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UNIVERSITY OF MIAMI

THE EFFECTS OF NURSERY HABITAT LOSS ON JUVENILE LEMON SHARKS, *NEGAPRION BREVIROSTRIS*

By

Kristine L. Stump

A DISSERTATION

Submitted to the Faculty
of the University of Miami
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THE EFFECTS OF NURSERY HABITAT LOSS ON JUVENILE LEMON SHARKS, *NEGAPRION BREVIROSTRIS*

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The Effects of Nursery Habitat Loss on Juvenile Lemon Sharks, *Negaprion brevirostris* (August 2013)

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The lemon shark, *Negaprion brevirostris*, is a large coastal elasmobranch that relies on shallow nearshore nursery areas for increased juvenile survival throughout its range. Habitat loss due to anthropogenic development has occurred globally at large scales, particularly in the coastal zone. In Bimini, Bahamas, where lemon sharks use mangrove-fringed lagoons and creeks as nurseries, the construction of a large resort and marina complex has altered the natural environment through mangrove removal, seabed dredging and the filling of wetlands. The Bimini system is one of the most well-studied in all elasmobranch literature. Given the wealth of pre-disturbance data, this study was a unique opportunity to quantify potential changes in lemon shark survival, growth, movement and prey resource availability in response to habitat loss. A telemetry study showed that despite the disturbance, juvenile lemon sharks continued to show strong site fidelity to the degraded nursery. However, a before-after control-impact (BACI) analysis of the marine faunal community showed that since the disturbance, there have been significant changes in overall community structure, as well as significant declines in multiple taxa. Mojarra, the most important prey item for juvenile lemon sharks within the nursery, experienced one of the most dramatic declines. A BACI analysis showed that post-disturbance, juvenile lemon shark annual growth rate within the degraded

nursery declined. In addition, survival models suggested that the disturbance negatively affected annual survival, particularly for the young-of-year, driving estimates to values which indicate that the anthropogenic disturbance lowered the nursery's ability to provide ample recruits to adult populations. With the threat of continued development within Bimini's lemon shark nurseries, it is important to consider precautionary management principles. Because many marine species rely on coastal habitats at some or even all life stages, the loss or degradation of these areas can have significant negative consequences on biodiversity. As one of the top predators within the system, lemon sharks are an important indicator of overall ecosystem health. In Bimini, juvenile lemon sharks are obligate residents of a nursery that has been degraded in terms of quality, complexity and resources, and these changes have had negative effects on their growth and survival. Habitat loss, particularly from anthropogenic disturbances, is likely one of the most significant threats to lemon shark populations. The protection of essential nursery habitats in Bimini may be critical to effective conservation and management of this species, and the importance of Bimini's lagoons as essential fish habitat in a nursery capacity should be weighed against future development plans.

For mom –
for your inspiration, confidence and unconditional love

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Thank you to the people of Bimini for making your island in the stream a wonderful home for the three years I was lucky enough to be on the rock with you. Special thanks to the Guerrier family for your infectious smiles.

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Chapter 1. Introduction

Habitat loss due to anthropogenic development has occurred globally at large scales, particularly in the coastal zone (Airoldi et al. 2008). Because many marine species rely on coastal habitats at some or even all life stages, the loss or degradation of these areas can have significant negative consequences on marine biodiversity (see Gray 1997 for a review). The response of each species to habitat loss is likely varied and dependent on many factors, including species-specific life history strategies. The lemon shark, *Negaprion brevirostris*, is a large coastal elasmobranch that relies on shallow nearshore nursery areas throughout its range for increased survival of its neonates and juveniles (Compagno 1984). In parts of its range, however, these nursery areas have been degraded by anthropogenic development. Given the wealth of research on lemon shark early life history (Appendix), this study aims to investigate the response of nursery-bound young-of-year and juvenile lemon sharks to nursery habitat degradation and loss. The specific aims of this research were to:

1. Investigate the effects of nursery habitat loss on young-of-year and juvenile lemon shark survival and growth (Chapter 2);
2. Determine if habitat loss resulted in changes to juvenile lemon shark prey availability (Chapter 3);
3. Compare young-of-year and juvenile lemon shark spatial movements before and after nursery habitat loss (Chapter 4); and
4. Employ an experimental design to determine the degree to which juvenile lemon sharks use the subtidal structural complexity within their nursery habitat as a refuge from predators (Chapter 5).

Many studies assessing the effects of anthropogenic disturbance lack data prior to the disturbance and must make comparisons to similar intact areas (e.g., Wiens & Parker 1995, Airoldi et al. 2008). In Bimini, Bahamas (Figure 1.1), where lemon sharks use the mangrove-fringed lagoons and creeks as nursery areas, a wealth of pre-disturbance data exist for both an area subjected to coastal development and nearby undisturbed nurseries (see Appendix). Therefore, this study was a unique opportunity to quantify actual changes in response to habitat loss in terms of survival, growth, movement and resource availability.

1.1 Sharks and nursery areas

To increase the effectiveness of species-specific and ecosystem-based management, there is a need to better identify and understand nursery habitats. Specifically, for an area to be considered a nursery, it must support a higher contribution of recruitment to adult populations than surrounding habitats through density, growth, increased juvenile survival, movement to adult habitats or any combination of these factors (Beck et al. 2001). The idea that some elasmobranch species use nursery areas was proposed as early as the turn of the 20th century (Meek 1916). Since then, there have been numerous studies investigating the use of nursery areas by many shark species (see Heupel et al. 2007 for a review). For continuity within the discipline and to provide a basis for testable hypotheses, Heupel et al. (2007) outlined three criteria which must be met in order for an area to be classified as a shark nursery:

1. Juvenile sharks must be encountered more commonly in the area in question than in other areas.

2. There must be a tendency for juvenile sharks to remain or return for long periods.
3. The area must be used by juvenile sharks repeatedly across years.

Using these guidelines, many shark species, including lemon sharks, have been confirmed as using nursery areas (McCandless et al. 2007 and references therein).

1.2 Mangroves as nursery habitat

Globally, in tropical and subtropical coastal marine environments, mangroves and adjacent habitats are important for many fish and invertebrates, particularly as nursery or intermediate environments for juveniles (see Faunce & Serafy 2006 and Nagelkerken et al. 2008 for reviews). An important functional role of subtidal mangrove habitat is as a complex structure that facilitates individuals' abilities to balance prey acquisition and refuging from larger predators (Laegdsgaard & Johnson 2001, Cocheret de la Moriniere et al. 2004). Many adult reef fishes are found in higher densities on reefs when there is mangrove habitat available nearby (Nagelkerken 2000, Nagelkerken & van der Velde 2002, Mumby et al. 2004, Dorenbosch et al. 2004), and commercial fisheries landings of species that use mangroves as nursery habitat are positively correlated with the amount of nearby mangrove shoreline (Aburto-Oropeza et al. 2008). An estimated 30-50% of global mangrove forests have been destroyed due to anthropogenic coastal development in the past 50 years (Valiela et al. 2001, Alongi et al. 2002, Donato et al. 2011). Research has shown significant declines in species richness and relative abundances in cleared sites (Williamson et al. 19994, Huxham et al. 2004, Shinnaka et al. 2007), and even partial clearing can have significant effects on community structure (Taylor et al. 2007).

1.3 Study site

In Bimini, Bahamas, an island group on the westernmost edge of the Great Bahama Bank (Figure 1.1), the mangrove-fringed lagoons and creeks provide nursery habitat for a number of species, including lemon sharks. Dominated by the red mangrove, *Rhizophora mangle*, a 3 km^2 lagoon known as the North Sound (Figure 1.1) is of particular importance not only to juvenile lemon sharks, but also to many other species of ecological, commercial and conservation concern (Afonso & Gruber 2007, Jennings et al. 2012). Since 1997, the construction of a large resort and marina complex has altered the natural environment, including significant seabed dredging and excavation for a deep navigational channel along the western edge of Bimini's main lagoon in 2001 (Gruber & Parks 2002). In 2005, the development encroached into the North Sound, where approximately 39% of the nursery's mangrove shoreline was cleared and filled (Figure 1.1, Jennings et al. 2012). Both the 2001 and 2005 construction pulses were conducted with little to no environmental mitigation such as silt curtains or turbidity barriers (Gruber & Parks 2002 and see Figure 3.2 of this work).

1.4 Study species

The lemon shark (*Negaprion brevirostris*) is a large coastal species ranging from New Jersey to Brazil (including the Gulf of Mexico) in the western Atlantic, the Gulf of California to Ecuador in the eastern Pacific, and in some areas along the coast of western Africa in the eastern Atlantic (Bigelow & Schroeder 1948, Springer 1950, Compagno 1984). It is a placentally viviparous carcharhinid that reproduces on a biennial cycle with a polyandrous mating system (Feldheim et al. 2004, DiBattista et al. 2008a). Like many carcharhinids, the lemon shark relies on nursery areas to maximize survival of the earliest life stages (Compagno 1984, Wetherbee et al. 2007, Reyier et al. 2008). Though adults are migratory over long distances, gravid adult females show strong philopatry to specific nursery grounds (Feldheim et al. 2002), possibly to natal nurseries (Feldheim et al. submitted). Litter size is typically between seven and 17, and pups are born at total lengths (TL) of approximately 55 – 65 cm after a ten to 12 month gestation period (Springer 1950, Compagno 1984). The lemon shark is a slow-growing species, with annual juvenile growth rate varying by location from approximately 3 to 11 cm/yr in Bimini, Bahamas; 20 cm/yr in Marquesas Keys, FL; and 21 – 27 cm/yr in Atol das Rocas, Brazil (Barker et al. 2005, Freitas et al. 2006). Maturity is reached at approximately 224 cm TL for males and 239 cm TL for females, or at ages of about 12 and 13 years, respectively (Compagno 1984, Brown & Gruber 1988). There is typically spatial separation in the activity spaces of juveniles, large juveniles and adults (Gruber et al. 1988, Franks 2007, Wetherbee et al. 2007, Reyier et al. 2008, Kessel et al. 2009, Guttridge et al. 2012), but where overlap does occur, lemon sharks can be cannibalistic (Vorenberg 1962).

The International Union for the Conservation of Nature (IUCN) classifies the lemon shark as Near Threatened. In parts of its range, the lemon shark is afforded protection. For example, in 2011, the entire archipelago of The Bahamas became a shark sanctuary, where the commercial harvest of any shark species was explicitly prohibited. In the United States, the harvest of lemon sharks was prohibited within Florida state waters in 2012. At the federal level, the National Oceanic and Atmospheric Administration’s (NOAA) Atlantic Highly Migratory Species (HMS) Management Plan specifically designates areas as essential fish habitat (EFH) for neonate and juvenile lemon sharks extending throughout most of both coasts of Florida and into parts of Louisiana and Texas (NOAA/NMFS 2009).

The mangrove-fringed lagoons and creeks of Bimini, Bahamas are an important nursery site for lemon sharks, and the system is one of the most well-studied in all elasmobranch literature (Castro 2011 and Appendix of this work). Neonates born in one of several of Bimini's specific nursery areas, including the North Sound, Sharkland, South Bimini, Pirate's Well and Bonefish Hole (Figure 1.1), are strongly site-attached to natal nurseries. Individuals remain almost exclusively within primary nurseries for up to three years following birth (Morrissey & Gruber 1993a, Gruber et al. 2001, Franks 2007, Chapman et al. 2009). One factor suspected to be an important driver of the residency period within these nurseries is the comparatively higher density of larger juveniles in the main lagoon (Figure 1.2; Franks 2007). By remaining within a more constrained primary nursery area, small juveniles may be decreasing the likelihood of encounters with these potential predators (Franks 2007, Guttridge et al. 2012).

While residents of primary nurseries, juveniles maintain relatively small (approximately 1 km^2) overlapping home ranges, with high reuse of areas along the mangrove fringe and no displays of territoriality (Morrissey & Gruber 1993b, Franks 2007). As juveniles, the sharks' movements are negatively correlated with both depth and distance from shore (Franks 2007), and they have been found to prefer rocky or sandy substrates as well as dense seagrass (Morrissey & Gruber 1993b, Franks 2007). Displacement studies have demonstrated that juvenile lemon sharks experimentally removed from Bimini and released at distances up to 16 km from their home range return to their nursery sites (Edrén & Gruber 2005).

Teleosts constitute the majority of juvenile lemon shark diet, followed by crustaceans (Cortés & Gruber 1990). Within Bimini's nurseries, mangrove-associated yellowfin mojarra (*Gerres cinereus*) dominate the diet through selective feeding, though diet can be highly plastic, and juveniles can be more opportunistic if conditions change (Reeve et al. 2009, Newman et al. 2010).

Using mark-depletion methods, Gruber et al. (2001) estimated first year survival in Bimini's nurseries to vary annually between 38% and 65%. Hoenig & Gruber (1990) estimated that if a lemon shark population were to be at equilibrium, young-of-year survival would need to be approximately 39% to maintain population stability. If first year survival is above this approximated level, it is likely that an important functional role of Bimini as a lemon shark nursery includes providing habitat for increased juvenile survival for future recruitment to the wider lemon shark population.

1.5 Dissertation structure

While much is known about the early life history of lemon sharks while they are restricted to nursery habitat in Bimini, it is not known how these sharks have responded to habitat degradation and loss. The four data chapters that follow use the abundant information on juvenile lemon sharks in Bimini, Bahamas (see Appendix) to determine what effects, if any, the loss of nursery habitat might have on resident young-of-year and juveniles in terms of survival, growth, prey availability, site fidelity and home range.

The availability of suitable nursery habitat may be a limiting factor for some shark populations (Springer 1967, Castro 1987). In addition, declines in growth have been shown to be indicators of broader habitat quality changes (Schindler et al. 2000, Gilliers et al. 2006). Using an 18-year mark-recapture dataset and a before-after control-impact design (BACI; Bernstein & Zalinski 1983), Chapter 2 explores the effects of large-scale habitat degradation and loss on the survival and growth of young-of-year and juvenile lemon sharks within Bimini's North Sound nursery.

While nursery-bound, neonate and juvenile lemon sharks rely on prey resources within primary nurseries, and many of these prey species are mangrove-associated (see Nagelkerken et al. 2008 for a review). The loss of subtidal mangrove habitat due to anthropogenic development could lead to a decline in many species, including those of particular importance in juvenile lemon shark diet (Williamson et al. 19994, Taylor et al. 2007, Shinnaka et al. 2007). Chapter 3 compares prey availability before and after habitat loss, using a BACI design, to determine if there have been post-disturbance changes in available resources.

Animals' habitat use can influence population dynamics, intra- and interspecific interactions, ecosystem structure and biodiversity (Morris 2003). At the individual level, movements are driven largely by the need to balance foraging opportunities with predation risk (e.g., Werner et al. 1983, Lima & Dill 1990, Bednekoff 2007, Brown & Kotler 2007, Heithaus et al. 2009, Wirsing & Heithaus 2009). Chapter 4 compares pre- and post-disturbance movement data to determine if there has been a change in home range, avoidance of degraded habitat, or emigration from disturbed areas after large-scale mangrove removal and dredge-and-fill within the North Sound nursery.

Laegdsgaard & Johnson (2001) suggested that one of the most important features of subtidal mangrove habitat is its structural complexity, which simultaneously provides foraging opportunities and minimizes predation risk. It has been hypothesized that the use of Bimini's mangrove-fringed lagoons and creeks as nursery areas by lemon sharks is linked to both resource availability and predator avoidance (Morrissey & Gruber 1993a, Franks 2007). While there have been several studies employing artificial mangroves to examine the role of structural refugia against predation for teleosts (e.g., Nagelkerken & Faunce 2008), this has not been tested for a large marine vertebrate. Chapter 5 is the first study to use an artificial mangrove system to investigate a shark's use of subtidal structural complexity as a refuge in the face of predation risk.

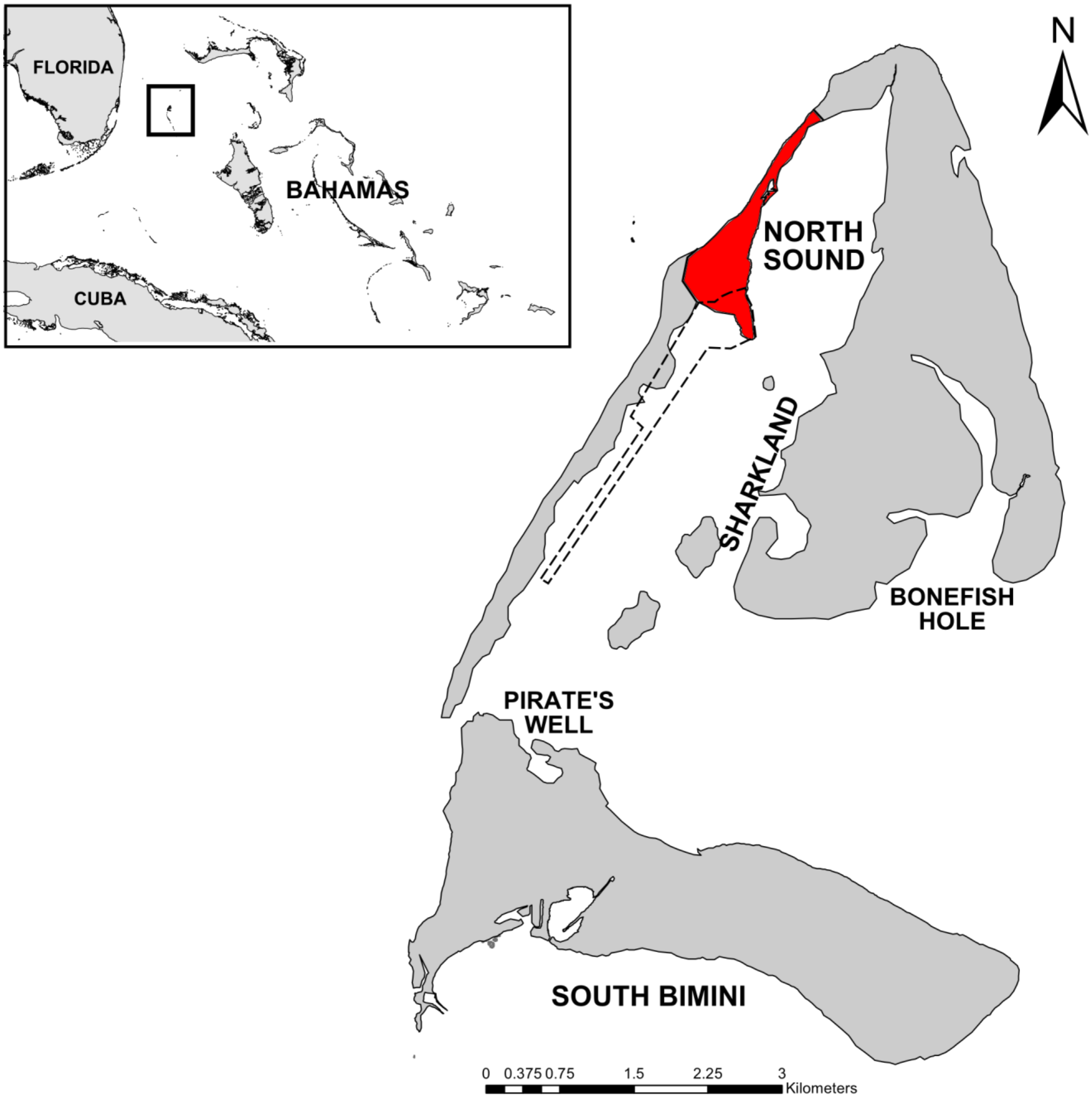


Figure 1.1 Bimini, Bahamas is an island group on the western edge of the Great Bahama Bank, approximately 86 km east of Miami, FL. Labels indicate specific locations of juvenile lemon shark nursery areas within the islands. Red shows the area of 2005 mangrove removal, which was subsequently filled with dredge material. Seabed dredging occurred in 2001 within the area outlined by the dotted line.

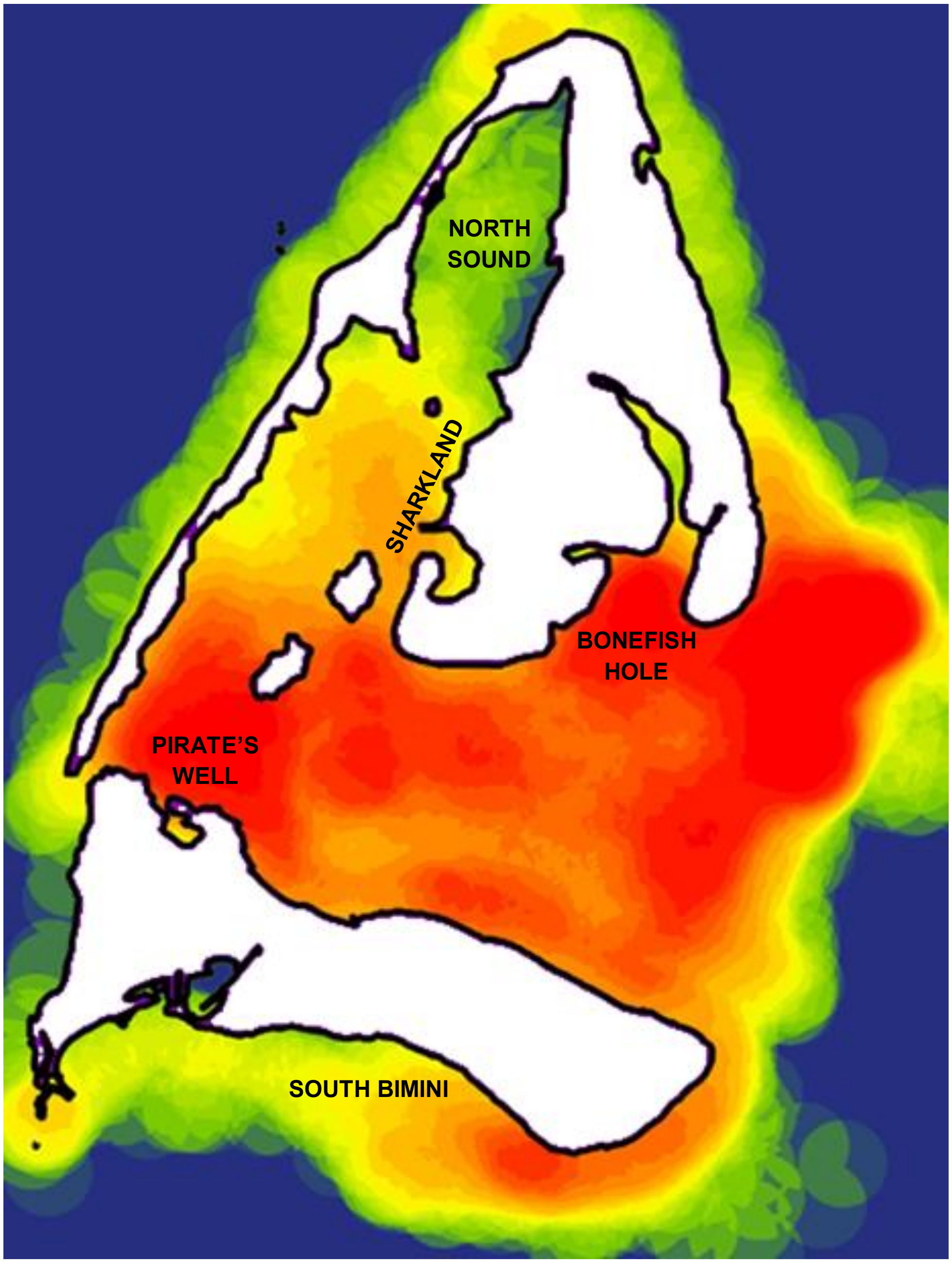


Figure 1.2. Estimated density of large juvenile lemon sharks around Bimini, Bahamas (adapted from Franks 2007). Densities were estimated from telemetry locations of lemon sharks greater than 120 cm total length between 1995 and 2005. Red indicates high numbers of recorded locations. Green indicates lower numbers of telemetry locations.

Chapter 2. Effects of nursery habitat loss on juvenile lemon shark survival and growth

2.1 Background

Many shark species use nursery areas for advantages which include ample prey abundance and protection from larger predators during vulnerable juvenile life stages (Branstetter 1990, Simpfendorfer & Milward 1993, Castro 1993, Heupel & Hueter 2002, Duncan & Holland 2006). The availability of suitable nursery habitat may be a limiting factor for some shark populations (Springer 1967, Castro 1987). In the U.S., since the Magnuson-Stevens Fisheries Conservation and Management Act (MSFCMA) required identification and consideration of essential fish habitat (EFH) for multiple life stages in fishery management plans, there has been an increased need for a better understanding of EFH for many shark species. Understanding the functional role of nurseries as EFH will help improve shark conservation and management (Heupel et al. 2007). In particular, it is important to characterize shark nurseries for coastal species, given the continuing rise of human populations and the concurrent rate of coastal habitat modification (Grubbs & Musick 2007, Heithaus 2007).

The lagoons around the islands of Bimini, Bahamas serve as a lemon shark (*Negaprion brevirostris*) nursery (Figure 2.1). The shallow, mangrove-fringed lagoons and creeks upon which they rely are the only such habitat available on the western side of the Great Bahama Bank. Around Bimini, neonates and juveniles are bound not only to the insular system in general, but also to specific nursery sites within particular bays and lagoons (Morrissey & Gruber 1993a, Franks 2007, Chapman et al. 2009). One of these important nurseries, the North Sound (Figure 2.1), has been subjected to large-scale anthropogenic disturbances during the construction of a resort and marina complex (Gruber & Parks 2002). Extensive dredging, mangrove removal, and wetlands-filling have occurred over several discrete time periods just outside of and within the North Sound.

Globally, habitat degradation and loss have been linked to negative effects on elasmobranchs, including decreased condition, increased pollutant-loading and even population declines (Lowe 2002, Gelsleichter et al. 2005, Simpfendorfer et al. 2010). Declines in growth rates of some fish taxa have also been shown to be indicators of broader ecosystem changes (Schindler et al. 2000, Gilliers et al. 2006). Therefore, it is important to follow the fates of these top predators as juveniles because they are potential indicators of overall ecosystem health. The current study uses long-term mark-recapture data and a before-after control-impact (BACI) design (Bernstein & Zalinski 1983) to study the effects of large-scale habitat degradation and loss on survival and growth of juvenile lemon sharks in a threatened nursery.

2.2 Methods

2.2.1 Study area and sampling

The effects of nursery habitat loss on juvenile lemon shark survival and growth were investigated in two nurseries: (1) the North Sound (NS), which directly experienced habitat loss, and (2) Sharkland (SL), a similar adjacent nursery where no habitat loss occurred (Figure 2.1.). While the two nurseries are adjacent to each other, telemetry data suggests that juvenile lemon sharks generally establish home ranges in one or the other, with little overlap between the two areas (Morrissey & Gruber 1993a, Franks 2007). Therefore, the undisturbed Sharkland nursery was considered in contrast to the disturbed North Sound nursery for before-after comparisons. Each year, from 1995 to 2012, juveniles were captured in both nurseries during annual gillnet surveys between the dates of 23 May and 23 June, shortly after parturition by adult females (Table 2.1). During the annual mark-recapture surveys, juveniles were captured in square mesh monofilament gillnets (180 m x 2 m, 5 cm mesh) following Gruber et al. (2001). Each individual was given an intramuscular, uniquely-coded passive integrated transponder tag (PIT, Destron-Fearing®), which does not affect behavior, survival or growth (Manire & Gruber 1991, Barker et al. 2005). Pre-caudal length (PCL) was recorded along with the PIT tag number on the first and all subsequent captures of each individual. In addition, a small fin clip (approximately 25 mm^2) was collected for DNA extraction used in genetic analyses (e.g., Feldheim et al. 2001, 2002, DiBattista et al. 2008a, Dibattista et al. 2009) and to help determine the juveniles' ages (see section 2.2).

2.2.2 Age determination

Neonate (Age-0) lemon sharks were easily identified by their umbilicus, which is fully open at birth, then slowly closes within the first few months post-parturition (Barker et al. 2005, Figure 2.2). For juveniles first captured as non-neonates, age was determined as follows. First, for sharks caught between 1995 and 2007, a genetic pedigree of sibling litters, reconstructed based on microsatellite analysis, was used to assign a year of birth to each juvenile (Feldheim et al. 2004, DiBattista et al. 2009). Second, for sharks first captured as non-neonates after 2007, beyond the temporal scope of the genetic database, age was assigned based on length-frequency analyses as reported by (Barker et al. 2005). The number of sharks for which age was estimated based on length was only 36 (N_{NS} = 11, N_{SL} = 25), or 1.86% of the total dataset.

2.2.3 Apparent survival and recapture probabilities

Using the program MARK (White & Burnham 1999), a dataset consisting of 1,935 (N_{NS} = 742, N_{SL} = 1193) individual juvenile lemon sharks captured during annual mark-recapture surveys in the North Sound and Sharkland between 1995 and 2012 was used to analyze models of survival and recapture probabilities. Because sharks Age-3 and older are likely to move away from their original nurseries (Morrissey & Gruber 1993a, Franks 2007, Chapman et al. 2009), survival and recapture estimates for this age class are confounded with emigration. Therefore, analyses were restricted to Age-0, Age-1 and Age-2 sharks, which remain highly site-attached. Juveniles generally stay within their natal nursery, but because the North Sound and Sharkland are adjacent to each other, sharks Age-2 and younger are occasionally captured in both. To confidently assign each shark to either the North Sound or Sharkland, individuals caught in both nurseries at any point up to and including Age-2 were excluded. A total of 112 sharks, or 5.5% of the dataset, was excluded in this way. Using similar methods for the mark-recapture data from 1995-2000, DiBattista et al. (2007) found no difference in results when this group was excluded.

For survival estimates in a study in which capture histories are binary (0 = not captured, or 1 = captured), it is important to confirm that there is a high probability of recapturing an individual that is indeed alive and still in the system (Letcher et al. 2005).

A set of seven candidate models (Table 2.2) were run in MARK to determine which of the mechanisms being tested best explains recapture probability (p, probability of catching individuals alive and present in the system) and then to estimate p. With an Akaike's Information Criteria (AIC) weight greater than 0.8, the model in which survival probability varies with age, $p_{(age)}$, was selected (Burnham & Anderson 2002). This recapture model was subsequently used as the recapture probability component in the suite of candidate survival models.

The program MARK was next used to analyze a set of 26 candidate models for apparent survival (phi, probability that individuals were alive and present in the system), which differed in how survival was affected by two major construction (i.e., ecosystem impact) events (Table 2.3). The first event was a large-scale dredging campaign just outside of the North Sound in 2001 (Figure 2.1). The second was large-scale mangrove removal in 2005 within the North Sound, where approximately 67 ha were cleared (Jennings et al. 2012, Figure 2.1). Candidate models allowed for combinations of these two events to have effects on juvenile lemon shark survival for either the year they occurred only (pulse) or continuing for the years following the event (press).

The Cormack-Jolly-Seber model was used as a starting point for apparent survival (Lebreton et al. 1992). Individuals were grouped into six categories according to nursery and age at first capture: NS Age-0, NS Age-1, NS Age-2, SL Age-0, SL Age-1 and SL Age-2. A previous study exploring growth using data from 1995-2006 reported no sex-based differences in juvenile survival (Jennings et al. 2008); therefore, sex was not included in the candidate model structures. All models were run using a sine link function, and variance was estimated using the 2ndPart method, as recommended by

White & Burnham (1999). Model selection was based on AICc weight; if no single model had an AICc weight greater than 0.8, parameter estimates were calculated using model averaging, weighted by the AICc weights (Burnham & Anderson 2002).

2.2.4 *Growth*

Juvenile lemon shark annual growth for three age classes (Age 0-1, Age 1-2 and Age 2-3) in two nurseries (North Sound and Sharkland) was analyzed using the annual mark-recapture dataset from 1995-2012. Annual growth was calculated for each individual from consecutive-year recaptures using the formula,

$$\text{Growth (cm/yr)} = \frac{\text{PCL2} - \text{PCL1}}{\Delta t}\ x\ 365 \qquad \text{(Equation 2.1)}$$

where PCL1 and PCL2 are the pre-caudal lengths at first and second capture occasions, respectively, and Δt is the time, in days, between captures. Similar to the survival analyses, individuals captured in both the North Sound and Sharkland at any point up to and including Age-3 were excluded. Growth data were square root-transformed to achieve normality (Shapiro-Wilks normality test, $p = 0.11$). An analysis of variance (ANOVA) was used to test for the effects of nursery, age, sex, year and the interactions of these factors on juvenile lemon shark growth.

