, there was no relationship between shark catch rates and the CPUE of teleosts at a particular sampling site. However, shark catch rates were significantly higher in regions where teleost CPUE was also higher (Table 1, Fig. 2).

Discussion

We found that shark catch rates in Florida Bay were spatially variable, but were not significantly correlated with physical factors, chlorophyll *a* levels or the abundance of teleosts at small spatial

[1] Electronic supplementary material is available for this article at http://www.dx.doi.org/10.1007/s10750-006-0148-6

Table 1. Influence of biotic and abiotic factors on catch rates of sharks in Florida Bay

Factor	$F_{1,42}$	*p*
Regional fish abundance	4.4	**0.04**
Sample site fish abundance	1.0	0.33
Depth	0.09	0.77
Temperature	0.6	0.43
Salinity	0.06	0.81
Turbidity	0.6	0.45
Chlorophyll *a*	0.03	0.86

Only fish over 2.0 cm TL were included in the analysis. Species mentioned in text were eliminated from analyses.

scales. Shark abundance was, however, greater in regions where teleost abundance was highest. A lack of covariation in marine predator abundance and their prey at small spatial scales with linked distributions at larger spatial scales is consistent with findings in other, primarily open, marine systems (e.g. Mehlum et al., 1999; Fauchald et al., 2000; Guinet et al., 2001). However, previous studies of marine predators have found that predator and prey distributions tend to coincide at small spatial scales when prey resources are predictable. For example, pied cormorants (*Phalacrocorax varius*) match the distribution of their prey at the scale of microhabitats and habitat patches in a seagrass ecosystem with predictable teleost distributions (Heithaus, 2005). Similarly, tiger sharks prefer shallow seagrass habitats where prey is most abundant (Heithaus et al., 2002) and basking sharks actively select energetically profitable patches of zooplankton (Sims & Quale, 1988). Because the spatial heterogeneity present in Florida Bay should lead to relatively predictable teleost distributions, a significant effect of teleost abundance on shark CPUE at the level of sampling sites might be predicted. However, sharks have relatively low feeding rates (Weatherbee & Cortes, 2004), and therefore, may not concentrate their movements in microhabitats of high prey abundance, especially when they are at risk of predation themselves and safer areas have lower prey abundance (Heithaus, 2004). Many of the sharks that we captured were juveniles, which often exhibit relatively restricted movements (e.g. lemon sharks, Morrissey & Grubber, 1993; blacktip sharks, Huepel & Hueter, 2002). Indeed, one blacktip shark that was tagged during this study was subsequently recaptured on two occasions within several kilometers of its release location. Therefore, it is possible that sharks remain within regions of high prey density even if they do not match prey abundance at small spatial scales.

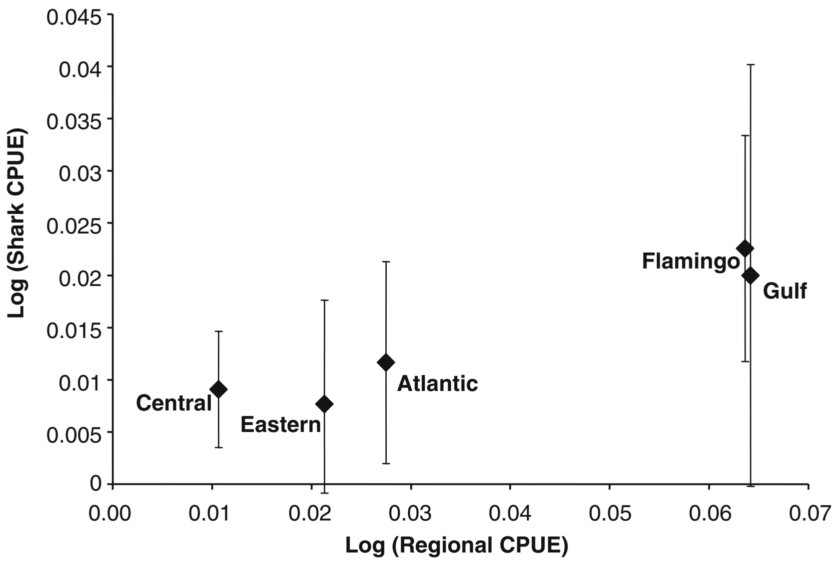

Figure 2. Influence of regional teleost abundance on shark catch rates. Error bars represent ± SE.

