Multi-Decadal Habitat Changes Mapped via Remote Sensing and Implications for

Juvenile Lemon Sharks (*Negaprion Brevirostris*) and their Nursery Areas.

By

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Dedication

In memory of my father for passing on his love of nature, curiosity, and sense of humour to get through the toughest challenges. I also dedicate this to my mother who supports me no matter how far I need to go to achieve my goals.

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Abstract

Many shark species are currently facing pressures from anthropogenic activities, including the loss of critical habitat. In Bimini, the Bahamas, mangroves, and seagrass beds provide nursery habitats for juvenile lemon sharks (*Negaprion brevirostris*), which show high site fidelity during their early years of life. Additionally, female lemon sharks show natal philopatry, meaning they will return to the nursery they were born in to give birth, making these areas critical to reproduction. Over the past two decades, coastal development has removed large areas of mangrove and created new islands in the Bimini lagoon, potentially reducing the overall viability of its nurseries. To understand the impacts of coastal development on two neighboring nursery areas, North Sound (NS) and Shark Land (SL), annual mangrove and seagrass extent was mapped from 1999 to 2020 using Landsat satellite remote sensing, random forest machine learning, and the automated adaptive signature generalisation algorithm (AASG). This resulted in 18 annual maps, with high overall accuracy in identifying seagrass vs. non-seagrass (82%) and vegetation vs. non-vegetated coastal habitat (99%), including mangroves, to a resolution of 30x30 m2. Satellite remote sensing revealed a clear effect of coastal development on seagrass extent, which decreased post development and subsequently re-bounded in 2 to 5 years. I then analysed the effects of habitat extent on annual individual shark survival estimates and body condition, calculated from a long-term mark-recapture dataset, using two generalised linear mixed models. The effects of coastal development on shark survival were less clear than effects on seagrass density and extent. In both nurseries, habitat extent did not significantly affect survival, possibly due to alternate habitat availability in other parts of the Bimini lagoon. However, the amount of annual habitat change differentially affected survival in both nurseries. Counter-intuitively, the NS nursery in closer proximity to development showed marginally increased survival probability in years with greater change, while the SL nursery showed decreased survival probability. Shark body condition showed a positive relationship to mangrove extent, suggesting that the loss of mangroves may result in foraging difficulty for sharks. Body condition was also reduced when seagrass extent increased post dredging in the NS, suggesting possible nutrient loading and trophic effects. My results highlight the nuanced impacts of coastal development on shark survival and emphasize the importance of mitigating construction impacts while protecting remaining mangrove and seagrass areas to ensure continued lemon shark resiliency.

List of Abbreviations and Symbols Used

AASG – Automatic Adaptive Signature Generalisation

BBFSF – Bimini Biological Field Station Foundation

BC – Body Condition

CHDSG – Consistent High-Density Seagrass

CMRI – Combine Mangrove Recognition Index

EW – East Wells

GLMM – Generalized Linear Mixed Model

HDSG – High Density Seagrass

IPCC – International Panel on Climate Change

IUCN – International Union for the Conservation of Nature

LCI – Lower Confidence Interval

LDSG – Low-Density Seagrass

MDSG – Mid-Density Seagrass

MPA – Marine Protected Area

NASA – National Aeronautics and Space Administration

NDVI – Normalized Difference Vegetation Index

NDWI – Normalized Difference Water Index

NIR – Near Infrared

NOAA – National Oceanic and Atmospheric Administration

NS – North Sound

OLI – Operational Land Imager

OR – Odds Ratio

PCL – Pre-Caudal Length

SB – South Bimini

SL – Shark Land

UCI – Upper Confidence Interval

USGS – United States Geological Survey

VIF – Variance inflation factor

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Chapter 1: General Introduction

Elasmobranchs, including sharks and rays, are important for the structure and functioning of marine ecosystems, such as the top-down regulation and stability of food webs, the maintenance of the integrity of coastal ecosystems such as seagrass beds which act as carbon sinks, and cycling of nutrients through egestion (Atwood et al., 2015; Barley et al., 2017; Ferretti et al., 2010; Hammerschlag et al., 2019; Rasher et al., 2017; Williams et al., 2018) Sharks and rays also provide economic value through tourism operations, with a revenue of 314 million USD globally per year (Cisneros-Montemayor, 2013). Currently, many shark and ray species worldwide are facing high risk of extinction due to their slow reproductive rates and high age at maturity, coupled with targeted fishing and bycatch as well as other anthropogenic pressures (Field et al., 2009). Habitat loss also plays an important role in elasmobranch declines, especially for species which require specific habitats for critical life history stages such as breeding, feeding or nursery areas [9,10].

In Bimini, the Bahamas, female lemon sharks (*Negaprion* brevirostris) show natal philopatry, reaching sexual maturity at approximately age 12 and giving birth to 3-18 pups on a biennial cycle in the specific nursery area in which they were born (Chapman et al., 2009, Feldheim et al., 2002, Feldheim et al., 2014). Juvenile lemon sharks then show high site fidelity to these nurseries, residing in the Bimini lagoon up to at least age-3 before moving further offshore (Franks, 2007; Morrisey & Gruber, 1993a). Juveniles between age-0 and age-1 show even further restricted home ranges within their nurseries of approximately 0.68 km^2 (Morrisey & Gruber, 1993a). The viability of these nursery areas relies on the presence of shallow waters and large expanses of mangroves which together provide protection from larger predators and habitat for prey species (Franks, 2007).

Extensive seagrass meadows in the lagoon additionally provide feeding areas for older juveniles as well as habitat for prey communities (Newman et al., 2007; Hussey et al., 2017)

Lemon sharks are currently listed as near-threatened on the IUCN red-list (Sundstrom, 2015), while the most recent stock assessment for the South-Eastern United States population of lemon sharks, which includes sharks residing in Bimini, has shown a 26% decline over the last two generations, approximately 36 years (Carlson et al., 2021; Hansell et al., 2020). While the Bahamian government designated the entirety of the Bahamas as a Shark Sanctuary in 2011 (Ward-Paige, 2017), which prohibits the landing of shark species, there have been few regulations in Bimini for the protection of habitats shown to be important to local shark species' life history (Ward-Paige, 2017), which is integral to the efficacy of species recovery initiatives (Kinney & Simpfendorfer, 2009). In 2001, North Bimini was proposed as an area of high priority for the creation of a Marine Protected Area by the Bahamian government and was listed as a MPA in 2009 by the Bahamas National Trust; however, no regulations have been implemented and mangrove habitats have continued to be degraded or removed for tourism development (Wise, 2014). In addition, extensive dredging for boating channels along with coastal development may have degraded or reduced seagrass habitat through sedimentation and smothering. One limitation to fully understanding the impacts of coastal development and construction on vegetated habitats and lemon shark nursery populations has been the minimal availability of long-term habitat data spanning coastal development over past decades.

Given limited *in-situ* habitat data, techniques such as remote sensing can fill important data gaps. Images collected by long-running satellite programs, such as NASA's

Landsat suite of satellites, can help to quantify coastal habitat distribution over several decades (Wilson et al., 2019; Wilson et al., 2020, Leblanc et al., 2021). Additionally, algorithms such as the automated adaptive signature generalization (AASG) have been used in other areas to effectively map habitat extents across several decades despite *in-situ* data limitations (Dannenberg et al., 2016). Maps can then be used to understand changes in both coastal vegetation (such as mangroves) and submerged aquatic vegetation (such as seagrass beds), allowing for consistent and comparable annual maps through time and the assessment of anthropogenic changes (Leblanc et al., 2021).

To understand demographic trends in the juvenile lemon shark populations in Bimini, a local conservation organization, the Bimini Biological Field Station Foundation (BBFSF), has run a standardized annual tagging program for young-of-the-year lemon sharks (Gruber et al., 2001). Sampling has occurred in two nurseries in the Bimini lagoon, North Sound (NS) and Shark Land (SL), since the mid 1990's from May to mid-June, with gill-nets being set perpendicular to shore in 3 locations in each nursery for approximately 6 nights, 72 hours total per nursery. All sharks caught in these nets are collected , measured, sexed and tagged with a passive integrated transmitter (PIT) tag and placed into semi-enclosed pens until the final night when released back into the area where they were caught (Gruber et al., 2001). Lemon sharks are a placentally viviparous species, meaning that young are fed through an umbilical cord in-utero (Feldheim et al., 2002). For the first few months after birth, when an umbilical scar is present, the size of the umbilical scar opening is measured for help in age determination (Barker, 2005). This extensive dataset allows for estimation of annual survival rates, by assessing whether an individual shark was re-captured in following years, and trends in survival rates over time.

By pairing annual lemon shark capture data with quantified habitat distribution data, my thesis aims to help better understand long-term impacts of habitat change on juvenile lemon shark survival and body condition. The second chapter of my thesis focuses on the analysis of satellite imagery to create maps of coastal habitat distribution from the late 1990s to 2020 to assess changes in habitat extent and distribution over the recent past. My third chapter focuses on the analysis of lemon shark survival from 1999 to 2017, and the abiotic and biotic factors influencing annual survival rates, including the effects of habitat changes. My results highlight the importance of vegetated habitat to lemon shark survival and increase our understanding of the impacts of habitat change on the viability of lemon shark populations in Bimini. This work can aid in determining mitigation measures for coastal development and construction and suggests that extending current protections to include not only the sharks themselves but also their critical habitat may be key to preventing further population declines.

Chapter 2: Analysis of two decades of Landsat satellite images reveals the impact of coastal development and mangrove deforestation on seagrass habitats in Bimini, the Bahamas

2.1 Introduction

Coastal environments are integral ecosystems for many aquatic species, including fish, crustaceans, and benthic species, and are frequently characterized by productive invertebrate (e.g., coral or oyster reefs) or vegetated (e.g., seagrass beds or mangroves) habitats (Barbier et al., 2011; Henseler et al., 2019; Seitz et al., 2014). These ecosystems have faced extensive pressures from human activities over past decades, particularly due to coastal development (Orth et al., 2006; Valiela et al., 2001; Waycott et al., 2009). Transformation of vegetated coastal habitats, including the removal of mangrove ecosystems and sediment infilling, can lead to the degradation of adjacent seagrass beds which require relatively clear water for photosynthesis (Lewis, 1976; Waycott, et al., 2009). Sedimentation can smother seagrass leaves, while suspension of sediment particles in the water column, and influx of nutrients fostering algal growth, can reduce light availability to seagrass shoots (Ellegaard et al., 2014; Huxham et al., 2018). In turn, the degradation or loss of seagrass habitats can impact survival of local faunal communities (Carbalo, 2006). Understanding the drivers of habitat change and the ecosystem consequences of coastal development is important for developing mitigation and restoration strategies. However, in many instances there is limited baseline information on existing habitats and their spatial extent pre-development, making it difficult to quantify the true extent of habitat loss or change(Brown et al., 2022).