2.3 Results

2.3.1 Recapture and survival probabilities

Of the seven candidate model structures of recapture probability (p), the most highly supported model indicated that recapture probability varies with age only (Table 2.2). Estimates of p for each age class calculated from this model are generally high (Figure 2.3).

Table 2.4 shows results for the candidate survival models. Unlike the recapture probability models, for apparent survival (phi) no one model had more than 80% of the AICc weights. However, two of the models received much stronger support than the others: one in which survival varies with age, nursery and (for North Sound young-of-the-year, YOY) mangrove removal effects (AICc weight = 0.46417) and one in which survival varies only with age and nursery (AICc weight = 0.26380). Model-averaged parameter estimates from the full set of candidate models, dominated by these two top models, show different patterns of age-specific apparent survival (phi) in the two nurseries (Figure 2.4a). Phi increases with age in the North Sound from 0.348 ± 0.03 for Age 0-1, to 0.604 ± 0.10 for Age 2-3 (Table 2.5a). In contrast, apparent survival is fairly similar among age classes in Sharkland, where estimates range only from 0.503 ± 0.02 for Age 0-1, to 0.437 ± 0.06 for Age 2-3. The model-averaged estimate of first-year apparent survival is approximately 44.9% higher in Sharkland than in the North Sound. In contrast, though highly variable due to smaller sample sizes, mean estimates of phi for Age 2-3 are 38.2% higher in the North Sound than in Sharkland.

Based on AICc weights, the best model is the one that includes an effect of 2005 mangrove removal on North Sound YOY survival; this model received 1.76x more support than the second model, in which there are no effects of construction (Table 2.4). The best model shows a marked decline in YOY survival co-occurring with deforestation. Parameter estimates from this model alone are similar to the model-averaged estimates and estimates of the second most-supported model. The exception is North Sound YOY survival from 2005-2006, during the mangrove removal, which the top model estimates to be 0.255 ± 0.05, or 26.7% lower than the model-averaged estimate for young-of-year in all other years (Figure 2.4b, Table 2.5b,c).

Of the factors included in the set of candidate models, nursery, age and construction effects consistently occurred in the best-supported models (Table 2.4). The estimated importance of these factors, based on the total AICc weights of the models in which they appear, strongly suggests that nursery, age and the 2005 mangrove removal were key to the high ranking of the model (Table 2.6). Specifically, based on combined AICc weights, the models in which the 2005 event was a pulse (affecting only that year) rather than a press (continued effects in subsequent years) were more supported (ΣAICc = 0.64143 and 0.06847, respectively). The importance of the effects of the 2001 dredging event, however, did not receive much support. When the data are categorized as before (1995-2004), during (2005-2006) and after (2007-2012) mangrove removal, apparent survival (phi) from the fully model-averaged estimates for each age class in each nursery show the decline in North Sound YOY survival during mangrove removal, while phi estimates both before and after are similar (Table 2.5d , Figure 2.5.). The model-averaged estimates of phi for all other age classes in both nurseries are relatively constant.

2.3.2 Growth

Analysis of variance results (ANOVA) show that there are significant effects of nursery, age and year on juvenile lemon shark growth (Table 2.7). In addition, there is a significant nursery-year interaction effect, indicating differential growth in the two nurseries among years. Sex was not a significant factor affecting growth, a result in agreement with previous studies (Barker et al. 2005, Freitas et al. 2006, Jennings et al. 2008).

Post-hoc pairwise comparisons of mean annual growth values for each age class in each nursery show significant differences (Table 2.8, Figure 2.6). In the North Sound, first-year growth was significantly slower than both Age 1-2 and Age 2-3 growth, while Age 1-2 and Age 2-3 growth did not differ from each other. In contrast, there was no difference in growth among age classes in Sharkland. First year and Age 1-2 growth were significantly slower in the North Sound than in Sharkland, whereas Age 2-3 growth was the same between the nurseries.

Although sample sizes were low in some years, growth increments were calculated for each of three age classes in each nursery for each year (Table 2.9). The data for the full time period 1995 – 2012 show high interannual variability in growth, but within each nursery, the three age classes appear to vary similarly over time (Figure 2.7). Within the North Sound, the lowest growth values recorded when n>1 during the 18-year mark-recapture study were between 2005 and 2007, after large-scale mangrove deforestation. However, these values were not significantly different from other years of the study, except for the five highest (1998-1999, 2002-2003, 2004-2005, 2008-2009 and 2009-2010; post-hoc Tukey test, $p < 0.05$).

Survival analyses suggested that the 2005 mangrove removal in the North Sound was an important event (Table 2.4). Therefore, a before-after control-impact (BACI) comparison was made on juvenile lemon shark growth, using 2005 as the impact date. An ANOVA on data from both nurseries combined showed significant effects of nursery, age and time (Table 2.10, Figure 2.8a). Mean growth after mangrove loss (5.51 ± 0.14 cm/yr, $n = 381$) was significantly lower than mean growth before deforestation (6.53 ± 0.13 cm/yr, $n = 446$). Post-hoc pairwise comparisons showed significant declines in growth before versus after 2005 within in each nursery (Tukey test, $p<0.01$; Figure 2.8b). To see if there was a similar pattern in North Sound YOY growth to the pattern in survival (YOY survival was low in 2005 and 2006, Figure 2.5), an ANOVA was run on the full growth dataset categorized as before (1995 – 2004, $n = 90$), during (2005 – 2006, $n = 19$) or after (2007 – 2012, $n = 68$). Model results show a significant effect of time ($F = 12.153$, $p<0.001$), and despite small sample size ($n = 19$), post-hoc pairwise comparisons detected that North Sound YOY growth in 2005 – 2006 was significantly slower than from 1995-2005 (Tukey test, $p=0.018$, Figure 2.9). However, 2005 – 2006 YOY growth was not significantly different from YOY growth between 2006 and 2012, nor were the before and after periods significantly different from each other (Tukey test, $p>0.05$).

2.4 Discussion

Using a long-term (18-year) mark-recapture dataset, the survival and growth of juvenile lemon sharks in a nursery experiencing major anthropogenic disturbance were explored. Survival model results suggest that large-scale mangrove removal within the North Sound nursery in 2005 negatively affected the juvenile lemon sharks therein, particularly young-of-year. In addition, a BACI analysis showed significant decreases in juvenile lemon shark growth rate in both the North Sound and the adjacent, but intact, Sharkland nursery after habitat loss occurred.

2.4.1 Survival

The survival model parameter estimates are likely robust to the important potential bias of emigration. Only the first three age classes were included in the analyses, and these are known to be highly site-attached, with little movement beyond the primary nursery (Morrissey & Gruber 1993a, Franks 2007). Individuals are occasionally captured in both the North Sound and Sharkland because of their close proximity to each other, but these sharks, up to and including Age-2 were excluded, thereby reducing the confounding effects of temporary emigration. In addition, model estimates of recapture probability (p) show there was a high probability of recapturing tagged individuals that survived and remained in the system.

Using mark-depletion analysis methods, Gruber et al. (2001) estimated YOY survival to be between 38 and 65%. Using the program MARK, DiBattista et al. (2007) estimated North Sound YOY survival to fall between 48 and 70%. Estimates from the current study are lower, with values from 25.5 to 35.7%. One possible reason for the difference is that the previous two studies used mark-recapture data from 1995 to 1999 and 1995 to 2000, respectively, so the full range of natural variation in annual survival was not represented as well as in the dataset which includes an additional 12 years. The current dataset also includes the length of time for neonates captured in 1995 to reach maturity, and there is evidence of Bimini-born females returning to the nurseries to give birth (Feldheim et al., submitted). Another possible reason for lower survival estimates in the current study is that both of the previous studies analyzed data collected prior to major habitat loss in the North Sound, and current estimates do in fact show real changes in the system since construction began. The survival model selection results show strong support for an effect of the 2005 mangrove removal on North Sound YOY survival. This top model is almost twice as supported as the second model, which includes the effects of age and nursery only. Based on the sums of AICc scores for models in which they appear, there is very strong support for differential effects of age and nursery on juvenile survival (Table 2.6), and YOY within the North Sound appear to be the most negatively affected by the 2005 habitat loss (Figure 2.5).

Despite the potential deleterious effects of dredging, including direct disturbance, water quality deterioration, sedimentation, trace metal release and smothering siltation (MacDonald et al. 1997, Riegl and Piller 2000, Feldheim and Edrén 2002, Gruber et al. 2002, Parsons 2004), the 2001 seabed excavation was not as strongly supported by the models as a major factor explaining changes in juvenile survival over time. This result is somewhat in contrast to the previous report of a decrease in North Sound YOY survival after dredging occurred. Using a survival regression analysis with blocked effects for year of capture, Jennings et al. (2008) reported a significant 23.5% decrease in North

Sound YOY survival from before (1995–2000) to after (2001–2006) when the 2001 dredging event was used as the impact in a BACI design. In the current study, using MARK to analyze data from 1995 to 2012, the effects of the 2001 dredging are not as strongly represented (Table 2.6). There are several possible reasons for this difference. First, the previous study was based on a smaller dataset encompassing a 12-year period. The expanded 18-year dataset may include a greater degree of variability in annual survival, thereby masking effects of the 2001 dredging. Second, the magnitude of the effects of 2005 mangrove removal on North Sound young-of-year, as predicted by model-averaged survival estimates, may overwhelm the effects of dredging, which may be small by comparison. Third, it is possible that despite the highly destructive dredging, including a 17% decrease in seagrass cover in the North Sound (Jennings et al. 2008), the majority of the impact was outside of the nursery (Figure 2.1), and juvenile lemon sharks were spared the most drastic effects.

Nursery-bound juvenile lemon sharks in Bimini rely on mangrove-associated species for prey (Cortés & Gruber 1990, Franks 2007, Newman et al. 2010), and also on subtidal mangrove structure and creeks as refugia from predators (Guttridge et al. 2012 and see Chapter 5, this work). It is not surprising that model results support the scenario in which the loss of a large portion of nursery habitat to anthropogenic development would have an effect on the juvenile lemon sharks, particularly young-of-year within the affected nursery. If habitat loss were indeed an important event within the North Sound, it is possible that survival estimates could be driven lower by emigration of juveniles out of the North Sound in search of more suitable habitat at earlier ages. However, it is unlikely that increased emigration out of the North Sound drives survival estimates for two reasons. First, the closest non-degraded habitat is the adjacent Sharkland nursery, and individuals captured in both the North Sound and Sharkland before Age-3 were excluded. Movement to other locations is unlikely, given the increased predation risk beyond the primary nursery (see Figure 1.2). In addition, no North Sound or Sharkland juvenile was ever captured in another nursery during extensive sampling for concurrent studies (Stump, unpublished data). Second, telemetry data show continued high site-fidelity to the North Sound for residents of all three age classes analyzed, even after the 2005 mangrove removal (see Chapter 4, this work).

Model-averaged estimates of survival indicate an average 18.75% decrease in mean survival for North Sound YOY in the year of the mangrove removal (Table 2.5d, Figure 2.5). Density-dependence was not addressed in the survival models. If first-year survival were in fact density-dependent, a coincidental higher neonate input concurrent with mangrove removal could potentially confound model results. The lower North Sound YOY survival between 2005 and 2006 could be due to (a) a larger number of individuals competing for resources, (b) a decline in habitat quality and resource availability due to habitat loss, (c) loss of natural refugia from predators, or (d) a combination of the three. Results of the growth analyses presented here, as well as resource data (Chapter 3) and risk effects data (Chapter 5), suggest that the decrease in survival is most likely a combination of these factors.

Using a Leslie matrix model, Hoenig & Gruber (1990) estimated that if a lemon shark population were to be at equilibrium, YOY survival would have to be approximately 39% to maintain a population stability. Prior to habitat loss in Bimini's North Sound nursery, first-year survival estimates were calculated to be 38-65% using mark-depletion methods (Gruber et al. 2001) and 48-70% using model-averaged estimates from candidate survival models evaluated with the program MARK (DiBattista et al. 2007). In both of these studies, despite non-trivial mortality, estimates of first-year survival were generally above the Leslie matrix approximation of 39% required for a stable population. The model-averaged estimate of North Sound YOY survival from the present study, which includes mark-recapture data over the course of two large-scale construction events, is approximately 35% (Table 2.5a). This value is just below the threshold predicted by the Leslie model to be necessary for population stability. In the most strongly supported model, North Sound YOY survival during the year of mangrove removal is pushed downward to approximately 25.5%, well below the predicted level necessary for stability (Table 2.5b). Although there is some uncertainty associated with the Leslie matrix approximation, current survival model estimates suggest that North Sound YOY survival generally hovers on the edge of contributing to this estimate for population sustainability, and large-scale anthropogenic disturbances could have negative consequences on the North Sound nursery's ability to recruit to the adult population. In contrast, first-year survival in the adjacent Sharkland nursery is estimated to be approximately 50% over time (Table 2.5a), and model-averaged estimates indicate that YOY survival was not negatively affected by the 2005 mangrove removal in the North Sound (Table 2.5d). Therefore, the burden of recruitment may fall more heavily on the non-degraded Sharkland nursery.

2.4.2 Growth

Annual growth rates were examined for three age classes of juvenile lemon sharks in two Bimini nurseries using an 18-year mark-recapture dataset encompassing multiple years of anthropogenic disturbances. In agreement with a previous study conducted on a smaller dataset prior to habitat loss, overall mean growth rates from Age 0-1 and Age 1-2 were slower in the North Sound than in Sharkland, but the same in both nurseries for Age 2-3 (Barker et al. 2005). While growth was the same among age classes within Sharkland, YOY sharks grew significantly slower than Age 1-2 and Age 2-3 sharks in the North Sound. ANOVA results showed that growth was affected by nursery, age and year. In addition, there was a significant interaction effect of nursery and year, indicating that there were nursery-specific differences in growth over time.

There was a high degree of interannual variability in growth over the 18-year sampling period. Sample sizes for many individual years were small (Table 2.9), which may partly explain why statistical tests could not detect significant differences among any but the highest and lowest years. However, age classes appeared to vary similarly year-by-year within nurseries (Figure 2.7), suggesting that local environmental conditions may be a driving factor in annual growth rates. Indeed, there can be connections between environmental conditions and biological responses in terms of elasmobranch growth rate (Hoenig & Gruber 1990), and changes in growth can indicate more broad changes in the environment (Schindler et al. 2000, Gilliers et al. 2006). Despite high interannual variation, a BACI analysis using the 2005 North Sound mangrove removal as the impact showed there was a significant overall decrease in growth since deforestation (Figure 2.2a), and post-hoc tests showed that each nursery experienced a decline in mean annual growth after 2005 (Figure 2.2b). Despite a small sample size, a significant decrease in growth was detected between 1995-2004 and 2005-2006, during mangrove removal (Figure 2.9). However, from 2007 – 2012, growth recovered to pre-deforestation levels.

This recovery is consistent with the survival model selection results that indicated the 2005 disturbance was a pulse rather than a press.

The significant decrease in North Sound YOY growth between 2005 and 2006 could be the result of a) increased numbers of juveniles competing for resources, b) a decline in prey availability or quality due to habitat loss, c) changes in foraging behavior caused by loss of refugia, or d) a combination of several factors. In order to lend support to one hypothesis over another, future work should explore the energetic needs for different age classes and relate those needs prey production in the North Sound. A diet study is also needed to ascertain if there was a shift in mean trophic level or trophic web to less energetically profitable prey in the diet of juvenile lemon sharks concurrent with habitat degradation.

2.5 Conclusion

With the threat of continued development within Bimini's lemon shark nurseries, it is important to consider precautionary management practices. As top predators within the insular system, lemon sharks are an important indicator of overall ecosystem health. Bimini's mangrove-fringed lagoons and creeks are the only such habitat on the western edge of the Great Bahama Bank. Juvenile lemon sharks appear not to move even between the primary nurseries in Bimini (Chapter 4), and there is no evidence that they would be able to move to other island systems. Because of the increased predation risk at even moderate distances from primary nurseries (see Figure 1.2, Gruber et al. 1988, Franks 2007, Guttridge et al. 2012), there is no viable alternative habitat within a reasonable distance of Bimini. Even if there were, displacement studies demonstrated that juvenile lemon sharks experimentally removed from Bimini and released at distances up to 16 km from their home range homed back to their original nursery sites (Edrén & Gruber 2005). It is not until approximately Age-6 that lemon sharks, as large juveniles, generally disperse to a wider area (Franks 2007, Chapman et al. 2009). It is not known to which geographical population or metapopulation Bimini juveniles recruit, as individuals are highly migratory after leaving shallow, coastal nurseries (Feldheim et al. 2002, Chapman et al. 2009). In 2011, The Bahamas established a shark sanctuary, banning shark-fishing throughout the country's Exclusive Economic Zone. Nearby, in 2010, Florida enacted legislation prohibiting the harvest of lemon sharks in state waters. While they are measures aimed at protecting older lemon sharks, a species listed by the International Union for the Conservation of Nature (IUCN) as near-threatened, they may not be enough to maintain stable populations if important nursery habitats are degraded to the point that they cannot produce enough viable recruits to adult populations. YOY and juvenile survival is related to population size (Gedamke et al. 2007), and even minor changes in YOY survival estimates can have significant effects on population dynamics (Hoenig & Gruber 1990). Habitat loss, particularly from anthropogenic disturbances, is likely one of the most significant threats to lemon shark populations. Therefore, management scenarios should consider multiple life stages, including neonates and juveniles. The protection of essential nursery habitat for juvenile lemon sharks in Bimini should be strongly considered in conservation and management efforts for the species, and the importance of Bimini's lagoons as essential fish habitat in a nursery capacity should be weighed against future development plans.

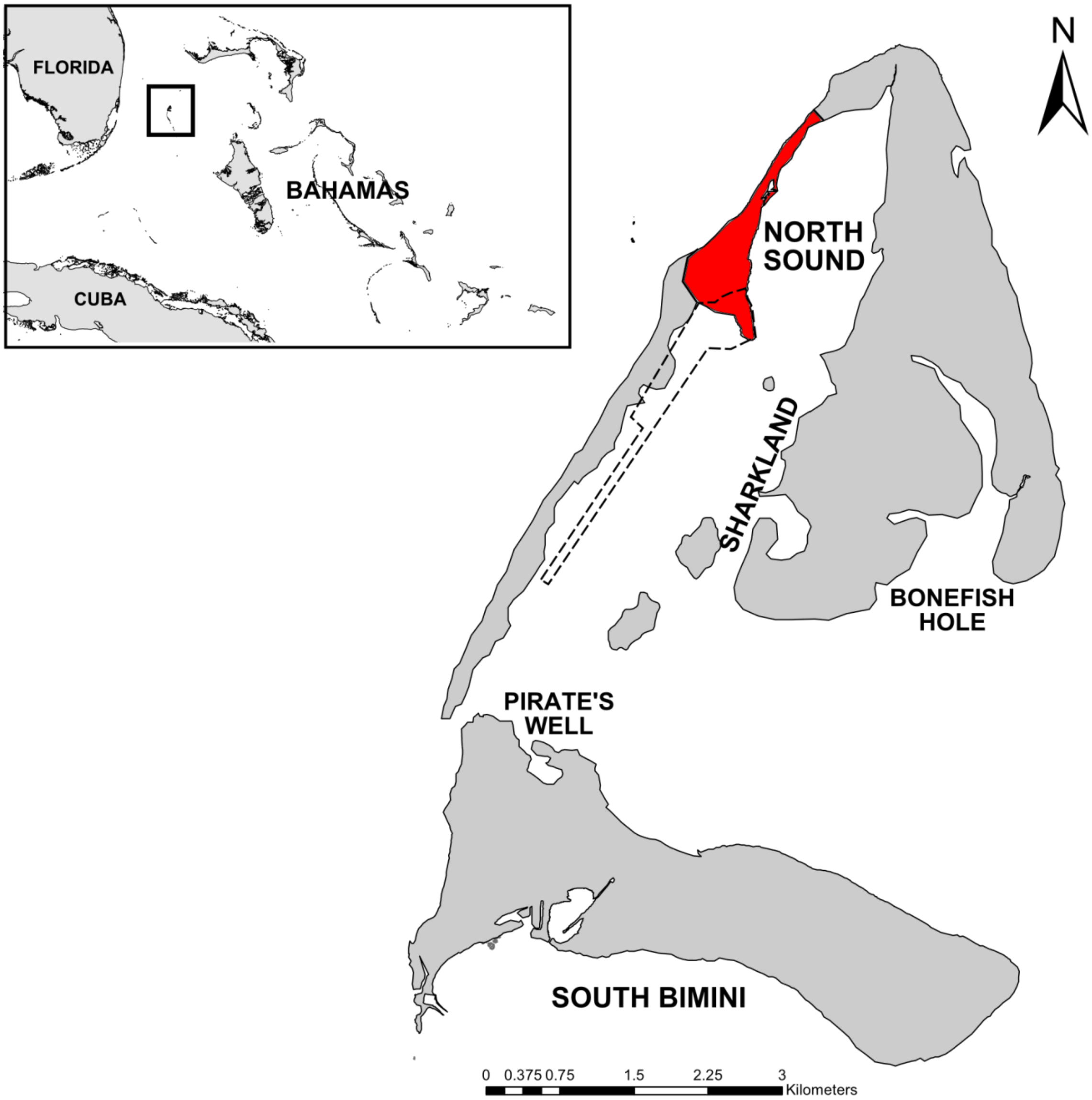
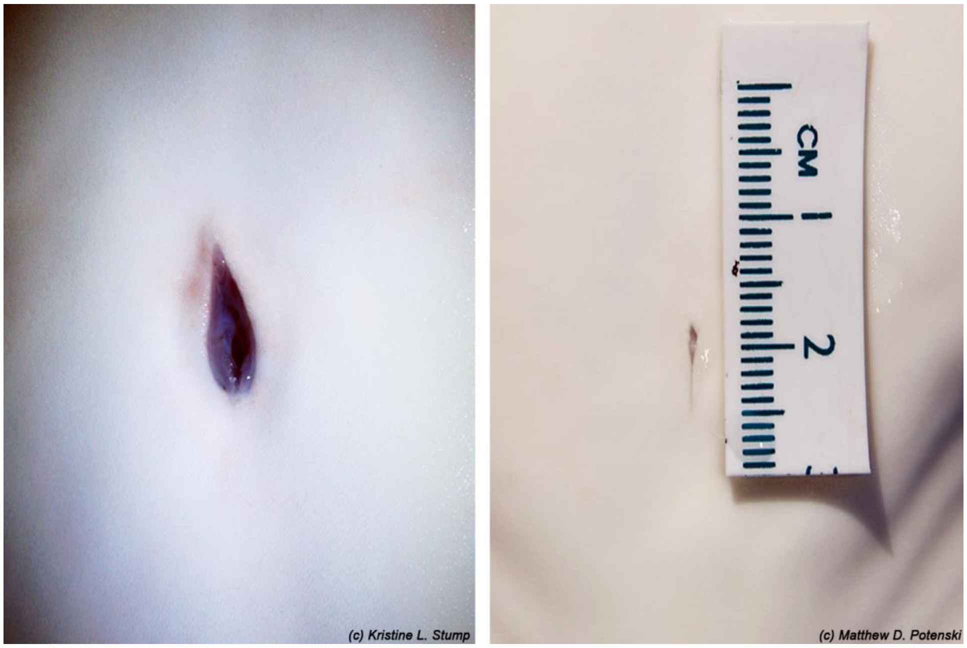


Figure 2.1. Bimini, Bahamas is an island group on the western edge of the Great Bahama Bank, approximately 86 km east of Miami, FL. Labels indicate specific locations of juvenile lemon shark nursery areas within the islands. Red shows the area of 2005 mangrove removal, which was subsequently filled with dredge material. Seabed dredging occurred in 2001 within the area outlined by the dotted line.

Table 2.1. Annual juvenile lemon shark mark-recapture sampling dates in the North Sound and Sharkland.

Year	North Sound	Sharkland
1995	2 - 5 June	7 - 11 June
1996	23 - 31 May	2 - 10 June
1997	26 May - 2 June	4 - 11 June
1998	26 May - 2 June	4 - 10 June
1999	25 - 29 May	31 May - 6 June
2000	21 - 29 May	21 May - 8 June
2001	5 - 10 June	13 - 21 June
2002	5 - 13 June	16 - 22 June
2003	9 - 19 June	31 May - 7 June
2004	4 - 10 June	13 - 22 June
2005	7 - 13 June	17 - 23 June
2006	10 - 19 June	1 - 8 June
2007	6 - 13 June	16 May - 4 June
2008	7 - 14 June	17 - 24 June
2009	3 - 10 June	13 - 20 June
2010	14 - 21 June	4 - 11 June
2011	7 - 14 June	26 May - 3 June
2012	1 - 7 June	13 - 20 June



(c) Kristine L. Stump

(c) Matthew D. Potenski

Figure 2.2. Examples of neonate umbilical scars. Left: fully open umbilical scar on a recently-born neonate. Right: half-closed umbilical scar on a neonate several weeks after birth.

Table 2.2. Model selection for estimating recapture probability (p) of three juvenile lemon shark age classes in the North Sound and Sharkland. Seven discrete recapture models were tested: (1) recapture probability is constant ($p_{(.)}$); (2) recapture probability varies with time ($p_{(t)}$); (3) recapture probability varies with age ($p_{(age)}$); (4) recapture probability varies with nursery ($p_{(nursery)}$); (5) recapture probability varies with birth cohort ($p_{(cohort)}$); (6) recapture probability varies with age and nursery but not birth cohort ($p_{(age+nursery)}$); and (7) recapture probability varies with age, nursery and cohort ($p_{(age+nursery+cohort)}$). Survival probabilities were set as constant through time, but different among age classes and nurseries for all models. Based on an Akaike's Information Criteria (AICc) weight of 0.881, the model in which recapture probability varies with age ($p_{(age)}$, in bold) was selected and used in all survival model structure tests.

Model	AICc	Delta AICc	AICc Weight	Model Odds Ratio	Number of parameters
$p_{(.)}$	4323.351	10.095	0.006	0.006	11
$p_{(t)}$	4339.495	26.240	0.000	0.000	26
$\mathbf{p_{(age)}}$	**4313.255**	**0.000**	**0.881**	**1.000**	**13**
$p_{(nursery)}$	4324.103	10.848	0.004	0.004	12
$p_{(cohort)}$	4333.952	20.697	0.000	0.000	28
$p_{(age+nursery)}$	4317.435	4.180	0.109	0.124	16
$p_{(age+nursery+cohort)}$	4389.182	75.927	0.000	0.000	109

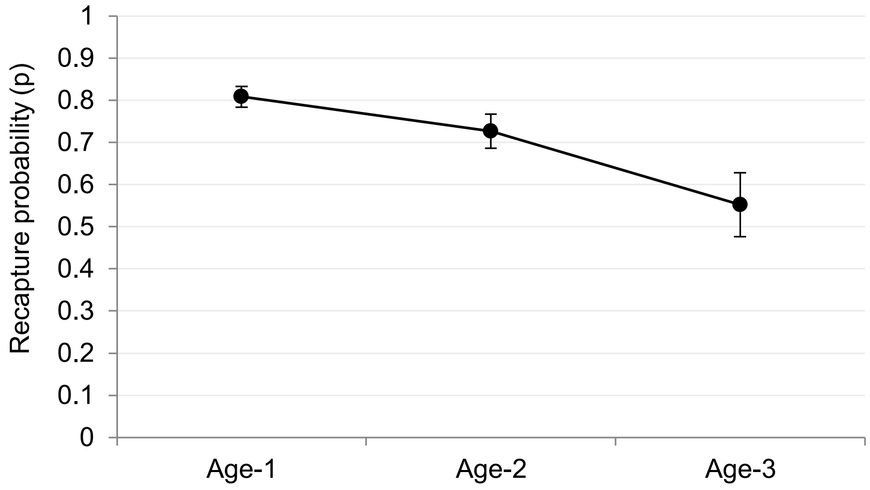
Table 2.3. Model descriptions for the 26 candidate survival models run on the 1995-2012 juvenile lemon shark mark-recapture dataset. NS = North Sound, YOY = young-of-year

Models Without Disturbance Effects	**Model Description**
phi$_{(.)}$	Survival is constant
phi$_{(t)}$	Survival varies with time
phi$_{(\text{cohort})}$	Survival varies with birth cohort
phi$_{(\text{age})}$	Survival varies with age
phi$_{(\text{nursery})}$	Survival varies with nursery
phi$_{(\text{age+nursery})}$	Survival varies with both age and nursery

Models with 2001 and 2005 Disturbance Effects	**Model Description**
phi$_{(\text{disturbance})}$ - 2001 pulse, 2005 pulse	Survival varies with disturbance; disturbance effects are restricted to the years 2001 and 2005 only
phi$_{(\text{disturbance})}$ - 2001 pulse, 2005 press	Survival varies with disturbance; 2001 effects are restricted to that year, and 2005 effects persist through 2012
phi$_{(\text{age+disturbance})}$ - 2001 pulse, 2005 pulse	Survival varies with age and disturbance; disturbance effects are restricted to the years 2001 and 2005 only
phi$_{(\text{age+disturbance})}$ - 2001 pulse, 2005 press	Survival varies with age and disturbance; 2001 effects are restricted to that year, and 2005 effects persist through 2012
phi$_{(\text{nursery+disturbance})}$ - 2001 pulse, 2005 pulse	Survival varies with nursery and disturbance; disturbance effects are restricted to the years 2001 and 2005 only
phi$_{(\text{nursery+disturbance})}$ - 2001 pulse, 2005 press	Survival varies with nursery and disturbance; 2001 effects are restricted to that year, and 2005 effects persist through 2012
phi$_{(\text{age+nursery+disturbance})}$ - 2001 pulse, 2005 pulse	Survival varies with age, nursery and disturbance; disturbance effects are restricted to the years 2001 and 2005 only
phi$_{(\text{age+nursery+disturbance})}$ - 2001 pulse, 2005 press	Survival varies with age, nursery and disturbance; 2001 effects are restricted to that year, and 2005 effects persist through 2012
phi$_{(\text{age+nursery+disturbance/NS/YOY})}$ - 2001 pulse, 2005 pulse	Survival varies with age and nursery, with disturbance effects on North Sound young-of-year only; disturbance effects are restricted to the years 2001 and 2005 only
phi$_{(\text{age+nursery+disturbance/NS/YOY})}$ - 2001 pulse, 2005 press	Survival varies with age and nursery, with disturbance effects on North Sound young-of-year only; 2001 effects are restricted to that year, and 2005 effects persist through 2012

Table 2.3 (continued)

Models with 2005 Construction Effects Only	**Model Description**
phi$_{\text{(disturbance)}}$ - 2005 pulse	Survival varies with disturbance; disturbance effects are restricted to the year 2005
phi$_{\text{(disturbance)}}$ - 2005 press	Survival varies with disturbance; 2005 disturbance effects persist through 2012
phi$_{\text{(age+disturbance)}}$ - 2005 pulse	Survival varies with age and disturbance; disturbance effects are restricted to the year 2005
phi$_{\text{(age+ disturbance)}}$ - 2005 press	Survival varies with age and disturbance; 2005 disturbance effects persist through 2012
phi$_{\text{(nursery+ disturbance)}}$ - 2005 pulse	Survival varies with nursery and disturbance; disturbance effects are restricted to the year 2005
phi$_{\text{(nursery+ disturbance)}}$ - 2005 press	Survival varies with nursery and disturbance; 2005 disturbance effects persist through 2012
phi$_{\text{(age+nursery+ disturbance)}}$ - 2005 pulse	Survival varies with age, nursery and disturbance; disturbance effects are restricted to the year 2005
phi$_{\text{(age+nursery+ disturbance)}}$ - 2005 press	Survival varies with age, nursery and disturbance; 2005 disturbance effects persist through 2012
phi$_{\text{(age+nursery+ disturbance/NS/YOY)}}$ - 2005 pulse	Survival varies with age and nursery, with disturbance effects on North Sound young-of-year only; disturbance effects are restricted to the year 2005
phi$_{\text{(age+nursery+ disturbance/NS/YOY)}}$ - 2005 press	Survival varies with age and nursery, with disturbance effects on North Sound young-of-year only; 2005 disturbance effects persist through 2012



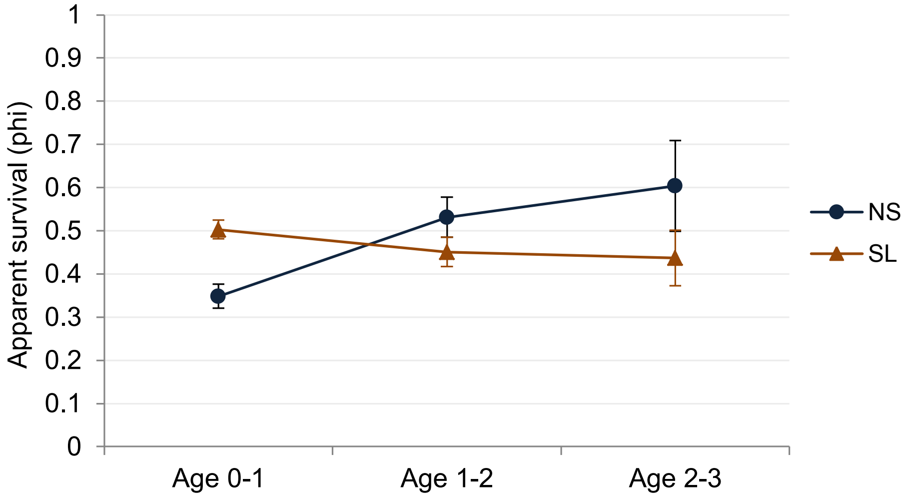
	Recapture probability (p)
Age-1	0.808 ± 0.02
Age-2	0.727 ± 0.04
Age-3	0.552 ± 0.08

Figure 2.3. Estimated recapture probability (p) for Age-1, Age-2 and Age-3 lemon sharks in the North Sound and Sharkland. Estimates were derived from the most highly-supported model, $p_{(age)}$(Table 2.2). Ages on the x-axis reflect the age at recapture for sharks tagged one year before. Exact values (±SE) are given below the graph.