The relationship between relative teleost abundance and shark abundance may have been obscured due to sampling limitations. Specifically, the rapid removal of bait from the longline in some locations, especially the Atlantic and Gulf regions, where relatively high teleost catch rates occurred, may have prevented an accurate estimation of shark abundance. Bait loss in these instances is likely due to the abundance of untargeted scavenger species, especially crabs. This problem was addressed in the calculation of shark CPUE by assuming bait loss occurred half way through the soak time. While it is likely that this technique only partially accounts for the high volume of bait loss in some regions, it is important that habitat- and region-specific rates of bait loss be considered in studies of elasmobranches that use hook-capture methods.

Our finding that shark abundance at a regional scale is related to the average abundance of teleosts within the region suggests that proposed increases in freshwater flow to Florida Bay may have profound consequences for the abundance and distribution of these top predators. Currently, the CERP project has not defined the restoration plans or goals for Florida Bay, but has initiated the Florida Bay & Florida Keys Feasibility Study. The goal of this study is to evaluate the Florida Bay ecosystem and determine the modifications that are needed to successfully restore water quality and ecological conditions of the Bay. As part of this feasibility study, an upper trophic level modeling component will be developed to consider the response of upper trophic level species, including fish and sharks, in an effort to provide recommendations for Florida Bay's restoration. Although the precise habitat alterations caused by CERP are yet to be determined, it is likely that the freshwater increase will alter the habitat quality throughout Florida Bay. Shark habitat selection at large spatial scales will likely be mediated by the response of their teleost prey to these habitat alterations. This in turn could lead to cascading effects in the ecosystem caused by top-down effects of sharks (reviewed in Heithaus, 2004). Further studies of links between patterns of shark abundance, including species-specific analyses, with biotic and abiotic factors will be of great value to predict the effects of proposed modifications on the distribution and abundance of sharks. Furthermore, studies that investigate the effects of sharks on other species within Florida Bay will provide important information on how changes to shark populations and habitat use may cascade through the community.

Conclusions

We found no relationship between shark distribution and physical features of the environment or phytoplankton primary productivity. Although shark CPUE was not affected by teleost abundance at a sampling site, shark abundance was positively correlated with mean teleost CPUE for a region. Due to sampling limitations in this study, further research across a longer temporal period and that examines the links between individual shark species and their prey will greatly enhance our understanding of these top predators in Florida Bay. This study suggests that shark abundance is likely to be impacted by changes to teleost communities that are predicted to occur during future anthropogenic changes to the Florida Bay ecosystem.

Acknowledgements

Fish and shark sampling in Florida Bay was conducted under Everglades National Park permit EVER-2005-SCI-0062 and Florida Fish and Wildlife Conservation Commission Permit 045R-855A. Todd Chandler, Matt Warren, Ray and Pat Heithaus, and Jeremy Vaudo assisted with field work. We also thank Andy Read, Danielle Waples, Dan Odell, and Jane and Onofre Torres for their advice and support. Funding was provided by NOAA/Coastal Oceans Program. This material also is based upon work supported by the National Science Foundation, Florida Coastal Everglades (FCE) Long-term Ecological Research program (DEB-9910514). Any opinions, findings, conclusions, or recommendations expressed in the material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. This publication also was supported partially by the National Sea Grant College Program of the United States Department of Commerce's National Oceanic and Atmospheric Administration under

NOAA Grant # R/MI-12. The views expressed herein do not necessarily reflect the views of any of these organizations. This is contribution #311 of the Southeast Environmental Research Center at Florida International University.

References

Butler, M. J. IV, J. H. Hunt, W. F. Herrnkind, M. J. Childress, R. Bertelsen, W. Sharp, T. Matthews, J. M. Field & G. Marshall, 1995. Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobster Panulirus argus. Marine Ecology Progress Series 129: 119–125.

Fauchald, P. K., E. Erikstad & H. Skarsfjord, 2000. Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81: 773–783.

