Florida International University
FIU Digital Commons

FIU Electronic Theses and Dissertations | University Graduate School

7-15-2010

Regional variation in tiger shark (Galeocerdo cuvier) abundance and habitat use

Kathryn Cameron
Florida International University, kcame003@fiu.edu

Follow this and additional works at: http://digitalcommons.fiu.edu/etd

Recommended Citation
Cameron, Kathryn, "Regional variation in tiger shark (Galeocerdo cuvier) abundance and habitat use" (2010). *FIU Electronic Theses and Dissertations.* Paper 260.
http://digitalcommons.fiu.edu/etd/260

This work is brought to you for free and open access by the University Graduate School at FIU Digital Commons. It has been accepted for inclusion in FIU Electronic Theses and Dissertations by an authorized administrator of FIU Digital Commons. For more information, please contact dcc@fiu.edu.

FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

REGIONAL VARIATION IN TIGER SHARK (*GALEOCERDO CUVIER*) ABUNDANCE AND HABITAT USE

A thesis submitted in partial fulfillment of the

requirements for the degree of

MASTER OF SCIENCE

in

BIOLOGY

by

Kathryn Elizabeth Cameron

2010

To: Dean Kenneth Furton
College of Arts and Sciences

This thesis, written by Kathryn Elizabeth Cameron, and entitled Regional Variation in Tiger Shark (*Galeocerdo cuvier*) Abundance and Habitat Use, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

_____
Maureen Donnelly

_____
James Fourqurean

_____
Michael Heithaus, Major Professor

Date of Defense: July 15, 2010

The thesis of Kathryn Elizabeth Cameron is approved.

_____
Dean Kenneth Furton
College of Arts and Sciences

_____
Interim Dean Kevin O'Shea
University Graduate School

Florida International University, 2010

DEDICATION

I would like to dedicate this thesis to the women scientists who are out there in the field; especially those who have helped make its completion possible.

To Lauren Yeager, Elizabeth Stoner, Caroline Peyer, and Kristin Kuehl, the example you set through your research provided me with a constant source of support.

And to my Mother, Penelope Bowen, who was an accomplished field scientist at a time when it was rare for women to do field work. You are my hero.

ACKNOWLEDGMENTS

I would first like to thank my committee members, Drs. Maureen Donnelly and James Fourqurean, who have helped shape me into a better scientist through their commitment to my education and scientific growth. I would also like to thank Drs. Phillip Stoddard and Rene Price, who both gave their time to foster my intellectual development at FIU.

I would like to thank both Dr. Robert Mauck and Robert McMillan, whose encouragement and direction led me here. I would like to also thank Dr. Aaron Wirsing, who provided both academic and financial support.

Thank you to my parents, who taught me to work hard and with integrity.

Thank you to my colleague, Adam Rosenblatt, without whom I would have had a very different graduate career. You have been my friend, my pillar, and my sounding board for creative scientific thinking. Every scientist needs a safe place to discuss ideas openly and you gave that to me.

I would like to especially thank my thesis advisor, Dr. Michael Heithaus, who taught me the realities of scientific research, and who helped me take control of my future. Mike, I am truly grateful for all you have given me.

Funding was provided by the FIU Summer Science and Judith Parker Scholarships, National Geographic, and the National Science Foundation.

My time spent in the Biological Sciences Department at FIU has helped shaped me as a scientist and guided me towards a future I am passionate about.

ABSTRACT OF THE THESIS

REGIONAL VARIATION IN TIGER SHARK (*GALEOCERDO CUVIER*) ABUNDANCE AND HABITAT USE

by

Kathryn Elizabeth Cameron

Florida International University, 2010

Miami, Florida

Professor Michael Heithaus, Major Professor

The purpose of this study was to investigate whether there is regional variation in the abundance and habitat use of tiger sharks (*Galeocerdo cuvier*) within in a model seagrass ecosystem. Abundance was determined with catch rates on drumlines and habitat preferences were investigated using acoustic tracking of large tiger sharks (n=4). I found spatiotemporal variation in the probability of catching at least one shark and in catch rates on days sharks were caught. In general, sharks were present throughout more of the year and in higher abundances in the northern region. Habitat use also varied between regions. In the northern region, sharks moved randomly with respect to habitat, while in the southern region sharks preferred shallow habitats. Although preliminary, these results suggest that large predator abundance and habitat use may vary over relatively small spatial scales and that such variation may be useful for elucidating their ecological role.

TABLE OF CONTENTS

CHAPTER PAGE

I. INTRODUCTION…….…… 1

II. METHODS…… 5
Study site…….....5
Fishing methods…….. 9
Tiger shark movements and habitat use….....10
Statistical analysis…….....11

III. RESULTS…….…… 16
Water temperature…….....16
Shark size distribution, sex ratio, and species assemblage…..……..16
Tiger shark abundance……..……..... 18
Tiger shark movement and habitat use……..... 20

IV. DISCUSSION……..…….. 24
Shark abundance……..……..... 24
Tiger shark movement and habitat use……...…….. 27
Significance……...…….....30

LITERATURE CITED……..…… 31

LIST OF FIGURES

FIGURE PAGE

1. Maps of study sites…….....……7

2. Randomization protocols …… .....……13

3. The frequency distribution of mean tiger shark (n=4) movement directions used for CRW randomization protocol…… .....……15

4. The probability of capturing at least one tiger shark in a fishing day in Herald Bight and Monkey Mia… .....……19

5. Tiger shark catch rate (sharks/hr) on days when at least one shark was caught…….....……20

6. Track paths for the four tiger sharks tracked in Herald Bight…….....……21

7. Tiger shark speed (km/hr) relative to shark total length…… .....…….22

8. The proportion of time spent in deep habitats by tiger sharks tracked in Herald Bight….....……24

I. Introduction

Recent studies have documented increased and widespread declines in populations of marine top predators (Pauly *et al.* 1998, Myers and Worm 2003, Myers *et al.* 2007). Since upper trophic level predators may influence ecosystem dynamics through top-down mechanisms (e.g., Estes *et al.* 1998, Pace *et al.* 1999, Frank *et al.* 2005, 2006, Heithaus *et al.* 2008), concerns have arisen that their declines could alter ecosystem functioning via trophic cascades. For example, in rocky reef ecosystems offshore of southwest Alaska, increased predation of sea otters (*Enhydra lutris*) by killer whales (*Orcinus orca*) in the 1990's released herbivorous sea urchins (*Strongylocentrotus sp.*) from otter predation (Estes and Duggins 1995, Estes *et al.* 1998, 2004). Increased urchin density resulted in an ecosystem phase-shift from an alga-dominated state (kelp forests) to a less productive herbivore-dominated state (urchin barrens) with reduced biodiversity (Estes and Duggins 1995, Estes *et al.* 1998, 2004, 2010). In another example, gradual declines in large sharks along the Atlantic seaboard since the 1970's may have led to increased densities of elasmobranch mesopredators (i.e., cownose ray, *Rhinoptera bonasus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, chain catshark, *Scyliorhinus retifer*, and smooth butterfly ray, *Gymnura altavela*). The release of mesopredators, particularly rays, appears to have played a role in the decline and/or continued depression of bivalve populations (i.e., bay scallops, *Argopecten irradians*, soft-shelled clams, *Mya arenaria*, hard clams, *Mercenaria mercenaria*, and oysters, *Crassostrea virginica*) (Myers et al. 2007, but see Heithaus *et al.* 2010 for a review of potential confounding factors).

Despite empirical support for strong top-down control in marine ecosystems, it is increasingly apparent that the ecological role of marine top predators is context-

dependent and additional studies are needed to determine the species and conditions that are likely to result in strong top-down control of marine systems (Gripenberg and Roslin 2007, Heck and Valentine 2007, Heithaus *et al.* 2008). Such studies, however, are generally hindered by the logistical difficulties of studying large-bodied and wide-ranging top predators in the ocean, and by a lack of pristine areas where top predators, like sharks, and their prey exist at near natural densities. Furthermore, a failure to account for the diversity of mechanisms through which predators can alter the dynamics of their prey populations and communities has hindered efforts to create predictive frameworks from model systems (Heck and Valentine 2007, Heithaus *et al.* 2008, 2009).

The mechanisms through which predators impact their prey and communities include, but are not limited to, direct predation ("consumptive effects") and non-consumptive effects (also called "risk effects"). These two mechanisms, alone or in combination, can alter abundance, distribution, and behavior of prey species (Schmitz *et al.* 2004, Preisser *et al.* 2005, Schmitz 2005, Creel and Christianson 2008, Heithaus *et al.* 2008). The recent understanding that non-consumptive effects may be as, or even more, important than direct predation in affecting prey population dynamics and community structure (Schmitz *et al.* 2004, Preisser *et al.* 2005, Creel and Christianson 2008, Heithaus *et al.* 2008) has led to increased interest in the role of risk effects in top-down control.