Table 2.4. Model selection for estimating apparent survival (phi) in Age-0, Age-1 and Age-2 lemon sharks in the North Sound and Sharkland. The first two models (in bold) received stronger support than any of the other models.

Model	AICc	Delta AICc	AICc Weights	Model Odds Ratio	Number of Parameters
phi$_{\text{(age+nursery+disturbance/NS/YOY)}}$ - 2005 pulse	**4312.1252**	**0.0000**	**0.46417**	**1.0000**	**14**
phi$_{\text{(age+nursery)}}$	**4313.2553**	**1.1301**	**0.26380**	**0.5683**	**13**
phi$_{\text{(age+nursery+disturbance/NS/YOY)}}$ - 2001 pulse, 2005 pulse	4314.1401	2.0149	0.16949	0.3651	15
phi$_{\text{(age+nursery+disturbance/NS/YOY)}}$ - 2005 press	4316.7279	4.6027	0.04647	0.1001	14
phi$_{\text{(age+nursery+disturbance/NS/YOY)}}$ - 2001 pulse, 2005 press	4317.2807	5.1555	0.03525	0.0759	15
phi$_{\text{(age+nursery+disturbance)}}$ - 2005 press	4319.2906	7.1654	0.01290	0.0278	21
phi$_{\text{(age+nursery+disturbance)}}$ - 2005 pulse	4320.3143	8.1891	0.00773	0.0167	21
phi$_{\text{(age+nursery+disturbance)}}$ - 2001 pulse, 2005 press	4329.1076	16.9824	0.00010	0.0002	29
phi$_{\text{(age+nursery+disturbance)}}$ - 2001 pulse, 2005 pulse	4330.6781	18.5529	0.00004	0.0001	29
phi$_{\text{(nursery)}}$	4332.5040	20.3788	0.00002	0	7
phi$_{\text{(nursery+ disturbance)}}$ - 2005 pulse	4334.9312	22.8060	0.00001	0	10
phi$_{\text{(nursery+ disturbance)}}$ - 2001 pulse, 2005 pulse	4335.5099	23.3847	0	0	12
phi$_{\text{(nursery+ disturbance)}}$ - 2005 press	4337.1470	25.0218	0	0	10
phi($_{\text{nursery+ disturbance)}}$ - 2001 pulse, 2005 press	4337.1608	25.0356	0	0	12
phi$_{\text{(disturbance)}}$ - 2001 pulse, 2005 pulse	4338.2322	26.1070	0	0	8
phi$_{\text{(disturbance)}}$ - 2001 pulse, 2005 press	4339.0730	26.9478	0	0	8
phi$_{\text{(.)}}$	4339.3639	27.2387	0	0	6
phi$_{\text{(disturbance)}}$ - 2005 pulse	4339.5972	27.4720	0	0	7
phi$_{\text{(disturbance)}}$ - 2005 press	4340.9030	28.7778	0	0	7
phi$_{\text{(age)}}$	4343.7043	31.5791	0	0	9
phi$_{\text{(age+disturbance)}}$ - 2005 pulse	4347.9641	35.8389	0	0	13
phi$_{\text{(age+disturbance)}}$ - 2005 press	4349.4330	37.3078	0	0	13
phi$_{\text{(age+disturbance)}}$ - 2001 pulse, 2005 pulse	4350.5008	38.3756	0	0	17
phi$_{\text{(age+disturbance)}}$ - 2001 pulse, 2005 press	4352.1824	40.0572	0	0	17
phi$_{\text{(cohort)}}$	4355.3450	43.2198	0	0	22
phi$_{\text{(t)}}$	4355.9045	43.7793	0	0	22

(a) Fully model-averaged



(b) phi$_{\text{(age+nursery+disturbance/NS/YOY)}}$ – 2005 pulse

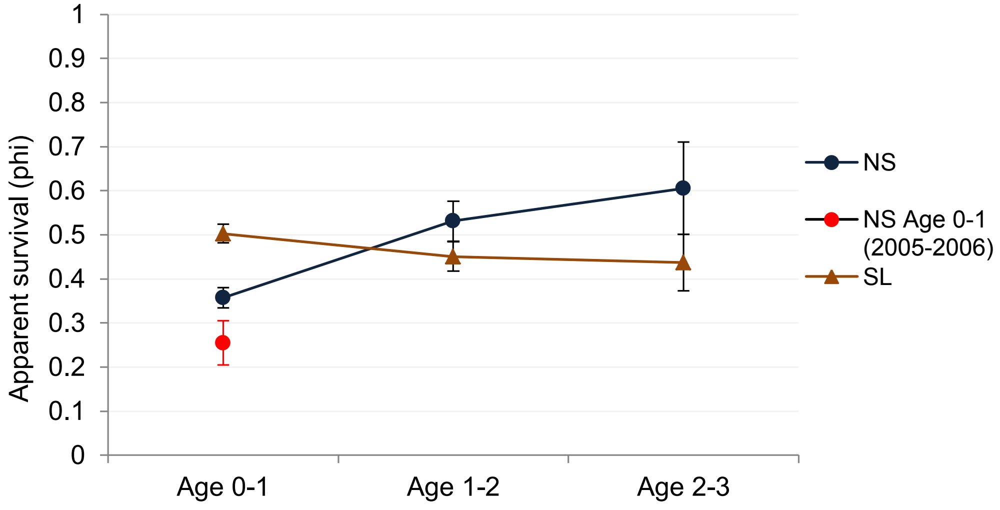


Figure 2.4. Estimates (±SE) of apparent survival (phi) for each age class in the North Sound (NS) and Sharkland (SL) for (a) the full candidate set, model-averaged and (b) the most-supported model (phi$_{\text{(age+nursery+disturbance/NS/YOY)}}$ – 2005 pulse). The most-supported model (b) indicates a distinct lower apparent survival (shown in red) for young-of-year sharks in the North Sound in 2005, following large-scale mangrove removal. NS = North Sound, YOY = young-of-year

Table 2.5. Estimated apparent survival (phi) from (a) model-averaged parameter estimates from the full candidate model set; (b) the most supported model; (c) the second-most supported model; and (d) fully-model averaged for each age class in each nursery before (1995-2004), during (2005-2006) and after (2007-2012)mangrove removal occurred within the North Sound. NS = North Sound, YOY = young-of-year

(a) **Fully model-averaged**

	North Sound	Sharkland
Age 0-1	0.348 ± 0.03	0.503 ± 0.02
Age 1-2	0.531 ± 0.05	0.451 ± 0.03
Age 2-3	0.604 ± 0.10	0.437 ± 0.06

(b) **phi$_{(age+nursery+disturbance/NS/YOY)}$ - 2005 pulse**

	North Sound	Sharkland
Age 0-1	0.357 ± 0.02	0.503 ± 0.02
Age 0-1 (2005-2006)	0.255 ± 0.05	-
Age 1-2	0.531 ± 0.05	0.451 ± 0.03
Age 2-3	0.606 ± 0.10	0.437 ± 0.06

(c) **phi$_{(age+nursery)}$**

	North Sound	Sharkland
Age 0-1	0.343 ± 0.02	0.503 ± 0.02
Age 1-2	0.531 ± 0.05	0.451 ± 0.03
Age 2-3	0.606 ± 0.10	0.437 ± 0.06

(d) **Fully-model averaged**

	North Sound			Sharkland		
	Age 0-1	Age 1-2	Age 2-3	Age 0-1	Age 1-2	Age 2-3
Before	0.352 ± 0.03	0.532 ± 0.05	0.604 ± 0.10	0.503 ± 0.02	0.450 ± 0.03	0.437 ± 0.06
2005-2006	0.286 ± 0.06	0.53 ± 0.05	0.605 ± 0.11	0.502 ± 0.02	0.452 ± 0.04	0.437 ± 0.07
After	0.352 ± 0.02	0.530 ± 0.05	0.604 ± 0.10	0.502 ± 0.02	0.451 ± 0.03	0.437 ± 0.06

Table 2.6. Relative estimated importance of factors to apparent survival model fit based on the full model suite. Estimated importance is the sum of AICc weights (Table 2.4) of models in which each factor is a component.

Factor	Estimated Importance
Nursery	0.99998
Age	0.99995
2005 Mangrove removal	0.73616
2001 Dredging	0.20488

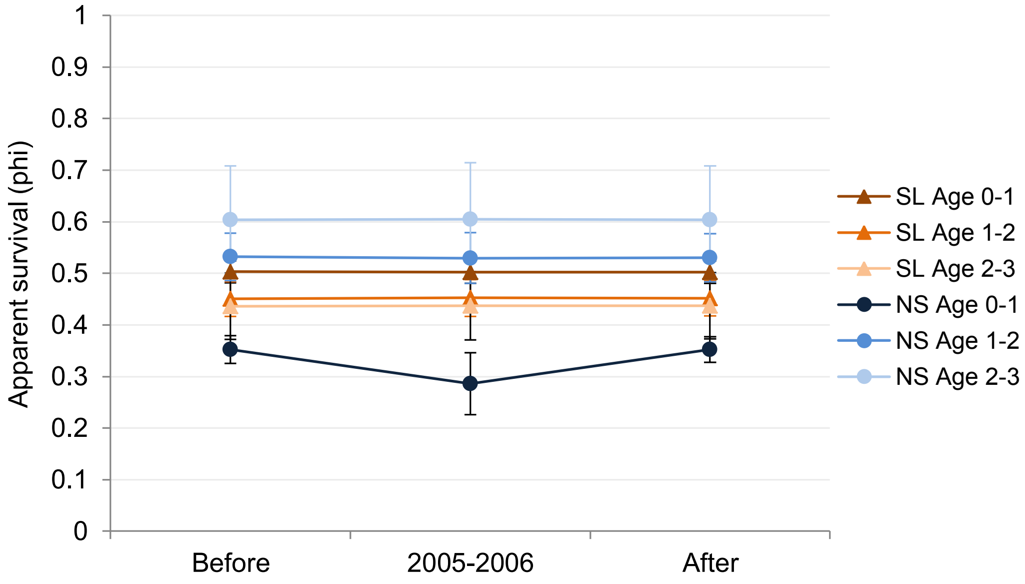


Figure 2.5. Model-averaged mean apparent survival (phi) estimates (±SE) the North Sound (NS) and Sharkland (SL) for Age 0-1, Age 1-2 and Age 2-3 before (1995-2004), during (2005-2006) and after (2007-2012) large-scale mangrove removal occurred within the North Sound nursery.

Table 2.7. Summary results of ANOVA model for factors affecting lemon shark growth. Growth data were square root-transformed to achieve normality (Shapiro-Wilks test, p = 0.11). Asterisks indicate significant factors and interactions.

Factors	df	SS	MS	F-value	p-value	
Nursery	1	15.03	15.032	64.090	<0.001	***
Age	2	3.94	1.969	8.394	<0.001	***
Sex	1	0.61	0.612	2.607	0.107	
Year	16	43.67	2.730	11.638	<0.001	***
Nursery x Age	2	0.03	0.013	0.054	0.947	
Nursery x Year	16	26.85	1.678	7.155	<0.001	***
Age x Year	29	6.61	0.228	0.972	0.509	
Nursery x Sex	1	0.15	0.151	0.643	0.423	
Age x Sex	2	0.17	0.087	0.369	0.692	
Sex x Year	16	4.11	0.257	1.096	0.355	
Nursery x Age x Year	26	5.80	0.223	0.951	0.535	
Nursery x Age x Sex	2	0.32	0.161	0.686	0.504	
Nursery x Sex x Year	15	2.90	0.193	0.825	0.650	
Age x Sex x Year	26	4.25	0.163	0.696	0.869	
Nursery x Age x Sex x Year	12	3.02	0.251	1.072	0.381	
Residuals	659	154.57	0.235			

df = degrees of freedom, SS = sum of squares, MS = mean square

Table 2.8. Mean annual growth in cm per year (±SE) for three age classes in the North Sound and Sharkland from 1995 - 2012. Asterisks indicate significant differences in Age 0-1 and Age 1-2 growth (post-hoc Tukey test; p<0.001 and p=0.03, respectively). Sample sizes for each group are in parentheses.

	North Sound		Sharkland
Age 0-1	4.819 ± 0.16 (177)	***	6.352 ± 0.14 (347)
Age 1-2	5.696 ± 0.30 (84)	*	6.774 ± 0.25 (141)
Age 2-3	6.115 ± 0.52 (30)		7.084 ± 0.35 (48)

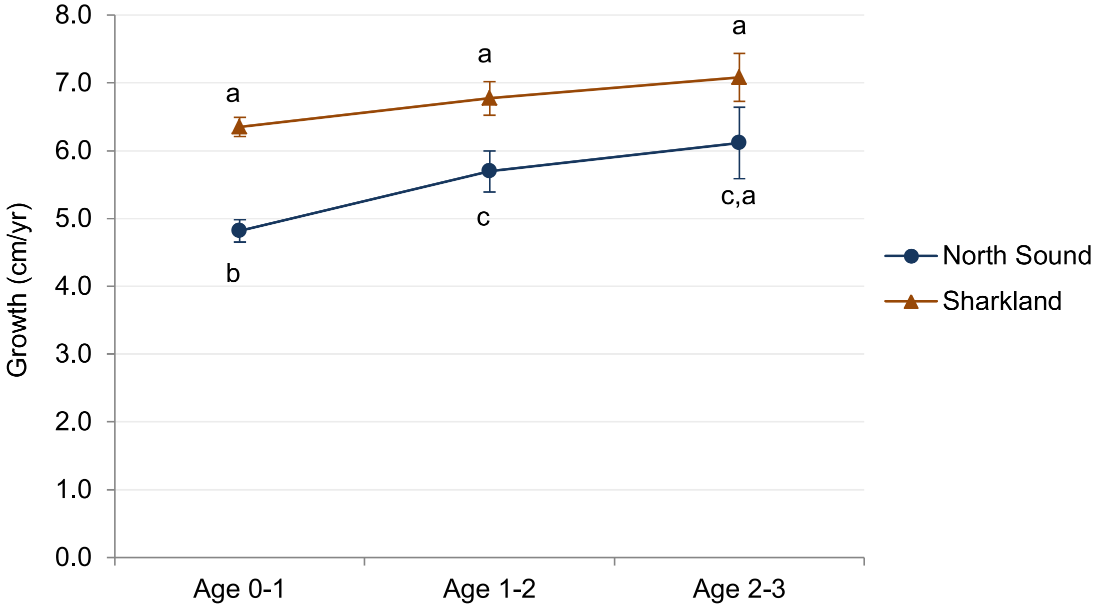


Figure 2.6. Mean annual growth (±SE) of three juvenile lemon shark age classes in the North Sound and Sharkland nurseries from 1995 to 2012. Lowercase letters indicate significant differences among groups (post-hoc Tukey test, $p<0.05$).

Table 2.9. Mean annual growth in cm per year (±SE) for each age class during each year in the North Sound and Sharkland. Sample sizes are in parentheses.

	North Sound	Sharkland		North Sound	Sharkland
1995-1996			**2004-2005**		
Age 0-1	4.24 ± 0.21 (9)	9.11 ± 0.11 (22)	Age 0-1	7.08 ± 0.25 (9)	5.04 ± 0.13 (18)
Age 1-2	(0)	(0)	Age 1-2	8.73 ± 012 (5)	6.79 ± 0.21 (4)
Age 2-3	(0)	(0)	Age 2-3	7.99 ± 0.19 (2)	6.16 ± 0.45 (5)
1996-1997			**2005-2006**		
Age 0-1	3.66 ± 0.14 (10)	6.67 ± 0.32 (8)	Age 0-1	3.39 ± 0.12 (19)	6.85 ± 0.14 (18)
Age 1-2	4.30 ± 0.12 (9)	8.84 ± 0.47 (7)	Age 1-2	2.97 ± 0.22 (5)	9.89 ± 0.31 (9)
Age 2-3	(0)	(0)	Age 2-3	3.92 ± 0.09 (3)	8.37 ± 0.55 (3)
1997-1998			**2006-2007**		
Age 0-1	3.96 ± 0.16 (10)	7.47 ± 0.07 (33)	Age 0-1	2.92 ± 0.07 (14)	4.19 ± 0.15 (17)
Age 1-2	4.65 ± 0.48 (5)	7.36 ± 0.67 (3)	Age 1-2	3.90 ± 0.29 (11)	3.52 ± 0.18 (9)
Age 2-3	6.98 ± 0.21 (4)	5.08 (1)	Age 2-3	3.15 ± 0.67 (3)	5.60 ± 0.34 (6)
1998-1999			**2007-2008**		
Age 0-1	6.52 ± 0.20 (12)	7.99 ± 0.13 (16)	Age 0-1	5.20 ± 0.21 (11)	6.65 ± 0.09 (31)
Age 1-2	9.05 ± 0.31 (10)	9.74 ± 0.29 (10)	Age 1-2	5.32 ± 0.43 (3)	8.68 ± 0.27 (8)
Age 2-3	9.28 ± 0.36 (3)	10.92 (1)	Age 2-3	6.37 ± 0.95 (3)	9.34 (1)
1999-2000			**2008-2009**		
Age 0-1	5.39 ± 0.08 (15)	6.60 ± 0.09 (26)	Age 0-1	5.32 ± 0.32 (4)	4.98 ± 0.12 (17)
Age 1-2	4.73 ± 0.19 (10)	7.61 ± 0.77 (3)	Age 1-2	7.84 ± 0.29 (6)	5.69 ± 0.15 (16)
Age 2-3	4.95 ± 1.04 (2)	7.44 ± 1.13 (3)	Age 2-3	12.30 (1)	5.93 ± 0.52 (3)
2000-2001			**2009-2010**		
Age 0-1	4.7 ± 0.28 (2)	4.84 ± 0.07 (23)	Age 0-1	6.34 ± 0.15 (17)	6.12 ± 0.06 (37)
Age 1-2	5.53 ± 0.24 (6)	6.09 ± 0.21 (13)	Age 1-2	5.7 ± 1.87 (2)	5.79 ± 0.12 (12)
Age 2-3	6.95 ± 0.97 (3)	9.11 ± 1.07 (2)	Age 2-3	6.45 ± 1.35 (3)	8.79 ± 0.46 (5)
2001-2002			**2010-2011**		
Age 0-1	4.51 ± 0.13 (10)	6.22 ± 0.24 (13)	Age 0-1	4.74 ± 0.16 (5)	5.27 ± 0.28 (9)
Age 1-2	(0)	6.46 ± 0.36 (7)	Age 1-2	4.65 ± 0.21 (3)	4.97 ± 0.15 (15)
Age 2-3	(0)	7.30 ± 0.61 (5)	Age 2-3	3.22 (1)	6.03 (1)
2002-2003			**2011-2012**		
Age 0-1	5.18 ± 0.41 (4)	6.98 ± 0.11 (26)	Age 0-1	4.76 ± 0.15 (17)	5.18 ± 0.13 (20)
Age 1-2	7.71 ± 0.11 (5)	10.01 ± 0.61 (6)	Age 1-2	5.15 ± 0.8 (2)	3.98 ± 0.49 (5)
Age 2-3	(0)	8.3 ± 0.52 (5)	Age 2-3	3.61 (1)	5.20 ± 0.38 (5)
2003-2004					
Age 0-1	5.00 ± 0.18 (9)	5.93 ± 0.23 (13)			
Age 1-2	3.4 ± 0.8 (2)	6.71 ± 0.12 (14)			
Age 2-3	2.15 (1)	6.42 ± 0.94 (2)			

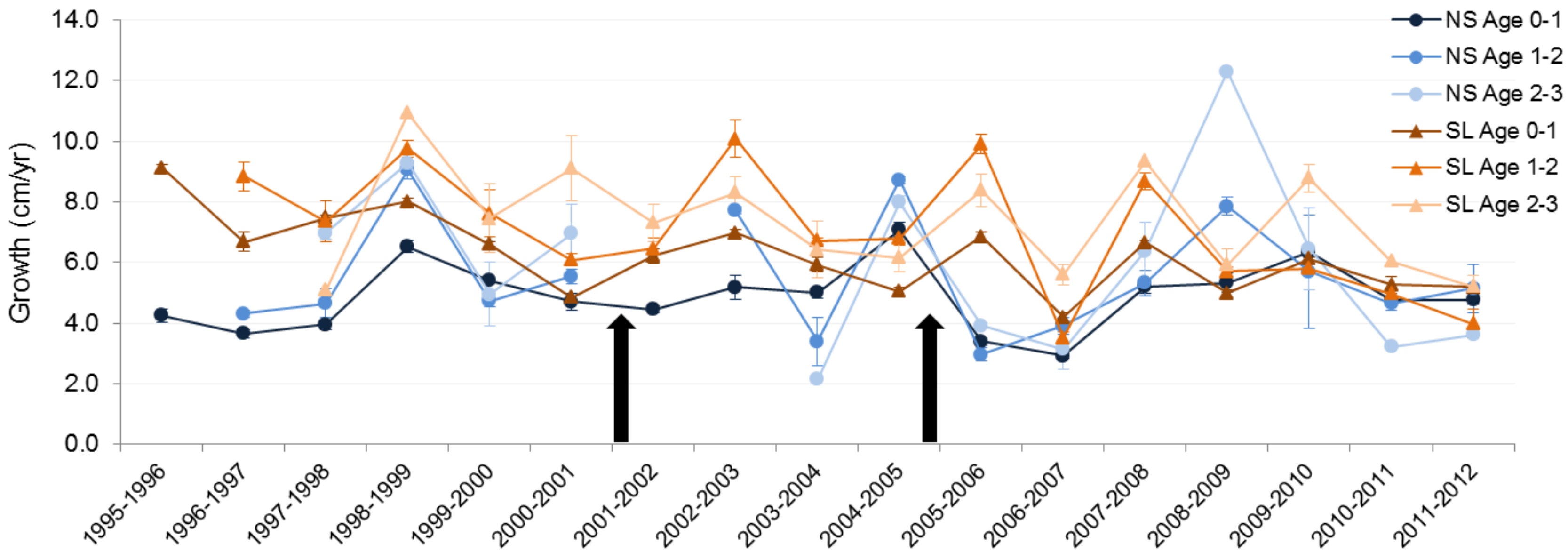


Figure 2.7. Mean annual growth (±SE) for each of three age classes in the North Sound (NS) and Sharkland (SL). Absent error bars indicate sample size was too small (n=1, Table 2.9) for that age class during that time period for SE estimation. Gaps in data indicate no growth information was available for that age class during that time period (n=0, Table 2.9). Black arrows show the timing of two large-scale construction operations: 2001 dredging just outside of the North Sound and 2005 mangrove removal within the North Sound (Figure 2.1).

Table 2.10. Summary of ANOVA model results for before-after control-impact (BACI) analysis of mangrove removal on juvenile lemon shark growth on combined North Sound and Sharkland data. “Time” refers to before versus after 2005. Asterisks indicate significant factors.

Factors	df	SS	MS	F-value	p-value	
Nursery	1	15.03	15.032	50.849	<0.001	***
Age	2	3.94	1.969	6.66	0.00135	**
Time	1	10.78	10.779	36.461	<0.001	***
Nursery x Age	2	0.18	0.090	0.305	0.73726	
Nursery x Time	1	0.00	0.003	0.01	0.9216	
Age x Time	2	0.76	0.382	1.291	0.27563	
Nursery x Age x Time	2	0.41	0.206	0.696	0.49908	
Residuals	815	240.93	0.296			

df = degrees of freedom, SS = sum of squares, MS = mean square

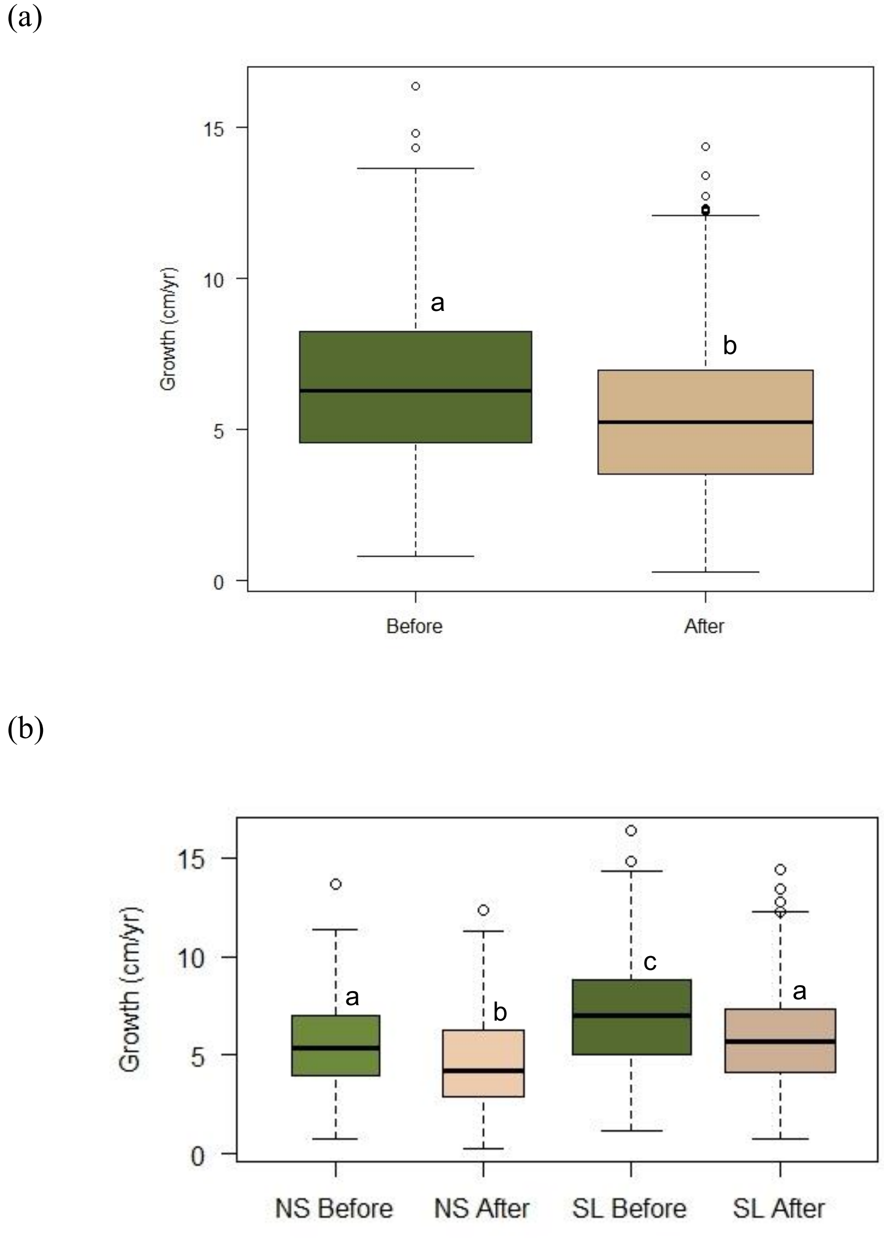


Figure 2.8. Before-after control-impact (BACI) analysis of juvenile lemon shark growth, with 2005 mangrove deforestation as the impact. (a) Overall median growth before and after mangrove removal (post-hoc Tukey test; $p<0.05$). Data represent three age classes in both North Sound and Sharkland nurseries combined. (b) Median growth in the North Sound (NS) and Sharkland (SL) before and after mangrove removal occurred within the North Sound. Lowercase letters indicate significant differences among groups (post-hoc Tukey test, $p<0.05$). Box plot width is proportional to sample size.

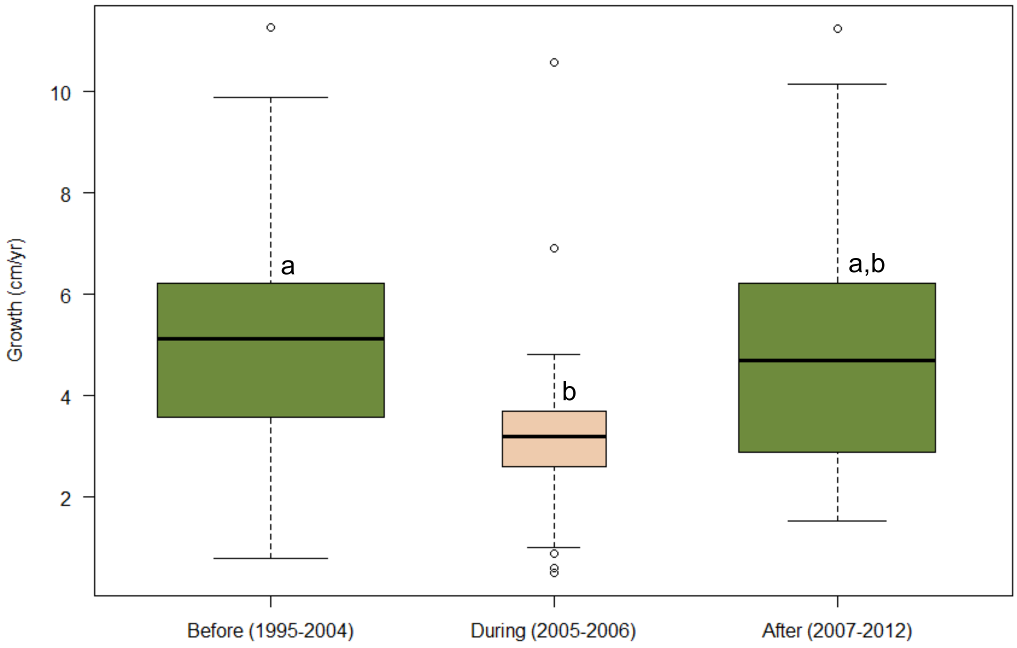


Figure 2.9. Median annual growth of North Sound young-of-year before, during and after mangrove deforestation. Lowercase letters indicate significant differences among groups (post-hoc Tukey test, $p<0.05$). Box plot width is proportional to sample size.

Chapter 3. Changes in faunal community structure following an anthropogenic disturbance within a lemon shark nursery

3.1 Background

In tropical and subtropical coastal marine environments, mangroves and adjacent habitats are important for many fish and invertebrates, often serving as nursery or intermediate environments for juveniles (see Nagelkerken et al. 2008 for a review). One of the most important functions mangroves provide is sub-surface structural complexity, which helps individuals balance foraging opportunities with predation risk (Laegdsgaard and Johnson 2001, Cocheret de la Moriniere et al. 2004). Though not all species are obligate inhabitants of mangroves during a life stage, many adult reef fishes occur in higher densities on reefs with available mangrove habitat nearby (Nagelkerken 2000, Nagelkerken and van der Velde 2002, Dorenbosch et al. 2004, Mumby et al. 2004). In the Gulf of California, fisheries landings are positively correlated with the amount of viable mangrove shoreline, and specifically with the amount of mangrove habitat being used by commercial species as nursery grounds (Aburto-Oropeza et al. 2008).

Despite their well-documented importance, mangroves worldwide are being lost due to development. In the past few decades, an estimated 30-50% of global mangrove forests have been destroyed (Valiela et al. 2001, Alongi 2002, Donato et al. 2011). Few studies have directly investigated the effects of mangrove deforestation on fish assemblages, but when they have, they reported that species richness and relative abundances were higher at mangrove sites than at cleared sites (Williamson et al. 1994, Shinnaka et al. 2007, Taylor et al. 2007) and that community structure overall differed significantly between natural and modified habitats (Huxham et al. 2004, Shinnaka et al.