Bimini, The Bahamas is a shallow pair of islands characterised by productive mangrove and seagrass habitats (Fig. 2.1). Bimini's mangroves and seagrass beds provide important nursery, foraging and spawning habitat for 175 species of fishes and invertebrates, including species such as the lemon shark *Negaprion brevirostris* (Edren and Gruber, 2005; Newman et al., 2007). Mangroves and shallow seagrass beds provide important protection from larger predators and habitat for prey species, including fish and crustacean species, allowing juvenile lemon sharks to grow and learn to hunt before heading further offshore (Gruber et al., 1988; Guttridge et al., 2011, 2012; Morrissey and Gruber, 1993; Newman et al., 2010). Individual lemon sharks have also been shown to exhibit natal philopatry, returning to the nursery they were born in to give birth themselves, and female lemon sharks return to Bimini to give birth biennially (Chapman et al., 2009; Feldheim et al., 2002, Feldheim et al., 2014). Three distinct lemon shark nursery areas exist in Bimini: North Sound, Shark Land and South Bimini (Fig. 1; Edren and Gruber, 2005).

Over the past several decades, Bimini has faced extensive coastal development. Since the late 1990s, construction has been ongoing for the development of tourist complexes in North Bimini and the Bimini lagoon. Notably, two major developments occurred in the early 2000's: In 2002, a boating channel was dredged in the Bimini lagoon and in 2005, mangrove and other terrestrial vegetation was removed and replaced with new sediment in Mosquito Point for the creation of Bimini Bay Resort, despite Mosquito Point being a well-documented mangrove habitat for lemon sharks within the North Sound nursery (Fig. 2.1; Gruber and Parks, 2002; Jennings et al., 2008; Black & Veatch, 2008). Currently, development is ongoing in the northern portion of the lagoon, with further removal of vegetation and creation of new islands using dredged sediment (Fig. 2.1;

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Matthew Smukall, personal communication). In South Bimini, development of roadways for the airport beginning in 2019 has resulted in further vegetation removal and sediment infilling, potentially impacting nearby habitat in the South Bimini lemon shark nursery (Fig. 2.1). Thus far, the full extent of terrestrial vegetation removal (including mangroves) and its impact on adjacent seagrass beds has not been fully quantified. While some habitat mapping surveys were conducted during specific years (Morrisey and Gruber 1993; Hussey, 2003; Kessel, unpublished results; Pellet, unpublished results), no surveys have consistently and comparably mapped habitat distribution across time to understand the potential long-term impacts of coastal development on vegetated habitats and their dependent fauna.
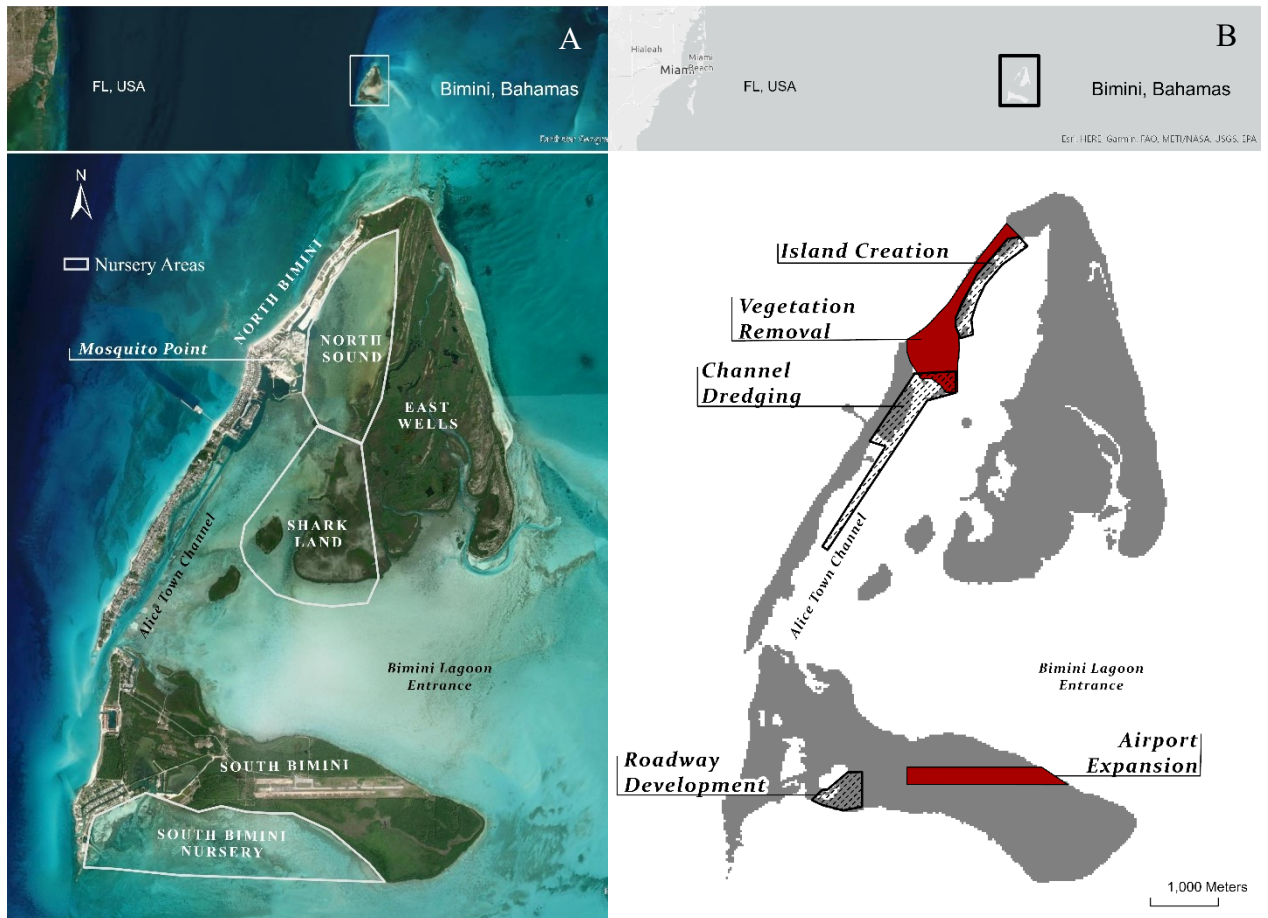
Fig. 2.1. Left: A 2020 true-color satellite image of Bimini, Bahamas (Maxar, 2020) with the three major lemon shark nursery areas delineated in white: North Sound, Shark Land and South Bimini, as well as the major island areas: North Bimini, East Wells and South Bimini and important landmarks (A, ArcGIS Pro v2.7.0, 2020). Right: Land areas of Bimini (grey) showing the major areas of development since 1999 highlighted in red and hash-marked areas. Insets on top show the location of Bimini off the coast of Florida, US (B).

Satellite remote sensing is a method that allows for consistent mapping of large areas of terrestrial and aquatic habitat (Klemas, 2016; Silva et al., 2008; Xie et al., 2008). Multispectral satellite remote sensing captures images on a regular basis across the globe and categorizes reflected light from the Earth's surface into several wavelengths (Aggarwal, 2003). Satellite images are captured in pixels which vary in spatial resolution, depending on the sensor used and viewing angle, and each of these pixels will have a specific amount of light reflected from each band given surface conditions (Aggarwal, 2003). By using image-based machine-learning classification, such as supervised random-forest classification models, pixels which reflect similar amounts of light in each band can be paired with *in-situ* habitat data to determine expected reflectance values for each habitat type; these expected values can then be used to map the distribution of habitats across unknown areas, where *in-situ* data has not been collected but pixels show similar spectral signature (Akar and Gungor, 2012; Zhafarina and Wicaksono, 2019; Zhang et al., 2021).

Satellite remote sensing has been successfully used to classify shallow marine environments and coastal habitats including seagrass beds and mangroves (e.g., Dogan et al., 2009; Rose et al., 2015; Poursanidis et al., 2021; Wilson et al., 2020). One long-running satellite series that is frequently used for habitat classification is NASA/U.S. Geological Survey's (USGS) Landsat suite of sensors, which includes Landsat 5 TM, Landsat 7 ETM+, Landsat 8 OLI and Landsat 9 (Darweesh et al., 2021; Hansen et al., 2001; Lauer

and Aswani, 2008; Palandro et al., 2008; Topouzelis et al., 2018). Together, these satellites have provided a publicly available and continuous time series of red, green, blue, and near-infrared (NIR) bands, with similar spectral range and wavelength categorization since 1984, at a spatial resolution of 30m (Suppl. Table S1; Chander et al., 2009; Irons et al., 2012; Masek et al., 2020). Images at a given location are collected at a temporal frequency of once every 16 days (USGS, 2022). One challenge when using these images for mapping of habitat is the lack of *in-situ* data availability across the entire time series. However, algorithms such as Automatic Adaptive Signature Generalization (AASG) can use just one classified reference map created with *in-situ* data from any single year to determine habitat coverage in years where *in-situ* data are lacking (Dannenberg et al., 2016). The algorithm achieves this by determining average reflectance in a specified band for each habitat type in the mapped reference image. If pixels in an unmapped image fall within a certain standard deviation of the average reflectance of certain habitat type and are in a location where that habitat type was previously identified in the mapped image, these pixels are then classified as that same habitat type and used to train a new random forest model to classify habitat types in the new unmapped image. (Dannenberg et al., 2016; Leblanc et al., 2021). By using freely available satellite imagery along with this algorithm, habitat extent can be monitored over time for changes due to natural or anthropogenic effects (Hakkenberg et al., 2020; Dannenberg et al. 2018; Leblanc et al., 2021).

In my second chapter, one year of available *in-situ* habitat data from May 2016 and the closest available Landsat-8 OLI satellite image from June 2016 were used to train a random forest model and create a reference map for terrestrial and aquatic habitats of Bimini. Using this reference map along with the AASG algorithm and freely available

Landsat 5, 7, 8 and 9 imagery, I created a time-series of terrestrial and aquatic habitat maps in Bimini over a 23-year period from 1999 to 2020. Through this time series, long-term changes in terrestrial vegetation cover were assessed along with their impacts on the distribution and density of adjacent seagrass beds within known lemon shark nursery areas: North Sound, Shark Land and South Bimini. My study results are placed in the context of habitat protection and conservation for juvenile lemon sharks and other species. Knowing long-term changes in habitat availability is essential for management and conservation planning going forward (Newman et al., 2007).