Not surprisingly, the relative importance and strength of risk effects varies with context (e.g., Nicieza 1999, van Oers *et al.* 2005, Figueria and Lyman 2007, Heithaus *et al.* 2009, Schmitz 2009, Wirsing *et al.* 2010). One key factor that influences the dynamics of risk effects is the habitat use pattern of predators. Indeed, habitat use is a key feature in understanding ecological systems because habitats contain the resources

required for survival and reproduction, and the context for interspecific interactions (Morris 2003). Resource availability often influences habitat use patterns of predators, especially when they are not at risk themselves. Most simply, optimal foraging theory predicts that, all else being equal, foragers, including top-predators, should select habitats with the highest net energy intake rates (MacArthur and Pianka 1966, Charnov and Orians 1973, Pyke 1984). Many factors influence energy intake rates of predators including prey abundance and availability, the number of competitors present, and anti-predator tactics of prey (Sih *et al.* 1998, Gende and Quinn 2004, Hebblewhite *et al.* 2005, Lecomte *et al.* 2008). The landscape in which predator-prey interactions take place can influence the probability of an encounter and the probability of a successful attack by the predator (i.e., the probability of prey escape; Hebblewhite *et al.* 2005). Therefore, studies of predator habitat use across a range of habitat configurations can provide important insights into the factors influencing the relative importance of risk effects in marine ecosystems.

Since 1997, the relatively pristine seagrass ecosystem of Shark Bay, Western Australia has been used as a model system for understanding the ecological role of a top-predator, in this case the tiger shark (*Galeocerdo cuvier*). Studies to date have focused on how tiger sharks influence their prey, and possibly community dynamics, through non-consumptive effects. Of particular interest is how spatiotemporal variation in tiger shark abundance and food availability influence habitat use decisions by their prey (Heithaus and Dill 2002, Heithaus *et al.* 2007a, Wirsing et al. 2007a, Heithaus *et al.* 2009) and the potential cascading effects of anti-predator decisions by prey. Seasonal and inter-annual variation in the abundance of tiger sharks in the study area (Heithaus

2001a, Wirsing *et al.* 2006), combined with studies of shark habitat preferences at multiple spatial scales (Heithaus *et al.* 2002, 2006), and surveys of food distributions, have allowed researchers to test predictions based on behavioral ecological theory (see Heithaus *et al.* 2009). For example, dolphins (*Tursiops aduncus*), dugongs (*Dugong dugon*), and pied cormorants (*Phalacrocorax varius*) reduce their use of productive, shallow foraging grounds when tiger shark abundances are high, and instead use deeper waters where these species have a lower predator encounter rate, but reduced access to food (Heithaus and Dill 2002, Heithaus 2005, Wirsing *et al.* 2007a). At smaller spatial scales, healthy green turtles (*Chelonia mydas*), bottlenose dolphins, and dugongs abandon productive seagrass interiors for less productive seagrass edge microhabitats where their escape probability is increased (Heithaus and Dill 2006, Heithaus *et al.* 2007a, Wirsing *et al.* 2007a, Heithaus *et al.* 2009).

While previous studies in Shark Bay have advanced our understanding of the potentially wide-reaching effects of sharks in marine ecosystems, these studies have been conducted primarily within a 150-km^2 study area with a single habitat configuration that allows for replication within the site. Regions within Shark Bay vary in the configuration of critical habitat types (i.e., arrangement of deep and shallow habitat patches) and it is possible that tiger shark abundance and habitat preference varies between sites within the bay. Expansion beyond a single study site in Shark Bay would be of value to understanding the ecological function of tiger sharks in Shark Bay and behavioral decisions made by their prey. Further, knowledge of shark ecology across a larger scale could help in elucidating the factors that influence the non-consumptive effects that predators have on their communities (e.g., Heithaus *et al.* 2009, Wirsing *et al.* 2010).

The objective of this study was to determine if seasonal patterns of tiger shark abundance, habitat preferences, and movement patterns varied between two regions of Shark Bay that contain similar prey communities but have different habitat configurations (i.e., spatial arrangement of shallow and deep water patches) and access to oceanic waters. In addition, I investigated whether the size distributions and sex ratios of tiger sharks varied between these two regions and whether there were differences in the structure of the community of top elasmobranch predators. These data are an important first step in developing testable hypotheses about the impact of habitat configuration on the nature of predator-prey interactions in Shark Bay and their effects on community dynamics. Additionally, the knowledge gained from this study provides the first step towards a deeper understanding of the potential effects of shark declines.

II. Methods

Study site

Shark Bay (approximately 25°45'S, 113°44'E; Figure 1a) is located in the subtropical zone of Western Australia, approximately 800 km north of Perth. The climate in the region is semi-arid, and the combination of minimal freshwater input (228 mm average rainfall, WA Bureau of Meteorology) and restricted water exchange between the ocean and bay, results in hypersaline conditions throughout the southern reaches of both the Eastern and Western Gulfs (Berry and Playford 1997). The approximately 15,000-km^2 bay is relatively shallow throughout with large expanses of nearshore shallows and offshore shallow seagrass banks (<4.0 m) surrounded by deeper waters (10-50 m depth). Shark Bay lies in a tidal transition zone with mixed tides that are mostly semi-diurnal

(Burling *et al.* 2003). The tidal range at the original sampling site, Monkey Mia, is 1.2 m (Burling *et al.* 2003).

In 1991 Shark Bay was listed as a World Heritage site in part because it contains some of the largest seagrass beds in the world (*ca*. 4000 km^2; Walker *et al.* 1988), which support large populations of megagrazers (e.g., dugongs, green sea turtles), piscivores (e.g., dolphins, pied cormorants, sea snakes), and their primary predator, tiger sharks (Heithaus 2001a,b, Wirsing *et al.* 2007a, Heithaus *et al.* 2007a, Kerford *et al.* 2008, Heithaus *et al.* 2009). Tiger sharks have not been subject to commercial fishing pressure within Shark Bay for over 15 years, and pressure prior to 1994 was from a single operator, working primarily in the Western Gulf (Heithaus 2001a). The relative isolation of the bay allows ecosystem dynamics to be studied in the absence of substantial human impacts.

My study was conducted in two sites along the eastern side of Peron Peninsula, in the Eastern Gulf of Shark Bay (Figure 1a). The Monkey Mia study site (MM), which has been the focus of past studies of tiger sharks and their prey, is located in Red Cliff Bay and surrounding waters up to 8 km offshore of the Monkey Mia Dolphin Resort (Figure 1b). At Monkey Mia, the deep habitats (>6 m) are interspersed with shallow banks (<2.5m at interior) that average 1.25 km in width and 4 km in length (Figure 1b). Virtually all the shallow habitat is accessible to tiger sharks and their prey at low tide. The Herald Bight study site (HB) is 30 km north of Monkey Mia and is closer to the mouth of the bay. The Herald Bight site includes the waters of Herald Bight, east of the