2007, Taylor et al. 2007). Taylor et al. (2007) reported that even a partial clearing of mangroves along the shore could significantly affect fish community structure.

Bimini, Bahamas, 85 km east of Miami, FL is a group of mangrove-fringed islands representing the only mangrove habitat on the western edge of the Great Bahama Bank (Figure 3.1). The shorelines, lagoons and creeks of this insular system, dominated by red mangroves (*Rhizophora mangle*) and adjacent seagrass and sand flats, provide habitat for myriad fish and invertebrates (Voss and Voss 1960, Afonso and Gruber 2007, Jennings et al. 2012). In particular, Bimini has well-documented lemon shark (*Negaprion brevirostris*) nurseries, where juveniles remain exclusively within primary nursery areas for up three years following birth (see Appendix, Morrissey and Gruber 1993a, Gruber et al. 2001, Franks 2007, Chapman et al. 2009).

A 3 km^2 lagoon known as the North Sound (Figure 3.1) is of particular importance not only to juvenile lemon sharks, but also to many other species of ecological, commercial and conservation concern (Jennings et al. 2012). Since 2005, construction of a large resort has encroached into the North Sound, where approximately 39% of the mangrove wetlands was cleared and filled (Figure 3.1; Jennings et al. 2012). Mangrove deforestation and dredge-and-fill was limited to a 0.36 km^2 area on the west side of the lagoon, while the east side remained intact (Figure 3.1). Often, this construction has occurred with little or no mitigation, with fill material flowing freely from what was once a mangrove wetland directly into the lagoon (Figure 3.2). Several researchers have suspected that there may be large effects of this disturbance on fish assemblages, including those of importance in juvenile lemon shark diets (Feldheim & Edrén 2002, Gruber & Parks 2002, Newman et al. 2010).

The objective of this study was to investigate the effects of anthropogenic habitat loss on mangrove-associated taxa within a lemon shark nursery. Specifically, the following questions were addressed:

1. Do taxonomic composition, abundance and biomass differ between disturbed and intact nurseries over time?
2. Do taxonomic abundance and biomass differ between deforested and intact sides of the disturbed nursery over time?
3. Are there differences between disturbed and intact habitats in mangrove-associated taxa that are the preferred juvenile lemon shark prey?

Many studies aimed at assessing biological effects of environmental disturbance lack data prior to the disturbance and must compare affected areas to similar intact areas (Wiens and Parker 1995, Airoldi et al. 2008). Here, a pre-disturbance community assemblage dataset exists for both a disturbed area and a nearby control (Newman et al. 2007) with which to compare data collected after the disturbance. Therefore, this study was a unique opportunity to quantify actual changes in an anthropogenically altered habitat using a before-after control-impact (BACI) experimental design (Bernstein and Zalinski 1983, Stewart-Oaten et al. 1986).

3.2 Methods

3.2.1 Data collection

Juvenile lemon shark prey community composition was investigated in two nurseries: (1) the North Sound, which experienced habitat loss, and (2) South Bimini, a similar, nearby undisturbed control nursery (Figure 3.1). Because neonates and juveniles feed primarily near shore (Newman et al. 2010, 2011), sampling was conducted within 200 m of the shoreline via seine net (75 m x 2 m, 5 mm mesh), following the methods described in Newman et al. (2007). All periods of the tidal cycle were sampled in both wet (May – October) and dry (November – April) seasons between October 2009 and September 2011, with all sampling conducted during daylight hours. Individuals captured were identified to the lowest taxonomic level possible, and the total numbers and wet weights of each taxonomic group were recorded before individuals were released onsite. Since the study was focused on juvenile lemon shark prey, gastropods were not included in analyses, as they are not known to be part of the lemon shark diet (Cortés and Gruber 1990, Newman et al. 2010). Similarly, flora such as seagrasses and algae were excluded because their presence in lemon shark stomach contents is incidental to feeding on benthic fish and invertebrates (Cortés and Gruber 1990). Abiotic environmental data were not available for the period 2000 – 2003, thereby precluding comparative analyses of those data.

3.2.2 Data Analysis

Abundance and biomass data were compared to data collected via identical methods between 2000 and 2003 (Newman et al. 2007), prior to habitat degradation within the North Sound, using a BACI design to examine faunal community differences between before and after sampling periods in both the control and disturbed nurseries. For continuity and comparison, species were aggregated to family level for analyses following Newman et al. (2007). To downweight the influence of rare families (Cao et al. 1997), only those which represented at least 5% in an index of relative importance (%IRI, calculated from abundance, weight and occurrence of taxa) from (Newman et al. 2007) were included in BACI statistical comparisons.

To visualize overall trends, Euclidean distance matrices were constructed from abundance and biomass data after $\log_{10}(x+1)$ transformation, followed by principal coordinate analysis (PCO) for all of the data combined and for each nursery individually. Faunal family vectors with a Pearson correlation greater than 0.2 were superimposed onto each PCO plot to investigate their linear correlation with the ordination axes. A non-parametric permutational analysis of variance (PERMANOVA; PRIMER 2006, PRIMER-E Ltd, Plymouth, UK) was used to test for differences among nurseries, time periods (before and after) and their interactions using Bray-Curtis resemblance matrices, unrestricted permutations of raw data, and Type III Sum of Squares (9999 permutations). Six samples (4% of total sampling effort) with zero catch were excluded. PERMANOVA, structured as outlined above, was also used to test for differences in mean abundance and biomass of families among time periods within the disturbed nursery alone to determine if there were differences among deforested and intact sides of the nursery.

A similarity-percentages analysis (SIMPER, PRIMER-E; Clarke 1993) was run on $\log_{10}(x+1)$-transformed data to identify which families contributed most to the differences in abundance and biomass before versus after habitat loss within the North Sound and South Bimini (Clarke 1993). For the families found in both before and after sampling periods within each of the two nurseries, differences in mean abundance and biomass per seine were tested for significance using Wilcoxon rank sum tests on $\log_{10}(x+1)$-transformed data. All such analyses were run in R (version 3.0.0).

To characterize community structure, three diversity indices were calculated for each seine for the two sampling periods in both the North Sound and South Bimini. First, richness (S) was calculated as the number of different families present for each time period within each nursery. Second, the Shannon Index (H'), based on proportional abundances, was calculated as:

$$H' = -\Sigma p_i \ln p_i$$

(Equation 3.1)

where p_i is the proportion of individuals in the i^{th} species. Finally, the Pielou Evenness Index (J') of observed diversity to maximum possible diversity was computed as:

$$J' = \frac{H'}{Hmax}$$

(Equation 3.2)

where H' is the Shannon Diversity and H_{max} is the maximum value of H' (equal to lnS; Magurran 1988). For each index, PERMANOVA structured as described above was used in a BACI design to test for differences among nurseries, time periods and their interactions.

3.3 Results

A total of 131 seines was pulled between 2009 and 2011 in the North Sound and South Bimini combined, and these were compared to a total of 550 seines from the period 2000 to 2003 (Table 3.1). The influence of rare families was downweighted by restricting comparative analyses to the 22 families each identified by Newman et al. (2007) as constituting greater than 5% of an IRI in the North Sound and South Bimini (Table 3.2).

PCO plots revealed a prior differentiation between the North Sound and South Bimini in terms of abundance and biomass that persisted after the disturbance (Figure

3.3). For abundance, the first two axes explained 54% of the variation, with strong orthogonal relationships of the families Gerreidae and Atherinidae. The ordination of biomass data was less clear, likely due to the inherent variability of this type of data. The first two axes explained 32% of variation, and the strongest linear relationship is in the family Gerreidae. Within the North Sound, PCO plots revealed a differentiation between mean abundances before and after the disturbance (Figure 3.4), as evidenced by the spatial separation of seines in the time periods on the ordination plane. There is strong linear correlation with the family Gerridae associated with the differentiation (Figure 3.4). The first two axes of the abundance PCO plot explained 55% of the variation. Such a differentiation is less apparent in the biomass PCO plot, where the first two axes explain 38% of the variation (Figure 3.4). In the South Bimini nursery, the reduced sampling effort from the period after the disturbance makes it difficult to discern any clear differentiation between time periods in terms of either abundance or biomass, though for abundance, the family Atherinidae is most strongly correlated with the overall variation (Figure 3.5).

PERMANOVA revealed that overall, there was a significant interaction of nursery and time period for abundance and biomass of families (Table 3.3). Within the disturbed North Sound nursery, a total of 46 faunal families was represented across both sampling periods (Table 3.4). Of the 26 families that were common to both sampling periods, the mean abundance per seine decreased significantly for five families: Atherinidae, Achiridae, Gerreidae, Hemiramphidae and Sphyraenidae; there was a significant increase only in Clupeidae (Table 3.4, Wilcoxon rank sum tests, $p<0.05$). There were significant declines in mean biomass per seine for Atherinidae and

Hemiramphidae, and a significant increase in Pisidae (Table 3.4, Wilcoxon rank sum tests, $p<0.05$). In the undisturbed South Bimini nursery, a total of 50 faunal families was represented across both sampling periods (Table 3.5). Of the 24 families common to both sampling periods, mean abundance per seine decreased significantly for only Haemulidae, Ostraciidae and Scaridae, while there were significant increases for six families: Belonidae, Gonodactylidae, Majidae, Portunidae, Sphyraenidae and Xanthidae (Table 3.5, Wilcoxon rank sum tests, $p<0.05$). Mean biomass per seine decreased for Haemulidae, Ostraciidae and Scaridae, while there were increases for Alphaeidae, Belonidae, Gonodactylidae, Majidae, Sphyraenidae and Xanthidae (Table 3.5, Wilcoxon rank sum tests, $p<0.05$). The families Gerreidae, Haemulidae, Lutjanidae, Penaeidae, Portunidae, Scaridae and Sphyraenidae were reported by Newman et al. (2010) as particularly important juvenile lemon shark prey species. The magnitude of changes in mean abundance and biomass per seine of these families in each nursery is shown in Figure 3.6. In the North Sound, Gerreidae, the most important prey family, decreased significantly in mean abundance by 52%, while in South Bimini, the decrease was not significant.

SIMPER analysis within the North Sound revealed that 16 groups were responsible for approximately 90% of the differences between sampling periods for both abundance and biomass (Figure 3.7a). The significant decline in Gerreidae, a ubiquitous and important juvenile lemon shark prey family, was disproportionately influential, contributing to 25.2% and 18.5% of the difference in overall abundance and biomass, respectively. In South Bimini, 18 families were responsible for approximately 90% of the differences between sampling periods for both abundance and biomass (Figure 3.7b), with the highly patchy Atherinidae family contributing to 21% of the difference in overall abundance.

PERMANOVA revealed that there were significant effects of both side and time within the North Sound, but no interaction (Table 3.6). Post-hoc pairwise comparisons showed that for mean abundance, both the disturbed and intact side of the nursery were significantly different between time periods (Tukey test; $p<0.001$). For biomass, only side was a significant factor (Table 3.6).

Table 3.7 shows mean values of richness, Shannon Index (H'), and the Pielou Evenness Index (J') for the North Sound and South Bimini for the sampling periods before and after habitat loss occurred in the North Sound. Results of PERMANOVAs used in a BACI design to test for differences in each of these indices among nurseries and time periods reveals a significant effect of time for richness, and a significant interaction of nursery and time for both H' and J' (Table 3.8). Despite similar decreases in mean richness for both the North Sound and South Bimini (Table 3.7), a post-hoc pairwise comparison detected a significant decline only in the North Sound (Tukey test, $p<0.01$). Changes in H' and J' were in opposite directions for the two nurseries, with both indices increasing in the North Sound and decreasing in South Bimini (Table 3.7); however, post-hoc pairwise comparisons indicated that only the changes in the North Sound were significant (Tukey test, $p<0.05$ and $p<0.01$, respectively).

3.4 Discussion

This study examined faunal community structure and diversity in a lemon shark nursery before and after large-scale habitat loss. Both the disturbed nursery and a nearby undisturbed nursery experienced changes over time in terms of mean abundance and biomass of faunal families, but the two nurseries differed in the magnitude and direction of those family-specific changes. In the disturbed nursery, there was a significant decline in mean abundance of Gerreidae, the most important lemon shark prey family, and this change was not limited to the side of the nursery that was deforested. Throughout the sampling areas within 200 m of the entire North Sound, there were declines in the mean abundance and mean biomass per seine of several taxa, including those important in juvenile lemon shark diet. Diversity indices revealed significant changes in community structure in the disturbed nursery after habitat loss.

3.4.1 Methodology

Ideally, a BACI analysis involves an asymmetrical design consisting of a disturbed site and several control locations (Underwood 1994). In Bimini, “before” data were available for the disturbed site and only one control site, thereby precluding conclusive assignment of causality of community changes to anthropogenic activity. However, before-after comparisons did reveal differences in temporal patterns of faunal abundance and biomass between the two locations over time, and the major difference between those locations was a large-scale anthropogenic disturbance.

A general characteristic of ecological surveys is that the number of species (or families) captured accumulates with increasing sampling effort until a point at which additional sampling adds only rare and transient species (Ugland et al. 2003). In the present study, sampling effort between 2009 and 2011 was less than between 2000 and 2003 (Table 3.1). To reduce the effects of this difference, BACI comparisons were limited to major taxa, defined as those constituting greater than 5% of an IRI as reported by Newman et al. (2007) (Table 3.2). Each of the 22 families in the reduced dataset was commonly encountered, and most were caught during both sampling periods in both nurseries. However, because the sampling effort in South Bimini was much lower during the time period after habitat loss, the resultant inflated standard errors may have decreased the power of statistical tests to detect significant differences in community- and family-level temporal comparisons in that nursery.

If there were seasonal differences in faunal communities, bias could be introduced through differences in seasonal sampling effort. However, the present study does not have this bias for two reasons. First, Newman et al. (2007) found very few seasonal differences during the 2000 to 2003 sampling period. Second, a chi-square test revealed no difference in sampling effort among seasons for the periods before and after habitat loss (Table 3.1).

3.4.2 Implications of results

Newman et al. (2010) found a high degree of overlap between juvenile lemon shark diet and mangrove-associated faunal communities. While changes occurred over time in both the disturbed and undisturbed control nursery, the direction and magnitude of those changes differed, particularly for the family Gerreidae, the most important juvenile lemon shark prey item (Newman et al. 2010). Prior to habitat loss, an IRI indicated that the family Gerreidae was the dominant prey item, accounting for approximately 70% of the North Sound juvenile lemon sharks' diet (Newman et al. 2010). There was a highly significant 52% decline in mean abundance per seine of this important prey family following mangrove degradation in the North Sound (Figure 3.7). Newman et al. (2010) also determined that the family Sphyraenidae was important to juvenile lemon shark diet in the North Sound (4% IRI), and this family experienced a significant 65% decline in mean abundance per seine following habitat loss (Figure 3.7). In the undisturbed South Bimini nursery, despite decreases and increases in mean abundance and biomass of Gerreidae, respectively, significant differences were not detected. However, there was a significant increase in both mean abundance and biomass for Sphyraenidae, another important lemon shark prey taxon.

Post-disturbance changes in mean abundance and biomass of taxa in the North Sound were not limited to the area of deforested and filled wetlands, but extended to the zone of sampling within 200 m of the shore on the opposite side of the nursery with an intact mangrove shoreline (Figure 3.1, Table 3.6). This result suggests that juvenile lemon sharks cannot simply shift to the other side of the lagoon and encounter more favorable foraging opportunities. Past telemetry and genetic data showed that juvenile lemon sharks remain within their primary nursery for the first three years after birth (Morrissey and Gruber 1993a, Franks 2007, Chapman et al. 2009), relying exclusively on the prey resources available within the nursery. Additionally, telemetry data collected after habitat loss indicates that there is no evidence to support the idea that juvenile lemon sharks emigrate from the disturbed nursery at younger ages, nor are they spending more time farther from shore within the disturbed nursery (Chapter 4). Therefore, juveniles appear to be bound to a system with significant declines in their prey resources, and these changes could have negative effects on their survival, growth and fitness.

Analysis of several diversity indices revealed nursery-specific patterns of change over time. Despite significant increases and decreases in mean abundance and biomass of a few taxa in the undisturbed nursery as well as changes in the diversity indices analyzed, statistical tests could not detect significant differences in overall community structure in terms of richness, diversity or evenness. However, the high standard error associated with the lower sampling effort in South Bimini may have limited the power of such tests to detect significant differences. In the disturbed North Sound, significant differences in each of these indices indicate post-disturbance changes at the community level. A simple measure of richness showed a reduction in the mean number of families per seine in the North Sound following habitat loss. The Shannon Index, however, indicated that after the disturbance, there was a slight increase in diversity. This counterintuitive result is potentially due to the sensitivity of the index to underlying species abundance distributions (Magurran 1988). Because the index is calculated using proportional abundances (Equation 3.1), the presence of strongly dominant taxa can push the diversity value downward. Often, disturbed communities experience an increase in dominance due to the proliferation of one or two taxa that are capable of taking advantage of new conditions (Connell 1978, Huston 1979, Airoldi et al. 2008). In the North Sound, however, the undisturbed state of the system was characterized by dominance of a few families, particularly Gerreidae and Atherinidae (Table 3.4), and both experienced significant declines between sampling periods. The significant increase in the Pielou Evenness Index confirms that a post-disturbance lessening of taxonomic dominance did indeed occur (Table 3.7). SIMPER results show that the decrease in Gerreidae mean abundance was the largest contributor to the difference between before and after sampling periods in the North Sound (Figure 3.5). In addition, the North Sound PCO plot shows that Gerreidae, specifically, was the family most strongly linearly correlated with the differentiation between before and after sampling periods (Figure 3.4).

3.5 Conservation and management implications

This study was a unique opportunity to quantify changes associated with an anthropogenic disturbance. The existence of a baseline community assemblage dataset in both a control and disturbed area allowed for direct comparisons of community structure and diversity before and after habitat loss. Comparisons revealed differences in temporal patterns of faunal abundance and biomass between the two locations over time, and the major difference between those locations was large-scale habitat loss. Declines in important juvenile lemon shark prey resources were not limited to the deforested shoreline. Using the simplest of diversity measures, family-level and community-level changes in abundance, biomass, richness, diversity and taxonomic dominance were found that are different in the disturbed system. The declines in mean abundance per seine of most taxa in the disturbed nursery, including those important in juvenile lemon shark diets, can have effects on the growth, survival and fitness of nursery-bound sharks in this insular system. Juvenile lemon sharks selectively forage on Gerreidae, which dramatically declined in mean abundance. In this community in which taxonomic abundances are dominated by a few families in the nursery's undisturbed state, a richness index better captures system changes than the Shannon Index, and a combination of indices is more informative than any singular index. This distinction has important implications for future work in this system, particularly with regard to environmental impact assessments associated with any additional proposed development.

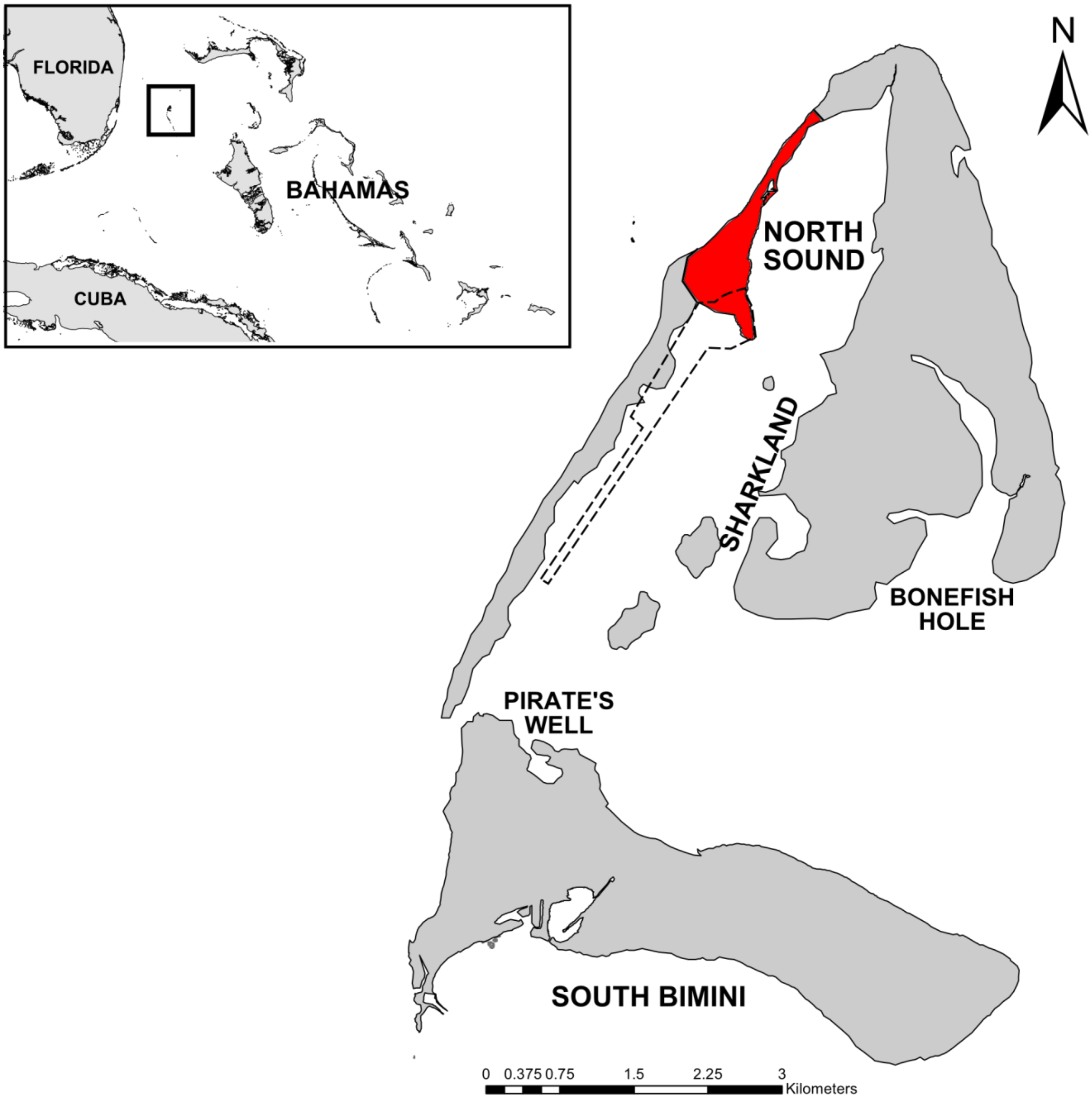


Figure 3.1 Bimini, Bahamas is an island group on the western edge of the Great Bahama Bank, approximately 86 km east of Miami, FL. Labels indicate specific locations of juvenile lemon shark nursery areas within the islands. Red shows the area of 2005 mangrove removal, which was subsequently filled with dredge material. Seabed dredging occurred in 2001 within the area outlined by the dotted line.

Figure 3.2. Construction activity within the North Sound, Bimini, Bahamas. Top: Fill material is dumped on the shoreline with no sediment mitigation barriers. Middle: Fill material is transported to an area deforested of mangroves and deposited along the shoreline. Bottom: Mounds of excavated fill material are piled behind a deep dredge pool in an area that had previously been a mangrove forest wetland. Plumes of sediment can be seen flowing into the nursery in the middle and bottom images.

Table 3.1. Effort (number of seines) before and after habitat loss occurred in the North Sound. There was no significant difference in effort among seasons (Wet: May - October, Dry: November – April) between the before and after sampling periods (Chi-square test, p>0.5).

	South Bimini (Control)			North Sound (Disturbed)		
	Wet	Dry	Σn	Wet	Dry	Σn
Before (2000-2003)	135	135	**270**	135	145	**280**
After (2009-2011)	19	18	**37**	32	62	**94**

Table 3.2. Families included in PERMANOVA analyses investigating changes in abundance, biomass and occurrence in the North Sound and South Bimini before and after habitat loss occurred in the North Sound. These 22 families each constituted greater than 5% of an index of relative importance (IRI) during the "before" sampling period (2000 – 2003; Newman et al. 2007).

Family	Description
Achiridae	Soles
Albulidae	Bonefishes
Atherinidae	Silversides
Belonidae	Needlefishes
Carangidae	Jacks
Chaetodontidae	Angelfishes and butterflyfishes
Dasyatidae	Whiptail stingrays
Gerreidae	Mojarras
Gobiidae	Gobies and sleepers
Haemulidae	Grunts
Labridae	Wrasses
Lutjanidae	Snappers
Monacanthidae	Filefishes
Ostraciidae	Trunkfishes
Penaeidae	Penaeid shrimps
Pisidae	Spider crabs
Pomacentridae	Damselfishes
Portunidae	Swimming crabs
Scaridae	Parrotfishes
Sparidae	Porgies
Sphyraenidae	Barracudas
Tetraodontidae	Puffers

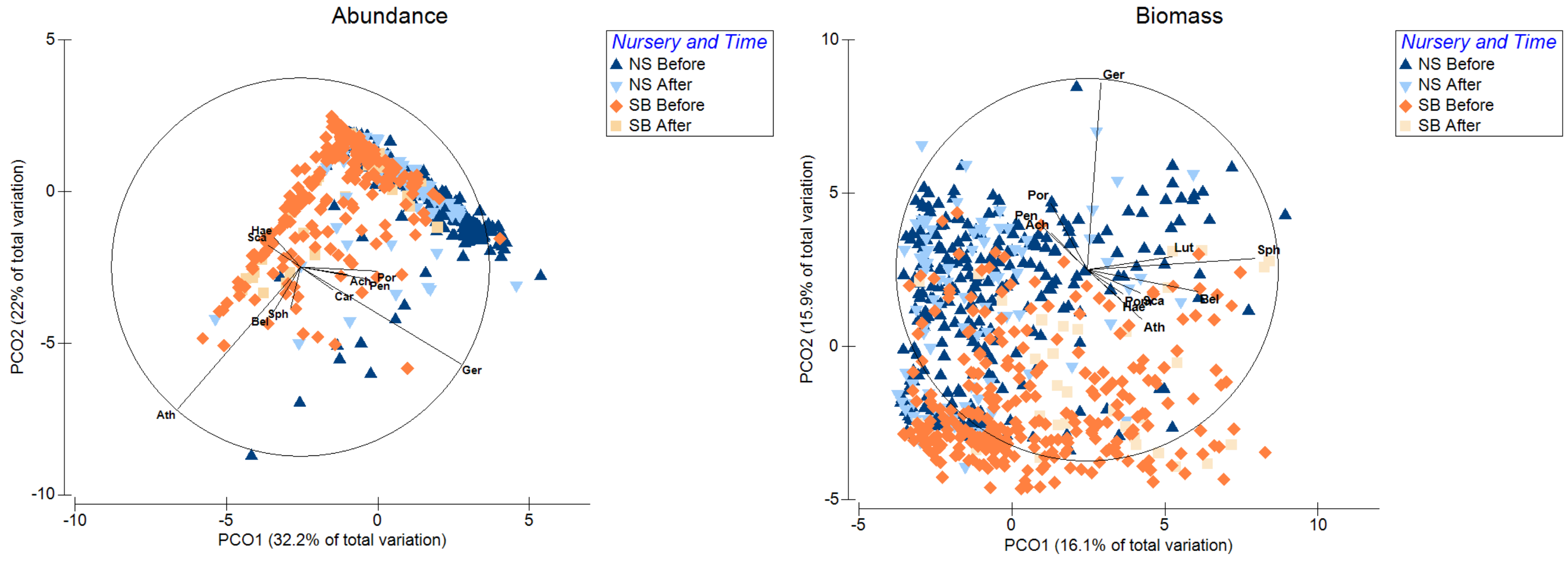


Figure 3.3. Principal coordinate analysis (PCO) plots for mean abundance and biomass of families captured in the North Sound and South Bimini before and after a disturbance in the North Sound. The first two axes of the abundance and biomass plots explain 54.2% and 32.0% of the variation, respectively. Data were $\log_{10}(x+1)$-transformed, and plots were based on Euclidean distances. Family vectors represent those with greater than a 0.2 Pearson correlation. Ach = Achiridae, Ath = Atherinidae, Bel = Belonidae, Car = Carangidae, Ger = Gerridae, Hae = Haemulidae, Lut = Lutjanidae, Pen = Penaeidae, Pom = Pomacentridae, Por = Portunidae, Sca = Scaridae, Sph = Sphyraenidae.

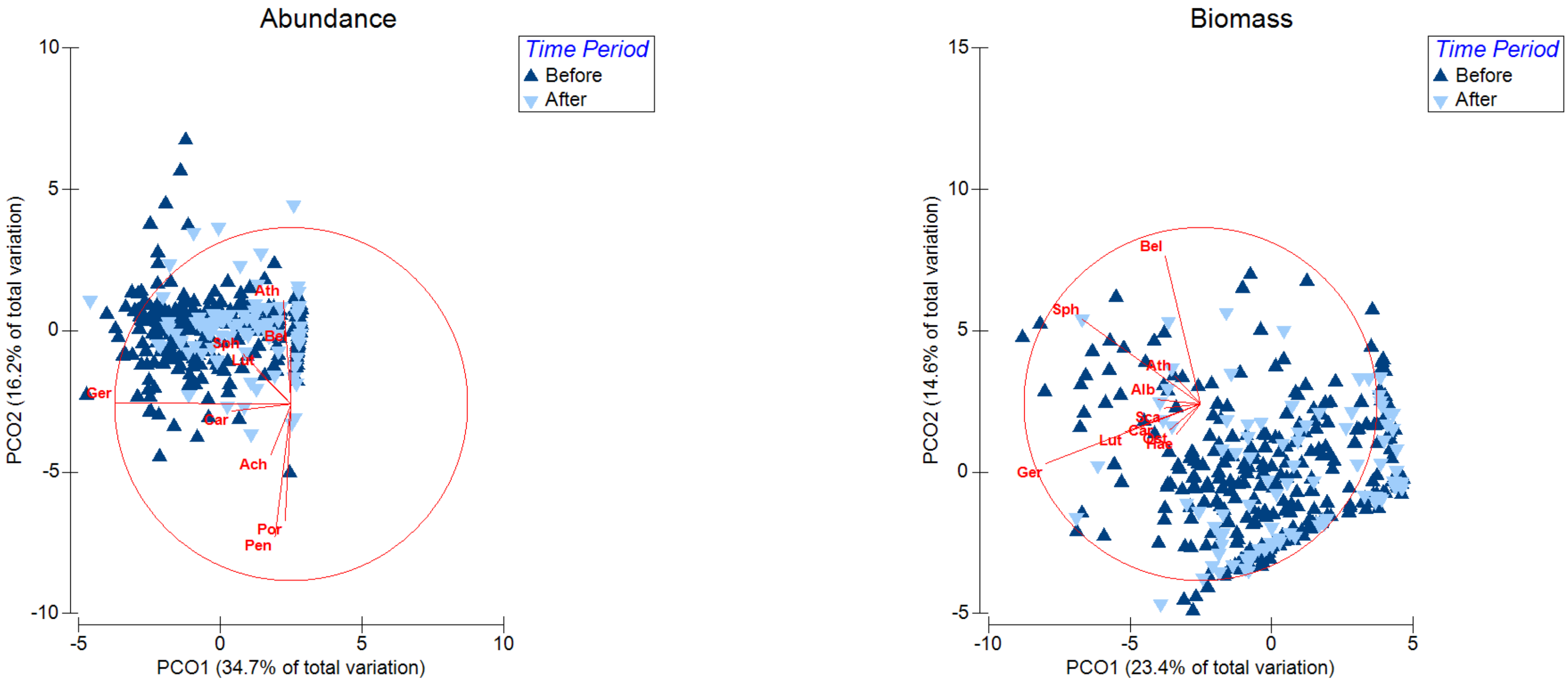


Figure 3.4 Principal coordinate analysis (PCO) plots for mean abundance and biomass of families captured in the North Sound before and after a disturbance. The first two axes of the abundance and biomass plots explain 54.9% and 38.0% of the variation, respectively. Data were $\log_{10}(x+1)$-transformed, and plots were based on Euclidean distances. Family vectors represent those with greater than a 0.2 Pearson correlation. Ach = Achiridae, Alb = Albulidae, Ath = Atherinidae, Bel = Belonidae, Car = Carangidae, Ger = Gerreidae, Hae = Haemulidae, Lut = Lutjanidae, Ost = Ostraciidae, Pen = Penaeidae, Por = Portunidae, Sca = Scaridae, Sph = Sphyraenidae.