2.2. Methods

2.2.1 Study region

Bimini resides on the western edge of the Grand Bahama Bank (25.7273° N, 79.2979° W), adjacent to the Gulf Stream and approximately 85 km east of Miami, Florida, USA (Fig. 2.1). Bimini consists of two main islands, North and South Bimini, surrounding a central shallow lagoon, with the eastern portion of North Bimini known as East Wells. Most of Bimini, other than the western ocean facing shore, is fringed by dense mangroves, primarily red (*Rhizopora mangle*) and black mangrove (*Avicennia germaninans*) in addition to other terrestrial vegetation consisting of mainly small shrubs, woody vegetation and herbaceous plants (Howard, 1950; Newman et al., 2007). The central lagoon consists of sandflats and seagrass beds dominated by turtle grass (*Thalassia testudinum*), shoal grass (*Halodule wrightii*) and manatee grass (*Syringodium filiforme*) (Fuentes et al., 2019). The lagoon area in North Bimini exhibits great temperature variation due to shallow water levels and low tidal flow as well as fluctuating salinity levels in sheltered areas of between 31-45‰ due to rainfall (Turekian and Newell, 1957). Seagrass species also dominate

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shallow habitats located off the south shore of South Bimini (Fuentes et al., 2019). Seagrass bed extent throughout Bimini varies seasonally, with summer being the time of highest extent for seagrass in the Bahamas, between March and August, while winter is considered the time of lowest seagrass extent, between September and February (Tussenbroek et al., 2014). Air temperature in the Bahamas varies from highs of 36.5°C in the summer to lows of 7.9°C in the winter while water temperature averages at 29.5°C in the summer and 22.2°C in winter months. Bimini also experiences a tropical cyclone season between mid-July to October (Bahamas Department of Meteorology, 2020; NOAA, 2023).

2.2.2 Training data

The primary training dataset of *in-situ* habitat types used for creation of the aquatic reference map came from Fuentes et al. (2016). In their study, 52 $1m^2$ quadrats were sampled across Bimini in June 2016, and percent coverage of species within each quadrat was estimated. For my thesis, habitat data was broken into two categories: seagrass (n=10) and non-seagrass habitat (n=42). Quadrats with less than 50% seagrass coverage were classified as non-seagrass habitat and labeled low-density seagrass/bare (LDSG/bare). Quadrats with greater than 50% seagrass coverage were considered seagrass habitat and were further separated into mid-density seagrass (MDSG), (50-75% seagrass; n=7), and high-density seagrass (HDSG), (75-100% seagrass; n=3). Additionally, previously created biotope maps of Bimini, developed by Jerome Pellet for Save Our Seas Foundation (SOSF) (unpublished results) and Hussey (2003), were used to add training data points (n=139) to other areas of the map through visual inspection and comparison to the false colour version of the 2016 satellite image in ArcGIS Pro (v2.7.0, 2020; Fig. S1.).

For the terrestrial reference map, no *in-situ* training data was available, thus training data points (n=483) for the May 2016 Landsat-8 reference image were created through visual inspection of vegetation patterns in ArcGIS Pro (v2.7.0, 2020) along with the biotope map by Pellet (unpublished results) and aerial images (Fig. S1). Habitat type was initially broken into 7 classes similar to the biotope map created by Pellet (unpublished results). These habitat classes included mangrove, developed, sand, maintained vegetation, other vegetation, inland lakes, and rocky outcroppings. However, through random forest classification accuracy trials, I determined that the highest accuracy across the time-series was achieved when only 2 classes were used: vegetated and bare, which included natural sand and urban developed land.

2.2.3 Satellite image selection

All available cloud-free satellite images collected within the study area by Landsat-5, 7, 8 and 9 between 1999-2020 were downloaded from the USGS Earth Explorer (https://earthexplorer.usgs.gov/). The image closest in time to *in-situ* habitat data collection (May 2016) was selected for creation of the reference maps. This image was taken by Landat-8 on May 8th, 2016 at 10:42 EST, with a tidal height of 0.8m. Subsequently, one cloud-free image was selected for each year from 1999 to 2020 when available, based on lowest wave action and least sun-glint resulting in highest water transparency. No cloud-free images were found in 2012 or 2013 due to a reduction in image acquisition frequency when Landsat 7 experienced a malfunction in the scan line corrector which caused pixel loss in captured images and Landsat 8 had not yet been launched (Zhang et al., 2007). To improve comparability of maps across time, images were selected as close to February as possible as most years had at least one image available in this month. February also

corresponds to the time of year with minimum seagrass extent and therefore provided a good point of reference for assessing seagrass coverage across time (Fourqurean et al., 2001). While February is 4 months apart from the reference image month, the AASG algorithm can predict habitat type across years and months, so this was not expected to cause mis-classification (Dannenberg et al., 2016). No habitat coverage analysis was carried out for 2005, 2008 or 2010 due to a lack of cloud-free satellite images in winter in these years (between December and March). In total, 18 images were selected for analysis. For the available images, the average tidal height at the time of image collection was 0.40 m with a standard deviation of +/- 0.28 m (NOAA, n.d.; Table S2).

2.2.4. Pre-processing of satellite images

All images were pre-processed for atmospheric correction using the fixed dark spectrum fitting approached with ACOLITE using default settings (Vanhellemont, 2019; Python v. 20221114.0). Land masks were then created in Sentinel Applications Platform (SNAP) (European Space Agency, 2021, v.9.0) by first using a threshold of 0.045 in the near-infrared (NIR) band and then manually editing these polygons in misclassified areas. A new land mask was created in each year where land was added or removed during coastal development. These land masks were then used to create terrestrial maps for each image in the time series. For aquatic maps, a land mask created during the year of greatest terrestrial extent in the time series (2017) and at low tide was used for all image years, to improve continuity of seagrass extent calculations across time. A deep-water mask was also applied for areas deeper than 5m, based on the National Oceanic and Atmospheric Administration (NOAA, 2005) bathymetric chart, to limit mapping to the extent of the documented lemon shark nurseries, focus on areas where seagrass and sand were dominant habitats based on

maps from Pellet (unpublished results), and to remain well within previously documented benthic habitat satellite detection thresholds (Hussey, 2003; Palandro, 2009).

2.3.5. Satellite image band selection

Specific bands were selected as predictor variables for the terrestrial and aquatic random forest models, based on their ability to improve random forest classification accuracy in the reference map as well as in the AASG algorithm time-series. For aquatic mapping, the red, green, and blue bands were used along with green-red and green-blue Lyzenga Depth-Invariant Index bands for water column correction. Lyzenga water column correction linearizes the relationship between different bands to accommodate for different water depths (Lyzenga, 1978). No vegetation indices were used for aquatic mapping, as the NIR band used in these indices does not penetrate the water's surface (Hartmann, 2016). For terrestrial mapping, the red, green, and blue bands were used as well as two calculated indices: the Combined Mangrove Recognition Index (CMRI) and the Normalised Difference Vegetation Index (NDVI = (red-NIR)/(red+NIR)). The CMRI uses a combination of the NDVI and Normalised Difference Water Index (NDWI = (green-NIR)/(green+NIR)) to increase band differentiation at the upper and lower ranges of the index and thus increase differentiation between mangrove and other habitats with CMRI equal to NDVI minus NDWI (Gupta et al., 2018). Both CMRI and NDVI have been shown to be the two most effective predictors for distinguishing vegetated from non-vegetated habitats, followed by the blue and green satellite image bands (Chen, 2020). While the short-wave infrared (SWIR) band was also found to be effective in past studies when mapping a single image, it is not consistently captured across the Landsat sensor systems and was thus excluded from analyses (Wang et al., 2018).

2.2.6 Reference image random forest classification

One terrestrial and one aquatic reference map were created using the May 2016 Landsat-8 image and a random forest model, using the RStudio caret package (v6.0-93) with 5-fold cross validation repeated 10 times (Kuhn, 2008; R Core Team, 2021). Random forest cross-fold validation was used as it produces the highest accuracy in classifying habitat maps and reduces misclassification of pixels (Ha et al., 2020). 50% of the training data set was not used in model building and was reserved to be used in a confusion matrix, to calculate both user's and producer's accuracy as well as overall accuracy and a kappa coefficient. User's accuracy was defined as the total reference pixels which were correctly categorised by the random forest model while producer accuracy is defined as the number of predicted pixels which matched reference data in each category. Overall accuracy was calculated as the average of producer and user accuracies across habitat classes. Additionally, the kappa coefficient assesses the accuracy of predictions as compared to random chance with any value greater than 0.61 being considered sufficient agreement of the predicted dataset with the expected data (McHugh, 2012).

2.2.7 Time-series mapping

Once the aquatic and terrestrial reference maps were created, the automatic adaptive signature generalisation (AASG) algorithm was used to classify habitats in years lacking or with sparse *in-situ* data by creating 'stable sites' to be used as pseudo-training data. The AASG algorithm defines stable sites in new images by calculating the average reflectance value for a specific band for each habitat class in the reference map and identifying pixels in the unmapped image which show reflectance values within a proportion of the standard deviation of the average reflectance value for each habitat type for the specified band

(Dannenberg et al., 2016). In this study, 0.25 of the standard deviation of the reflectance value of the chosen band was used for both the terrestrial and aquatic maps as this increased class specificity. For terrestrial maps, the NDVI layer was used for classification of stable sites, while for aquatic maps the green band was used; these bands showed the greatest spectral differentiation between habitat classes in the reference map. The AASG algorithm then used a random forest model to classify each of the new images, using the created stable sites as training data (Dannenberg et al., 2016).

To assess the reliability of produced AASG aquatic habitat class maps, *in-situ* data from 1999, 2003, and 2020 were used in map validation (Fig. S2). For the 1999 map, test data points of seagrass and sand habitat were created by viewing a 1993 map of seagrass and sand polygons of the North Sound, from transect surveys by Morrissey and Gruber (1993), along with the 1999 Landsat-5 false colour image in ArcGIS Pro (n = 38, v2.7.0, 2020). For 2003, test data points were adapted from plant survey quadrats completed by Kessel (unpublished results) where a $1m^2$ quadrat was placed at locations in the North Sound and South Bimini shark nurseries and percent cover of seagrass, leaf litter, red algae and bare substrate within the quadrat were quantified; these quadrats were then classified into LDSG/bare, MDSG and HDSG as described above for the Fuentes et al. (2016) quadrat training data (n = 30). To assess accuracy of the 2020 map, data collected during acoustic receiver range testing in March of 2020 was used (n = 119, Cormier et al., unpublished results). Data points along range-testing transects were classified as either seagrass, seagrass/sand, sand/seagrass, or sand based on visual inspection. Only data points classified as sand or seagrass were used for assessment of map accuracy to reduce the chance of misclassification. For accuracy assessments of both 1999 and 2020 bottom-

habitat maps, pixels classified by AASG as LDSG/bare were considered 'sand' and pixels classified as either MDSG or HDSG were considered 'seagrass'.