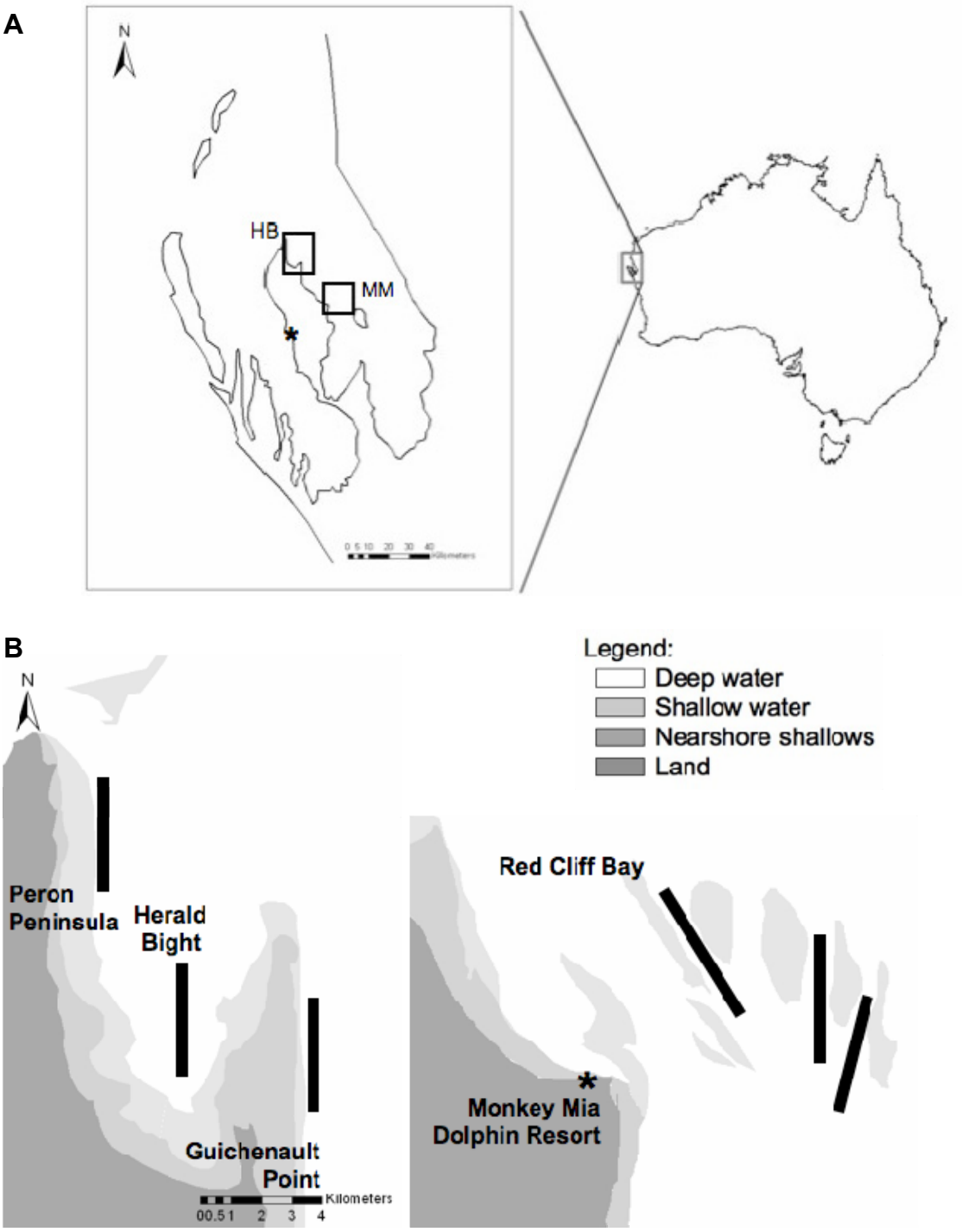

Figure 1: Maps of study sites, (A) Herald Bight and Monkey Mia, are within 30 km of one another and located in the Eastern Gulf of Shark Bay. The town of Denham (*) lies on the Western Gulf.
(B) Herald Bight (left) and Monkey Mia (right) differ in the configuration of shallow and deep habitats. Fishing zones used in this study are indicated with black lines.

northern tip of Peron Peninsula (approximately 25°34'S, 113°32'E), and the waters surrounding Guichenault Point, approximately 10 km east of Peron.

The two sites have nearly identical proportions of shallow-to-deep water (MM: 15:85, HB: 14:86), but differ in the configuration of these two habitat types (see Figure 1b). Unlike the more complex mosaic of deep and shallow habitats at the Monkey Mia site, the Herald Bight site is composed almost entirely of deep, open water with nearshore seagrass shallows and one long seagrass bank extending from the exposed sand spit at Guichenault Point (Figure 1b). Bank widths at Herald Bight range from as little as 100 m to 1.7 km and banks average 7.5 km in length. Large areas of the nearshore shallows and the seagrass shallows extending north of Guichenault Point are inaccessible to large tiger sharks on most low tides.

Mean monthly water temperatures vary temporally in Shark Bay, ranging from 14°C in the cold season to 25°C in the warm season (Heithaus 2001a, Wirsing *et al.* 2006). Previous studies at Monkey Mia have found positive correlations between water temperature and both shark (Heithaus 2001a) and dugong abundance (Wirsing *et al.* 2007a). Additionally, other prey species such as dolphins, pied cormorants, and healthy green sea turtles, appear to alter their foraging behavior and habitat use during the cold season in response to a reduction in the number of tiger sharks encountered (Heithaus and Dill 2002, Heithaus 2005, Heithaus *et al.* 2007a, Wirsing *et al.* 2007b, Heithaus *et al.* 2009, Dunphy-Daly *et al.* 2010). Because of these documented temporal variations, I compared shark abundances between the study sites in both warm and cold seasons.

Fishing methods

Spatial and temporal variation in the relative abundance of tiger sharks was investigated using catch rates on drumlines. Each drumline consisted of a single 4-5 kg Danforth anchor attached to 30 m of rope that terminated in a buoy line with three 20 cm diameter foam buoys and a 25 L sealed plastic barrel of air. Hook lines were tied to the buoy line with 1 m of rope spliced to 1 m of chain, equipped with a Mustad 13/0 J shark hook. Because of disruptions to the supply of standard bait (Australian salmon), hooks were baited with approximately 1 kg of sea mullet (also called striped mullet, *Mugil cephalus*), Australasian snapper (*Pagrus auratus*) or blue-lined emperor (*Lethrinus laticuadus*). Previous fishing studies found no significant effect of these bait types on tiger shark catch rates in the Monkey Mia study area (Wirsing *et al.* 2006). On each fishing day (n>4/month/site), 10 lines, spaced 0.4 km apart, were set in one of three deep-water fishing zones located at each site (Figure 1b). It is not possible to assess catch rates in shallow water habitats because of high rates of bait loss to non-target species, primarily northwest blowfish (*Lagocephalus sceleratus,* Heithaus 2001a). Lines were set at or near dawn and allowed to soak for three hours before the initial check. At initiation of set, water temperature, tide (i.e., flood, high, ebb, or low), and cloud cover were recorded. The depth and GPS location was recorded for each fishing line. After the initial check, no more than two hours elapsed between succeeding checks. Missing bait was replaced and recorded.

When a shark was captured, it was brought alongside the boat and the anchor was retrieved. This allowed the boat to move with the shark as it swam forward slowly, which minimized stress. All sharks were measured (total length, fork length, and

precaudal length), sex was determined on the basis of the presence or absence of claspers, tagged with an individually numbered plastic roto tag, and then released by cutting the hook.

Tiger shark movements and habitat use

Habitat preferences of sharks in Herald Bight were determined via acoustic tracking (e.g., Heithaus *et al.* 2002). Sharks were selected for tracking on the basis of the timing of capture (before 1300 to allow sufficient track durations), size (>270 cm to be comparable to studies in the MM site), and condition (swimming strongly on the line). Prior to tagging sharks chosen for the tracking study, all other fishing hooks were collected and any other sharks were processed and released. For each shark that was tracked (n = 4), a VEMCO (Shad Bay, Nova Scotia) V32 transmitter was attached to the first dorsal fin using two plastic cable ties after routine processing. Transmitters measured 12 cm in length and transmitted between 28.5 and 32.8 kHz.

Tracking took place from a 5.5 m research vessel using a VEMCO V-11 directional hydrophone and VR-60 acoustic receiver. Sharks were tracked until time of day or weather conditions forced me from the water. Every five minutes I recorded the GPS position of the boat, the direction to the shark, the approximate distance of the shark from the boat (based on strength of signal), and the shark's habitat. During tracking, I kept the boat 150-250 m from the shark's estimated position and I changed the boat's position relative to the shark frequently to avoid affecting its behavior.

Statistical analysis

Water temperature

Water temperature was compared between the two sites separately for each season with paired t-tests because of a difference in data collection. Water temperatures at Herald Bight and during both warm seasons (2009 and 2010) at Monkey Mia were measured from the boat's depth sounder (Northstar Explorer 660), mounted at the stern of the vessel approximately 45 cm below the water surface. In the 2009 cold season, equipment malfunction prevented the collection of temperature data from the research vessel while at Monkey Mia. Instead, water temperatures from the Pearl Farm, a floating house permanently moored in Red Cliff Bay and taken 1 m below the water surface, were used in place of MM temperatures (linear regression on log-transformed temperatures, R^2=0.94, F_5=68.5, p=0.001). Note that analyses of differences in temperature among zones reflect variation in temperature among days on which shark fishing occurred rather than comparisons between zones on the same days (i.e., reflects conditions during sampling rather than absolute differences in environmental conditions).

Shark abundance, sex ratios, and size distributions

Variation in the probability of catching at least one tiger shark and the catch rates of tiger sharks on those days when sharks were caught were compared across seasons and between sites using a conditional approach (e.g., Serafy *et al.* 2007), which is useful for data sets that include a large proportion of zeros. Instead of employing non-parametric methods, the ecological relevance of the data is maintained by separating the data into two parts, the probability of catching at least one shark and catch rate, resulting in a

conditional model. For the probability of catching at least one shark, days when no sharks were caught were designated with a zero and days on which at least one shark was caught were designated with a one. These data were fit to a binomial distribution, and the effects of site (MM or HB), season (warm or cold) and their interaction were tested with a generalized linear model (GLM), run in JMP 6.0. I calculated catch rates by dividing the number of sharks captured on a day by the total hours spent fishing on that day. I assumed that bait was lost, or sharks were captured, halfway between the last check when bait was present and the time when bait loss or shark capture was detected (e.g., Heithaus 2001a). Daily catch rates were log transformed and fit with a GLM (run in JMP 6.0) to test for effects of site, season, and their interaction.

I tested for spatial and temporal variation in the sizes of tiger sharks with ANOVA in Sigma Stat 3.5. Differences in sex ratios were investigated by comparing the number of individuals of each sex (males assigned a 0 and females assigned a 1, fit to binomial distribution) in each site and season using chi-square in JMP 6.0.

Tiger shark movements and habitat use

Assessing habitat preferences can be difficult when using tracking data. The expected proportion of time an individual spends in each habitat type, even if they do not exhibit a preference, can vary with starting location of the track, duration of the track, and habitat configuration (e.g., Heithaus *et al.* 2002, 2006). For these reasons, it is often not valid to compare the observed habitat use of an individual to the overall availability of habitats in a study area. In order to overcome these difficulties, I used three Monte Carlo randomization procedures (Heithaus *et al.* 2002), to assess tiger shark habitat preferences.

These procedures recreate random tracks for each tracked shark based on different rules of movement.