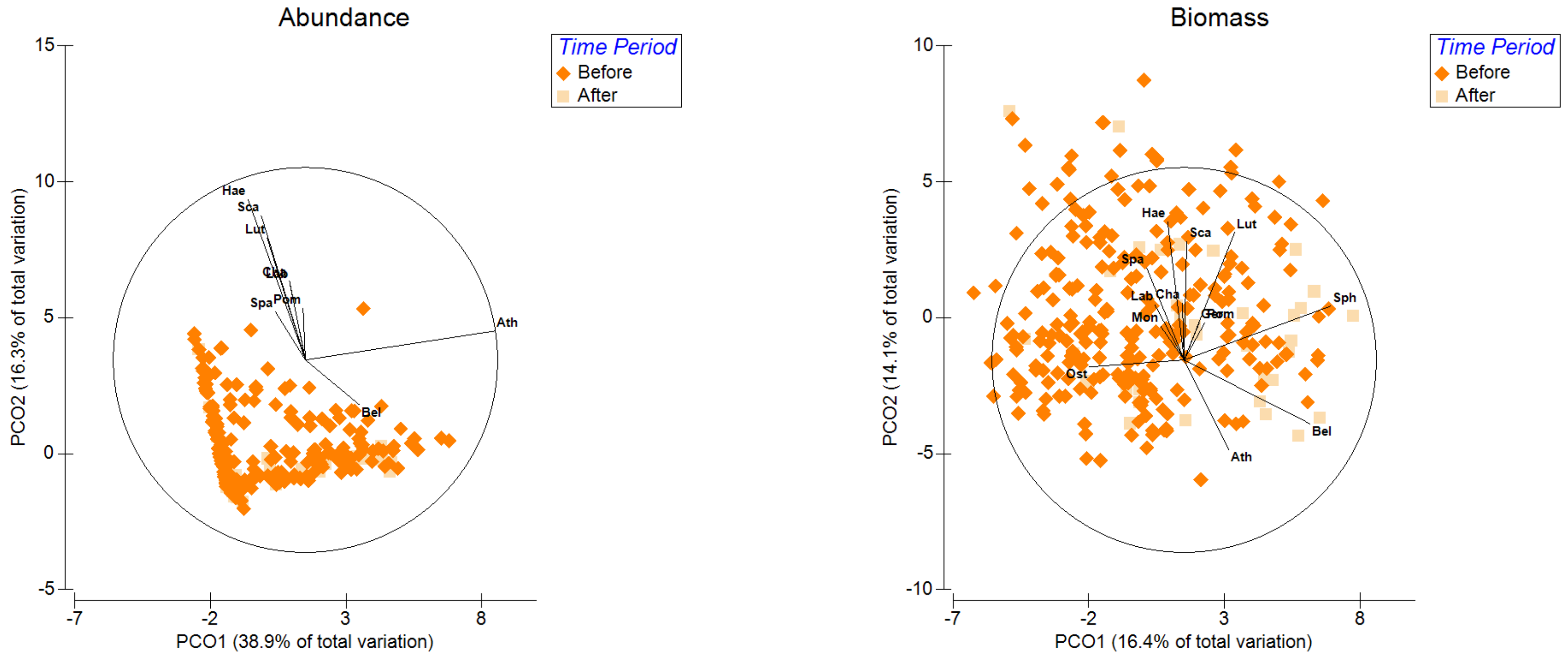


Figure 3.5. Principal coordinate analysis (PCO) plots for mean abundance and biomass of families captured in undisturbed South Bimini before and after a disturbance occurred in the North Sound. The first two axes of the abundance and biomass plots explain 55.2% and 30.5% of the variation, respectively. Data were $\log_{10}(x+1)$-transformed, and plots were based on Euclidean distances. Family vectors represent those with greater than a 0.2 Pearson correlation. Ath = Atherinidae, Bel = Belonidae, Cha = Chaetodontidae, Ger = Gerreidae, Hae = Haemulidae, Lab = Labridae, Lut = Lutjanidae, Mon = Monacanthidae, Ost = Ostraciidae, Pom = Pomacentridae, Sca = Scaridae, Spa = Sparidae, Sph = Sphyraenidae

Table 3.3. Permutational analysis of variance (PERMANOVA) results used in a before-after control-impact (BACI) design to test for differences in mean (a) abundance and (b) biomass of catch data in the North Sound and South Bimini (Nursery) both before and after (Time Period) habitat loss occurred in the North Sound. Asterisks indicate significance level (** = p<0.01, *** = p<0.001). df = degrees of freedom, SS = sum of squares, MS = mean square. Pseudo-F is similar to a traditional ANOVA F-statistic but does not have a known distribution under a true null hypothesis (Anderson et al. 2008). p(perm) = permutational p value.

(a) Abundance

	df	SS	MS	Pseudo-F	p(perm)	
Nursery	1	128000	128000	49.866	0.0001	***
Time Period	1	13516	13516	5.2479	0.0002	***
Nursery x Time Period	1	9930	9931	3.8558	0.0012	**
Residuals	672	1730000	2576			

(b) Biomass

	df	SS	MS	Pseudo-F	p(perm)	
Nursery	1	105000	105000	39.477	0.0001	***
Time Period	1	12134	12134	4.5523	0.0002	***
Nursery x Time Period	1	11155	11155	4.1851	0.0003	***
Residuals	672	1790000	2665			

Table 3.4. Mean abundance (count) and mean biomass (g) per seine (±SE) in the North Sound for each family. Asterisks indicate significant differences (Wilcoxon rank sum tests; * = p<0.05; ** = p<0.01; *** = p< 0.001). Values of 0.00 indicate the family was present, but at mean abundances or biomass per seine less than 0.01. NP = not present in any samples.

	Abundance			**Biomass**		
	Before		After	Before		After
Achiridae	0.54 ± 0.10	*	0.18 ± 0.09	1.78 ± 0.36		1.34 ± 0.40
Albulidae	0.19 ± 0.08		0.21 ± 0.10	127.71 ± 108.41		330.72 ± 173.01
Alphaeidae	0.00		NP	0.00		NP
Atherinidae	01.17 ± 89.96	***	35.31 ± 25.17	305.41 ± 283.08	***	76.32 ± 47.41
Batrachoididae	NP		0.06 ± 0.03	NP		12.5 ± 6.28
Belonidae	4.52 ± 1.06		3.84 ± 0.96	90.71 ± 33.85		96.14 ± 37.35
Bothidae	0.01 ± 0.01		NP	0.02 ± 0.01		NP
Carangidae	0.15 ± 0.03		0.08 ± 0.04	0.72 ± 0.18		2.36 ± 1.37
Chaetodontidae	0.01 ± 0.01		NP	0.08 ± 0.04		NP
Clupeidae	0.01 ± 0.01	***	0.22 ± 0.12	0.10 ± 0.06	*	2.54 ± 1.52
Cynoglossidae	0.01 ± 0.01		NP	0.04 ± 0.03		NP
Cyprinodontidae	0.01 ± 0.01		NP	0.01 ± 0.01		NP
Dasyatidae	0.00		NP	0.98 ± 0.98		NP
Diogenidae	NP		0.01 ± 0.01	NP		9.24 ± 9.24
Ephippidae	0.01 ± 0.01		NP	0.06 ± 0.04		NP
Epialtidae	0.01 ± 0.01		NP	1.25 ± 0.88		NP
Fistulariidae	0.00		NP	0.03 ± 0.03		NP
Gerreidae	69.16 ± 7.05	***	33.24 ± 15.79	496.05 ± 88.49		477.30 ± 127.47
Gobiidae	0.01 ± 0.01		NP	0.01 ± 0.01		NP
Gonodactylidae	0.00		0.05 ± 0.02	0.02 ± 0.02		0.19 ± 0.10
Haemulidae	0.42 ± 0.13		0.03 ± 0.02	6.19 ± 2.07		0.62 ± 0.44
Hemiramphidae	1.19 ± 0.26	**	0.88 ± 0.78	6.49 ± 1.72	**	3.77 ± 2.47
Hippolytidae	0.00		NP	0.00		NP
Labridae	0.02 ± 0.01		NP	0.19 ± 0.09		NP
Loliginidae	0.01 ± 0.01		NP	0.06 ± 0.06		NP
Lutjanidae	0.55 ± 0.11		0.38 ± 0.11	17.87 ± 4.04		12.75 ± 6.55
Majidae	0.02 ± 0.01		0.12 ± 0.04	0.41 ± 0.25	***	7.63 ± 4.01
Monacanthidae	0.05 ± 0.01		0.02 ± 0.01	0.37 ± 0.41		0.02 ± 0.02
Ostraciidae	0.24 ± 0.04		0.17 ± 0.05	61.97 ± 13.02		24.86 ± 0.76
Panuliridae	0.01 ± 0.01		0.05 ± 0.05	0.01 ± 0.01		11.27 ± 11.27
Paralychthidae	0.00		NP	0.06 ± 0.06		NP
Penaeidae	7.29 ± 4.01		4.09 ± 1.14	2.41 ± 0.48		2.00 ± 0.54
Pisidae	0.06 ± 0.02		NP	0.18 ± 0.09		NP
Pomacanthidae	NP		0.01 ± 0.01	NP		0.01 ± 0.01
Portunidae	2.36 ± 0.37		2.51 ± 0.71	16.44 ± 2.63		22.89 ± 11.53
Pseudosquillidae	0.00		NP	0.01 ± 0.01		NP
Rynchocinetidae	0.00		NP	0.00		NP
Scaridae	0.27 ± 0.08		0.03 ± 0.02	5.58 ± 1.69		0.98 ± 0.76
Scorpaenidae	0.00		0.01 ± 0.01	0.01 ± 0.01		0.29 ± 0.29
Sparidae	0.13 ± 0.06		0.01 ± 0.01	3.34 ± 1.25		0.12 ± 0.12
Sphyraenidae	1.29 ± 0.20	**	0.45 ± 0.11	119.56 ± 32.07		71.51 ± 26.21
Syngnathidae	0.11 ± 0.03		0.03 ± 0.02	1.88 ± 1.32		0.02 ± 0.01
Synodontidae	0.03 ± 0.01		0.06 ± 0.03	1.57 ± 0.55		2.57 ± 1.44
Tetraodontidae	0.74 ± 0.10		0.60 ± 0.12	6.05 ± 1.06		5.34 ± 2.08
Triglidae	0.00		NP	0.03 ± 0.03		NP
Xanthidae	NP		0.05 ± 0.03	NP		0.09 ± 0.05

Table 3.5. Mean abundance (count) and mean biomass (g) per seine (±SE) in South Bimini for each family. Asterisks indicate significant differences (Wilcoxon rank sum tests; * = p<0.05; ** = p<0.01; *** = p< 0.001). Values of 0.00 indicate the family was present, but at mean abundances or biomass per seine less than 0.01. NP = not present in any samples.

	Abundance			**Biomass**		
	Before		After	Before		After
Acanthuridae	0.06 ± 0.02		NP	0.41 ± 0.17		NP
Achiridae	0.01 ± 0.01		0.03 ± 0.03	0.07 ± 0.05		0.13 ± 0.13
Albulidae	0.02 ± 0.02		NP	16.85 ± 12.02		NP
Alphaeidae	0.04 ± 0.02		0.05 ± 0.04	0.00	**	0.02 ± 0.02
Antennariidae	0.00		NP	0.06 ± 0.03		NP
Atherinidae	67.78 ± 19.96		53.70 ± 15.92	87.92 ± 31.06		60.38 ± 18.75
Aulostomidae	0.01 ± 0.01		NP	0.13 ± 0.07		NP
Batrachoididae	0.02 ± 0.66		0.05 ± 0.04	0.11 ± 0.07		0.14 ± 0.11
Belonidae	4.46 ± 0.66	*	9.22 ± 2.42	177.91 ± 56.63	*	454.45 ± 149.45
Bothidae	0.01 ± 0.01		NP	0.07 ± 0.04		NP
Carangidae	0.11 ± 0.02		0.11 ± 0.08	48.64 ± 22.21		0.50 ± 0.35
Chaetodontidae	0.08 ± 0.02		0.05 ± 0.05	0.33 ± 0.10		0.26 ± 0.26
Cheloniidae	0.01 ± 0.01		NP	63.15 ± 54.49		NP
Clupeidae	362.88 ± 335.53		2.54 ± 2.54	140.72 ± 128.53		24.16 ± 24.16
Dactylopteridae	0.01 ± 0.01		NP	1.08 ± 0.79		NP
Dasyatidae	0.1 ± 0.03		NP	1618.69 ± 463.58		NP
Echeneidae	0.02 ± 0.01		NP	1.01 ± 0.98		NP
Fistulariidae	0.00		NP	0.22 ± 0.22		NP
Gerreidae	6.38 ± 1.90		3.97 ± 1.81	49.20 ± 9.4		84.03 ± 29.00
Ginglymostomatidae	0.01 ± 0.01		NP	25.63 ± 18.31		NP
Gobiidae	0.29 ± 0.06		0.19 ± 0.07	0.89 ± 0.18		0.50 ± 0.24
Gonodactylidae	0.01 ± 0.01	***	0.11 ± 0.05	0.02 ± 0.02	***	0.28 ± 0.19
Haemulidae	5.23 ± 1.21	*	1.43 ± 1.01	34.01 ± 7.75	*	30.7 ± 19.26
Hemiramphidae	0.43 ± 0.16		NP	35.85 ± 7.75		NP
Hippolytidae	0.43 ± 0.16		NP	0.01 ± 0.01		NP
Holocentridae	0.00		NP	0.03 ± 0.03		NP
Labridae	0.35 ± 0.09		0.14 ± 0.07	1.48 ± 0.38		1.64 ± 1.25
Labrisomidae	0.01 ± 0.01		NP	0.01 ± 0.01		NP
Lutjanidae	1.47 ± 0.28		1.14 ± 0.40	35.92 ± 6.81		197.78 ± 161.73
Majidae	0.02 ± 0.01	*	0.11 ± 0.06	0.02 ± 0.01	*	0.4 ± 0.26
Monacanthidae	0.16 ± 0.04		NP	0.84 ± 0.28		NP
Mullidae	0.22 ± 0.12		NP	2.23 ± 1.30		NP
Ostraciidae	0.50 ± 0.06	**	0.16 ± 0.09	158.94 ± 24.22	**	22.08 ± 11.44
Palaemonidae	0.00		NP	0.00		NP
Panuliridae	0.01 ± 0.01		NP	1.48 ± 1.48		NP
Penaeidae	0.11 ± 0.03		0.03 ± 0.03	0.16 ± 0.05		0.00
Pisidae	0.09 ± 0.02		NP	0.13 ± 0.04		NP
Pomacentridae	0.17 ± 0.04		0.03 ± 0.03	0.73 ± 0.15		0.05 ± 0.05
Portunidae	0.1 ± 0.02	*	0.35 ± 0.16	2.94 ± 1.19		1.66 ± 1.09
Pseudosquillidae	0.00		NP	0.02 ± 0.02		NP
Scaridae	2.87 ± 0.5	***	0.54 ± 0.44	18.53 ± 3.84	***	4.45 ± 4.34
Scorpaenidae	0.01 ± 0.01		NP	0.11 ± 0.01		NP
Serranidae	0.00		NP	0.19 ± 0.19		NP
Sparidae	0.44 ± 0.08		0.24 ± 0.16	58.75 ± 12.35		38.84 ± 27.21
Sphyraenidae	1.48 ± 0.21	**	2.24 ± 0.35	167.07 ± 31.75	**	380.51 ± 215.18
Squillidae	0.02 ± 0.01		NP	0.06 ± 0.03		NP
Syngnathidae	0.02 ± 0.01		NP	0.03 ± 0.01		NP
Synodontidae	0.02 ± 0.01		NP	0.26 ± 0.17		NP
Tetraodontidae	0.11 ± 0.02		0.03 ± 0.03	12.64 ± 5.31		0.17 ± 0.17
Xanthidae	0.01 ± 0.01	***	0.27 ± 0.09	0.01 ± 0.01	***	0.33 ± 0.13

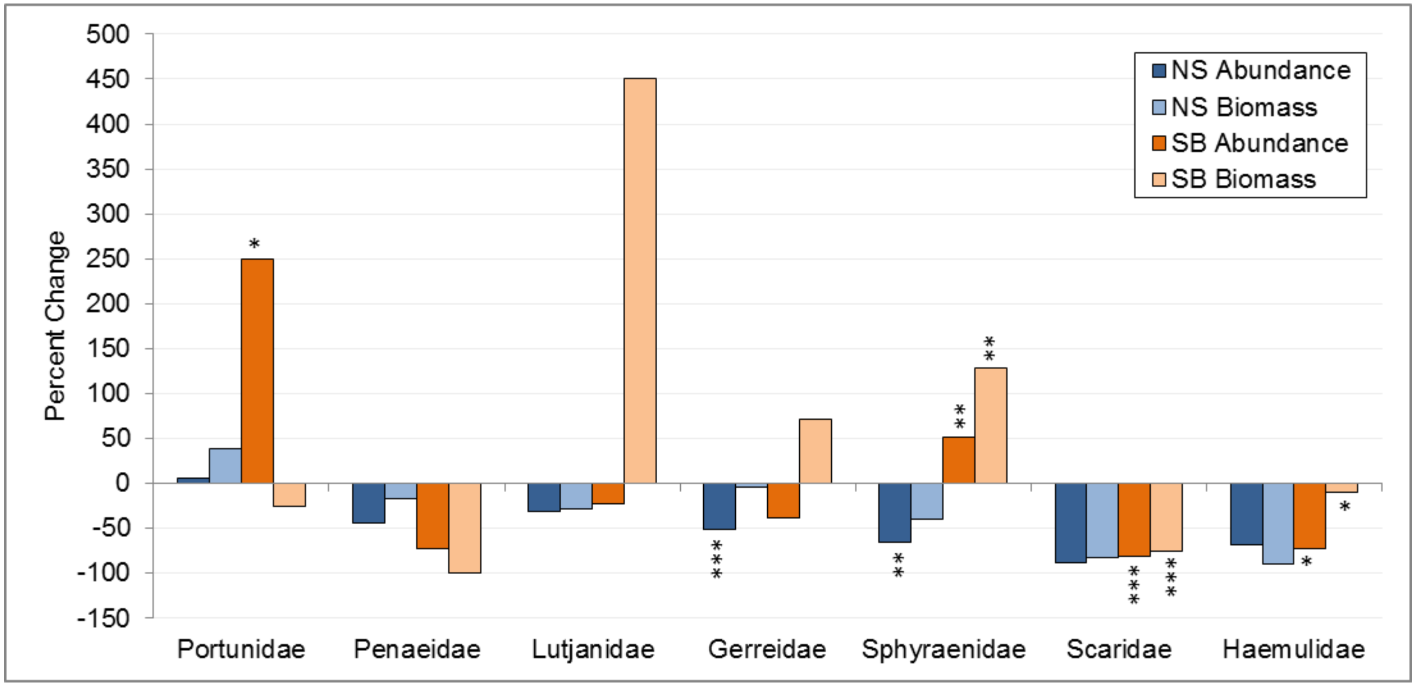
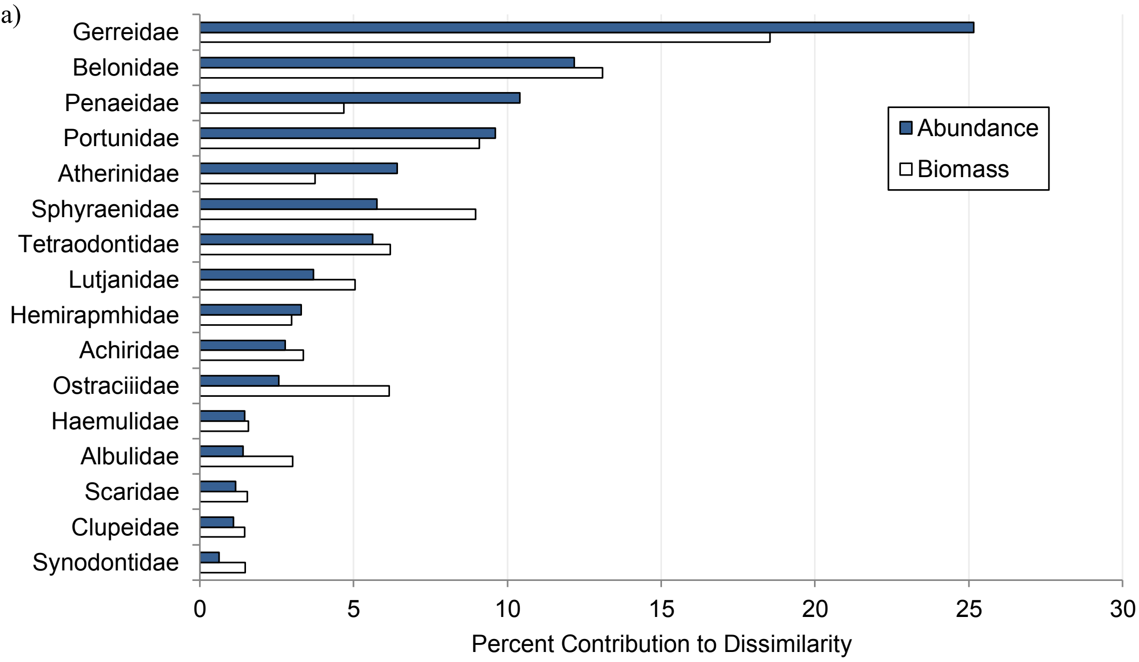


Figure 3.6. Magnitude of changes in mean abundance and biomass of seven important juvenile lemon shark prey families (Newman et al. 2010) in the North Sound (NS) and South Bimini (SB). Asterisks indicate significance level (* = p<0.05, ** = p<0.01, *** = p<0.001) as reported in Table 3.4 and Table 3.5.

Figure 3.7. Family contribution to dissimilarity before and after habitat loss for abundance and biomass in (a) the North Sound and (b) South Bimini (SIMPER, PRIMER-E). All data were $\log_{10}(x+1)$-transformed, and Bray-Curtis similarity matrices were used. Cumulatively, the 16 families in the North Sound and 18 families in South Bimini accounted for approximately 90% of the differences between time periods within their respective nurseries.

(a)



(b)

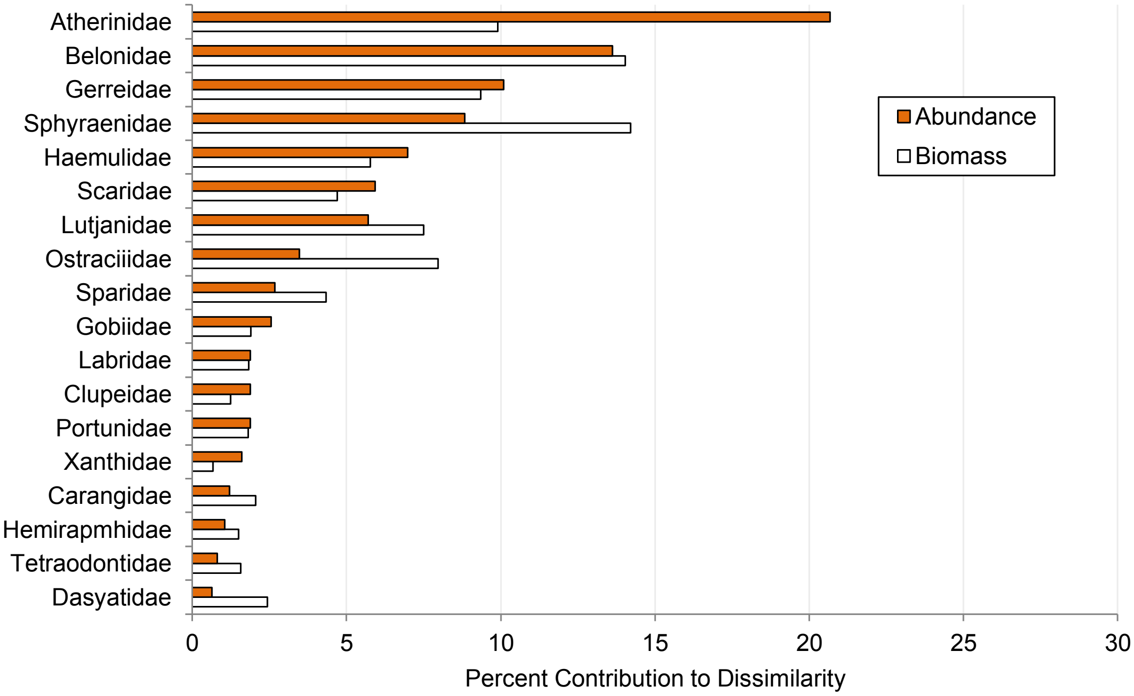


Table 3.6. Permutational analysis of variance (PERMANOVA) results testing for differences in mean (a) abundance and (b) biomass and of catch data on the disturbed and intact sides (Side) within the North Sound both before and after (Time Period) habitat loss. Asterisks indicate significance level (** = p<0.01, *** = p<0.001). df = degrees of freedom, SS = sum of squares, MS = mean square. Pseudo-F is similar to a traditional ANOVA F-statistic but does not have a known distribution under a true null hypothesis (Anderson et al. 2008). p(perm) = permutational p value.

(a) Abundance

	df	SS	MS	Pseudo-F	p(perm)	
Side	1	10646	10646	4.7622	0.0006	***
Time Period	1	12001	12001	5.3684	0.0002	***
Side x Time Period	1	1604.3	1604.3	0.71763	0.6523	
Residuals	368	822690	2235.6			

(b) Biomass

	df	SS	MS	Pseudo-F	p(perm)	
Side	1	9308	9308	3.8463	0.0008	***
Time Period	1	3916.9	3916.9	1.6186	0.1244	
Side x Time Period	1	2675.2	2675.2	1.1055	0.3636	
Residuals	368	890550	2420			

Table 3.7 Mean diversity index values (±SE) for the North Sound and South Bimini before and after habitat loss occurred in the North Sound. Asterisks indicate significant differences (Tukey test; * = p<0.05, ** = p<0.01). S = species richness, H' = Shannon Index, J' = Pielou Evenness Index.

	North Sound (Disturbed)			**South Bimini (Control)**	
	Before		After	Before	After
S	4.49 ± 0.11	**	4.00 ± 0.20	5.01 ± 0.15	4.5 ± 0.33
H'	0.74 ± 0.03	*	0.79 ± 0.05	0.95 ± 0.03	0.83 ± 0.09
J'	0.55 ± 0.02	**	0.65 ± 0.03	0.65 ± 0.02	0.60 ± 0.05

Table 3.8. Permutational analysis of variance (PERMANOVA) results used in a before-after control-impact (BACI) design to test for differences in (a) richness, (b) Shannon Index and (c) Pielou Evenness Index in the North Sound and South Bimini before and after habitat loss occurred in the North Sound. Asterisks indicate significance level (** = p<0.01, *** = p<0.001). df = degrees of freedom, SS = sum of squares, MS = mean square. Pseudo-F is similar to a traditional ANOVA F-statistic but does not have a known distribution under a true null hypothesis (Anderson et al. 2008). p(perm) = permutational p value.

(a) Richness (S)

	df	SS	MS	Pseudo-F	p(perm)	
Nursery	1	538.73	538.73	2.7048	0.0775	
Time Period	1	843.94	843.94	4.2371	0.0278	*
Nursery x Time Period	1	101.11	101.11	0.50764	0.5538	
Residuals	678	135040	199.18			

(b) Shannon (H’)

	df	SS	MS	Pseudo-F	p(perm)	
Nursery	1	1046	1045.8	1.0154	0.3499	
Time Period	1	401	401.41	0.38975	0.8605	
Nursery x Time Period	1	4414	4413.9	4.2857	0.006	**
Residuals	678	698280	1029.9			

(c) Evenness (J’)

	df	SS	MS	Pseudo-F	p(perm)	
Nursery	1	529.03	529.03	0.82842	0.4027	
Time Period	1	302.44	302.44	0.4736	0.6089	
Nursery x Time Period	1	3862.5	3862.5	6.0483	0.0056	**
Residuals	678	413820	638.61			

Chapter 4. Juvenile lemon shark spatial movements before and after nursery habitat loss

4.1 Background

Population dynamics, intra- and interspecific interactions, biodiversity and ecosystem structure are all influenced by animals' habitat use (Morris 2003). At the individual level, animal movements are driven largely by the need to balance prey acquisition with mortality risk (e.g., Werner et al. 1983, Lima & Dill 1990, Bednekoff 2007, Brown & Kotler 2007, Heithaus et al. 2009, Wirsing & Heithaus 2009). Many elasmobranchs use inshore nursery areas for the advantages of ample prey and protection from predators (e.g., Branstetter 1990, Simpfendorfer & Milward 1993, Castro 1993, McCandless et al. 2007), and the availability of such habitats may be a limiting factor for some shark populations (Springer 1967, Castro 1987). To identify and ultimately protect these habitats, it is important to understand how animals use nurseries as essential fish habitat (EFH) during early life stages (Simpfendorfer & Heupel 2004).

The shallow, mangrove-fringed lagoons and creeks of Bimini, Bahamas serve as lemon shark (*Negaprion brevirostris*) nurseries (Figure 4.1) as defined by Heupel et al. (2007). There, in the only such habitat on the western edge of the Great Bahama Bank, juveniles remain within specific primary nursery areas for several years (Morrissey & Gruber 1993a, Franks 2007, Chapman et al. 2009). While residents of primary nurseries, juvenile lemon sharks maintain relatively small, overlapping home ranges, with high reuse of areas along the mangrove fringe and no displays of territoriality (Morrissey & Gruber 1993a, Franks 2007). The presence of juveniles is negatively correlated with both depth and distance from shore (Franks 2007). Strong site fidelity has been shown through displacement and homing studies, which demonstrated that juveniles return to specific primary nursery sites from experimental displacement distances of up to 16 km (Edrén & Gruber 2005).

Globally, habitat loss has threatened several elasmobranchs species such as leopard sharks, *Triakis semifasciata* and sawfish, *Pristis pectinata* (Carlisle & Starr 2009, Simpfendorfer et al. 2010). In Bimini's North Sound nursery (Figure 4.1), the construction of a resort and marina has created a significant anthropogenic disturbance in the form of large-scale mangrove removal and dredge-and-fill activities (Gruber & Parks 2002). The effects of this disturbance on nursery-bound juvenile lemon sharks are unknown. The objective of this study, therefore, was to compare movement data from before and after habitat loss to determine if there were changes in movement patterns in response to the disturbance. Specifically, the following questions were addressed:

1. Do juveniles continue to exhibit site fidelity to the degraded nursery?
2. Is there an increase in size and extent of home range to areas beyond the disturbed North Sound?
3. Has there been a shift away from extensive shoreline use following mangrove removal, dredging and filling in the North Sound?

A before-after control-impact (BACI) design (Bernstein & Zalinski 1983) was used to compare pre- and post-disturbance movement patterns.

4.2 Methods

4.2.1 Study site, animal capture and transmitter implantation

In Bimini, Bahamas, the North Sound is a 3 km^2 semi-enclosed lagoon which experienced an anthropogenic disturbance in the form of large-scale mangrove removal in 2005, while the nearby South Bimini nursery remained undisturbed (Figure 4.1). Juvenile lemon sharks (Age-0 to Age-2) from the two geographically distinct nurseries were captured for use in this telemetry study. The South Bimini nursery was used as a contrasting nursery to the North Sound because pre-disturbance movement data also exist for South Bimini. In both locations, sharks were captured via gillnet following the methods described in Gruber et al. (2001). Individuals to be implanted with transmitters were transported to a holding pen, where they were measured, weighed and tagged with a passive integrated transponder (PIT, Destron Fearing®) tag.

Coded Transmitters (CTs) and Coded High Power Transmitters (CHPs, Sonotronics, Inc., Tucson, AZ) with battery life ranging from nine to 36 months were surgically implanted in the peritoneal cavity of juvenile lemon sharks. The weight in water of each CT and CHP ranged from 9.5 g to 12 g. It has been shown that at less than 2% of a shark's body weight, these transmitters do not affect behavior or growth (Morrissey & Gruber 1993a). Each acoustic transmitter emitted a unique combination of pulses at specific frequencies (70 – 83 kHz) that could be audibly identified when within range of a directional hydrophone (DH-4, Sonotronics, Inc.) and an ultrasonic receiver (USR-08, Sonotronics, Inc.), which converted the high-frequency pings to audible pulses. For example, a transmitter with the aural code 4-7-8 emitted four pulses followed by a pause, seven pulses followed by a pause, and eight pulses followed by a longer pause, at which point the cycle would repeat. Prior to implantation, all transmitters were range-tested to ensure they could be heard within the normal operating range of the hydrophone (up to approximately 100 m).