To assess the reliability of AASG terrestrial habitat class maps, test data sets were created for 1999, 2011 and 2020 to be used in map validation (n = 115, 140, 144, respectively, Fig.S3). Since no *in-situ* datasets were available for terrestrial maps, coordinates of bare and vegetated habitat for each year were created by viewing the false colour Landsat satellite images from 1999, 2011 and 2020 in ArcGISPro (v2.7.0, 2020).

2.2.8 Assessment of habitat change across time-series

Habitat extent in hectares (ha) was calculated using R (R Core Team, 2021 v.4.1.1) for each habitat type in each year for each nursery area, North Sound, Shark Land and South Bimini, as well as for adjacent terrestrial areas, namely North Bimini, East Wells, and South Bimini (Fig.1). Number of pixels for a given habitat was converted to ha assuming a pixel nominal surface area of 0.09 ha (i.e., 30 m x 30 m = 900 m^2).

Additionally, to determine areas which showed consistent HDSG (CHDSG) coverage, a HDSG variability map was created by stacking all created aquatic maps and calculating the percent of times that a pixel was classified as HDSG across the 18 image, 23-year time series. Pixels classified as high-density seagrass in ≥75% of maps (~13/18 images) were considered as CHDSG. This map was then used to assess how HDSG extent in individual years differed from CHDSG distributions.

2.3. Results

In total, 16 maps were created of terrestrial and aquatic vegetation (Fig. 2.2), with terrestrial vegetation being classified in 2 categories, bare and vegetated, and aquatic

habitat being classified into 3 categories, low-density seagrass/bare (LDSG/bare), mid-density (MDSG) and high-density (HDSG) seagrass. Patterns in seagrass and terrestrial vegetation are described below in section 2.3.1.
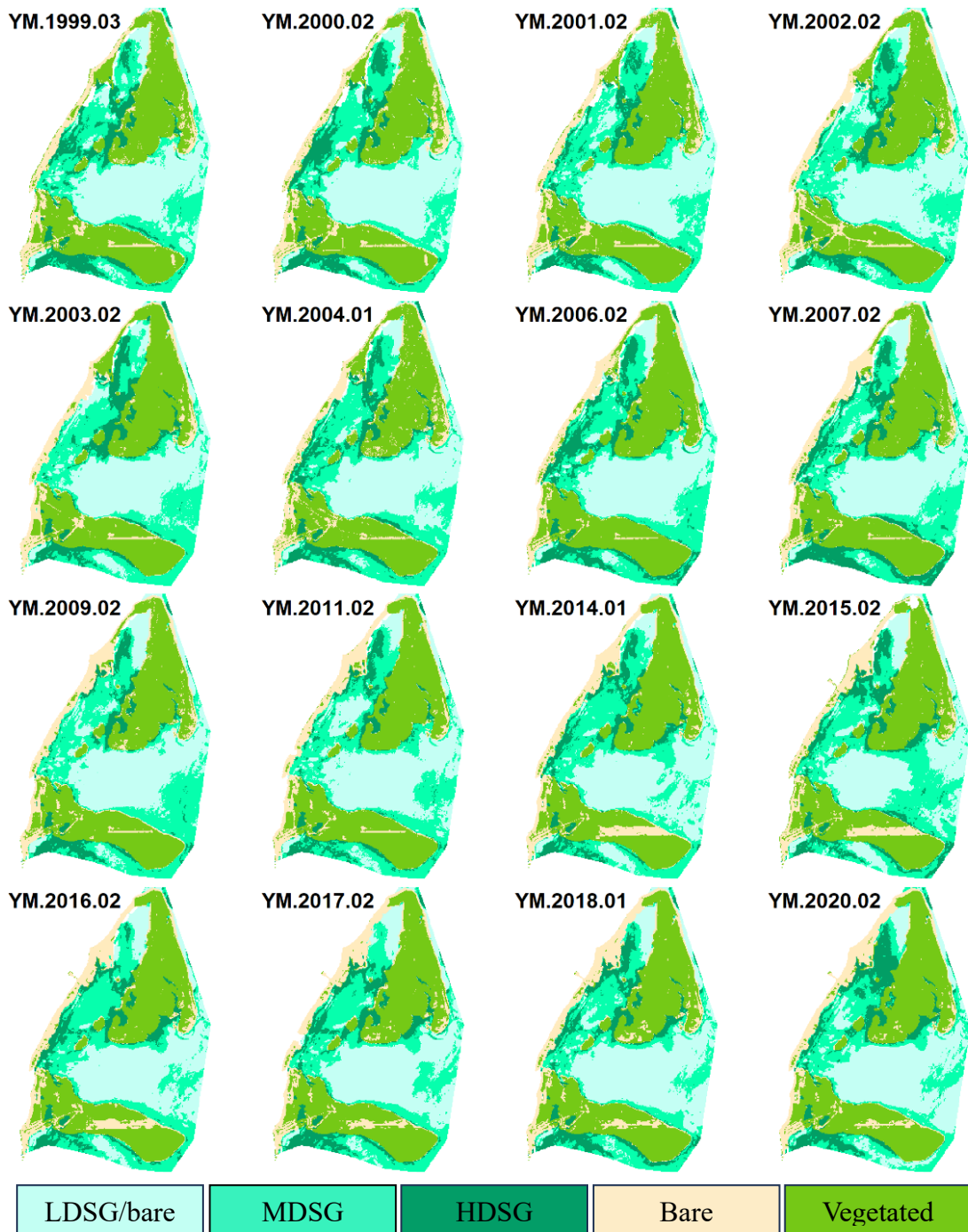
Fig. 2.2 Maps of aquatic and terrestrial habitats in Bimini during the winter from 1999-2020. Terrestrial areas show vegetated and bare habitat while aquatic areas show high-density seagrass (HDSG), mid-density seagrass (MDSG) and low-density seagrass/bare habitat (LDSG/bare). The upper left corner of each image identifies the Year and Month of the satellite image (YM).

2.3.1 Habitat-type map accuracy

The aquatic and terrestrial reference maps (created from the May 2016 Landsat-8 image, *in-situ* data and random forest model) showed high overall accuracy, with values of 94% and 98%, respectively, and high kappa coefficients values of 0.91 and 0.98 (Table 2.1).

For the AASG created aquatic maps, accuracy decreased, but was still relatively high when assessing seagrass vs. non-seagrass areas. Bottom type classification in 1999 and 2020 both showed an overall accuracy of 82% in identifying areas of LDSG/bare vs. areas of MDSG/HDSG with kappa coefficients of 0.64 and 0.63, respectively (Table 2). In 1999, user accuracy ranged from 76-88% and producer accuracies ranged from 75-89% across classes. In 2020, user and producer accuracies were slightly lower for some classes, ranging from 63-100%, with user accuracy at a minimum of 73% for seagrass habitat and producer accuracy being a minimum 63% for LDSG/bare. When assessing the ability for AASG to classify seagrass densities, accuracy decreased further. In the 2003 map, overall accuracy was 59% with a kappa coefficient of 0.42, based on the data obtained from Kessel (unpublished results). Overall accuracy was lowest for MDSG at 50%, while the algorithm showed the highest accuracy in predicting LDSG/bare, at 73%, followed by HDSG with an accuracy of 67.5% (Table 2.2).

For the AASG created terrestrial maps, overall accuracy in identifying vegetated vs. bare habitat was very high, with an average of 99% and an average kappa coefficient of 0.99 (Table S2). The terrestrial map created in 2011 was the only habitat map which

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showed less than 100% accuracy and less than 1.0 kappa, with an overall accuracy of 98%

and a kappa of 0.97 due to the misclassification of 2 out of 64 bare habitat coordinates as

vegetated (Table S2).

Table 2.1. Confusion matrix for the 2016 aquatic reference image showing number of pixels classified as LDSG/bare, MDSG and HDSG, according to reference data collected by Fuentes et al. (2016), and the number of pixels classified as each of those habitat types by the random forest model. Numbers in bold show the number of correctly identified points in each class.

Year: 2016		*In-situ Data*			
	Class	LDSG/ Bare	MDSG	HDSG	User's Accuracy
Classified Map	LDSG/ Bare	**8**	0	0	100%
	MDSG	0	**10**	1	90%
	HDSG	0	1	**15**	93%
	Producer's Accuracy	100%	90%	93%	**Overall Accuracy: 94%** **Kappa Coefficient: 0.91**

Table 2.2. Confusion matrix for the AASG created aquatic maps showing number of pixels classified as LDSG/bare, MDSG or HDSG compared to reference data collected in 1993 by Gruber and Morrisey (1993) adapted for 1999, in 2003 by Steve Kessel (unpublished results) and in 2020 by Emily Cormier (unpublished results). Numbers in bold show the number of correctly identified points in each class.

Year: 1999		*In-situ Data*		
	Class	LDSG/Bare	MD/HDSG	User's Accuracy
Classified Map	LDSG/Bare	**15**	2	88%
	MD/HDSG	5	**16**	76%
	Producer's Accuracy	75%	89%	**Overall Accuracy: 82%** **Kappa Coefficient: 0.64**

Year: 2003		*In-situ Data*			
	Class	LDSG/Bare	MDSG	HDSG	User's Accuracy
Classified Map	LDSG/Bare	**7**	0	0	100%
	MDSG	6	**5**	2	38%
	HDSG	2	3	**7**	58%
	Producer's Accuracy	46%	62%	77%	**Overall Accuracy: 59%** **Kappa Coefficient: 0.42**

Year: 2020		*In-situ Data*		
	Class	LDSG/Bare	MD/HDSG	User's Accuracy
Classified Map	LDSG/Bare	**38**	0	100%
	MD/HDSG	22	**59**	73%
	Producer's Accuracy	63%	100%	**Overall Accuracy: 82%** **Kappa Coefficient: 0.63**