The simplest, but most conservative protocol is the step randomization method (RZ). In this method, an individual track was decomposed into component "moves." Each move included both the distance and direction of movement between successive observed GPS positions. The order of each move was randomized and a new track was recreated that began and ended at the observed locations (see Heithaus *et al.* 2002 for illustration). The RZ protocol assumes that sharks move between two fixed locations for some underlying reason, but they do not have a preference for the habitats they use while in transit (Figure 2).

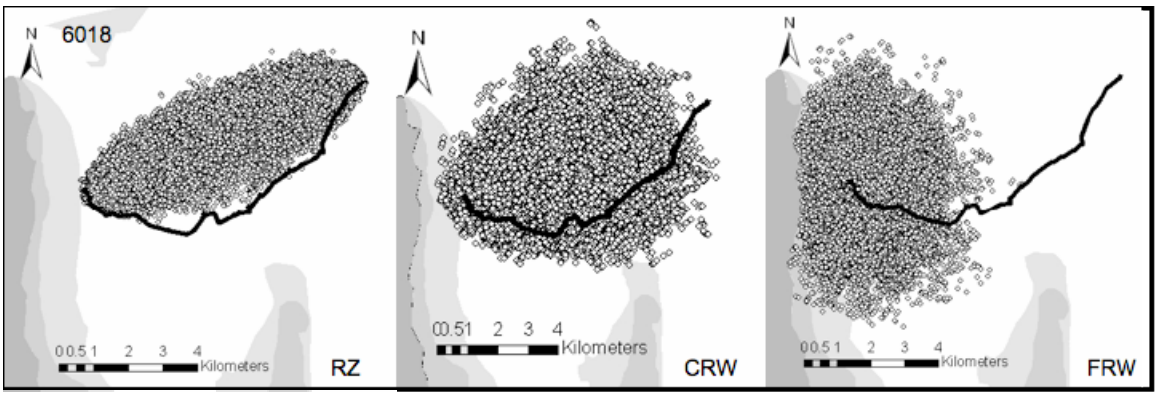

Figure 2: Randomization protocols: location fixes for three randomization protocols based on the observed track of shark 6018. In the RZ method, all points cluster around the original track and all tracks start and end at the observed points. The underlying tendency to move east is maintained in the CRW method, while the FRW produces a symmetrical cloud of points around the start location with the exception of movements onto land. The black line in each panel illustrates the observed track.

The second protocol is a full random walk (FRW). The FRW protocol assumes that animals move a particular distance between position fixes for an underlying reason, that they choose the direction to travel at each position fix, and that the direction of travel is

random. To create random tracks based on tiger sharks, the observed distance for each move was maintained, but reordered randomly as in the RZ method. The direction of travel (between 1 and 360°) of each move was selected completely at random.

The final protocol is a correlated random walk (CRW), which like the FRW does not assume that all randomized tracks will end at the observed final location of the track (Figure 2). Instead, CRW assumes that animals move an observed total distance for a particular reason (i.e., the total distance traveled by the shark was the same for every randomized track), but the direction of each move is correlated to the average movement direction of the population sample. To create random tracks, move distances were randomly reordered, as in the FRW, but the direction of travel for each move was determined using a two-step process. First, the direction of each move was allocated to a 45° bin (e.g., NNE, ENE, ESE, etc.) on the basis of the observed probabilities of moves from all observed shark tracks (each individual contributed one set of proportions of moves, Figure 3). Second, the exact angle of the move within each bin was selected randomly, therefore each direction within a 45° bin was equally likely to be selected. Therefore, the CRW created tracks that have longer distances between the starting and ending point than those of the FRW.

For all randomization procedures, 1000 random tracks were generated and mapped into a GIS map of the study site (ArcView 9.3, ArcGIS 9). The habitat (shallow or deep) was assigned to the end point of each move (Figure 2) and the proportion of fixes per habitat was calculated for each random track. In the FRW some random tracks moved onto land. These tracks were removed from the analysis and new random tracks were generated until 1000 tracks that did not move onto land were obtained. If >97.5%

of the random tracks displayed less use of a habitat than observed, I considered an individual to have a significant preference for a habitat (i.e., $p<0.025$ for a two-tailed test). Similarly, if >97.5% of random tracks displayed greater use of a habitat type than the observed track, I considered an individual to show a significant avoidance of a habitat. All randomization protocols are conservative and unlikely to predict a habitat preference, even if one exists (low type I error). However, they are subject to relatively higher Type II error, especially when the arrangement of habitat patches does not allow sharks to easily access them over the duration of the track (Heithaus *et al.* 2002).

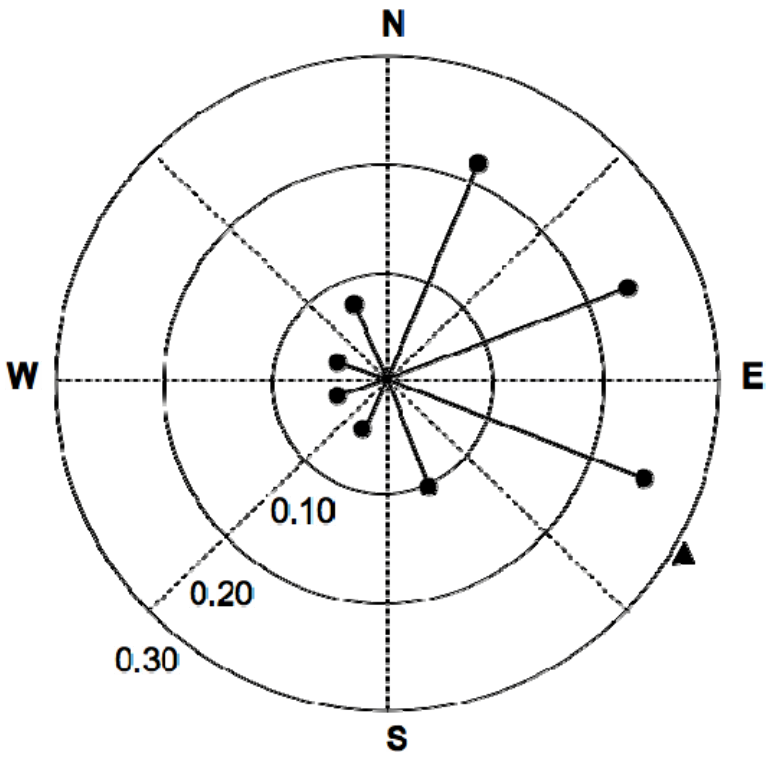

Figure 3: The frequency distribution of mean tiger shark (n=4) movement directions used for CRW randomization protocol. Arrow outside of circles is the mean direction (122.3°).

Habitat preference at the population level was determined with G-tests and using individuals as single data points. The G-test compared the number of moves that ended in a shallow habitat for observed tracks to expected tracks based on the three randomization protocols and habitat availability (e.g., Heithaus *et al.* 2002).

Shark speed and displacement were compared between observed tracks and expected tracks that had different end points from the observed track (CRW and FRW; linear regression, R Development Core Team, 2009, R 2.1) to determine if sharks were moving in a more or less directional manner than predicted (Turchin 1998, Bergman *et al.* 2000). I used logistic regression to test for the effect of shark length on swimming speed.

III. Results

Water temperature

Water temperatures during warm season sampling did not vary significantly between Monkey Mia (mean=27.7 ± 1.1°C SD) and Herald Bight (mean=25.1 ± 1.1°C SD (paired t-test, n=3, DF=2, t=4.3, p=0.55). However, during the single cold sampling season, water temperatures during sampling days in Herald Bight (mean=14.8 ± 1.2°C) were significantly colder than during those at Monkey Mia (mean=17.8 ± 1.16°C, paired t-test, n=3, df=2, t=4.3, p=0.007).

Shark size distribution, sex ratio and species assemblage

I fished for a total of 26 days in MM (16 warm, 10 cold) and 30 in HB (21 warm, 9 cold). I captured 34 tiger sharks between 156 and 376 cm in MM and 69 tiger sharks between

162 and 387 cm in HB. Tiger shark total length varied significantly between sites ($F_{1, 100}$ = 4.09, p = 0.04) and seasons ($F_{1, 100}$ = 4.27, p = 0.04), but there was no significant interaction ($F_{1, 100}$ = 0.33, p = 0.64). On average, sharks were larger at Herald Bight (301 cm TL ± 46 SD) than Monkey Mia (283 cm TL ± 55 SD) and during the warm season (300 cm TL ± 53 SD) compared to the cold season (281 cm TL ± 33 SD).

The sex ratio of my sample of tiger sharks was female-biased (1:4.7 male:female). There was no significant variation in the sex ratios by season ($\chi^2_{1, 101}$ = 1.34, p = 0.25), or site ($\chi^2_{1, 101}$ = 1.48, p = 0.22), and there was no interaction between site and season ($\chi^2_{1, 101}$ = 2.51, p = 0.11).

I recaptured six tiger sharks in Monkey Mia that had previously been tagged in that site as far back as 2004. In Herald Bight, I recaptured two tiger sharks previously captured outside of Herald Bight. The first was initially tagged at Monkey Mia in 2008. I was unable to read the ID number on the second tag, so this individual may have been tagged at Monkey Mia or elsewhere along the coast by the Department of Fisheries. Two tiger sharks were recaptured in Herald Bight, one in 2009 and one in 2010, both of which were tagged in Herald Bight during 2009. I did not recapture any tiger sharks in Monkey Mia that I had tagged in Herald Bight.