While sharks were temporarily immobilized in tonic immobility in an inverted position at the surface of the water (Watsky & Gruber 1990), a small (2-3 cm) incision was made through the abdominal wall into the peritoneal cavity, anterior to a pelvic fin. A CT or CHP transmitter was placed internally, and the incision was closed with Ethicon, Inc. 2-0 or 3-0 braided silk non-absorbable sutures. Individuals were then retained in the holding pen to recover and monitored daily for approximately seven to ten days. Once the incision site was healed, sutures were removed.

4.2.2 Data collection

When ready for release, telemetered sharks were transported back to their site of capture. Active tracking began immediately upon release and continued until sundown. For all subsequent tracking sessions, crews of three to four volunteers performed boat-based manual tracking of telemetered sharks for periods of up to eight hours. Three types of tracking occurred: 1) positional fixes were obtained for all sharks within a particular area, 2) a search for sharks was followed by a continuous track for the rest of the day on the first shark encountered, and 3) long-term tracks (24 to 36 hr) were conducted on specific individuals. For long-term tracks, teams rotated out after eight-hour shifts, with a new crew arriving on-site to continue the track without pause.

Skiff-based tracking crews consisted of at least three individuals: 1) a tracker positioned on the bow with a hydrophone and receiver, 2) a data recorder, and 3) a boat operator. Once a telemetered shark was encountered, its unique transmitter code was recorded, along with the GPS location of the boat (Garmin Ltd., GPS 72H$^{\text{TM}}$), the bearing to the shark (estimated by compass) and an estimated distance (in meters) of the signal (based on audible signal intensity). During the tracking period, the position, bearing and distance were recorded every five minutes. Distance estimates were potentially biased due to environmental conditions including substrate type, depth and sea surface conditions, all of which can affect the range of signal transmission (Franks 2007). In addition, listener bias may have contributed to variance in distance estimation. To reduce the effects of these biases, all volunteers were rigorously trained in active telemetry techniques, including practice sessions using dummy transmitters placed at known distances over various substrates and depths. During their first week of tracking actual sharks, new volunteers were paired with experienced trackers who would help determine distance estimates in the field.

To prevent altering shark behavior during the tracking process, crews remained at distances of 30 – 100 m from the telemetered sharks (Franks 2007). When possible, the boat engine was turned off and the skiff pushed through the shallow water to follow sharks as quietly as possible. Often, sharks entered areas too shallow for the skiffs, at which point the tracker would follow on foot, carrying the hydrophone and receiver. Using these methods, distances from the shark to the tracker were confidently estimated within 10 m (Morrissey & Gruber 1993a, Franks 2007).

4.2.3 Data Analysis

Data treatment

The full telemetry dataset consisted of sharks tracked in both the North Sound and South Bimini for this study from 2009 to 2011, as well as sharks tracked prior to North Sound habitat disturbance, from 2003 to 2005 (Franks 2007). Individuals tracked from 2003 to 2005 were captured, implanted with transmitters and tracked in the same manner as in the present study (Franks 2007). Data from both time periods were treated identically, as outlined below, allowing for a BACI analysis of juvenile lemon shark movements.

Though telemetered sharks were tracked immediately upon release, the first 24 hours of data were excluded due to the potential for post-handling and post-release effects on movement and behavior (see Sundstrom et al. 2001 for a review). In addition, if telemetered sharks were caught during gillnet surveys for concurrent studies (see Chapter 2), tracking data from the first 24 hours post-release on such occasions were also excluded. Sharks tracked over a period of less than one month and/or less than seven total hours were excluded from all analyses due to lack of sufficient data. For age-based analyses, data from an individual shark were included in an age category if the shark was tracked for at least one month with a minimum of seven hours of tracking during that age range. Because the North Sound nursery is immediately adjacent to the Sharkland nursery (Figure 4.1), some individuals' home ranges overlapped the two locations. To confidently assign juveniles as North Sound sharks, individuals for which more than approximately 25% of tracking locations were in Sharkland were excluded from all analyses. Positional fixes for the sharks were estimated from the recorded GPS locations of the tracking boat and the signal bearing and distance estimates using an Excel Geometry Function add-in (Spherical Earth Geometry: Angle and Distance Measurements, National Marine Mammal Laboratory 2000).

Franks (2007) found a significant autocorrelation of juvenile lemon shark estimated positions in the Bimini system such that the time-to-independence (TTI) of positional fixes was conservatively estimated to be 180 minutes. For statistical analyses, therefore, each shark's track was subsampled for locations occurring at intervals of greater than 180 minutes. In addition, because space use is largely a function of the availability of resources and mortality risk (Lima & Dill 1990) and there is relatively small seasonal variation in prey resources in the North Sound and South Bimini (Newman et al. 2007), movement data were considered in total, rather than by season. All statistical analyses were performed in R (version 3.0.0).

Site fidelity

To determine if juvenile lemon sharks exhibited site fidelity to a particular nursery, observed data were compared to correlated random walk (CRW) movement paths. CRWs were simulated for each individual shark using the Geospatial Modeling Environment (GME, Beyer 2009) for ArcGIS 10.0. Each CRW's step-length was drawn from a frequency distribution of step-lengths between successive positional fixes in the full observed datasets (i.e., prior to subsampling for a 180 minute TTI). Each step-length was paired with a randomly selected angle integer value between 0^o and 360^o. The number of steps for each CRW was set equal to the number of steps in the observed dataset for each shark. A land boundary of Bimini's shorelines was added as a constraint to prevent random movements onto unavailable habitat. One hundred simulated CRWs were created for each individual. The Mean Center tool (Spatial Statistics Toolbox, ArcGIS 10.0) was used to identify the geographic center of the simulated points, and the distance of each point in the CRW to the center of activity was calculated. Similarly, the distance of each observed point to the observed dataset's center of activity for each shark was also calculated. Mean distances from the CRWs and observed datasets were tested for significant differences using a Wilcoxon rank sum test.

Home range

The GME for ArcGIS 10.0 was used to estimate home range for each shark via the nonparametric minimum convex polygon (MCP) method (Mohr 1947) using the datasets subsampled for a 180 minute TTI. The MCP method estimates home range size by creating the smallest convex polygon that incorporates all tracking locations. MCPs were generated for 1) each shark's total set of tracking locations, and 2) data separated into Age-0, Age-1 and Age-2 for ontogenetic comparisons. All sharks used in this study were originally captured as neonates during annual gillnet surveys, so age was easily determined by the presence of an open umbilicus at the time of first capture (see Chapter 2, section 2.2). Prior to calculation of MCP area, a land mask was applied to exclude the islands themselves from polygon areas. A generalized linear model (GLM) was applied in a BACI design to test for differences in home range size, with the 2005 mangrove removal serving as the impact. Because the MCP method can be sensitive to sampling effort (Grubbs 2010), the GLM included a sampling factor which incorporated the number of different days each shark was tracked.

Distance from shore

To investigate juvenile lemon sharks' movements in relation to the shoreline, ArcGIS was used to calculate the straight-line distance of each location to the closest shore for all points in the datasets subsampled for a 180 minute TTI. A BACI design was employed, using the 2005 North Sound mangrove removal as the impact, to test for effects of age, nursery and time period (before: 2003-2005, after 2009-2011) on the sharks' mean distance from shore.

4.3 Results

Between 2009 and 2011, a total of 28 juvenile lemon sharks ranging from Age-0 to Age-2 were surgically implanted with acoustic transmitters in two nurseries (Table 4.1). Four individuals (North Sound: n = 3, South Bimini: n = 1) were excluded from analyses because they were not tracked for more than one month. Two individuals (North Sound: n = 2) were excluded because they were tracked for less than seven total hours. Two individuals were excluded from categorization as North Sound sharks because they were found more than 25% of the time in the adjacent Sharkland nursery (Table 4.2). There was no movement between the North Sound and South Bimini nurseries. Data from a total of 17 juvenile lemon sharks ranging from Age-0 to Age-2 tracked between 2003 and 2005 (North Sound: n = 9, South Bimini: n = 8), prior to habitat loss in the North Sound, were used for comparisons and met the same minimum data requirements as the current dataset (Franks 2007, Table 4.3).

4.3.1 Site fidelity

Before proceeding with home range analyses, the existence of site fidelity was first established for each shark by comparing observed tracking locations to 100 simulations of correlated random walks (CRWs, Figure 4.2) with land masks. Wilcoxon rank sum tests comparing the mean distance from each point to the center of activity in both the observed data and CRWs showed that all juveniles' movements were significantly different than randomly generated tracks (Table 4.4). Therefore, nursery-specific site fidelity was established for all individuals tracked between 2009 and 2011. Site fidelity had previously been established for all sharks tracked between 2003 and 2005 via similar methods (Franks 2007).

4.3.2 Home range

Total area of home ranges calculated for each individual shark via the nonparametric MCP method are given in Table 4.5. The range of estimates was similar in both nurseries before and after habitat disturbance (North Sound before: 0.214 – 2.459 km^2; North Sound after: 0.11 – 2.51 km^2; South Bimini before: 0.348 – 2.079 km^2; South Bimini after: 0.332 – 1.084 km^2). The data were normally distributed without transformation (Shapiro-Wilk normality test, $p = 0.25$). A generalized linear model (GLM) detected significant effects of both sampling effort and nursery on MCP area (Table 4.6). MCP area estimates of home range size were also calculated for Age-0, Age-1 and Age-2 sharks in both the North Sound and South Bimini before and after the disturbance occurred in the North Sound (Table 4.7). To account for differences in sampling effort among ages, nurseries and time periods, the number of days each individual was tracked was included as a factor in the GLM (Table 4.8). The GLM detected a significant slightly positive relationship between sampling effort and MCP area (Table 4.9, Figure 4.3). In addition, MCP area was significantly larger in the North Sound than South Bimini (Table 4.9, Figure 4.4). There were no significant effects of time period, age or any interaction of factors.

4*.3.3 Distance from shore*

The proportion of tracking locations falling within 50 m bins at increasing distances from shore are shown in Figure 4.5 for each age class in the North Sound and South Bimini both before and after habitat disturbance. Mean distances from shore for each age class in the North Sound and South Bimini before and after the disturbance are given in Table 4.10. An ANOVA was used for a BACI design to test for significant effects of age, nursery and time period on the shark's mean distance from shore. Prior to analysis, data were square root-transformed to achieve normality (Shapiro-Wilk, p = 0.29). Only a significant nursery effect was detected (Table 4.11), and Figure 4.6 shows the sharks' higher mean distance from shore in the North Sound compared to South Bimini.

4.4 Discussion

In the shallow, tropical mangrove-fringed nurseries of Bimini, Bahamas, juvenile lemon sharks were found not to have altered home range patterns following a large-scale anthropogenic disturbance. Despite significant mangrove removal within the nursery, tracked individuals continued to exhibit strong site fidelity to the North Sound and remained, on average, within close proximity of the denuded shoreline.

4.4.1 Methodology

Analyses of animal movements through the use of acoustic telemetry are particularly difficult due to the inherently autocorrelated nature of animal movements (Swihart & Slade 1997, Legendre 1993). Because resources and risk vary in time and space, animal locations tend to be clustered when the environment is heterogeneous (Legendre 1993). In addition, the ability to collect long-term tracking data at ecologically meaningful time scales is often limited by human resources (Simpfendorfer & Heupel 2004). For traditional statistical analyses, which assume sample independence, the effects of autocorrelation can be reduced by establishing a TTI of positional fixes; however, these reduced datasets come at the cost of losing potentially valuable information (Swihart & Slade 1997, Legendre 1993, De Solla et al. 1999). In the present study, this trade-off was balanced by employing ample human resources to collect data over sufficient time scales for meaningful comparisons after accounting for TTI.

Diel effects have often been observed in studies of elasmobranch behavior and habitat use (e.g., Nelson & Johnson 1970, Carey & Scharold 1990, Holland et al. 1993). In Bimini, Bahamas, large juvenile lemon sharks (150 – 230 cm total length) exhibit east-west diel activity patterns (Gruber et al. 1988). The majority of small juvenile (62.2 – 98.4 cm total length) lemon shark tracking in the current study was conducted during the day, but in the over 14 hours of nighttime tracking on sharks included in the analyses, no individual ever left its primary nursery or otherwise moved beyond locations at which it was tracked during daylight hours. In addition, no telemetered individuals were ever detected outside of their respective primary nurseries on a passive acoustic monitoring array in place around the wider insular system for a concurrent study (Stump, unpublished data). Therefore, in contrast to the known movements of large juveniles, it is likely that there were either no diel differences in movements of small juvenile lemon sharks, or if there were, they were at finer scales than the movements characterized for comparisons made here.

The MCP method for home range estimation is a common, though limited, measure of space use (Harris et al. 1990). Specifically, estimates of home range size can be positively correlated with sampling effort (Grubbs 2010). Results of a GLM which included sampling effort as a factor did indeed detect a significant positive relationship between the number of days an individual was tracked and MCP area. However, after accounting for this bias in the model, a significant effect of nursery on MCP area was still detected. This difference is likely due to the difference in depth and topography between the North Sound, which is a large expanse of shallow water, and South Bimini, where depth quickly increases with increasing distance from shore (Morrissey and Gruber 1993b, Franks 2007). The MCP method was preferred here over kernel utilization distributions, which generally do not allow for the inclusion of habitat constraints such as land masks for aquatic organisms in kernel estimation (Getz et al. 2007).

4.4.2 Site fidelity

All tracked individuals exhibited strong site fidelity to their respective nurseries. Despite significant declines in lemon shark prey in the North Sound (see Chapter 3) and the loss of important subtidal mangrove structure as refugia (see Chapter 5), home ranges of individuals captured in the degraded North Sound were restricted to the immediate area. This finding highlights the importance of parturition site selection by gravid adult females, which, despite being highly migratory, are known to be philopatric to Bimini (Feldheim et al. 2002, 2004). While the mechanisms of fine-scale (i.e., nursery-specific) site selection are unknown (Feldheim et al. 2002), there is evidence in support of philopatry specifically to natal nurseries (Feldheim et al., submitted). Because neonates and juveniles appear to be obligate residents of the natal nursery (S. Gruber, unpublished data), the continued presence of neonates in the North Sound each year (see Chapter 2) suggests that adult females have not altogether avoided the degraded habitat. With continued philopatry to habitats vulnerable to anthropogenic disturbance, the effects of disturbances can occur at individual, community and population levels (see Knip et al. 2010 for a review). For example, avian breeding success is greatly reduced in the face of even mild anthropogenic disturbances (see Hockin et al. 1992 for a review), and golden lion tamarin (*Leontopithecus rosalia*) groups experienced higher predation rates in degraded forests (Raboy et al. 2004 and references therein). Sharks that remain in habitats of deteriorating quality can also suffer increased mortality (Snelson & Bradley 1978, Smith & Abramson 1990, Knip et al. 2010 and references therein).

4.4.3 Home range and shoreline use

There were no post-disturbance differences in either the size of sharks' home ranges in the North Sound or the mean distance from the shore, suggesting that there were no behavioral changes in overall space use within the disturbed nursery. Only a nursery effect was significant, as home range size was smaller and inshore use higher in South Bimini in both time periods. The South Bimini nursery is deeper and more exposed to larger predators than the semi-enclosed North Sound (Figure 4.1, Franks 2007). Results, therefore, are in agreement with other elasmobranch studies which highlight the importance of physical characteristics of habitat in terms of risk assessment in driving nursery-scale movement patterns (Heupel & Hueter 2002, Chapman et al. 2007, Papastamatiou et al. 2009, Guttridge et al. 2012).

Ontogenetic increases in elasmobranch activity space and home range have been documented in many species (e.g., Wetherbee et al. 2007, Yeiser et al. 2008). In the current study, however, no differences among age classes were found in home range size or shoreline use in either nursery over time. Often, when a lack of correlation is found between age and home range size, it is due to insufficient tracking durations for complete home range characterization and/or little variability in the size of sharks tracked (see Grubbs 2010 for a review). In this study, significant human resources were expended for long tracking durations, suggesting that the latter may be a more likely explanation for the lack of difference in home range size among age classes. The range in total length of telemetered sharks among all age classes varied only from 62.2 to 98.4 cm total length, and home range size likely increases along a continuum rather than discrete expansions (Grubbs 2010). In addition, in constrained subtropical lagoons, such as in Bimini, home ranges are generally small, and individuals use much of the available space while nursery-bound (Holland et al. 1993, Garla et al. 2005, Papastamatiou et al. 2009).

Understanding ontogenetic movement patterns is essential for identifying and ultimately protecting vulnerable habitats that are critical to survival (Simpfendorfer & Heupel 2004). In the North Sound, no age class moved away from or expanded beyond the primary nursery in response to degradation of a large portion of the mangrove-fringed shoreline. Not only do the juveniles remain site-attached to their natal nursery, but they also continue to show the same overall distribution patterns within it, with no avoidance of denuded areas in terms of either usage or distance. The exact timing of an ontogenetic shift out of the North Sound likely varies among individuals (Morrissey & Gruber 1993a, Franks 2007, Chapman et al. 2009), but for the first three years, sharks appear to be behaviorally bound to the 3 km^2 area despite changes in habitat quality. Juveniles, therefore, are particularly vulnerable to disturbances within the nursery, which can have negative effects on survival and growth (see Chapter 2). Even though there were significant post-disturbance decreases in the mean abundance of their prey (see Chapter 3), juveniles remained within the North Sound. This finding suggests that predation risk beyond the North Sound, where there is an increased likelihood of encounters with predators such as larger conspecifics (see Figure 1.2, Gruber et al. 1988, Franks 2007, Guttridge et al. 2012), is potentially a major driver which keeps juveniles from emigrating despite decreased habitat quality.

4.5 Conclusion

In Bimini, Bahamas, juvenile lemon sharks are obligate residents of specific natal nurseries. Tracking data show that despite large-scale habitat destruction, juveniles remain site-attached to the disturbed nursery and continue to use the degraded habitat in a manner similar to pre-disturbance use. Telemetry data show that despite suitable alternative habitats within the insular Bimini system, juveniles continue to remain within the disturbed natal nursery. As the only available nursery habitat on the western edge of the Great Bahama Bank, there is no viable alternative within a reasonable distance of Bimini. In addition, gravid adult females, which exhibit philopatry, have not avoided the North Sound as a parturition site after the disturbance. Therefore, juveniles are bound to the degraded North Sound and are particularly vulnerable to the anthropogenic disturbances within. It is possible that continued development could push the ecosystem to the point where the area could no longer produce enough viable recruits to maintain the adult population of Bimini recruits. Therefore, it is important to consider coastal zone management scenarios that protect these essential nursery habitats and weigh future development plans against species-specific and ecosystem-wide conservation and sustainability goals.

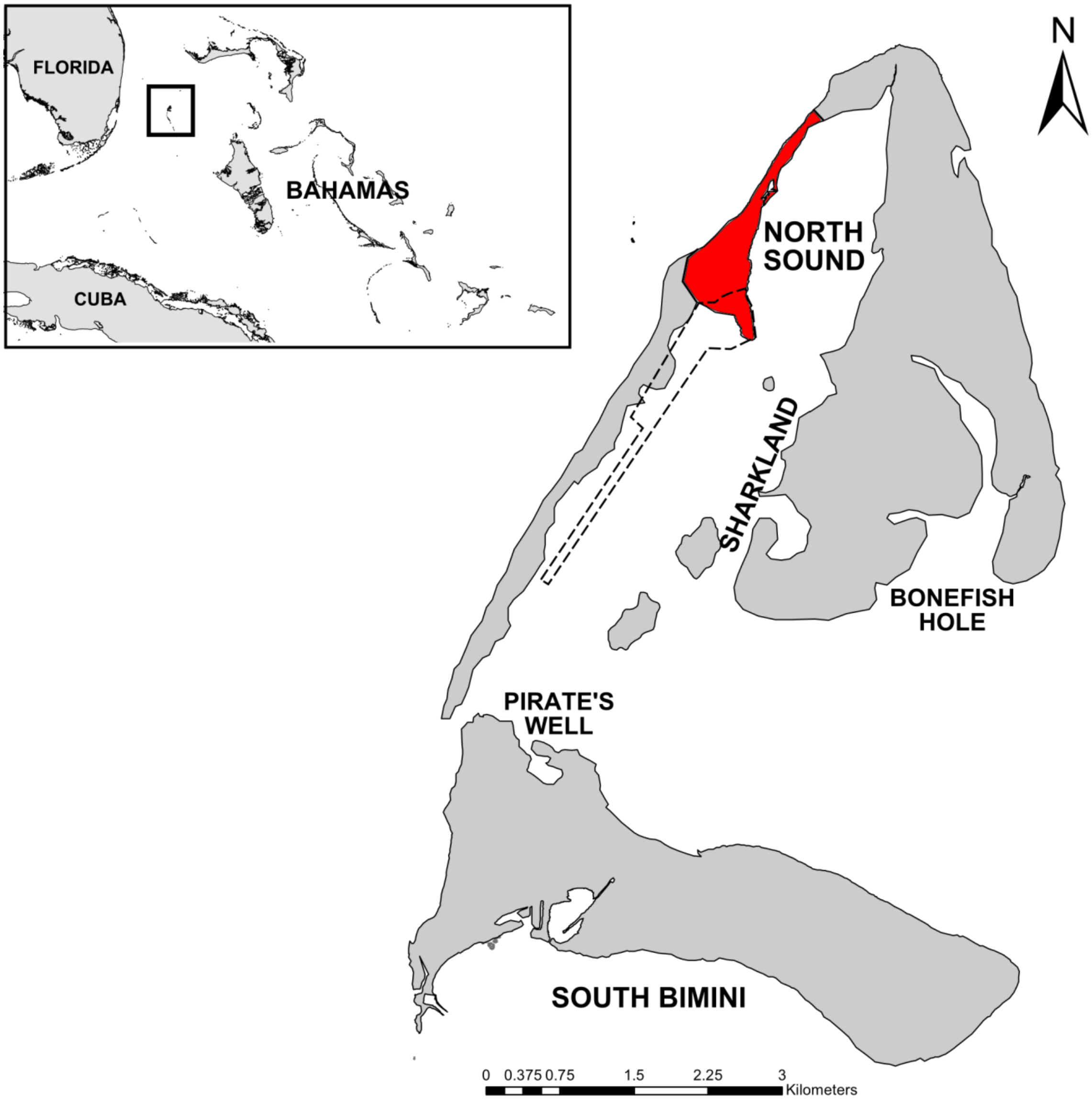


Figure 4.1 Bimini, Bahamas is an island group on the western edge of the Great Bahama Bank, approximately 86 km east of Miami, FL. Labels indicate specific locations of juvenile lemon shark nursery areas within the islands. Red shows the area of 2005 mangrove removal, which was subsequently filled with dredge material. Seabed dredging occurred in 2001 within the area outlined by the dotted line.

Table 4.1. Sharks implanted with acoustic transmitters between 2009 and 2011. Bold indicates individuals included in analyses. Values for hours tracked reflect totals after exclusion of data for the first 24 hr period post-release for each individual.

Nursery	Transmitter ID	PIT Tag	Sex	YOB	Age at Release	Age Last Heard	Size at Release (TL in cm)	Release Date	Last Heard	Days at Liberty	Hours Tracked
North Sound	3576	4A7F773A10	F	2008	1	1	72.2	27-Jun-09	19-Oct-09	112	34.00
North Sound	**3384**	**4A322F4174**	**M**	**2007**	**2**	**2**	**78.0**	**28-Jun-09**	**7-Oct-09**	**99**	**85.42**
North Sound	6868	4B183E4B10	F	2008	1	1	72.0	31-Jul-09	31-Jul-09	0	0.00
North Sound	5657	4A73164448	F	2009	0	0	61.4	4-Aug-09	11-Aug-09	7	3.08
North Sound	5658A	4B1B107709	M	2009	0	0	63.2	15-Sep-09	1-Oct-09	16	12.83
North Sound	**387**	**4A7F716620**	**M**	**2008**	**1**	**2**	**74.2**	**9-Oct-09**	**27-Jun-10**	**258**	**40.67**
North Sound	**478**	**4A34713E21**	**M**	**2008**	**1**	**3**	**71.2**	**10-Dec-09**	**28-Nov-11**	**708**	**123.42**
North Sound	**587**	**4A33485270**	**F**	**2008**	**1**	**1**	**73.1**	**20-Jan-10**	**12-Mar-10**	**52**	**13.67**
North Sound	5788	4B04237C33	F	2009	0	1	70.2	22-Jan-10	18-Apr-11	446	31.33
North Sound	**4456**	**4A7328590E**	**F**	**2009**	**0**	**0**	**65.7**	**26-Jan-10**	**23-Apr-10**	**87**	**14.83**
North Sound	**3344**	**4A73284302**	**M**	**2009**	**0**	**1**	**66.8**	**28-Jan-10**	**27-May-10**	**119**	**26.67**
North Sound	**3377**	**4B1A692329**	**F**	**2009**	**1**	**2**	**68.0**	**25-May-10**	**28-Nov-11**	**543**	**82.59**
North Sound	**356**	**4A737C3856**	**F**	**2009**	**1**	**2**	**70.4**	**29-May-10**	**2-Aug-11**	**423**	**53.92**
North Sound	**4457**	**4B7B43556A**	**M**	**2010**	**0**	**1**	**62.2**	**7-Aug-10**	**4-Aug-11**	**357**	**11.25**
North Sound	5678	4B7B444052	F	2010	0	0	54.9	11-Aug-10	22-Sep-10	41	3.50
North Sound	**5558**	**4B7B480153**	**M**	**2010**	**0**	**1**	**64.4**	**5-Sep-10**	**13-May-11**	**248**	**11.58**
North Sound	**5878**	**4B7B4B0A71**	**M**	**2010**	**0**	**1**	**67.4**	**5-Sep-10**	**23-Jul-11**	**318**	**19.33**
North Sound	4668	4B7B4B1D02	F	2010	0	0	63.0	20-Sep-10	23-Jul-11	39	3.25
North Sound	**3345**	**4A720F4520**	**F**	**2009**	**1**	**2**	**71.6**	**25-Nov-10**	**28-Nov-11**	**363**	**58.83**
North Sound	**5566**	**4B7B495825**	**M**	**2010**	**0**	**1**	**64.8**	**25-Nov-10**	**23-Oct-11**	**328**	**23.00**
North Sound	**5658**	**4A734D6775**	**F**	**2009**	**1**	**2**	**70.4**	**30-Nov-10**	**23-Jun-11**	**203**	**40.50**
North Sound	**5688**	**4B0273650E**	**F**	**2009**	**1**	**2**	**66.8**	**30-Nov-10**	**4-Aug-11**	**244**	**25.42**
South Bimini	4868	4B190B4046	F	2009	0	0	64.2	29-Jul-09	13-Aug-09	14	5.75
South Bimini	**5787**	**4B187D3811**	**F**	**2009**	**0**	**0**	**71.4**	**6-Oct-09**	**22-Feb-10**	**136**	**45.75**
South Bimini	**355**	**4B18063B38**	**F**	**2008**	**1**	**1**	**76.6**	**15-Nov-09**	**11-Feb-10**	**86**	**11.75**
South Bimini	**588**	**4B185F0E32**	**M**	**2008**	**1**	**2**	**79.1**	**22-Nov-09**	**5-Aug-10**	**253**	**54.75**
South Bimini	**6887**	**4A33607B56**	**M**	**2007**	**2**	**3**	**85.2**	**4-Dec-09**	**17-Apr-11**	**493**	**64.00**
South Bimini	**4667**	**485860666D**	**M**	**2011**	**0**	**0**	**63.4**	**24-Aug-11**	**23-Oct-11**	**59**	**61.42**

YOB = year of birth, TL = total length

Table 4.2. Percentage of positional fixes by area for each shark tracked in the North Sound (NS), Sharkland (SL) and South Bimini (SB), along with original site of capture. All sharks with a value in the %Other column were tracked just outside the edge of the North Sound, in a shallow area just south of southernmost extent of the mangrove removal (Figure 4.1). Sharks originally captured in the North Sound but tracked for more than approximately 25% of the time in Sharkland were excluded from analyses.

Transmitter ID	Capture Location	%NS	%SL	%SB	%Other
356	North Sound	98.15	0.62	0	1.24
387	North Sound	94.47	5.53	0	0.61
478	North Sound	99.86	0	0	0.14
587	North Sound	73.78	25.00	0	1.22
3344	North Sound	100	0.00	0	0
3345	North Sound	91.50	1.13	0	7.37
3377	North Sound	93.24	1.61	0	5.15
3384	North Sound	99.22	0.78	0	0
3576	North Sound	16.42	83.58	0	0
4456	North Sound	100	0	0	0
4457	North Sound	82.22	0.74	0	17.04
4668	North Sound	100	0	0	0
5558	North Sound	97.84	0	0	2.16
5566	North Sound	100	0	0	0
5657	North Sound	100	0	0	0
5658	North Sound	92.18	5.76	0	2.06
5678	North Sound	100	0	0	0
5688	North Sound	100	0	0	0
5788	North Sound	15.69	84.31	0	0
5878	North Sound	74.57	25.43	0	0
5658A	North Sound	91.56	0	0	8.44
355	South Bimini	0	0	100	0
588	South Bimini	0	0	100	0
4667	South Bimini	0	0	100	0
4868	South Bimini	0	0	100	0
5787	South Bimini	0	0	100	0
6887	South Bimini	0	0	100	0

Table 4.3. Sharks implanted with acoustic transmitters between 2003 and 2005 (Franks 2007) included in the “before” dataset for the before-after control-impact (BACI) design. Values for hours tracked reflect totals after exclusion of data for the first 24 hr period post-release for each individual.

Nursery	Transmitter ID	PIT Tag	Sex	YOB	Age at Release	Age Last Heard	Size at Release (TL in cm)	Release Date	Last Heard	Days at Liberty	Hours Tracked
North Sound	357	423B416C5E	M	2002	0	1	69.1	18-Apr-03	28-Jul-03	100	19.12
North Sound	366ns	411C324613	F	2001	2	3	75.0	10-Aug-03	26-Jun-04	316	61.00
North Sound	455	4234490149	F	2003	0	0	71.2	30-Oct-03	3-Apr-04	153	50.58
North Sound	777	4234473605	F	2002	1	3	73.0	6-Mar-04	2-Jun-05	446	53.92
North Sound	446	44556A562C	F	2004	0	0	71.2	26-Jun-04	12-Mar-05	256	33.25
North Sound	347	42344D0903	M	2003	1	2	70.0	18-Aug-04	18-Aug-05	360	39.58
North Sound	345ns	4234485540	M	2003	1	1	64.4	23-Aug-04	12-Dec-04	109	7.00
North Sound	3365	445C707F6F	M	2004	0	0	62.2	12-Sep-04	12-Dec-04	90	15.08
North Sound	334	44565A6B51	F	2004	0	1	65.8	16-Apr-05	18-Aug-05	122	7.25
South Bimini	366sb	42324D5776	F	2002	0	1	71.5	22-Mar-03	4-Jul-03	102	22.17
South Bimini	333	4234557F12	M	2002	1	1	65.6	24-May-03	4-Apr-04	310	68.33
South Bimini	345sb	423B420128	M	2002	1	1	75.6	13-Aug-03	6-Nov-03	83	37.67
South Bimini	367	41370A2235	F	2001	1	2	80.0	2-Dec-03	16-Apr-05	494	95.50
South Bimini	3336	423B523139	F	2003	1	2	69.8	24-Jul-04	17-Nov-05	473	119.17
South Bimini	233	451C5B1B05	F	2004	1	1	71.2	6-Jul-05	6-Feb-06	210	39.00
South Bimini	344	4232506D40	M	2004	1	1	73.2	4-Aug-05	19-Feb-06	195	32.92
South Bimini	223	411C2D607A	M	2005	0	0	65.4	26-Aug-05	30-Jan-06	154	12.67

YOB = year of birth, TL = total length

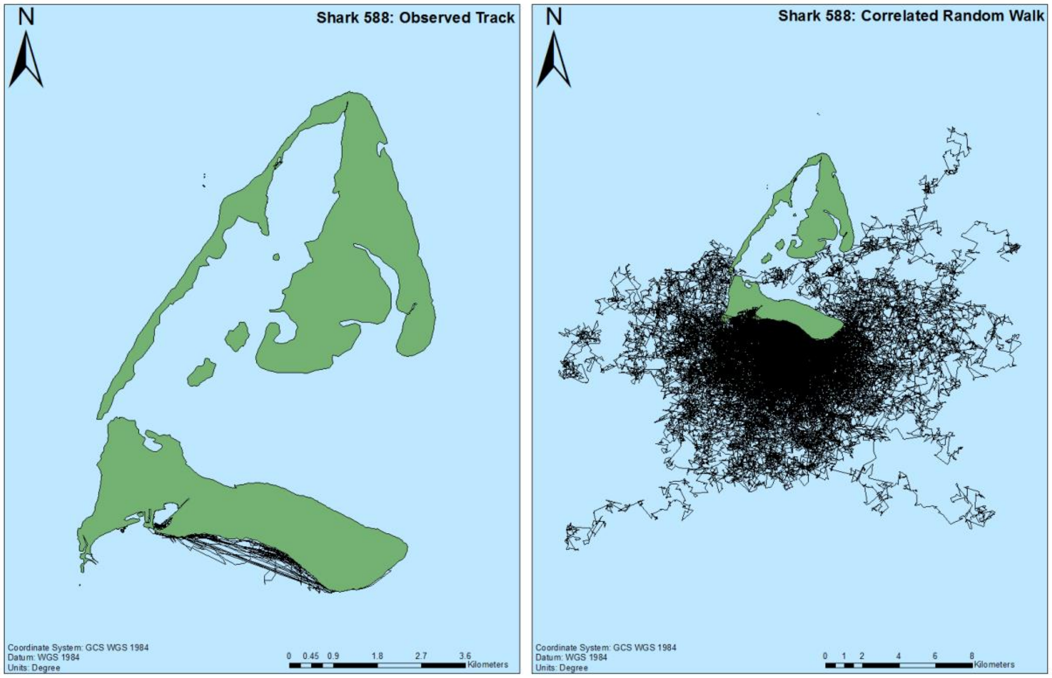


Figure 4.2. An example of the observed track (left) and 100 simulated correlated random walks (CRWs, right) of one South Bimini juvenile (Shark 588, Table 4.1).