2.3.2. Habitat extent from 1999 to 2022 in aquatic and terrestrial zones

2.3.2.1 Terrestrial vegetation trends
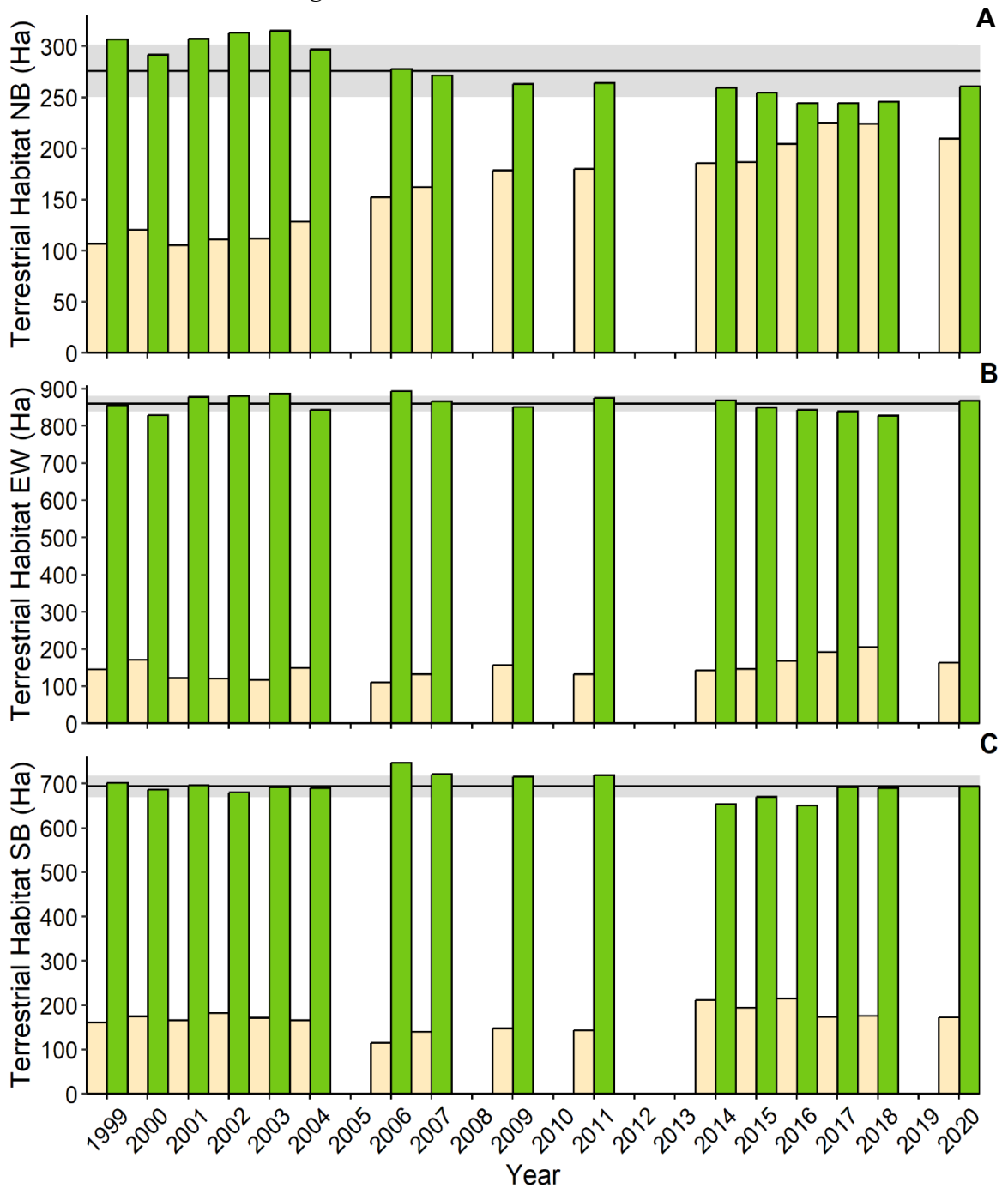
Fig. 2.3. Hectares (ha) of vegetated (green bars) and bare (yellow bars) terrestrial habitat per year in each of the three terrestrial areas studied: North Bimini (NB, A), East Wells (EW, B) and South Bimini (SB, C). Grey bar across plot shows the mean (dark line) and standard deviation (grey bar) for vegetated habitat extent calculated across the entire time series.

Terrestrial habitat coverage trends from 1999 to 2020 differed between regions of Bimini (Fig. 2.3). North Bimini showed the greatest changes in vegetation extent with an average of 276 ha and standard deviation +/- 25 (Fig. 2.3A). Here, vegetated habitat decreased from 314 ha 2003 to 263 ha in 2009, with losses especially in Mosquito Point in 2006, 2007 and 2009 (Fig. 2, YM_2006_02, YM_2007_02, YM_2009_02) where most development occurred for Bimini Bay Resort. Vegetated habitat extent then remained relatively consistent in mapped years of 2011, 2014 and 2015, but in 2016 vegetation extent decreased again, with bare habitat doubling and continuing to increase up to 2018, reaching a maximum of approximately 228 ha with the creation of new islands (Fig.2.3, YM_2017_02). By 2020, vegetated habitat had rebounded slightly, with a net loss of 46 ha of vegetation since 1999, while bare habitat had approximately doubled from 106 ha to 209 ha (Fig. 2.3A).

In East Wells, vegetation extent remained relatively constant over the entire period of observation (Fig. 2.3B). On average, vegetation extent was 860 ha (SD +/- 20) with a minimum of approximately 828 ha in 2000 and 2018 and a maximum of 893 ha in 2006. Bare habitat covers a small proportion of East Wells at an average of 152 ha (SD +/- 27), as this area remains mostly untouched by development. By 2020, both vegetated and bare habitat had both increased by approximately 1%, possibly due to a difference in tidal height between years which exposed or covered areas of vegetation and barren habitat (Fig. 2.3B).

In South Bimini, terrestrial vegetation extent remained relatively constant from 1999 to 2004 with an average of 691 ha (SD +/- 7) (Fig. 3C). In 2006, terrestrial vegetation increased and remained high until 2011. However, in 2014, vegetation extent decreased below 1999 levels, partly due to the expansion of the airport runway (Fig. 2,

YM_2014_01), but then rebounded likely due to vegetation re-growth which overtook sections of the runway that remained unused (Fig. 2.2, YM_2017_02; Dean Grubbs, personal communications). By 2020, vegetated habitat had decreased overall by 9 ha while bare habitat had increased by 13 ha since 1999.

2.3.3.2 Aquatic vegetation trends
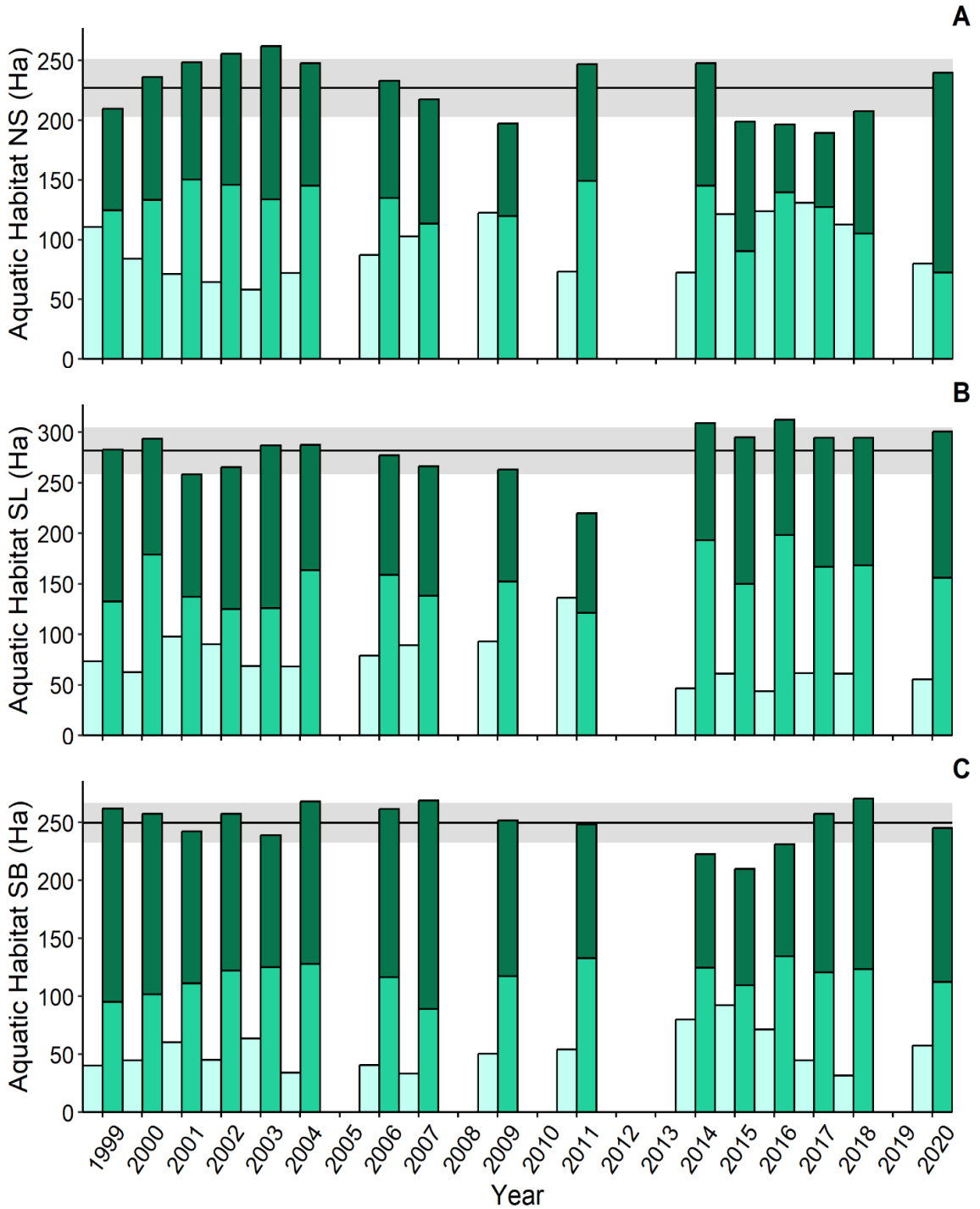
Fig. 4. Hectares (ha) of non-seagrass (LDSG/Bare, light blue) and seagrass habitat including HDSG (dark green) and MDSG (aquamarine) per year in each of the three nursery habitats studied: North Sound (NS, A), Shark Land (SL, B) and South Bimini (SB, C). Grey bar across plot shows the mean (dark line) and standard deviation (grey bar) for vegetated habitat extent calculated across the entire time series.