Tiger sharks were the only shark species captured during my sampling at MM. In Herald Bight tiger sharks accounted for 86% of sharks captured (n_{all}=80). Other shark species included pigeye sharks (*Carcharhinus amboinensis*, n=4, 5%), spottail sharks (*Carcharhinus sorrah*, n=4, 5%), bronze whalers (*Carcharhinus brachyurus*, n=2, 2%), and sandbar sharks (*Carcharhinus plumbeus*, n=1, 1.25%).

Tiger shark abundance

The probability of capturing at least one tiger shark did not vary significantly between the two study sites, although the interaction of site and season approached significance (Table 1), trending toward a higher probability of capturing at least one tiger shark in Herald Bight than in Monkey Mia in winter (Figure 4).

Table 1: Generalized linear model testing the effect of season, site, and their interaction on the probability of capturing at least one tiger shark during a day of fishing.

	DF	Chi-Square	P-value
Season	1	1.74	0.19
Site	1	2.66	0.10
Season*Site	1	3.58	0.06

Tiger shark catch rates on days that sharks were present were significantly higher in Herald Bight than in Monkey Mia (Figure 5). The interaction of site and season on catch rates was marginally non-significant (Table 2), but the presence of a trend was likely driven by relatively higher catch rates in Herald Bight in the cold season while catch rates at Monkey Mia were higher in the warm season.

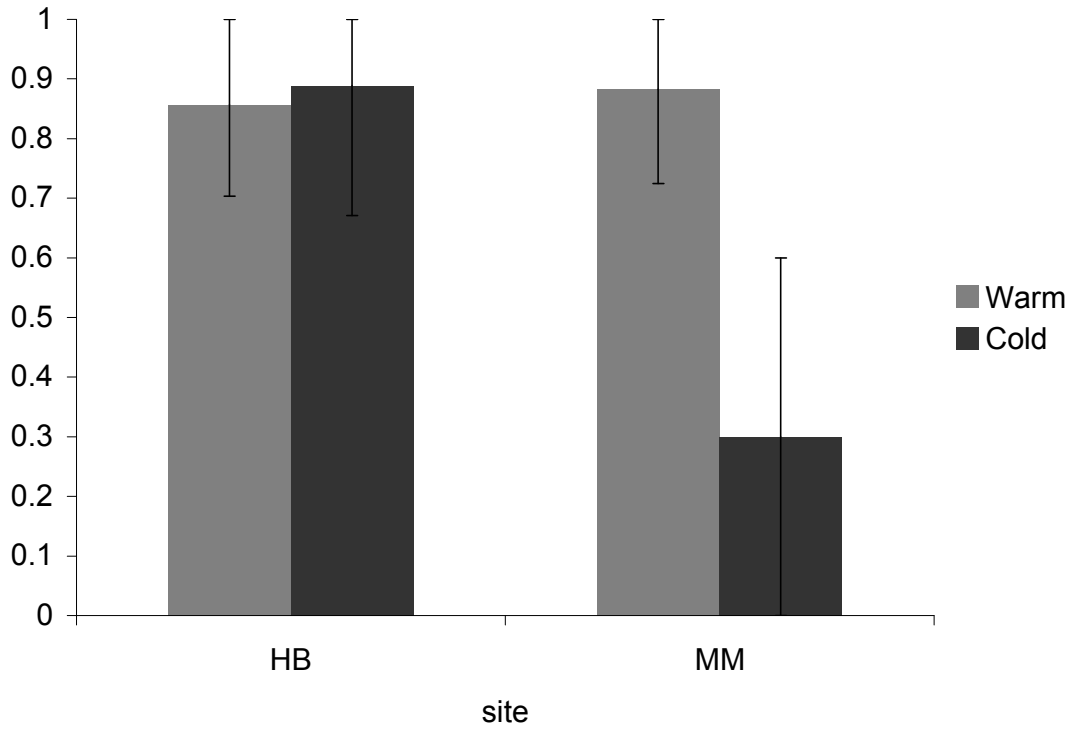

Figure 4: The probability of capturing at least one tiger shark in a fishing day in Herald Bight and Monkey Mia. Although not significant, there was a trend towards higher probabilities of capture in Herald Bight in the cold season compared to Monkey Mia. Error bars are standard error.

Table 2: Generalized linear model testing the influence of season, site, and their interaction on the catch rate of tiger sharks.

	DF	Chi-Square	P-value
Season	1	0.51	0.47
Site	*1*	*17.87*	*<0.0001*
Season*Site	1	3.61	0.06

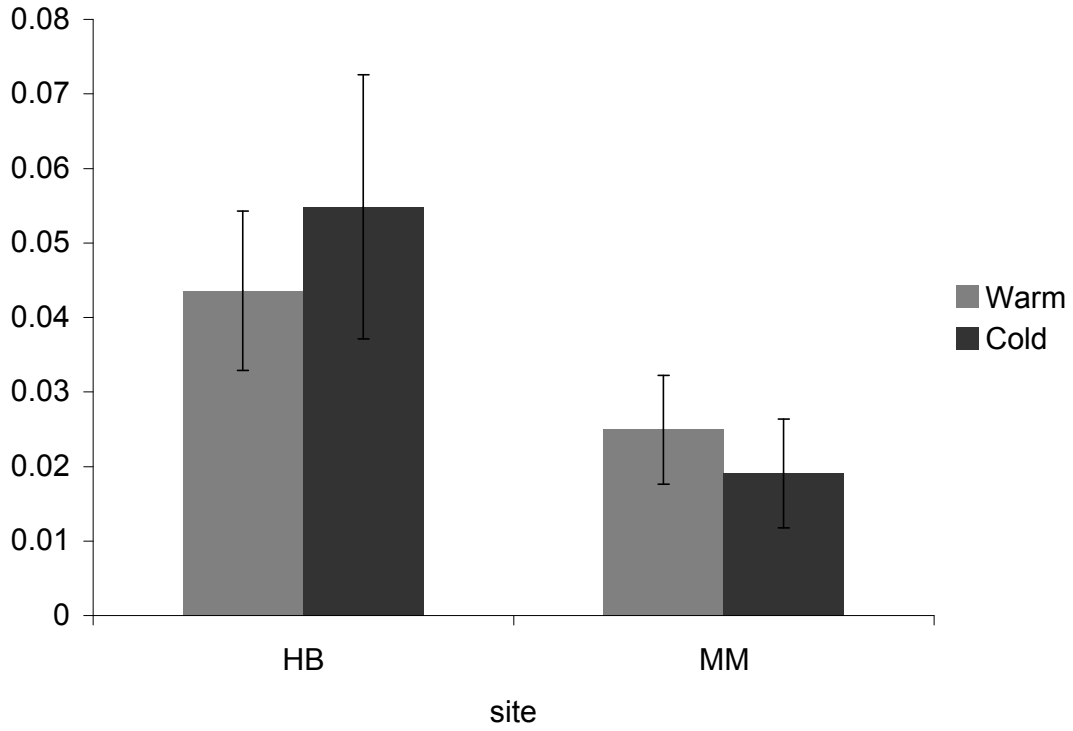

Figure 5: Tiger shark catch rate (sharks/hr) on days when at least one shark was caught. Error bars are standard error.

Tiger shark movement and habitat use

Tiger sharks tracked in Herald Bight (n=4) generally moved from west to east (Figure 6). The net-squared displacement of expected tracks created with the FRW method was significantly less than observed tracks (Table 3, G-test, G=63.33, $p<0.005$), indicating that the tracks were directional, and movements were not made randomly.