Table 4.4. Results of tests of site fidelity for sharks between 2009 and 2011. Mean distances of each point in a correlated random walk (CRW MD) to its center of activity were compared to mean distances of each point to the center of activity of observed data (OBS MD) using a Wilcoxon rank sum test. Asterisks indicate significant differences.

Shark	Nursery	CRW MD	OBS MD	W	p	
356	North Sound	3724.97 ± 9.64	350.8 ± 10.35	41284171	<0.001	***
387	North Sound	2706.34 ± 8.97	739.11 ± 16.76	21481692	<0.001	***
478	North Sound	5496.1 ± 8.8	497.13 ± 7.35	216184420	<0.001	***
587	North Sound	1156.88 ± 6.68	572.02 ± 13.78	2057307	<0.001	***
3344	North Sound	1236.8 ± 5.13	589.91 ± 15.6	7580689	<0.001	***
3345	North Sound	3612.75 ± 9.01	846.96 ± 12.56	46333862	<0.001	***
3377	North Sound	4465.52 ± 9.68	634.11 ± 12.12	96257396	<0.001	***
3384	North Sound	4789.53 ± 9.46	590.61 ± 8.77	102147112	<0.001	***
4456	North Sound	1910.42 ± 9.06	393.47 ± 24.16	2950362	<0.001	***
4457	North Sound	1340.57 ± 7.72	494.91 ± 27.25	1553357	<0.001	***
5558	North Sound	1622.04 ± 9.12	335.88 ± 20.72	1837314	<0.001	***
5566	North Sound	2174.98 ± 9.39	525.67 ± 19.17	7053730	<0.001	***
5658	North Sound	2531.58 ± 8.08	429.14 ± 19.47	22241924	<0.001	***
5688	North Sound	2836.21 ± 10.25	583.22 ± 27.74	8683261	<0.001	***
5878	North Sound	1824.04 ± 7.7	742.27 ± 21.73	4610671	<0.001	***
355	South Bimini	1605.64 ± 8.63	954.39 ± 44.06	1517206	<0.001	***
588	South Bimini	3263.89 ± 9.30	1014.75 ± 19.73	37268392	<0.001	***
4667	South Bimini	2358.45 ± 5.9	217.06 ± 2.97	53713454	<0.001	***
5787	South Bimini	1812.37 ± 5.77	324.87 ± 19.50	28556016	<0.001	***
6887	South Bimini	2509.0 ± 5.53	632.49 ± 23.06	53974910	<0.001	***

W = Wilcoxon statistic

Table 4.5. Total minimum convex polygon (MCP) area in km^2 for each shark in the North Sound and South Bimini before and after habitat loss occurred in the North sound. MCP areas were calculated from tacking datasets subsampled for positional fixes occurring at intervals greater than 180 minutes.

North Sound				**South Bimini**			
Before (2003-2005)		After (2009-2011)		Before (2003-2005)		After (2009-2011)	
Shark	MCP	Shark	MCP	Shark	MCP	Shark	MCP
334	1.091	3384	1.735	366sb	0.359	5787	0.332
345ns	0.55	387	2.51	344	0.378	355	0.98
347	1.357	478	1.863	223	0.348	588	1.084
357	0.564	587	1.009	345sb	0.791	6887	0.155
366ns	1.446	4456	0.786	367	2.079	4667	0.171
446	2.459	3344	1.852	3336	2.078		
455	0.772	3377	2.457	333	1.491		
777	1.895	356	0.821	233	0.348		
3365	0.214	4457	0.512				
		5558	0.11				
		5878	0.898				
		3345	2.342				
		5566	1.409				
		5658	1.325				
		5688	1.246				

Table 4.6. Results of generalized linear model (GLM) used to test for differences in overall minimum convex polygon (MCP) area for sharks in the North Sound and South Bimini (Nursery) before and after (Time Period) habitat loss occurred in the North Sound, accounting for potential effects of sampling effort (Days) on MCP area estimation. Asterisks indicate significance level (** = 0.01, *** = 0.001).

	df	SS	MS	F-value	p-value	
Days	1	1.6127	1.6127	22.061	<0.001	***
Time Period	1	0.002	0.002	0.028	0.869	
Nursery	1	0.7218	0.7218	9.874	0.004	**
Days x Time	1	0.1354	0.1354	1.852	0.184	
Days x Nursery	1	0.0454	0.0454	0.621	0.437	
Time x Nursery	1	0.0133	0.0133	0.182	0.673	
Days x Time x Nursery	1	0.1058	0.1058	1.461	0.237	
Residuals	29	2.1199	0.0731			

df = degrees of freedom, SS = sum of squares, MS = mean square

Table 4.7. Minimum convex polygon (MCP) area in km^2 for Age-0, Age-1 and Age-2 sharks in the North Sound and South Bimini before and after habitat loss occurred in the North Sound. Values in parentheses indicate sample size.

	North Sound		**South Bimini**	
	Before (2003-2005)	After (2009-2011)	Before (2003-2005)	After (2009-2011)
Age-0	1.15 ± 0.67 (3)	0.61 ± 0.14 (6)	0.16 ± 0.1 (2)	0.25 ± 0.08 (2)
Age-1	0.90 ± 0.15 (5)	1.30 ± 0.19 (9)	0.64 ± 0.16 (7)	1.01 ± 0.03 (2)
Age-2	1.05 ± 0.46 (3)	1.47 ± 0.25 (5)	1.51 ± 0.01 (2)	0.57 ± 0.42 (2)

Table 4.8. Number of different days each shark was tracked at each age in each nursery before and after habitat loss. Values are the total number of days from tracking datasets after subsampling for positional fixes occurring at intervals greater than 180 minutes.

	North Sound		
	Time	Shark	Days
Age 0	Before	455	12
		3365	12
		446	24
	After	5558	9
		3344	11
		4456	14
		4457	14
		5566	16
		5878	22
Age 1	Before	777	3
		358	5
		334	15
		345	16
		347	17
	After	5566	9
		478	10
		587	10
		5688	19
		387	20
		3345	28
		5658	31
		356	51
		3377	57
Age 2	Before	347	10
		366	19
		777	32
	After	356	13
		3384	24
		3345	24
		3377	25
		478	43

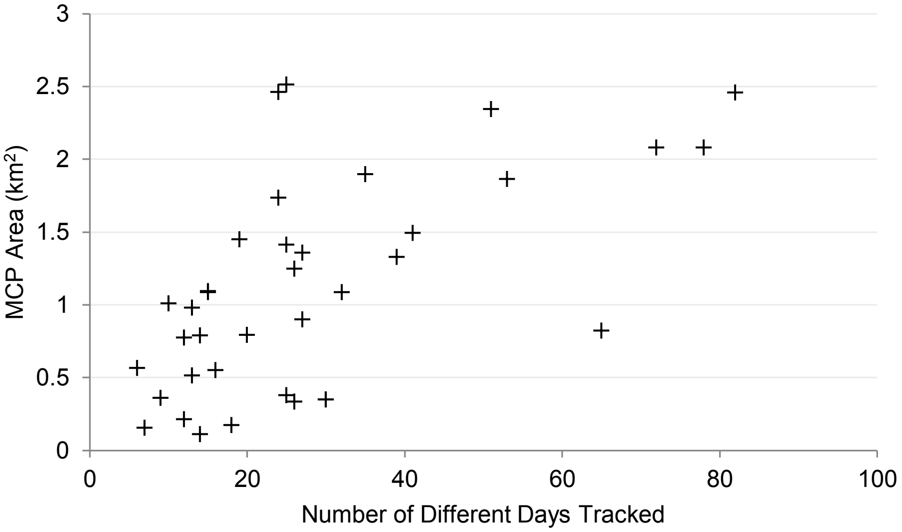
	South Bimini		
	Time	Shark	Days
Age 0	Before	366	4
		223	13
	After	4667	18
		5787	26
Age 1	Before	366	5
		367	19
		345	20
		344	25
		233	30
		333	41
		3336	62
	After	355	13
		588	23
Age 2	Before	3336	20
		367	55
	After	6887	7
		588	9

Table 4.9. Results of generalized linear model (GLM) to test for differences in minimum convex polygon (MCP) area among ages and nurseries before and after (Time Period) habitat loss occurred in the North Sound, accounting for potential effects of sampling effort (Days) on MCP area estimation. Asterisks indicate significance level (** = 0.01, *** = 0.001).

	df	SS	MS	F-value	p-value	
Days	1	3.42	3.42	16.09	0.001	***
Time Period	1	0.29	0.29	1.348	0.257	
Age	2	1.38	0.7	3.239	0.057	
Nursery	1	2.21	2.21	10.41	0.004	**
Days x Time	1	0	0	0.006	0.939	
Days x Age	2	0.98	0.5	2.298	0.122	
Time x Age	2	1.22	0.6	2.878	0.076	
Days x Nursery	1	0.52	0.52	2.423	0.133	
Time x Nursery	1	0.02	0.02	0.092	0.765	
Age x Nursery	2	0.21	0.1	0.498	0.614	
Days x Time x Age	2	0.53	0.3	1.24	0.307	
Days x Time x Nursery	1	0.28	0.28	1.313	0.263	
Days x Age x Nursery	2	0.5	0.2	1.169	0.328	
Time x Age x Nursery	2	0.26	0.1	0.617	0.548	
Days x Time x Age x Nursery	2	0.48	0.2	1.119	0.343	
Residuals	24	5.1	0.2			

df = degrees of freedom, SS = sum of squares, MS = mean square

(a)



(b)

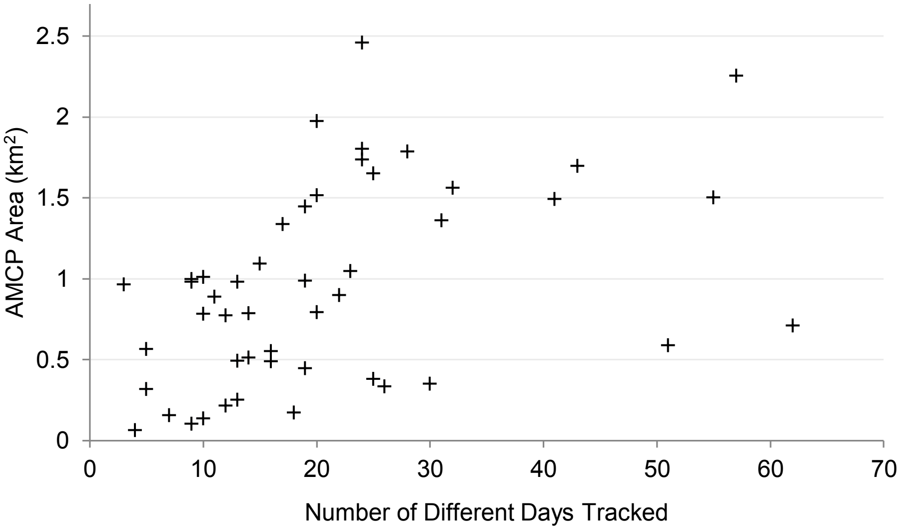


Figure 4.3. Estimated minimum convex polygon (MCP) area as a function of sampling effort for (a) each shark's full dataset, within-shark ages combined (n = 37), and (b) fully separated into ages (n = 48). The number of different days tracked was calculated from each individual's dataset of independent positional fixes (i.e., a subsampled dataset of points greater than 180 minutes apart).

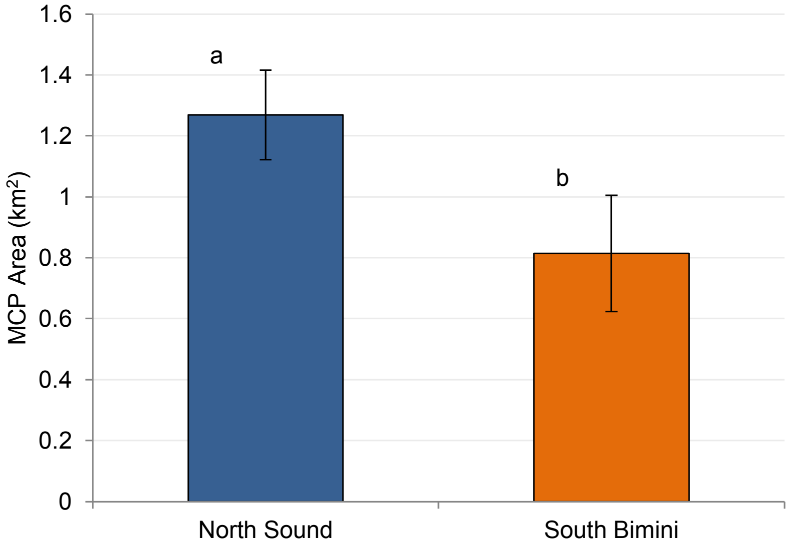


Figure 4.4. Minimum convex polygon (MCP) area (±SE) in the North Sound (1.27 ± 0.14) and Sharkland (0.81 ± 0.19). Data represent all ages and both time periods (before and after) within in each nursery, as a generalized linear model found no significant differences among those groups (GLM, $p>0.05$). Lowercase letters indicate significant differences (GLM, $p=0.004$).

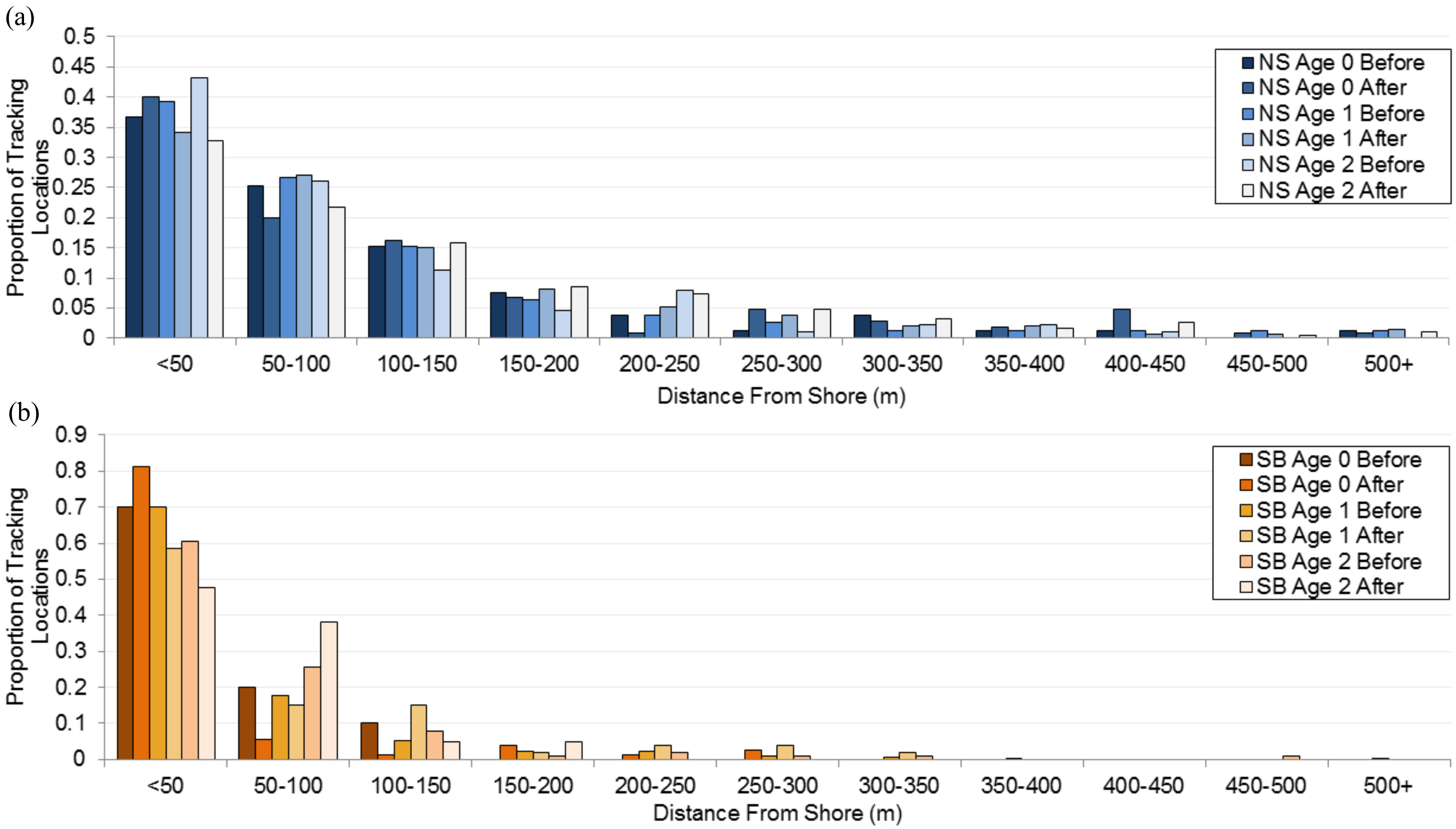


Figure 4.5. Proportion of tracking locations by age and time period per distance-from-shore bins in for (a) the North Sound and (b) South Bimini. Proportions were calculated from subsampled datasets of each shark's tracking data in which positional fixes were greater than 180 min apart.

Table 4.10 Mean distance from shore in meters (±SE) for each age class in the North Sound and South Bimini before and after habitat disturbance occurred in the North Sound. Values in parentheses indicate sample size.

	North Sound		**South Bimini**	
	Before (2003-2005)	After (2009-2011)	Before (2003-2005)	After (2009-2011)
Age 0	105.85 ± 29.92 (3)	117.17 ± 28.1 (6)	33.15 ± 10.94 (2)	41.88 ± 12.44 (2)
Age 1	106.81 ± 17.62 (5)	124.6 ± 18.91 (9)	43.61 ± 6.38 (7)	67.81 ± 6.78 (2)
Age 2	87.49 ± 10.65 (3)	116.27 ± 15.94 (5)	62.43 ± 8.14 (2)	52.34 ± 11.19 (2)

Table 4.11. Results of analysis of variance (ANOVA) to test for differences in distance from shore among ages and nurseries before and after (Time Period) habitat loss occurred in the North Sound. Asterisks indicate significance.

	df	SS	MS	F-Value	p-value	
Age	2	0.51	0.25	0.062	0.941	
Nursery	1	143.52	143.52	35.103	<0.001	***
Time Period	1	6.97	6.97	1.704	0.200	
Age x Nursery	2	1.84	1.84	0.450	0.641	
Age x Time Period	2	0.30	0.30	0.074	0.929	
Nursery x Time Period	1	0.00	0.00	0.001	0.980	
Age x Nursery x Time Period	2	3.84	1.92	0.467	0.629	
Residuals	36	147.19	4.09			

df = degrees of freedom, SS = sum of squares, MS = mean square

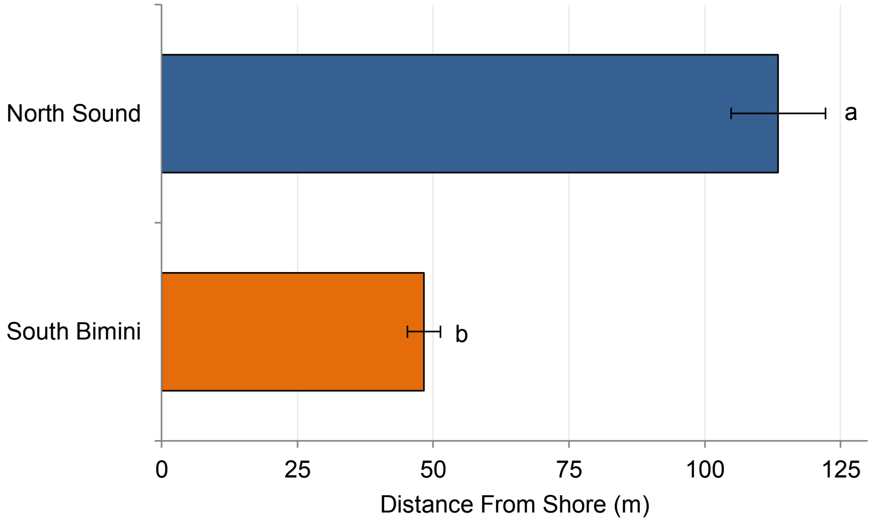


Figure 4.6. Mean distance from shore in meters (±SE) in the North Sound (113.55 ± 8.70, n = 31) and South Bimini (48.29 ± 3.05, n = 17). Values represent all ages and time periods combined within each nursery. Lowercase letters indicate significant differences (ANOVA, $p < 0.001$).

Chapter 5. Hunted hunters: an experimental test of the effects of predation risk on juvenile lemon shark habitat use

5.1 Background

5.1.1 Non-consumptive predator-prey interactions

Predators influence prey behavior, feeding rates, movement patterns, habitat use, morphology and population structure as a result of both direct and indirect interactions (Lima and Dill 1990, Peckarsky et al. 1993, Boonstra et al. 1998, Creel et al. 2005, Creel and Christianson 2008, Cresswell 2008). Historically, studies investigating predator-prey interactions have focused on direct predation (Boutin 1995, Eberhardt et al. 2003, White & Garrott 2005). In recent years, however, the importance of risk effects - behavioral changes in prey as a result of perceived predation threat (Heithaus et al. 2008a) - has been demonstrated in both marine and terrestrial systems (Lima 1998, Creel et al. 2005, Creel & Christianson 2008, Heithaus et al. 2009). To date, however, there have been no experimental manipulations investigating the effects of predation risk on large marine vertebrates.

Antipredatory behavioral responses are major factors influencing habitat use in many marine vertebrates. For example, Indian Ocean dolphins (*Tursiops aduncus*), green turtles (*Chelonia mydas*), pied cormorants (*Phalacrocorax variax*), and dugongs (*Dugong dugong*) shift from shallow, productive seagrass foraging areas to deeper, and safer, but less productive habitats when their predator the tiger shark (*Galeocerdo cuvier*) is present (Heithaus and Dill 2002, Heithaus et al. 2007, Heithaus et al. 2008b). Despite recent observational studies of risk effects on large marine vertebrates in the wild, there is a lack of research using experimental manipulations of predator presence, due likely to difficulties associated with maintaining large marine predators in captivity for experimental trials. Such studies could reveal and quantify important relationships between predator-prey interactions and their effects on habitat use.

Several shark species are apex predators in the marine environment, and these tend not to engage in antipredatory behavior as adults. However, small-bodied species and juveniles of larger species inhabit a mesopredator trophic level (Heithaus 2004, 2007, Ferretti et al. 2010) and are therefore subject to risk of predation by larger sharks (Springer 1967, van der Elst 1979, Compagno 1984, Harvey 1989), including larger conspecifics (Snelson et al. 1984, Clarke 1971, Wetherbee et al. 1990). Hence, many species use nursery areas which limit contact with larger sharks to manage this risk (e.g., Springer 1967, Castro 1993, Simpfendorfer and Milward 1993, Heupel and Hueter 2002, Heithaus 2004 and 2007, Grubbs 2010, Knip et al. 2010).

5.1.2 Mangroves as nursery areas

Mangroves, which commonly fringe low energy, shallow shorelines at tropical and subtropical latitudes (Lugo & Snedaker 1974), provide important subtidal nursery habitats for juvenile teleosts (see Faunce and Serafy (2006) for a review). Laegdsgaard and Johnson (2001) suggested one of the most important aspects of mangrove habitat for juvenile teleosts is structural complexity, which both maximizes prey resource availability and minimizes predation risks. In terms of refuge function, abiotic factors such as structural complexity, shade, and turbidity are all thought to reduce predation risk (Robertson & Blaber 1992, Cocheret de la Moriniere et al. 2004, Verweij et al. 2006). Individuals of many species seek refuge in mangrove structural complexity below the waterline as a habitat-specific escape tactic when a predation threat is perceived (Cocheret de la Moriniere et al. 2004).

Bimini, Bahamas (Figure 5.1) serves as nursery area for juvenile lemon sharks (*Negaprion brevirostris*), meeting the criteria proposed by Heupel et al. (2007) (and see Chapter 1). Adult females are philopatric, returning to their natal lagoon for parturition (Feldheim et al. 2002, Feldheim et al. 2004, DiBattista et al. 2008a). Juveniles remain highly site-attached to mangrove-fringed primary nurseries for several years before expanding their home ranges into the wider, less protected lagoon (Morrissey & Gruber 1993a, Franks 2007, Chapman et al. 2009). Although there is separation of activity spaces between small and large juvenile lemon sharks within the insular Bimini system (Gruber et al. 1988, Chapman et al. 2009), ontogenetic habitat shifts are continuous and likely related to a perceived decrease in predation risk concurrent with an increase in body size (Grubbs 2010). The difference in body size at which a juvenile lemon shark perceives less of a predation risk from larger sharks, including conspecifics, is unknown.

The North Sound lemon shark nursery has recently undergone large-scale mangrove removal via clear-cutting, dredging and filling, including approximately 37% (or 67 hectares) of the mangrove-fringed shoreline within the nursery (Jennings et al. 2012). Prior to mangrove loss in the North Sound, DiBattista et al. (2007) discovered that smaller, slower-growing individuals had higher survival. In the years following mangrove removal, effects have already been seen, including a release of selection pressure against faster-growing individuals of all ages (DiBattista et al. 2010), but a decrease in overall first-year survival by 23.5% in the years immediately following intense dredging (see Chapter 2 and Jennings et al. 2008). It has been hypothesized that use of these mangrove-fringed shorelines by juveniles is linked to both resource availability and predator avoidance (Franks 2007, Morrissey and Gruber 1993a, 1993b). The relative importance of each of these characteristics in driving juvenile movements within the primary nursery has rarely been investigated, but a recent study on wild individuals suggests predator avoidance is likely a driving factor (Guttridge et al. 2012).

Although mangrove shorelines are often major components of juvenile sharks' nursery habitat, the hypothesis that juvenile sharks use mangroves to avoid predators has never been empirically tested using experimental manipulations. Observing predator-prey interactions between two sharks in the natural environment is difficult due to relatively large-scale free-ranging movements, as well as the rarity of these interactions. This study aims to address the juveniles' use of mangrove structure in the face of a perceived predation risk.

5.2 Objectives

The objectives of this study were to investigate the small-scale use of artificial mangrove structure by small juvenile lemon sharks as an antipredatory response to predation risk, and to examine the relationship between body size and fine-scale habitat use in the presence of a predator. Specifically, the following hypotheses were tested:

1. A large juvenile lemon shark is perceived as a predation threat by small juvenile lemon sharks.
2. Small juvenile lemon sharks use artificial mangrove structure within the experimental configuration as a habitat-specific refuge in the presence of a potential predator more than when solitary or when with a size-matched conspecific.

3. There is a negative relationship between body size and use of artificial mangrove structure in the presence of a potential predator.

While there have been several studies on teleosts using artificial mangroves to examine structural refugia against predation (e.g., Nagelkerken and Faunce 2008), this study is the first to employ a similar design to investigate elasmobranchs. In addition, it is the first experimental study to focus on interactions between juvenile sharks and a predator to quantify the risk effects of predation on habitat use.

5.3 Methods

5.3.1 Study Site and Sharks

Bimini, Bahamas, an island group on the westernmost edge of the Great Bahama Bank (Figure 5.1), is dominated by red mangrove (*Rhizophora mangle*) shorelines. Juvenile lemon sharks used for this study were captured via gillnet following the methods described in Gruber et al. (2001). Upon capture, sharks were transported to a nearby holding pen, where they were later measured (pre-caudal length, PCL and total length, TL), weighed and tagged with a passive integrated transponder (PIT, Destron Fearing®) tag. A total of 15 juveniles from three age-classes (Age-0 to Age-2) was used for the study. Of these, 12 were trial sharks ($\bar{x}$ = 57.0 cm ± 6.1 cm PCL), and three were used only as size-matched conspecifics ($\bar{x}$ = 56.7 cm ± 1.2 cm PCL) in experimental treatments. For predator-presence trials, an Age-5 large juvenile lemon shark of 116 cm PCL (150 cm TL) was captured within Bimini's central lagoon using the block rig technique described in Kessel (2010) and transported to the trial pen. The large juvenile was acclimated for two days in the pen before trials began.

Juvenile test sharks were held in circular 5 m-diameter plastic mesh (5 cm x 5 cm) pens on a shallow, sandy flat adjacent to the trial pen. While in the holding pens, test sharks were exposed to natural ambient conditions including tidal and lunar cycles, as well as natural temperature and salinity fluctuations. There was no underwater visibility from the holding pens to the trial pen. The three additional juveniles retained for size-matched conspecific treatments were held in a nearby separate but identical circular 5 m-diameter mesh pen to eliminate the possibility of the formation of any associative interactions between test sharks and size-matched conspecifics prior to trial runs (Guttridge et al. 2009). All individuals were fed to satiation every third day with fresh and/or frozen local fish; feeding was intended to exclude confounding effects of foraging behavior within the trial pen.

A 10 m x 10 m trial pen was constructed with materials described above adjacent to the holding pens (Figure 5.2). The trial pen was divided into three sectors of equal size, demarcated by orange concrete rings. Artificial mangrove units (AMUs) similar to those described in Cocheret de la Moriniere et al. (2004) were embedded in one sector of the pen. AMUs (80 cm x 80 cm x 150 cm) were constructed of PVC piping (diameter = 2 cm) at a density of 56 pipes/m^2, a value obtained by measuring the mean density of red mangrove prop roots in a representative area of the North Sound lemon shark nursery. The units were spaced evenly in a repeating pattern within one sector of the trial pen, mimicking the natural mangrove shoreline of the lagoon and allowing juvenile test sharks to swim between and behind the artificial structures. An adjacent 4 m-high observation tower allowed for a complete view of the trial pen. At the midpoint of one side of the trial pen, a 2 m^2 acclimation pen was built between the trial pen and the observation tower, separated by a wooden trap door (1.5 m x 1.5 m) that could be operated from the observation tower. The wooden door blocked the test shark's view of the trial pen during acclimation periods.

5.3.2 Treatments and Trials

Juvenile lemon shark space use within the trial pen was observed in three treatments: 1) a solitary test shark, 2) a test shark in the presence of a size-matched conspecific and 3) a test shark in the presence of a large juvenile conspecific. Treatments (1) and (2) represented non-predation threat scenarios, while treatment (3) introduced a potential predator. Trials were conducted using a balanced design. There were 72 total trials conducted with 12 different test individuals. Each shark underwent each treatment a total of two times: once with AMUs on one side of the pen, and once with AMUs on the opposite side to account for any inherent bias for a particular side of the test pen. Therefore, each test shark underwent six total trials. At the completion of each trial, the test individual was returned to the holding pen until it was randomly selected for another trial. For treatments (1) and (2), the order of both shark and treatment were randomized. However, all trials with the large juvenile conspecific were condensed into a one-week period due to the logistical difficulties of maintaining a large shark in semi-captive conditions. Therefore, all trials with the large juvenile were conducted with AMUs on one side of the pen; the units were then moved to the opposite side, and treatment (3) trials were conducted again. In both cases, the order of test shark individuals was randomized.