Aquatic vegetation trends often mirrored trends in adjacent terrestrial areas (Fig. 2.3 and 2.4, Fig. 2.2). In the North Sound (Fig. 2.4A), like terrestrial vegetation in North Bimini (Fig. 2.3A), seagrass extent decreased from 262 ha in 2003 to 198 ha in 2009. Unlike terrestrial vegetation, however, seagrass extent rebounded after 2009, increasing to 248 ha by 2011. Then in 2015, parallel to the increase in bare terrestrial habitat with the creation of new islands (Fig. 2.3A), a gradual decrease in seagrass began and continued until 2017, reaching a low of 189ha (Fig. 2.4A). To assess the significance of the loss of seagrass in 2017, areas of HDSG in this year were compared to areas CHDSG in the variability map (Fig. 2.5A). While patches of CHDSG exist in the West side of the North Sound in the variability map, these patches were not visible in 2017 (Fig. 2.5B). However, seagrass did rebound by 2020 with total seagrass at 240ha and LDSG/bare habitat at 80 ha (Fig. 2.4A, Fig. 2.2)

In Shark Land, seagrass coverage also showed similar trends to terrestrial vegetation coverage in North Bimini (Fig. 2.4B; Fig. 2.3A). While some fluctuation occurred between 1999 and 2003, there was no distinct trend in extent until 2004, when seagrass extent began decreasing until 2011. However, seagrass rebounded by 2014 and remained high up to 2020, showing no observed change in extent due to the creation of islands in 2017. By 2020, seagrass covered a total of 300 ha and LDSG/bare covered ~55 ha, exhibiting an increase in seagrass extent of 18ha since 1999 (Fig. 2.4B).

In South Bimini, seagrass extent stayed relatively constant between 1999 and 2011 (Fig. 2.4C). Seagrass extent overall showed a slight decreasing trend from 2011 to 2015, simultaneously to the decrease in terrestrial vegetation in South Bimini (Fig. 2.3C), but then rebounded in 2018. Between 2018 and 2020, seagrass decreased again by 25 ha,

possibly due to the construction of roadways in South Bimini (Fig. 2.3C; Fig. 2.2). Seagrass

extent in South Bimini showed a net loss of 17 ha from 1999 to 2020. (Fig. 2.4C).

Outside of the nursery areas, other changes in seagrass extent were visible in the

time-series maps (Fig. 2.2). For example, a channel is visible in a LDSG/bare area in 2002

and 2003 following dredging activities (Fig. 2.2; YM_2002_02, YM_2003_02). However,

no clear decrease in seagrass occurred during these years within nursery habitats (Fig. 2.4)
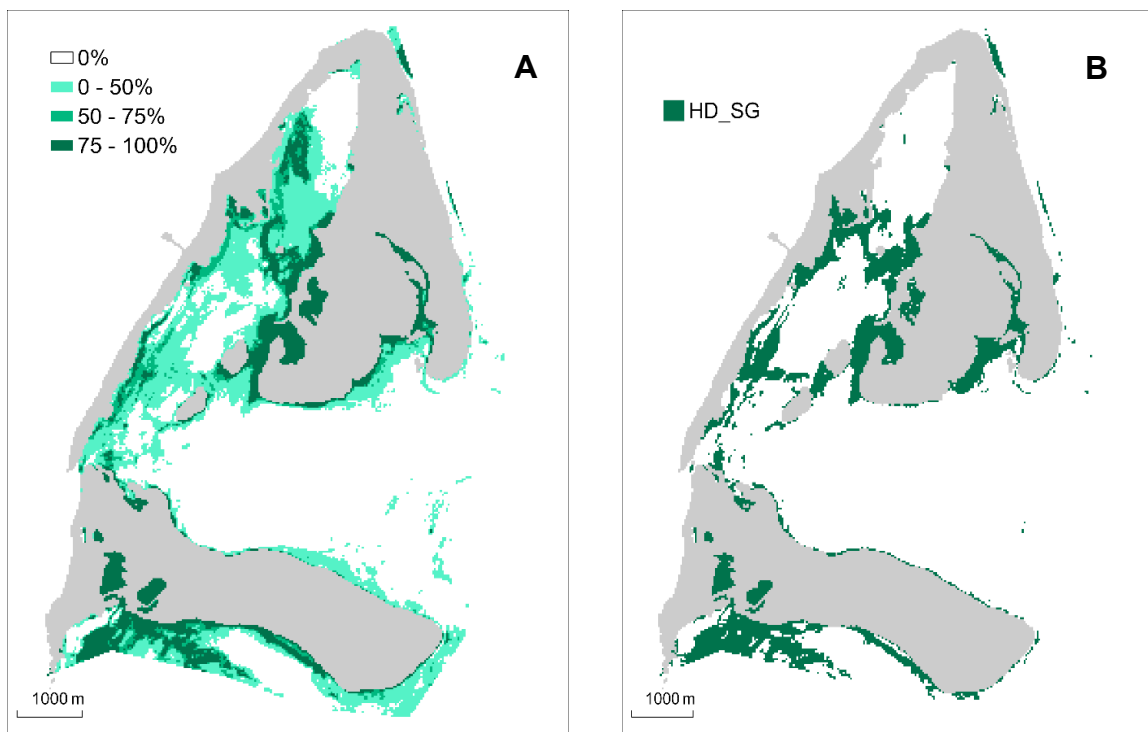
Fig. 2.5. Consistent high-density seagrass map (CHDSG) of Bimini (i.e., percent of image years where pixels classified as HDSG over the 18 years of data availability) (A) and the 2017 aquatic habitat map showing HDSG distribution, with little to no HDSG occurring in the North Sound (B). The grey areas correspond to the land mask while white areas correspond to a bathymetry greater than 5m and areas never classified as HDSG.

2.4. Discussion

Mapping coastal habitat extent over time helps to document habitat change and

understand the potential consequences for species and communities relying on these

habitats. We used a combination of remote sensing imagery, *in-situ* habitat data and the AASG approach to map and quantify changes in terrestrial and aquatic habitats in Bimini, the Bahamas over a 21-year time period from 1999-2020. These habitats are important nursery and foraging grounds for many species and identifying the magnitude and main drivers of habitat can help to inform conservation and management efforts (Newman, 2007).

2.4.1 Effectiveness of the AASG algorithm in mapping vegetation time series

The AASG-based classification of aquatic maps showed good overall accuracy (82%) and kappa coefficients (0.64) in classifying seagrass and non-seagrass areas (Table 2.2). This highlights the moderate effectiveness of the AASG algorithm in mapping seagrass extent in years lacking *in-situ* data for training. The AASG algorithm approach applied to the Landsat time series in my thesis showed similar accuracy to other methods used to identify habitats in years without *in-situ* data, such as spectral indices or creation of pseudo-ground truth data from high resolution imagery (Liang et al., 2023; Lyons et al., 2012), but with less user input required. However, when differentiating mid-density seagrass from high-density seagrass, overall accuracy and kappa values decreased (59%, 0.49; Table 2.2), which is important to consider when interpreting results and assessing seagrass bed recovery or loss, especially if assessing changes in mapped areas from high-density to mid-density seagrass or vice-versa. The AASG based terrestrial mapping showed very high overall accuracy (97%) and kappa coefficients (0.97) and demonstrated the effectiveness of the algorithm in mapping vegetated vs. non-vegetated habitats in the terrestrial zone (Table S2).

Overall, our maps were able to show long-term trends in the spatial extent of terrestrial and aquatic vegetation. Maps of aquatic vegetation showed interannual variability, which is expected due to potential changes in nutrient composition, temperature, and sediment deposition between years (Fourqurean et al., 2001). However, changes in spatial extent of seagrass were more pronounced in specific areas of Bimini. Areas which experienced the greatest interannual variation in seagrass extent included the east entrance to the island's inner lagoon, where shifting sand occurs with tidal and wind changes (Fig. 2.1, Fig. 2.2; Marba et al., 1993). Conversely, the two lemon shark nursery areas in the northern lagoon showed more consistent seagrass coverage across years, and low inter-annual variation, especially near terrestrial areas of intact vegetated habitat (Fig. 2.5A). In these nursery areas, years in which seagrass did show marked decreases in extent were often matched with years of pronounced terrestrial development and vegetation loss as well as sediment infilling as revealed by the terrestrial maps.

2.4.2 Effects of coastal development on aquatic habitats

Change in terrestrial vegetation extent showed impacts on adjacent seagrass density and distribution, especially in the North Sound and Shark Land nurseries. During coastal vegetation removal from 2004 to 2009 (Jennings et al., 2008), terrestrial vegetation decreased by 135 ha. At the same time, seagrass extent decreased in the North Sound and Shark Land by 65 and 24 ha, respectively. When new coastal islands were created between 2014 to 2017, as seen by the increase in bare habitat in terrestrial maps (Fig. 3A), seagrass density and extent also decreased drastically in the North Sound (Fig. 2.2, 2015-2017; Fig. 4A). The loss of high-density seagrass is especially clear when comparing to the whole time series, where high density seagrass was identified in the North Sound in 75-100% of

years but was not present in 2017 (Fig. 2.5). In both cases of seagrass loss concurrent with change in terrestrial vegetation, new land was being built through sediment deposition and infilling (Fig. 2.2). Seagrass density and loss could thus be due to sedimentation from dredging and movement of sediment, which may cover aquatic plants and cause die-offs when sediment is suspended in the water column and limits sunlight (Short and Wyllie-Echeverria, 1996; Durako et al., 2001). However, in 2002, when a boating channel was dredged along the western edge of the Bimini lagoon (Gruber and Parks, 2002), little to no change occurred in seagrass density and extent in nursery areas, possibly due to the distance of at least 780m between nurseries and the dredged channel, potentially limiting sediment deposition.

2.4.3 Rebound in seagrass extent after seagrass loss events

Unlike terrestrial habitat loss, decreasing or disappearing seagrass patches during coastal development often returned to pre-development status over time. The regrowth of these seagrass beds, however, occurred over different time scales. After continuous loss of 64 ha from 2003 to 2009, seagrass extent in the North Sound rebounded in just 2 years to almost pre-disturbance levels by 2011 (Fig. 2.4A). At the same time, seagrass loss of 68 ha in Shark Land occurred over 8 years from 2003 to 2011 and took 4 years to rebound (Fig. 4B). This may be due to differing seagrass species in these two areas, as species often vary in their ability to recover after disturbance events, depending on several factors including shoot turnover speed, colonisation strategy and seed dormancy ability (Erftemeijer et al., 2006; Kilminster et al., 2015). Seagrass species were not distinguishable based on Landsat satellite imagery due to low spatial and spectral resolution but may be identifiable with higher resolution hyperspectral imagery (Pettorelli et al., 2014). Seagrass in the North

Sound also shows differing responses to disturbance events. In 2004, seagrass loss occurred over a 5-year period while in 2015 the same extent of seagrass loss occurred in just 1 year. After the latter event, it then took approximately 4 years for seagrass to rebound, approximately double the time it took after the previous disturbance, when the rebound period was only two years. There are two factors which may impact seagrass rebound in this case. Firstly, it is possible that the cause of perceived losses of seagrass differed between the two events, with the 2015 event being caused by a rapid deposition of a larger amount of sediment on top of the seagrass. If the depth of sediment becomes too great, the seagrass will no longer be able to grow, potentially leading to complete die-off, which would decrease the ability of the seagrass to recover, leading to slower recovery times (Marba et al., 2015). Secondly, it is possible that seagrass community structure changed after the 2004 event, leading to a different disturbance response; areas potentially previously covered in *Halodule wrightii* in the North Sound, which show a low resilience to disturbance, may have been replaced by slower colonising, more resilient species such as *Thalassia testudinum,* as has been shown in other similar shallow coastal habitats in Florida and Australia (Durako et al., 2001; Kilminster et al., 2005). Such species-specific changes are not detectable from remote sensing imagery and would require more in-depth field research.