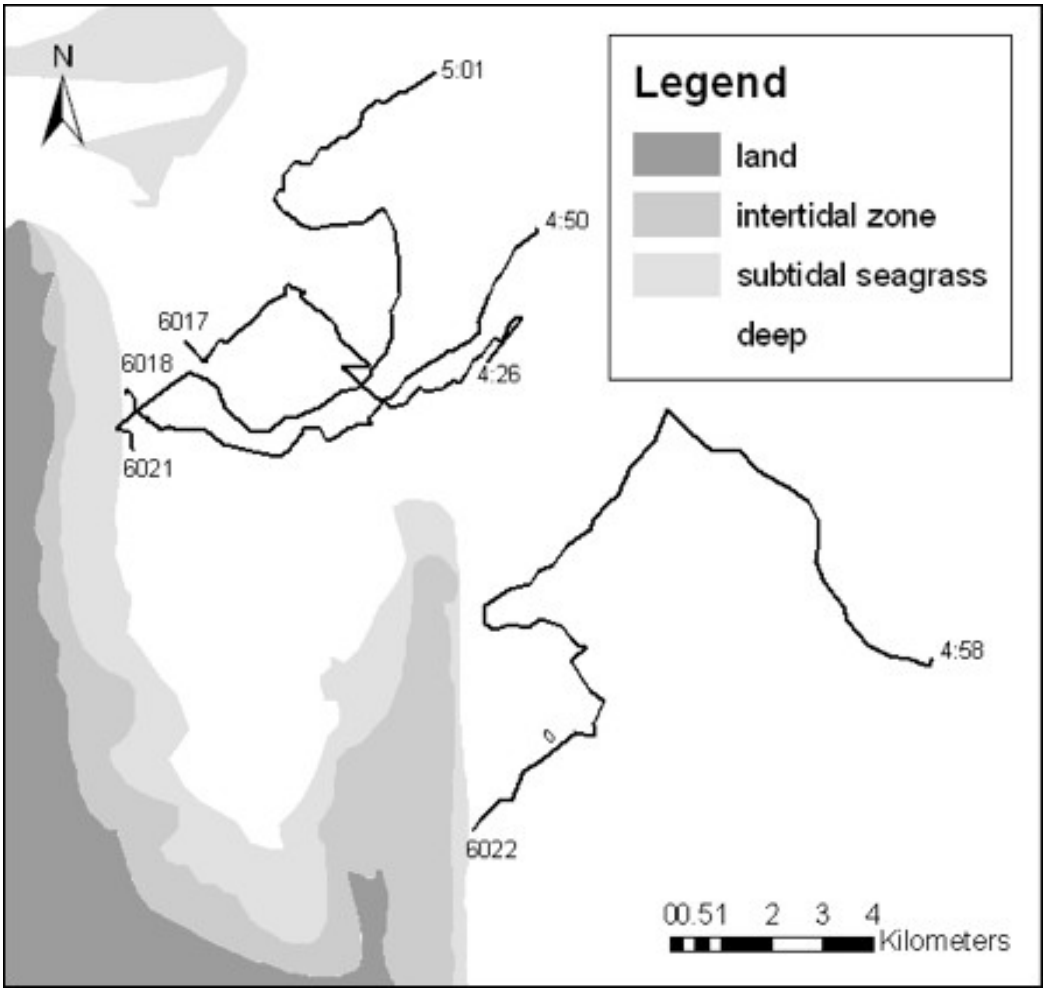

Figure 6: Track paths for the four tiger sharks tracked in Herald Bight. All tracks originated in deep habitats. Starting points are designated with shark identification numbers.

However, the net-squared displacement of expected tracks based on the CRW method was significantly greater than the displacement of observed tracks (Table 3, G-test, $G=15.27$, $p<0.01$), indicating the average movement direction of the observed tracks was less directional than expected and that the sharks may be remaining in the region without exhibiting site attachment. The speed of observed tiger sharks (mean=3.23 km/hr ± 0.5

SD) was influenced by total length (Figure 7, R^2=0.96, p=0.02), but displacement was not (R^2=0.16, p=0.59).

Table 3: Net-squared displacements of observed tracks and expected tracks based on two randomization protocols. CRW displacements are significantly greater than observed (G=15.27, p<0.01) while FRW displacements are significantly less than observed (G=63.33, p<0.005).

Shark	Observed displacement squared	CRW net-squared displacement	FRW net-squared displacement
6017	1.79	2.98	0.21
6018	3.24	1.79	0.15
6021	3.49	7.43	0.24
6022	3.76	18.62	0.39

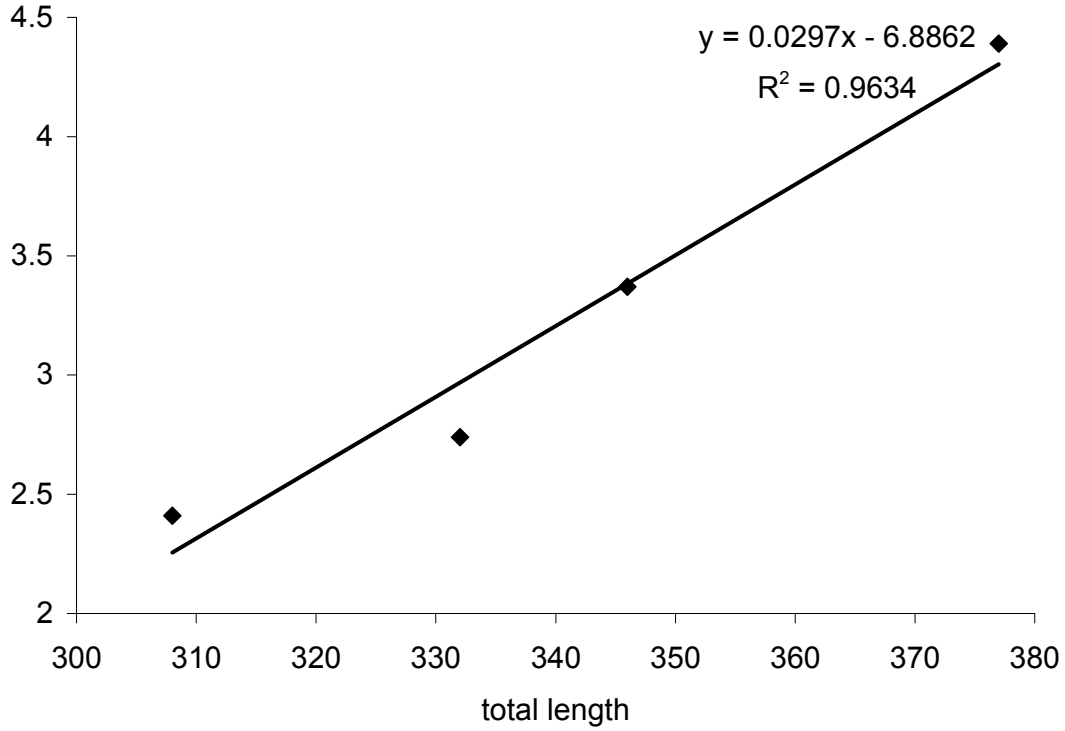

Figure 7: Tiger shark speed (km/hr) relative to shark total length (linear regression, R^2=0.96, p=0.02).

Overall, sharks in HB (n=4) spent only 1% of the observed time in shallow habitats, even though 14% of the available habitat is shallow in Herald Bight (Figure 8). Only one observed position fix from all sharks occurred in a shallow habitat. At the population level, the FRW method suggests that sharks might use deep habitats preferentially (G-test, G=10.36, $p<0.025$, Figure 8), but no other randomization methods suggested a potential habitat preference (G-test, RZ: G=0.96, $p>0.5$, CRW: G=1.17, $p>0.5$, HA: G=1.21, $p>0.5$). Furthermore, none of the randomization procedures indicated that observed use of deep habitats was significantly greater than that expected by random movements for any individual (Table 4).

Table 4: Observed proportion of location fixes in deep habitats for tracks of four tiger sharks and the number of randomly generated tracks (n=1000) that predicted less use of shallow habitats than observed. No significant habitat preferences were detected for either habitat.

Shark	Observed	RZ	CRW	FRW
6017	1.0	0	0	0
6018	1.0	0	0	0
6021	0.98	773	806	259
6022	1.0	0	0	0

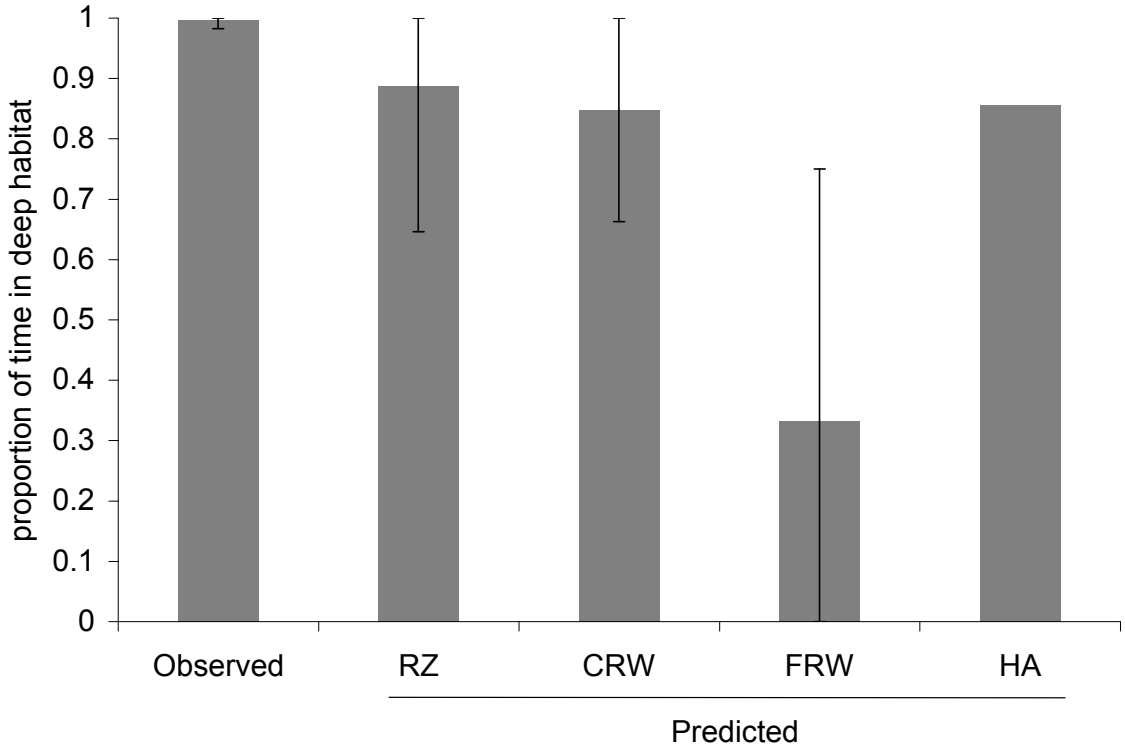

Figure 8: The proportion of time spent in deep habitats by tiger sharks tracked in Herald Bight: compared to tracks expected based on randomization protocols and habitat availability (HA). Error bars are 95% CI.