At the start of each trial, a test shark was moved with minimal handling from its holding pen to the acclimation pen via 100 L plastic transport box and allowed to recover from handling stress for a period of 15 minutes (Guttridge et al. 2009). Following the recovery and acclimation period, the trap door was opened, and the test shark was free to move into the test pen. The moment of entry marked the start of a 30 minute trial. If the treatment involved a size-matched conspecific or a large juvenile, that individual was already within the test pen before the start of the trial. The following behaviors were recorded using the program JWatcher (JWatcher Video V1.0, Macquarie University and UCLA):

1) Fright responses (avoidance, defined as “give-way” (Myrberg and Gruber 1974) or acceleration, similar to Myrberg and Gruber’s (1974) “explosive glide”, but more generally a marked increase in swimming speed);
2) Time spent swimming socially when a second conspecific was present (within one body length of the second conspecific, either swimming in parallel or following (Myrberg and Gruber 1974); and
3) Time spent in each sector (recorded when head and pectoral fins entered the sector).

Water temperature ($\bar{x}$= 27.62°C ± 2.07), depth ($\bar{x}$= 63.91cm ± 23.74), and salinity ($\bar{x}$ = 34.67 ± 4.29 were recorded at the start and end of each trial. Wind speeds during trials were less than 20 kt, and trials were conducted between the hours of 0800 and 1800 to ensure complete visibility of the test pen.

5.3.3 Data Analysis

Nominal trial duration was 30 minutes ($\bar{x}$ = 29:47 ± 0:49), and analyses investigated the proportion of each trial period dedicated to a particular behavior or sector. Prior to analysis, all data were tested for normality, and, where appropriate, log(x+0.5) or arcsine transformed. Before analyzing the effects of the different treatments, treatments with AMUs on the left versus the right side were compared using a paired t-test. As no significant differences were detected between trials conducted with AMUs on either side of the pen for each treatment ($p>0.05$), trials for both sides were averaged for each individual. A Kruskal-Wallis rank sum test with post-hoc pairwise comparisons was used to test for differences in time spent within the AMU sector and number of fright responses during each of the three treatments. Because not all trials lasted the full 30-minutes, only the first 28 minutes, 55 seconds, the length of the shortest trial, were analyzed. Analysis of the proportion of time spent engaged in social swimming in the presence of a size-matched conspecific and a sub-adult conspecific was performed using a Wilcoxon rank sum test. To investigate the effect of body length (PCL) on the proportion of time spent within the sector containing AMUs in the presence of a large juvenile, a linear regression model was fitted to the data. All analyses were carried out in R, version 3.0.0.

5.4 Results

Solitary test sharks exhibited virtually no fright responses per trial ($\bar{x} = 0.29 \pm 0.14$ SE), while test sharks paired with a size-matched conspecific were similarly low ($\bar{x} = 0.50 \pm 0.12$ SE; Figure 5.3). When in the presence of the large juvenile conspecific, however, test sharks demonstrated a significantly higher number of fright responses per trial ($\bar{x} = 7.92 \pm 0.19$ SE; PERMANOVA with post-hoc pairwise comparisons, $p<0.001$), with one individual peaking at 47. Not surprisingly, test sharks demonstrated a significantly higher proportion of the trial period engaged in social swimming with size-matched conspecifics ($\bar{x}$ = 0.566 ± 0.066 SE) than with the large juvenile conspecific ($\bar{x}$ = 0.078 ± 0.026 SE; Wilcoxon rank sum test, $p<0.001$; Figure 5.4).

There were significant differences among treatments in the use of the trial pen sector containing the artificial mangrove units (Figure 5.5). When solitary, the mean proportion of time sharks spent in the AMU sector was ($\bar{x}$ = 0.14 ± 0.04 SE). For test sharks in the trial pen with a size-matched conspecific, the mean proportion of time spent in close proximity to AMUs was $\bar{x}$ = 0.08 ± 0.04 SE. In contrast, the mean AMU use of test sharks exposed to predation threat in the form of a large juvenile conspecific was 0.28 ± 0.07 SE, with one individual reaching up to 0.85. PERMANOVA with post-hoc pairwise comparisons on arcsine-transformed data showed statistically significant differences in AMU use between treatments of test sharks with size-matched conspecifics and test sharks in the presence of a large juvenile ($p<0.05$). There was a negative relationship between body size and AMU use in the presence of the potential predator (Figure 5.6), with some of the smaller sharks using the AMUs during over 60% of the trial period. There were no significant effects of temperature, salinity or depth on any treatments (Table 5.1).

5.5 Discussion

This study examined the effects of perceived predation risk on the fine scale habitat use of an elasmobranch in controlled experimental conditions. Results support the hypothesis that juvenile lemon sharks view larger conspecifics as potential predators.

As social animals (Guttridge et al. 2009, Guttridge et al. 2011), juveniles exhibited social swimming behaviors with size-matched conspecifics, but the presence of a large juvenile conspecific elicited fright responses. Juveniles sought the refuge of the artificial mangrove structure more often in the presence of a large juvenile conspecific than when solitary or when paired with a size-matched conspecific. As expected, results showed a negative relationship between body size and AMU use in the presence of a potential predator, indicating individual sensitivity to predation risk based on size.

Heithaus et al. (2009) proposed that prey make habitat use decisions based on a combination of both prey abundance and predation risk, suggesting that the predators' effects on prey habitat use are landscape-specific and vary with resource availability, predator abundance and habitat-specific escape tactics. Here, confounding effects of foraging behavior were controlled for while manipulating risk effects within an experimental environment. During trials in the absence of a large juvenile, the perceived risk of encountering a predator was as close to zero as possible in the semi-captive experimental setting; in the presence of a potential predator, the encounter was inevitable within the confines of the trial pen. As a result, fine scale habitat use reflected the antipredatory behavioral decisions of each individual test shark to its own perceived risk of predation.

The dramatic increase in fright responses (Figure 5.3) by small juveniles in the presence of the large juvenile, combined with the low or nearly absent levels of social swimming of test sharks with the large juvenile, suggest the Age-5 conspecific was indeed considered to be a predation threat by juveniles up to Age-2. Although there have been known occurrences of intraspecific predation on juvenile lemon sharks by larger juveniles (Vorenberg 1962, Wetherbee et al. 1990, Morrissey and Gruber 1993a, 1993b) interactions have rarely been observed in the wild. In Bimini, Guttridge et al. (2012) recorded two such wild observations, and juveniles exhibited strong flight responses on both occasions.

Grouping behavior among conspecifics provides several advantages, including a decrease in individual risk to predation (Bertram 1978, Pulliam and Caraco 1984, Holland et al. 1993, Krause and Ruxton 2002, Heithaus 2004) and earlier predator detection through shared vigilance (Lazarus 1979, Treherne & Foster 1980, 1981, Childress & Lung 2003, Heupel & Simpfendorfer 2005). The fact that the proportion of time spent near the AMUs was significantly lower with a size-matched conspecific than with a larger juvenile conspecific, but did not significantly differ between the solitary test shark and the test shark with the large juvenile may be related to the advantages of grouping. Grouping may be responsible for a decrease in the sharks' use of the AMU refuge when paired with a size-matched conspecific in the form of a "boldness" effect (Krause and Ruxton 2002, Webster et al. 2007).

The fact that the difference in AMU use between solitary sharks and those with a size-matched conspecific was not statistically significant may be a result of low sample size or a consequence of the conditions of the experiment. Habituation to predator presence is known to occur in experimental manipulations (Schleidt et al. 1983). The mean number of fright responses per trial in the presence of the large juvenile decreased by approximately 64% between test sharks' first and second trial with the potential predator, suggesting habituation. However, no statistical significance was detected

(Wilcoxon rank sum, p=0.23, log10(x+0.5)-transformed data); this result may be due to low sample size (n = 12), which limits the power of the test to detect differences.

The test sharks with the size-matched conspecific spent more time engaging in grouping behavior than did the test shark with the large juvenile (Figure 5.4). Size-matched grouping in lemon sharks is well established (Guttridge et al. 2009, Guttridge et al. 2011), and the high number of interactions observed here between size-matched conspecifics was expected. Nearly absent proximity between the test shark and the large juvenile suggests avoidance, likely due to a perceived predation risk. The existence of any period of sociality at all between the test sharks and the large juvenile may be the effects of forced interactions within the confines of the 10 m x 10 m trial pen, as well as habituation during the trial period.

Body size is an important determining factor in habitat use of numerous animal taxa (e.g., Werner et al. 1983, Stamps 1983, Wahle 1992, Bystrom et al. 2003). Ontogenetic shifts in shark habitat use have been associated with a change in or expansion of diet and activity space (Springer 1967, Grubbs 2010). Prior to the present investigation, there have been few studies demonstrating a relationship between body size and antipredatory behavior in sharks. Guttridge et al. (2012) found strong correlations between juvenile lemon shark body size and the use of a mangrove-fringed refuge area, where smaller juveniles used the refuge on more occasions and for longer periods than larger juveniles. Size-related refuge use may be due to a decrease in antipredator behavior with increased body size (Werner and Hall 1988, Bouskila et al. 1998). Results of the present study support this idea, showing a negative relationship between body size and use of the AMU refuge in the presence of a predator (Figure 5.6). Increased AMU use by smaller juveniles in the presence of a larger juvenile suggests a higher perception of risk. Therefore, juvenile lemon shark habitat use was strongly related to individual risk assessment, and a habitat-specific escape tactic was used within the confines of the experimental configuration.

Mangrove prop roots are important for predator avoidance in juvenile teleosts (Cocheret de la Moriniere et al. 2004, Verweij et al. 2006, Nagelkerken & Faunce 2008). This study is the first to use artificial mangrove structures to examine predator-prey interactions in a shark species. Here, the increased use of AMUs in the presence of a predator suggests that this type of structure is an important refuge for juvenile lemon sharks. The structural complexity provides small-scale habitat that enables juvenile lemon sharks, like juvenile teleosts, to evade potential predators. Several studies in Bimini investigating juvenile lemon shark habitat use have suggested sharks use the mangrove-fringed nursery areas during early development to avoid larger predatory sharks (see Figure 1.2 and Morrissey and Gruber 1993b, Franks 2007, Chapman et al. 2009, Guttridge et al. 2011). Here, the first quantitative experimental support for this idea is presented, highlighting the importance of the presence of mangrove structure within the nurseries in antipredatory behavioral responses.

5.6 Conclusion

This study suggests the importance of mangrove structure as a habitat-specific escape tactic within a lemon shark nursery. In addition, it provides insights mechanisms influencing ontogenetic habitat shifts from primary to secondary nurseries and gives evidence that perceived predation risk is an important factor in determining the timing of these shifts. The negative correlation between body size and AMU use implies that juvenile lemon sharks are sensitive to individual predation risk based on size and are capable of assessing the potential threat of a larger shark. The exact size difference at which a conspecific changes from a companion to a predator is unknown, but results here show that at least an Age-5 large juvenile lemon shark was perceived as a predation threat to up to Age-2 juveniles. Predation risk was a driving force behind small-scale habitat use, and these behavioral decisions can have impacts at local and larger scales. While the scale of meters within the experimental design may not fully explain population-level patterns, the results are instructive in that they are a first look at the underlying mechanisms driving such patterns. The sharks' use of artificial structures mimicking natural mangrove shorelines may have important management and mitigation implications, particularly in environments such as Bimini and beyond, where mangrove habitats within nurseries have been lost due to coastal development. Natural habitats are desired for optimal ecosystem function, but if development does occur, it is important to consider restoration of the refuge function of mangrove shorelines, perhaps by requiring developers to add structural complexity to modified habitats.

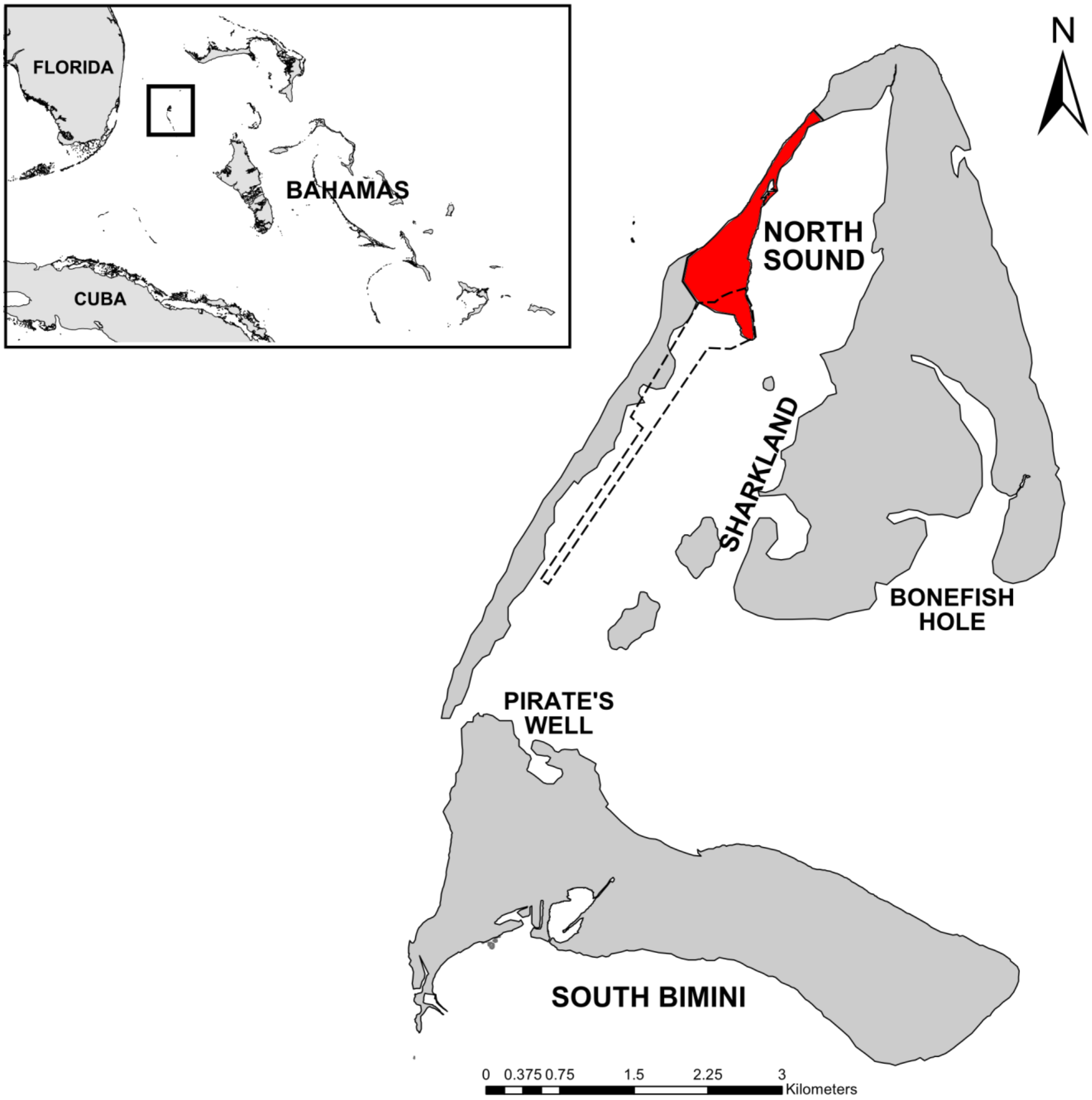


Figure 5.1 Bimini, Bahamas is an island group on the western edge of the Great Bahama Bank, approximately 86 km east of Miami, FL. Labels indicate specific locations of juvenile lemon shark nursery areas within the islands. Red shows the area of 2005 mangrove removal, which was subsequently filled with dredge material. Seabed dredging occurred in 2001 within the area outlined by the dotted line.

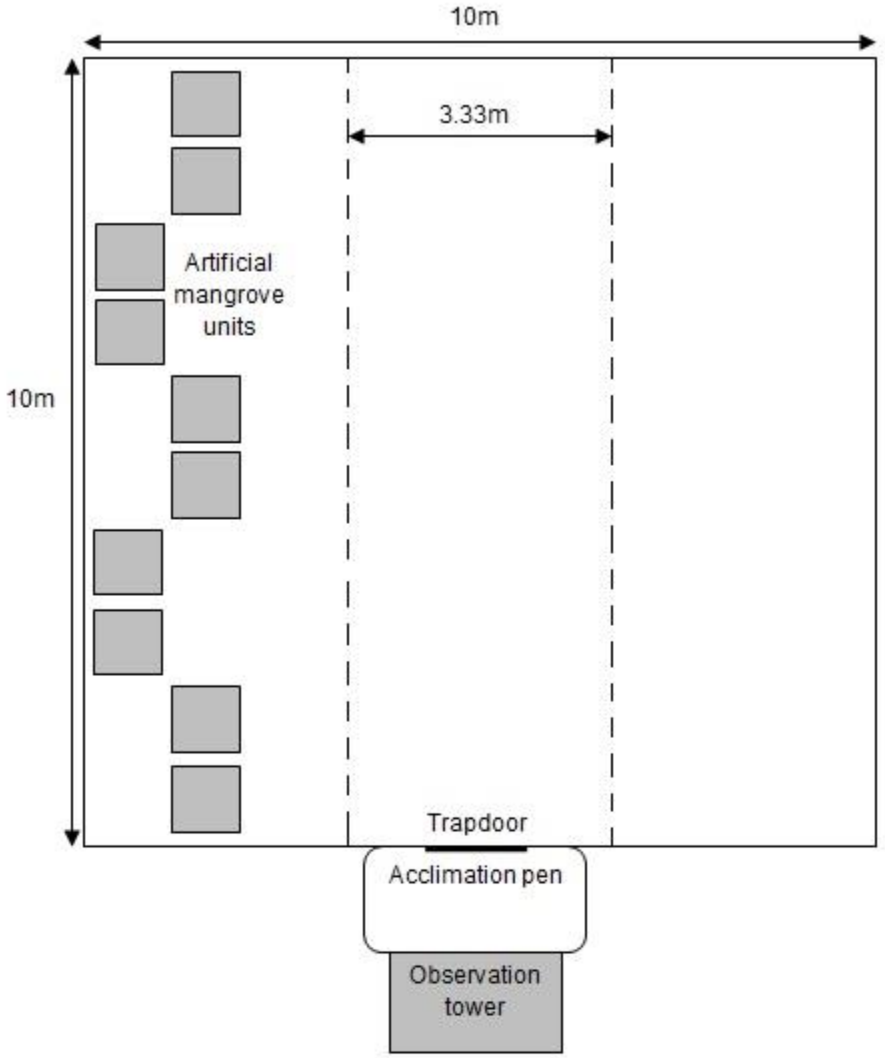


Figure 5.2. Schematic of trial pen. The trial pen (10 m x 10 m) was demarcated into three equally-sized sectors (dotted lines). Artificial mangrove units (AMUs, gray squares) are depicted in one sector of the pen and are spaced 20 cm apart, allowing juvenile lemon sharks access to areas around and behind AMUs. A 2 m^2 acclimation pen was adjacent to the test pen, separated by a wooden trap door blocking visual cues to the test pen during the acclimation period. The 4 m tall observation tower allowed for a complete view of the pen.

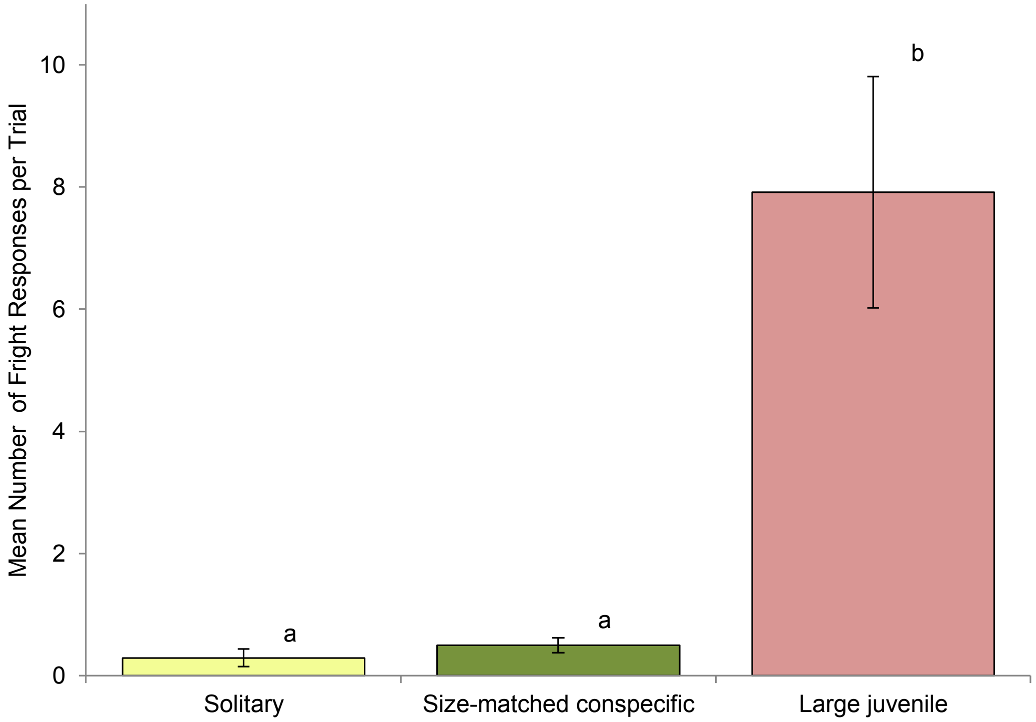


Figure 5.3. Number of fright responses per treatment. There was no difference in the number of fright responses per trial between the solitary ($\bar{x}$ = 0.29±0.14 SE) and size-matched conspecific ($\bar{x}$ = 0.50±0.12 SE) treatments (PERMANOVA with post-hoc pairwise comparisons, $\log_{10}(x+0.5)$-transformed data, $p = 0.251$). Significant differences (indicated by lowercase letters) were found between treatments of the solitary test shark and a large juvenile conspecific ($\bar{x}$ =7.92±1.90 SE) and between treatments of the test shark with a size-matched conspecific and a large juvenile (PERMANOVA with post-hoc pairwise comparisons, $p<0.001$).

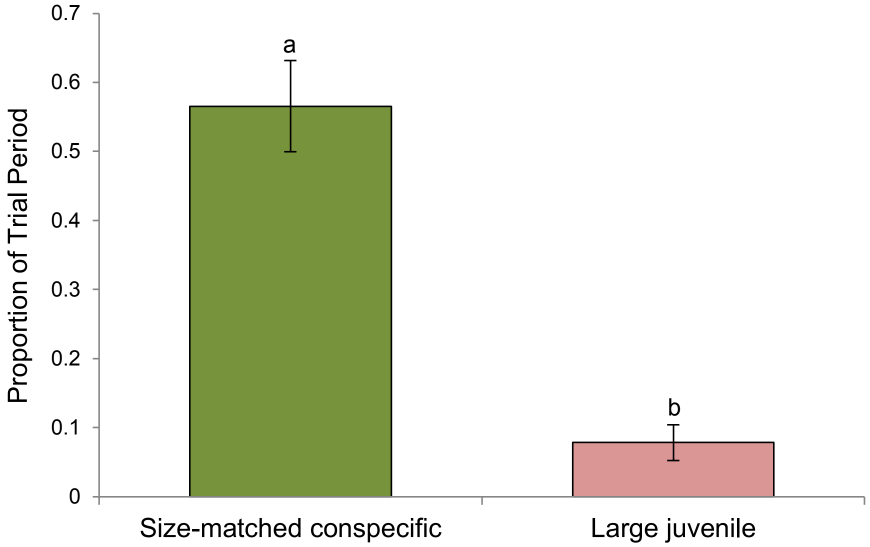


Figure 5.4. Proportion of trial period that juvenile lemon sharks spent interacting socially with size-matched or larger juvenile conspecifics. Test sharks spent a highly significant proportion of the trial period (PERMANOVA, arcsine transformed-data, $p<0.001$) interacting socially with size-matched conspecifics ($\bar{x}$ = 0.57±0.07 SE) compared to when with a larger juvenile conspecific ($\bar{x}$ = 0.08±0.03 SE).

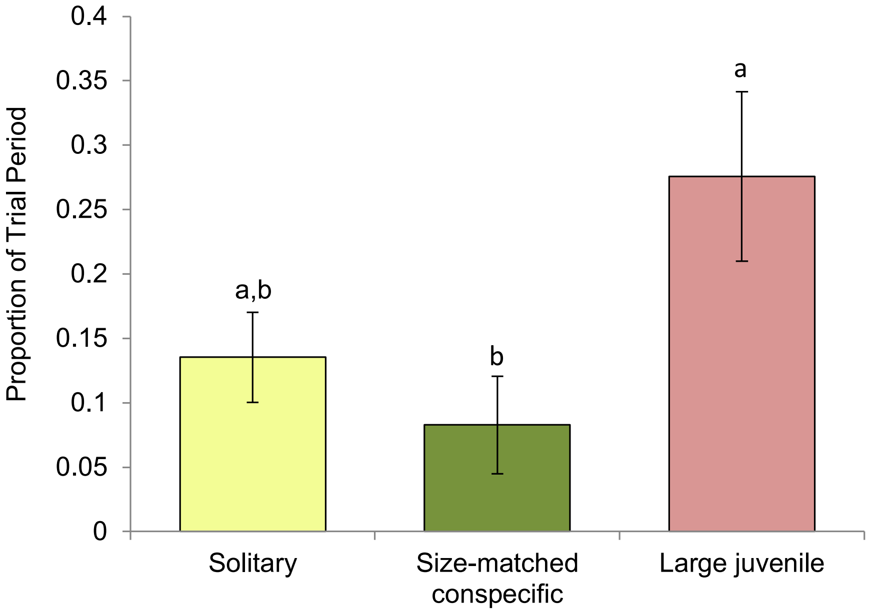


Figure 5.5. Proportion of time spent near artificial mangrove units (AMUs) per treatment. Lowercase letters indicate a significant difference in test sharks' use of AMUs between treatments with a size-matched conspecific ($\bar{x}$ = 0.08±0.04 SE) and with a large juvenile ($\bar{x}$ = 0.28±0.07 SE; PERMANOVA and post-hoc pairwise comparisons, $p<0.05$), but not between trials of the solitary shark ($\bar{x}$ = 0.14±0.04 SE) and the test shark with a size-matched conspecific.

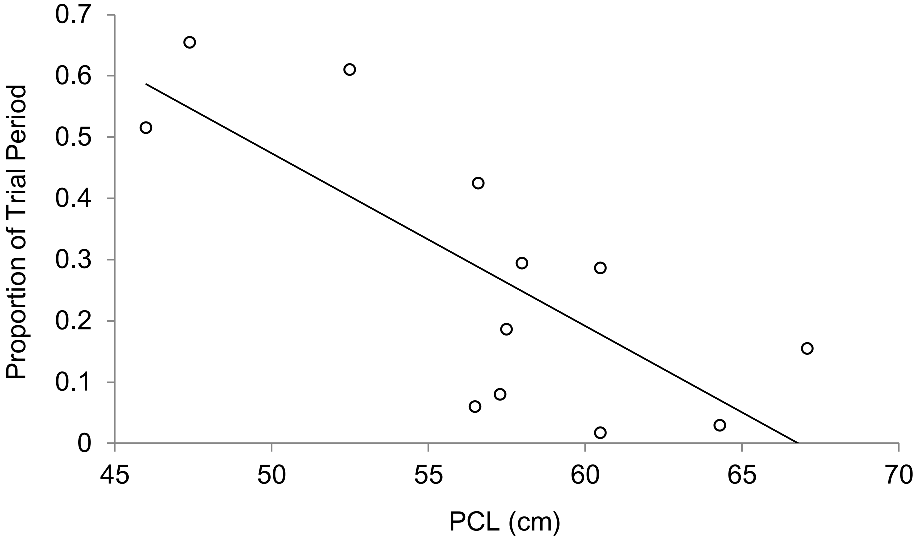


Figure 5.6. Relationship of small juvenile body size to use of artificial mangrove units (AMUs) in the presence of a large juvenile conspecific. A strong negative relationship between AMU refuge use and shark size indicates that body size is a factor in an individual's perception of predation threat ($R^2 = 0.5779$; $p<0.01$) and leads to differences in fine-scale habitat use.

Table 5.1. Results of PERMANOVA testing for effects of abiotic variables on the number of fright responses per trial, proportion of trial period engaging in social behavior and proportion of trial period spent near artificial mangrove units (AMU). A generalized linear model was used to test each variable across all treatments. Data were transformed as indicated.

	Variable	**Data transformation**	**p-Value**
Fright response	Depth	$\text{Log}_{10}(x+0.5)$	0.251
	Temperature	$\text{Log}_{10}(x+0.5)$	0.373
	Salinity	$\text{Log}_{10}(x+0.5)$	0.255
Social behavior	Depth	Arcsine	0.140
	Temperature	Arcsine	0.493
	Salinity	Arcsine	0.123
AMU use	Depth	Arcsine	0.061
	Temperature	Arcsine	0.565
	Salinity	Arcsine	0.544

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Appendix. A partial list of research conducted in Bimini, Bahamas.

Topic Area	Literature	
Lemon shark movements, habitat use and home range	Gruber et al. (1988) Morrissey and Gruber (1993a) Morrissey and Gruber (1993b) Correia et al. (1995) Edrén and Gruber (2005)	Franks (2007)* Chapman et al. (2009) Kessel (2010)* DiGirolamo et al. (2012) Guttridge et al. (2012)
Lemon shark diet	Cortes and Gruber (1990) Cortes and Gruber (1992) Reeve et al. (2009)	Newman et al. (2010) Newman et al. (2011) Pettitt-Wade et al. (2011)
Lemon shark breeding biology	Feldheim et al. (2001b) Feldheim et al. (2002a) Feldheim et al. (2004) DiBattista et al. (2008a)	DiBattista et al. (2008b) DiBattista et al. (2009) DiBattista et al. (2010)
Lemon shark survival and abundance	Manire and Gruber (1993) Gruber et al. (2001) DiBattista et al. (2007) Gedamke et al. (2007)	Jennings et al. (2008) Kessel (2010)*
Lemon shark growth	Barker et al. (2005) DiBattista et al. (2007)	Jennings et al. (2008)
Lemon shark behavior	Sundstrom et al. (2001) Guttridge et al. (2009a) Guttridge et al. (2009b) Guttridge et al. (2010) O'Connell et al. (2010)	Spaet et al. (2010) Guttridge et al. (2011) Guttridge et al. (2012) Guttridge et al. (2013)
Lemon shark physiology and sensory biology	Rasmussen and Gruber (1993) Sundstrom and Gruber (1998) Gleiss et al. (2009)	O'Connell et al. (2010) Spaet et al. (2010)
Methodology	Brown and Gruber (1988) Manire and Gruber (1991) Sundstrom et al. (2001)	Feldheim et al. (2002b) Sundstrom and Gruber (2002)

Appendix (continued)

Topic Area	Literature	
(Methodology continued...)	Sundstrom and Gruber (1998)	Barker et al. (2005)
	Sundstrom et al. (1998)	Gedamke et al. (2007)
	Feldheim et al. (2001a)	Gleiss et al. (2009)
	Gruber et al. (2001)	Guttridge et al. (2010)
Effects of habitat loss	Feldheim and Edrén (2002)	Jennings et al. (2008)
	Gruber and Parks (2002)	DiBattista et al. (2010)
	Gruber et al. (2002)	
Abiotic environment	Newell and Imbrie (1955)	Hussey (2003)**
	Turekian (1957)	Pettitt-Wade et al. (2011)
	Squires (1958)	DiGirolamo et al. (2012)
	Jacobsen (1987)*	
Bimini flora and fauna	Laubenfels (1949)	Snelson et al (1990)
	Pearse (1951)	Strong et al (1990)
	Andrew and Andrew (1953)	Corcoran and Gruber (1999)
	Clarke (1955)	Silliman and Gruber (1999)
	Renaud (1956)	Newman and Gruber (2002)
	Squires (1958)	Hussey (2003)**
	Voss and Voss (1960)	Newman et al. (2004)
	Kanciruk and Herrnking (1976)	Afonso and Gruber (2007)
	Clarke (1977)	Newman et al. (2007)
	Jacobsen (1987)*	Jennings et al. (2012)

* = Doctoral dissertation, ** = Master’s thesis,