2.4.4 Ecosystem impacts of nursery habitat changes

Since satellite imagery relies on light reflected from the Earth's surface, it is impossible to determine whether an area classified as LDSG/bare is truly a low-density area or whether mid or high-density seagrass is buried under sediment and their seed bank and root rhizomes still exist (Leblanc et al., 2021). However, whether seagrass density

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decreases, or seagrass is buried, similar ecological consequences may result. For example, when sediment deposition occurs as a result of human activities, sessile benthic species, such as sponges and bivalves, and certain early life stages, such as fish eggs or larvae, may be buried and trapped in sediment, resulting in an overall decrease in survival and diversity (Carballo, 2006; Fraser et al., 2017). Changes in abundance and diversity may have impacts on the trophic ecology of the area, leading to a shift in food availability and diet of local species higher in trophic levels, including lemon sharks which rely heavily on specific species for their diet (Diehl, 1992; Newman et al., 2007; Tilman et al., 2014). Even shifts in seagrass species composition, which may have occurred after seagrass loss events in Bimini as discussed above, can have impacts on associated fauna and trophic communities (Tussenbroek et al., 2014). In addition to seagrass loss or community change effects, coastal development can induce stressors such as noise and water pollution, which may exacerbate the impacts of habitat loss on lemon sharks (Gelsleichter et al., 2005; Kemp et al., 2005; de Vincenzi et al., 2021). As female lemon sharks are natally philopatric and return biennially to specific nurseries to give birth, these seagrass and nursery areas are important to juvenile lemon shark survival (Chapman et al., 2009; Feldheim et al., 2002). Thus far, intensive coastal developments have been shown to result in a decrease in juvenile lemon shark survival and growth rates prior to 2008 (Jennings et al., 2008). The current study provides improved spatio-temporal information on changes in seagrass and terrestrial vegetation extent, allowing for further long-term studies of the link between lemon shark reproduction, survival and diet and habitat loss, especially in identified years of high seagrass loss such as in 2017.

2.4.5 Development impacts on ecosystem services

In addition to the ecological impacts of development, ecosystem services of coastal environments may also be affected. For example, mangrove and seagrass habitats provide important carbon sequestration services (Donato et al., 2011; Murdiyarso et al., 2015; Serrano et al., 2019). One hectare of mangrove removal corresponds approximately to 350 metric tonnes (mt) of carbon, the equivalent to a release of 1415 mt CO_2, meaning that potentially 77,825 mt of CO_2 were released to the atmosphere due to coastal development in North Bimini, assuming that a large proportion of the removed habitat was made of mangroves (IPCC, 2014; Kauffman et al., 2020). Seagrass species also provide carbon sequestration through sediment accretion within their root-rhizome system (Duarte et al., 2005), and the loss or removal of these rhizomes would release 108 mt of stored carbon and 396 mt of CO_2 per hectare, depending on the age of the seagrass meadow (Marba et al., 2015). Further, if areas are recolonized by faster growing seagrass species with shallow root rhizomes, carbon-sequestration abilities may be reduced for these beds (McLeod et al., 2011). In turn, seagrass beds which have been previously disturbed also show lower resilience to hurricane impacts, and continuously compounding effects of anthropogenic and natural disturbance events have been shown to eliminate seagrass beds in other parts of the Caribbean (Tussenbroek et al., 2014; Whitfield et al., 2002). Some high-density seagrass beds have persisted in Bimini for over 20 years (Fig. 5; Fig.2) and thus provide important carbon sequestration services (IPCC, 2014). These seagrass habitats also exist near East Wells, which has been proposed both as a Marine Protected Area (MPA) and as a new area for development (Black & Veatch International, 2008). Based on the relationship between coastal development and loss of seagrass in other areas of Bimini, it

is important to consider potential seagrass impacts if more coastal development was to occur.

2.5.6 Satellite mapping limitations

While satellite imagery is a useful tool in understanding changes in vegetation coverage over time and space, important limitations must be considered. One limitation is the availability of cloud-free images. For my thesis, I had initially planned to map bottom-habitat during the months of maximum seagrass extent from March-August. Unfortunately, spring and summer correspond to some of the cloudiest months in Bimini, precluding interannual comparison due to the lack of satellite images (Tussenbroek et al., 2014). Additionally, some technological issues in the Landsat satellite suite reduced satellite imagery acquisition rates; for example, when Landsat-7 experienced a scan-line corrector malfunction in 2003 (Zhang et al., 2006). Another limitation in time-series satellite mapping is the lack of *in situ* data for training and ground-truthing classified satellite maps. In this analysis, some misclassification may have occurred in cases where aquatic habitats other than seagrass, such as *Sargassum* spp. or deep-water channels, were not adequately represented in the training dataset. Additionally, the classification between mid and high-density seagrass may also show greater uncertainty as seagrass density data was obtained from 1m x 1m sampling quadrats while satellite imagery was obtained at 30m x 30m pixels. AASG model performance also showed decreased reliability when defining high density vs mid-density seagrass, indicating that these classes may not be reliably identified through the time series.

Nonetheless, Landsat satellite imagery provides an effective way to assess general trends in vegetated habitat extent over space and time at a low cost (Banskota et al., 2014;

Lyons at al., 2012; Wilson et al., 2020). While validation data did not exist for all years, the random forest model and AASG algorithm show high accuracy in predicting vegetated vs. non-vegetated habitat in both the aquatic and terrestrial zone in selected years, in agreement with a previous study that used this method (Leblanc et al., 2021).

2.5 Conclusion

By using Landsat satellite images along with the AASG algorithm, terrestrial and aquatic habitat classification and spatial extent was documented in Bimini from 1999 to 2020, allowing for a better understanding of interannual seagrass dynamics and the impacts of terrestrial development on the aquatic environment. Some changes in seagrass extent due to development were expected, such as the loss of high-density seagrass during channel dredging in 2002, while other seagrass changes were revealed through the newly created habitat maps, such as in the North Sound from 2016 to 2018, where seagrass density and distribution decreased following the creation of islands. Assessing the relationship between terrestrial development and seagrass loss can help to identify important mitigation efforts for future developments. As the most pronounced impacts on seagrass occurred directly adjacent to island creation and sediment deposition, this study emphasizes the importance of mitigation of sedimentation through silt curtains, to reduce travel of sediment from construction sites to adjacent seagrass areas, which has been recommended in previous ecological impact assessments, but not effectively implemented (Black & Veatch International, 2008). The habitat maps and analysis methods used for this study could and should be used to monitor coastal development progress and potential future impacts. Finally, time series also pinpointed areas of consistent seagrass coverage that have existed for over 20 years. These areas should be prioritised for protection as they not only offer

carbon sequestration but are also valuable in maintaining the ecosystems within the lemon

shark nurseries, as I explore in my next chapter.

Chapter 3: Coastal development in a shark nursery: impacts of habitat changes on juvenile lemon shark survival in Bimini, the Bahamas from 1999-2017

3.1. Introduction

Habitat loss has been an important factor in the decrease of some shark populations around the world (Dulvy et al., 2021). These impacts can be particularly pronounced when occuring within critical habitat areas, which includes feeding, breeding, and nursery areas. Nursery areas can be especially important as they allow for the protection of young age classes and replenishment of shark populations (Kinney & Simpfendorfer, 2009). Nursery areas are often characterized by shallow and sheltered habitats for early life stages and are classified as areas where juvenile sharks are more commonly encountered, where they remain or return for extended periods of time, and where an area is repeatedly used across time or multiple pupping classes (Heupel et al., 2007).

Lemon sharks are large-bodied marine predators that occur across the North Atlantic Ocean and range from the United States to Western Africa and from New Jersey to Northern Brazil (Castro, 2011). Two main populations have been identified in the Western North Atlantic, a Northern Hemisphere stock, including the South-Eastern United States, Bahamas, and Caribbean; and a Southern Hemisphere stock (Ashe et el., 2015). Lemon sharks are currently listed as near-threatened on the IUCN red-list (Sundstrom, 2015), with the most recent stock assessment for the South-Eastern United States population of lemon sharks showing a decline of 26% over the last two generations, approximately 36 years (Carlson et al., 2021; Hansell et al., 2020).

Lemon sharks (*Negaprion brevirostris*) are known to use distinct nurseries during their first years of life, moving off to deeper water in subsequent years (Franks, 2007; Murchie et al., 2010; Weatherby et al., 2007). One well-studied lemon shark nursery area exists in Bimini, the Bahamas. Bimini is a pair of small islands at the Westernmost edge of the Great Bahamas Bank and on the Eastern edge of the Gulf Stream (Fig. 3.1), making it the only area of mangrove habitat on the Western edge of the bank. The Northern part of Bimini surrounds a shallow lagoon characterised by seagrass beds and fringed with mangroves while the southern part exhibits deeper waters, more complex fringing mangroves and extensive seagrass meadows and coral reefs (Newman et al., 2007). Three distinct nursery areas have been previously identified: North Sound, Shark Land and South Bimini (Fig. 3.1). Female lemon sharks give birth in these nurseries on a biennial cycle to between 2 and 18 pups between May and June (Feldheim et al., 2002). In North Sound and Shark Land, the Bimini Biological Field Station Foundation has been conducting annual sampling of newborn lemon sharks through standardised gillnet sampling and mark-recapture using Passive Integrated Transponders (PIT) (Gruber et al., 2001). Past research has shown that individuals born in these nursery areas typically reside within these habitats for at least the first 3 years and display strong site attachment, with very little movement between areas (Franks, 2007; Morrisey & Gruber, 1993a). Further, young of the year sharks use very small home-ranges of only ~0.68 km^2 (Morrisey & Gruber, 1993a). Within nursery areas, individuals show not only ontogenetic expansion of space use and habitat (i.e. increasing range with increased size) but also diel and inter-annual changes to movement behavior (Gruber et al., 1988; Guttridge et al., 2012). These movements are influenced heavily by predator avoidance and prey availability. For example, individuals show

preference for shallower water and mangrove edges, which provide protection from predators, and become more exploratory during low tides, when larger predator movement is limited (Guttridge et al., 2012). Density of seagrass beds has been shown to impact habitat use of individuals, with juveniles showing preference for moderate density seagrass areas (Kressler et al., in press) but avoiding the densest seagrass beds, possibly due to the difficulty of catching prey (Carlson et al., 2022; Franks, 2007; Morrisey and Gruber, 1993b). These studies show that seagrass beds and mangroves provide important habitat for juvenile lemon sharks during their first years of life.