IV. Discussion

Shark abundance

I found differences in catch rates of tiger sharks between two study sites that are relatively close in proximity. At Monkey Mia, tiger sharks were unlikely to be captured in the cold season, and when they were, few were caught. In contrast, most fishing days during the warm season resulted in capturing at least one shark and catch rates were relatively high on days that sharks were caught. The pattern I observed at Monkey Mia is consistent with previous studies in Monkey Mia, although inter-annual variations in cold season shark densities have been documented (Heithaus 2001a, Wirsing *et al.* 2006).

Unlike Monkey Mia, sampling at Herald Bight resulted in substantial captures of tiger sharks in both seasons. The probability of catching at least one tiger shark remained high across both the warm and cold seasons and was similar to the probability of catching at least one shark at Monkey Mia during the warm season. Catch rates on days sharks were present were relatively similar between seasons at Herald Bight, although somewhat higher in the cold season. Additionally, all catch rates at Herald Bight were higher than at Monkey Mia regardless of season, suggesting a higher overall density of tiger sharks in the Herald Bight study site.

Although the results presented here are based on a single cold season of data collection, the high catch rates of tiger sharks in Herald Bight merits additional exploration. There are several hypotheses to explain the apparent regional differences in the temporal variation in tiger shark abundance. First, prey availability may not change during the cold season at Herald Bight as it does in Monkey Mia. Dugongs, a primary prey for tiger sharks, have been documented to abandon the Monkey Mia study site when water temperatures drop below 18°C, likely for physiological reasons (Anderson 1986, Wirsing et al. 2007a). Additionally, catch rates of large tiger sharks (>3.5 m TL) in the Monkey Mia study site were found to have a positive correlation to dugong abundance (Wirsing *et al.* 2007c). Transect surveys of dugongs in the Herald Bight site in 2009 (conducted concurrently with shark sampling, see Wirsing *et al.* 2007a for methods of dugong surveys) showed consistently high densities of dugongs across seasons while patterns of dugong density in Monkey Mia maintained the typical pattern of low dugong densities when water temperatures dropped and higher densities when water temperatures were above 18°C (unpublished data). Therefore, these preliminary data suggest that tiger

shark abundance may be positively correlated to dugong abundance in Herald Bight, like at Monkey Mia, but that both dugong and tiger shark abundance may remain high year-round at Herald Bight, at least in some years.

Another possible explanation for high tiger shark densities during the cold season in Herald Bight is water temperature. Herald Bight, which is further north, is closer to the Indian Ocean, and was expected to have warmer water temperatures during the winter than Monkey Mia. Some shark species make seasonal migrations away from colder winter water temperatures or will abandon foraging grounds when water temperatures decline rapidly (Knip *et al.* 2010). However, the water temperatures recorded during the single cold season of sampling were significantly colder in Herald Bight than at Monkey Mia, so it is unlikely that water temperature is responsible for the difference in tiger shark density between the sites.

Alternatively, the increased proximity of the Herald Bight study site to open oceanic waters may in part be responsible for the lack of temporal variation tiger shark density. Tiger sharks are capable of traveling thousands of kilometers (Kohler *et al.* 1998, Heithaus *et al.* 2007b, Meyer *et al.* 2009). Therefore, it is possible that the sharks caught in Herald Bight during the cold season are making regular forays to Herald Bight from the Indian Ocean to forage on resident animals. Round trip movements between different foraging grounds have been documented in tiger sharks in Hawaii (Meyer *et al.* 2009) and could apply to tiger sharks in Shark Bay (Heithaus *et al.* 2002). Since tiger shark abundance has been linked to dugong abundance (Wirsing *et al.* 2007c), sharks may not include Monkey Mia in winter trips because dugongs are not present in high densities at that site.

These data are based on two warm sampling periods and one cold sampling period. Previous catch rate data from Monkey Mia documented interannual variation in seasonal shark abundance (Wirsing *et al.* 2006). It is possible that the 2009 cold season represented an unusually high density of tiger sharks in Herald Bight. As such, additional years of sampling at Herald Bight are recommended to strengthen the findings from this study.

During my sampling, I found that tiger sharks were the only species captured at Monkey Mia, but other species made up 14% of the captures in Herald Bight. This is likely the result of relatively low sample sizes. Nine other species of sharks have been captured on drumlines in the Monkey Mia study area (Heithaus 2001a, Wirsing *et al.* 2006) and the only species captured in Herald Bight not captured in Monkey Mia was the spot tail shark (*Carcharhinus sorrah*). Spot tail sharks, however, were only captured on 4 days in 2010. A full investigation of differences in the community structure of sharks between the sites would require larger sample sizes than I had and the use of other gear types that are more likely to capture species other than tiger sharks.

Tiger shark movement and habitat use

Expected tracks produced with CRW had higher displacement rates (km/hr) than observed tracks, while tracks produced with FRW had much lower displacement than the observed tracks. Together, these results suggest that sharks are not highly site-attached in Herald Bight (higher displacements than FRW), but are not rapidly moving out of the region (lower displacements than CRW, Bergman *et al.* 2000). Interestingly, sharks tracked at Monkey Mia displayed greater displacements than predicted by CRW

suggesting that they were transiting through the region (Heithaus *et al.* 2002). Because of the small sample size in this study, more studies are needed to gain further insights into residency patterns and movements of tiger sharks in the Herald Bight region. However, during the course of this study, two tiger sharks previously tagged in Monkey Mia were recaptured in Herald Bight, and therefore, the differences in habitat use between the sites are more likely explained by context-dependent behavioral changes rather than variation in habitat preferences between two separate populations.

Previous research in Monkey Mia found that large tiger sharks (n=45) preferred shallow habitats to deep ones (Heithaus *et al.* 2002). Tiger sharks used shallow habitats 36% of the time, which was 1.6 times greater than predicted using RZ and CRW randomization protocols (Heithaus *et al.* 2002). At the individual level, however, no significant habitat preference was detected for 23 of the 45 (51%) sharks tracked, while 19 sharks (42%) preferred shallow and only 3 (7%) preferred deep. Deep water accounts for the same amount of available habitat in Herald Bight (86%) as it does at Monkey Mia (85%) where tiger sharks were found to prefer shallow habitats (Heithaus *et al.* 2002). Expected habitat use described by the three randomization protocols did not detect a habitat preference for tiger sharks in Herald Bight. These data illustrate the importance of large sample sizes and longer track during in studies of habitat use, and suggests that further work is needed to fully understand habitat preferences, or lack thereof, in tiger sharks found in Herald Bight. The possibility of regional variation in habitat preference, especially since individual tiger sharks were observed to move between the study sites, merits further study.

In addition to low sample sizes, the position of track starting locations relative to the habitat configuration in Herald Bight may reduce the probability of detecting significant habitat preferences. Three of the four sharks were tagged just east of a large peninsula (Figure 5) and would have had to move towards land in order to use shallow habitats. While these sharks had greater access to deep water east of their tagged location, they could have moved inshore to access shallow habitat if it was preferred over deep. A significant preference for deeper habitats would be virtually impossible to detect (high Type II error) because of the lack of available shallow habitats along the path sharks followed.

It is possible that the sharks tracked in this study responded to the stress of capture and tagging by abandoning the study site and moving into deeper water. However, the sharks chosen for tagging were swimming strongly on the hook and generally processed and released within 15 minutes. Additionally, footage from tiger sharks captured in Monkey Mia and equipped with an animal-borne video cameras (AVEDS) were found to immediately return to stereotyped swimming behavior and some individuals began foraging within minutes of release (Heithaus *et al.* 2001, 2002). Since AVEDS were larger than the transmitters that I used and required longer handling times, it is unlikely that stress responses played a large role in habitat use decisions by the sharks in this study.

Two sites, located in the same relatively pristine coastal bay that are separated by only 30 km, support similar community structure and are connected by movements of large sharks and other megafauna, do not appear to have the same spatiotemporal patterns of tiger shark abundance or habitat use. If the differences observed here are upheld by

future studies, then the spatiotemporal pattern of tiger shark risk effects may also vary. Previous research at Monkey Mia found that lowered shark abundances in the cold season released prey from some risk effects (Heithaus and Dill 2002, Heithaus *et al.* 2007a, Wirsing et al. 2007a, Heithaus *et al.* 2009). Prey that had abandoned more productive foraging grounds during the warm season returned to these habitats when shark numbers declined (Heithaus and Dill 2002, Heithaus 2005, Heithaus *et al.* 2007a, Wirsing *et al.* 2007a, Heithaus *et al.* 2009). High shark catch rates year round at Herald Bight may increase the overall intensity of prey risk effects in Herald Bight and prevent the seasonal changes prey habitat use observed in Monkey Mia.