Fretwell, S. D. & H. L. Lucas Jr., 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16–36.

Guinet, C., L. Dubroca, M. A. Lea, S. Goldsworthy, Y. Cherel, G. Duhamel, F. Bonadonna & J. P. Donnay, 2001. Spatial distribution of foraging in female Antarctic fur seals Arctocephalus gazella in relation to oceanographic variables: a scale-dependent approach using geographic information systems. Marine Ecology Progress Series 219: 251–264.

Heithaus, M. R., 2001. The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes 61: 25–36.

Heithaus, M. R., L. M. Dill, G. J. Marshall & B. Buhleier, 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier)* in a seagrass ecosystem. Marine Biology 140: 237–248.

Heithaus, M. R., 2004. Predator–prey interactions. In Carrier, J. C., J. A. Musick & M. R. Heithaus (eds), Biology of Sharks and their Relatives. CRC Press, Boca Raton: 487–521.

Heithaus, M. R., 2005. Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. Marine Biology 147: 27–35.

Heupel, M. R. & R. E. Hueter, 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Marine and Freshwater Research 53: 543–550.

Hugie, D. M. & L. M. Dill, 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45: 151–169.

Light, S. S. & J. W. Dineen, 1994. Water control in the Everglades: a historical perspective. In Ogden, J. C. (ed.), Everglades: The Ecosystem and its Restoration. St. Lucie Press, Delray Beach, Florida, 47–84.

Matheson, R. E. J., D. K. Camp, S. M. Sogard & K. A. Bjorgo, 1999. Changes in seagrass-associated fish and crustacean communities in Florida Bay mud banks: the effects of recent ecosystem changes?. Estuaries 22: 534–551.

McPherson, B. E. & R. B. Halley, 1996. The South Florida Environment – A Region under Stress. Circular 1134, United States Geological Survey, Reston, Virginia.

Mehlum, F., G. L. Hunt Jr., Z. Klusek & M. B. Decker, 1999. Scale-dependent correlations between the abundance of Brünnich's guillemots and their prey. Journal of Animal Ecology 68: 60–72.

Morrissey, J. F. & S. H. Gruber, 1993. Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 2: 425–434.

Ogden, J. C., J. A. Browder, J. H. Gentile, L. H. Gunderson, R. Fennema & J. Wang, 1999. Environmental management scenarios: ecological implication. Urban Ecosystems 3: 279–303.

Robblee, M. B., T. R. Barber, P. R. Carlson Jr., M. Durako, J. W. Fourqurean, L. K. Muehlstein, D. Porter, L. A. Yarbro, R. T. Zieman & J. C. Zieman, 1991. Mass mortality of tropical seagrass *Thalassia testudinum* in Florida Bay (USA). Marine Ecology Progress Series 71: 297–299.

Rudnick, D. T., Z. Chen, D. L. Childers, J. N. Boyer & T. D. Fontaine III, 1999. Phosphorus and nitrogen inputs to Florida Bay: the importance of the Everglades watershed. Estuaries 22: 398–416.

Sih, A, 1984. The behavioral response race of predators and prey. American Naturalist 123: 143–150.

Simpfendorfer, C. A., A. B. Gotreid & R. B. McAuley, 2001. Size, sex, and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environmental Biology of Fishes 61: 37–46.

Sims, D. W. & V. A. Quayle, 1998. Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393: 460–464.

Sogard, S. M., G. V. N. Powell & J. G. Holmquist, 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. Bulletin of Marine Science 44: 179–199.

Thayer, G. W. & A. J. Chester, 1989. Distribution and abundance of fishes among basin and channel habitats in Florida Bay. Bulletin of Marine Science 44: 200–219.

Thayer, G. W., G. V. N. Powell & D. E. Hoss, 1999. Composition of larval, juvenile, and small adult fishes relative to changes in environmental conditions in Florida Bay. Estuaries 22: 518–533.

Weatherbee, W. M. & E. Cortes, 2004. Food consumption and feeding habits. In Carrier, J. C., J. A. Musick & M. R. Heithaus (eds), Biology of Sharks and their Relatives. CRC Press, Boca Raton: 225–246.