Significance

Top-predators often drive marine ecosystem functioning and, in some cases, stability, through trophic cascades. Predators not only kill and eat prey, but also have non-consumptive effects, altering foraging behavior (e.g., Ripple and Beschta 2006), use of refuges (e.g., Gelwick 2000), and physiological processes (e.g., Mateo 2007). Three main drivers influence these "risk" effects: predator hunting mode, anti-predator tactics of prey, and the landscape in which interactions occur (Heithaus *et al.* 2009, Schmitz 2009). In this study, I found that there were apparent differences in the seasonal patterns of tiger shark density and habitat use between two sites that vary in their landscape (i.e., the arrangement of habitat types) and access to oceanic waters but not in prey community assemblage. These differences in patterns of top predator abundance offer a rare opportunity for future studies to examine how habitat configuration influences predator-prey interactions and the potential cascading consequences for lower trophic levels.

LITERATURE CITED

Anderson PK. 1986. Dugongs of Shark Bay, Australia: seasonal migration, water temperature and forage. *National Geographic Research* 2 (4): 473-490.

Berry PF and PE Playford. 1997. Biology of modern *Fragum erugatum* (Mollusca, Bivalvia, Cardiidae) in relation to deposition of the Hamelin Coquina, Shark Bay, Western Australia. *Marine and Freshwater Research* 48: 415-420.

Bergman CM, JA Schaefer, SN Luttich. 2000. Caribou movement as a correlated random walk. *Oecologia* 123: 364-374.

Burling MC, CB Pattiaratchi, GN Ivey. 2003. The tidal regime of Shark Bay, Western Australia. *Estuarine Coastal and Shelf Science* 57: 725-735.

Charnov EL and GH Orians. 1973. Optimal foraging: Some theoretical explorations.

Creel S and D Christianson. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23 (4): 194-201

Estes JA and DO Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* 65: 75–100.

Estes JA, MT Tinker, TM Williams, DF Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473-476.

Estes JA, EM Danner, DF Doak, B Konar, AM Springer, PD Steinberg, MT Tinker, TM Williams. 2004. Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Sciences* 74: 621-638.

Estes JA, MT Tinker, JL Bodkin. 2010. Using ecological function to develop recovery criteria for depleted species: sea otters and kelp forests in the Aleutian Archipelago. *Conservation Biology* 24 (3): 852-860.

Figueira WF and SJ Lyman. 2007. Context-dependent risk tolerance of the bicolour damselfish: courtship in the presence of fish and egg predators. *Animal Behaviour* 74: 329-336.

Frank KT, B Petrie, JS Choi, WC Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308: 1621-1623.

Frank KT, B Petrie, NL Shackell, JS Choi. 2006. Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecology Letters* 9: 1096-1105.

Gelwick FP. 2000. Grazer identity changes the spatial distribution of cascading trophic effects in stream pools. *Oecologia* 125: 573-583.

Gende SM and TP Quinn. 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology* 82 (1): 75-85.

Gripenberg S and T Roslin. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos* 116: 181-188.

Hebblewhite, M. EH Merrill, TL McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. *Oikos* 111: 101–111.

Heck Jr. KL and JF Valentine. 2007. The Primacy of Top-down Effects in Shallow Benthic Ecosystems. *Estuaries and Coasts* 30(3): 371-381.

Heithaus MR. 2001a. 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 MR. 2001b. Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *Journal of Zoology* 253: 53-68.

Heithaus MR. 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.

Heithaus MR and LM Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology 83* (2): 480-491.

Heithaus MR and LM Dill. 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos* 114: 257-264.

Heithaus MR, LM Dill, GJ Marshall, B Buhleier. 2002. Habitat use and foraging behavior in tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. *Marine Biology* 140: 237-248.

Heithaus MR, A Frid, AJ Wirsing, LM Dill, JW Fourqurean, D Burkholder, J Thomson, and L Bejder. 2007a. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *Journal of Animal Ecology* 76: 837-844.

Heithaus MR, A Frid, AJ Wirsing, and B Worm. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23 (4): 202-210.

Heithaus MR, A Frid, JJ Vaudo, B Worm, AJ Wirsing. 2010. Unraveling the ecological importance of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds.) Sharks and Their Relatives II: Biodiversity, Adaptive Physiology, and Conservation. CRC Press, Boca Raton, FL, pp 607-633.

Heithaus MR, IM Hamilton, AJ Wirsing, LM Dill. 2006. Validation of a randomization process to assess animal habitat preference: microhabitat use of tiger sharks in a seagrass ecosystem. *Journal of Animal Ecology* 75: 666-676.

Heithaus MR, GJ Marshall, BM Buhleier, LM Dill. 2001. Employing Crittercam to study habitat use and behavior of large sharks. *Marine Ecology Progress Series* 209: 307-310.

Heithaus MR, AJ Wirsing, LM Dill, LI Heithaus. 2007b. Long-term movements of tiger sharks satellite-tagged in Shark Bay, Western Australia. *Marine Biology* 151: 1455-1461.

Heithaus MR, AJ Wirsing, D Burkholder, J Thomson, LM Dill. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78: 556-562.

Kerford M, AJ Wirsing, MR Heithaus, LM Dill. 2008. Danger on the rise: diurnal tidal state mediates an exchange of food for safety by the *Hydrophis elegans*. *Marine Ecology Progress Series* 358: 289-294.

Kohler NE, JG Casey, PA Turner.1998. NMFS Cooperative shark tagging program, 1962-93: An atlas of shark tag and recapture data. *Marine Fisheries Review* 60 (2): 1-87.

Knip DM, MR Heupel, CA Simpfendorfer. 2010. Sharks in nearshore environments: models, importance, and consequences. *Marine Ecology Progress Series* 402: 1-11.

Lecomte N, V Careau, G Gauthier, JF Giroux. 2008. Predator behavior and predation risk in the heterogeneous Arctic environment. *Journal of Animal Ecology* 77: 439-447.

MacArthur RH and ER Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100: 603-609.

Mateo JM. 2007. Ecological and hormonal correlates of antipredator behavior in adult Belding's ground squirrel (*Spermophilus beldingi*). *Behavioral Ecology and Sociobiology* 62: 37-49.

Meyer CG, TB Clark, YP Papastamatiou, NM Whitney, KN Holland. 2009. Long-term movement patters of tiger sharks Galeocerdo *cuvier* in Hawaii. *Marine Ecology Progress Series* 381: 223-235.

Morris DW. 2003. Toward and ecological synthesis: a case for habitat selection. *Oecologia* 136: 1-13.

Myers RA and B Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283.

Myers RA, JK Baum, TD Shepherd, SP Powers, CH Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315: 1846-1850.

Nicieza AG. 1999. Context-dependent aggregation in Common Frog *Rana temporaria* tadpoles: influence of developmental stage, predation risk and social environment. *Functional Ecology* 13 (6): 852-858.

Pace ML, JJ Cole, SR Carpenter, JF Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14 (12): 483-488.

Pauly D, V Christensen, J Dalsgaard, R Froese, and F Torres, Jr. 1998. Fishing down marine food webs. *Science* 279: 860-863.

Preisser EL, DI Bolnick, and MF Bernard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86 (2): 501-509.

Pyke GH. 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, 15: 523-575.

Ripple WJ and RL Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* 230: 96-106.

Schmitz OJ, V Krivan, O Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7: 153-163.

Schmitz OJ. 2005. Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management. *Oecologia* 145: 225-234.

Schmitz OJ. 2009. Effects of predator functional diversity on grassland ecosystem function. *Ecology* 90 (9): 2339-2345.

Serafy JE, M Valle, CH Faunce, J Luo. 2007. Species-specific patterns of fish abundance and size along a subtropical mangrove shoreline: An application of the delta approach. *Bulletin of Marine Science* 80 (3): 609-624.

Sih A, G Englund, D Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13 (9): 350-355.

Turchin P. 1998. Quantitative analysis of movement. Sinauer, Sunderland.

Walker DI, GA Kendrick, AJ McComb. 1988. The distribution of seagrass species in Shark Bay, Western Australia, with notes on their ecology. *Aquatic Botany* 30 (4): 305-317.

Wirsing AJ, MR Heithaus, LM Dill. 2006. Tiger shark (Galeocerdo cuvier) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort. *Marine Biology* 149: 961–968.

Wirsing AJ, MR Heithaus, LM Dill. 2007a. Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Animal Behaviour* 74: 93-101.

Wirsing AJ, MR Heithaus, LM Dill. 2007b. Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. *Animal Behaviour* 74: 1085-1091.

Wirsing AJ, MR Heithaus, LM Dill. 2007c. Can measures of prey availability improve our ability to predict the abundance of large marine predators? *Oecologia* 153: 563-568.

Wirsing AJ, KE Cameron, MR Heithaus. 2010. Spatial responses to predators vary with prey escape mode. *Animal Behaviour* 79 (3): 531-537.

van Oers K, M Klunder, PJ Drent. 2005. Context dependence of personalities: risk-taking behavior in a social and nonsocial situation. *Behavioral Ecology* 16 (4): 716-723.