As with many shark species, however, lemon sharks are experiencing anthropogenic impacts in critical habitat areas, especially over the past several decades. In North Bimini, creation of resort properties has resulted in the dredging and removal of mangrove habitats as well as the creation of new islands with dredged sediments (Black & Veatch, 2008; Chapter 2). Based on previously collected and analysed remote sensing Landsat suite satellite imagery, coastal development has resulted in a removal of 46 hectares (ha) of terrestrial vegetation (mainly mangroves) since 1999, and 57 ha of new sediment being deposited for the creation of islands in the North Sound (Chapter 2). Additionally, the movement and removal of sediment has changed seagrass extent in years following development, with seagrass extent reducing post-development and taking up to 5 years to rebound (Chapter 2). Since 2017, seagrass has been increasing in extent in the North Sound of Bimini (Chapter 2), possibly due to influx of nutrients from dredged materials in previously low nutrient areas (Nayar et al., 2007). Loss of mangroves and change in seagrass extent or density may affect lemon shark survival through loss of refuges and changes in prey availability or diversity (Stump, 2013). Additionally,

secondary effects of the development and construction itself, including noise and pollution, has been shown to impact juvenile shark species in other coastal nurseries (Gelsleichter et al., 2005; Wheeler et al., 2020).

Past studies in Bimini have shown some negative impacts of coastal development on juvenile lemon shark survival in specific years, especially during initial dredging for a boating channel in 2001 and mangrove removal in 2005 (Jennings et al., 2007; Stump, 2013). However, the long-term effects of vegetation removal and change on juvenile lemon shark survival have not been fully investigated, partly due to the lack of long-term habitat data. Thanks to recently mapped habitat data using Landsat 7 satellite imagery (Chapter 2), a 20-year long time series of coastal development and aquatic habitat change now exists for both North Sound and Shark Land nurseries, allowing for the assessment of resulting impacts on juvenile lemon shark survival.

In this study, I used long-term satellite imagery habitat mapping efforts in combination with mark-recapture sampling to assess the impacts of habitat change on both juvenile shark survival rates and body condition within two distinct nurseries: North Sound and Shark Land. Long-term habitat mapping was used to calculate the extent of seagrass and coastal vegetation in each year and quantify the change in terrestrial and aquatic vegetation extent from year to year, as a measure of coastal development impacts. These measures were used as a proxy of habitat availability for juvenile lemon sharks. Habitat extent and change, along with a suite of population and individual level variables including age, population size and body condition, were used as predictors of lemon shark survival in a binomial generalised linear mixed model (GLMM) to determine which factors significantly affected lemon shark survival and in which way. Another GLMM was also

created with lemon shark body condition as a response, to determine impacts of the same variables on overall shark fitness. It was expected that in years with greater development and lower mangrove or seagrass extent, survival and body condition would decrease in juvenile lemon sharks. It was also expected that survival rates and body condition would be more impacted in the North Sound due to its proximity to coastal development projects. Understanding how coastal development impacts juvenile lemon shark survival and fitness will aid in determining potential mitigation measures for future construction, which is planned for Bimini, as well as increase scientific knowledge on the importance of seagrass and mangrove vegetation for the viability of lemon shark nurseries.

3.2. Methods

3.2.1 Study site

Bimini resides on the westernmost edge of the Grand Bahama Bank (25.7273° N, 79.2979° W), adjacent to the Gulf Stream and approximately 85 km east of Miami, Florida, USA (Fig. 3.1). Bimini consists of two main islands, North and South Bimini, surrounding a central shallow lagoon, with the eastern portion of North Bimini known as East Wells. Most of Bimini, other than the western ocean-facing shore, is fringed by dense mangroves while the central lagoon consists of sandflats and seagrass beds (Fuentes et al., 2019; Newman et al., 2002). The central lagoon contains two well-documented lemon shark nursery areas, North Sound and Shark Land (Gruber et al., 2001). North Sound extends to the northernmost point of Bimini and is surrounded by land on three sides, while Shark Land is on the southwestern portion of East Wells and is much more open to the surrounding lagoon (Fig. 3.1).
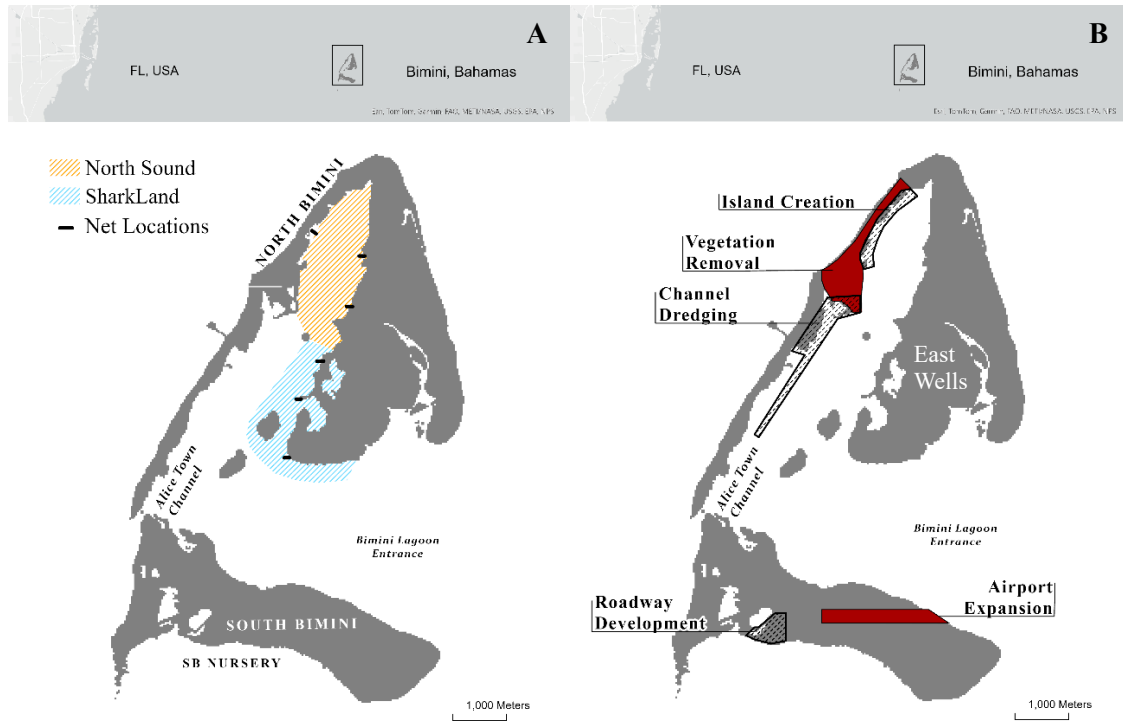
Fig. 3.1. Net locations of annual mark-recapture sampling within the two Bimini lagoon lemon shark nurseries, North Sound and Shark Land, as well as the major island areas (grey), North Bimini and South Bimini, and important landmarks (A, ArcGIS Pro v2.7.0, 2020). Right: Land areas of Bimini (grey) showing the major areas of development since 1999 highlighted in red and hash-marked areas. Insets on top show the location of Bimini off the coast of Florida, USA (B).

3.2.2. Lemon shark data

Since 1995, the Bimini Biological Field Station Foundation (BBFSF) has sampled the juvenile lemon shark population in the North Sound and Shark Land, between mid-May to early June (Gruber et al., 2001). Across 6 nights, three 180-foot gill nets are set at fixed locations in each nursery, totaling approximately 72 hours of survey per nursery (Fig. 3.1). Sharks caught in the nets are measured, sexed, and tagged with a PIT tag. They are then placed into enclosed pens until the final night when they are released back into the area of capture. Since lemon sharks are a placentally viviparous species, neonates are born

with an umbilical scar, which allows for determination of young of the year (Feldheim et al., 2002). If the umbilical scar is not fully healed, the opening is also measured (Gruber et al., 1993). If a shark is re-captured in subsequent years, the above measurements are recorded for the unique shark ID. In this study, data from 1999 to 2019 were used to match the available long-term satellite imagery data on mangrove and seagrass extent (Chapter 2). These annual surveys capture approximately 99% of the total lemon shark population within the survey area, allowing for accurate estimates of population size in the nursery in a given year and comparison between years (Franks, 2007). No field work had been completed during this thesis. Long-term data had been collected under Bahamas Department of Marine Resources permit MAMR/FIS/17B.

3.2.3 Survival calculations

Survival of individuals was recorded as a binomial with 0 indicating the shark was not recaptured and 1 that it was re-captured from $year_i$ to $year_{i+1}$ .. If the shark was caught in any years past $year_{i+1}$, it was also marked as '1' during all previous years, indicating survival. Age estimates for each shark were based on Dhellemmes et al. (2017). In short, sharks with open umbilical scars were considered age-0 and were aged in subsequent years according to their year of birth. Any sharks who did not have an open umbilical scar at the time of capture were aged based on total length and the age-growth relationships of DiBattista et al. (2007). In this study, survival data was limited to age-0 to age-1 and age-1 to age-2, as juvenile lemon sharks have been demonstrated to begin emigrating from their nursery at approximately age-3 and therefore disentangling survival from emigration is difficult for older juveniles (Guttridge et al., 2012). Survival was determined for sharks

caught up to 2019, but only sharks caught up to 2017 were used in modelling to allow for at least 2 years post initial capture were a shark to be recaptured.

To estimate annual age-0 survival rates, the number of age-0 sharks marked '1' for 'survived' was divided by the total number of age-0 sharks caught in that year. To estimate overall survival rate regardless of age class, the number of sharks marked with '1' was divided by the total number of sharks caught in that year. Annual survival rate estimates were measured as a proportion, ranging from 0 to 1. DiBattista et al., (2007) previously estimated that the recapture probability for an age-0 shark that was alive at age-1 was 0.99 and the recapture probability for an age-1 shark that was alive at age-2 was 0.92, meaning that survival estimates based solely on a shark being re-caught should be fairly robust.

3.2.4 Body condition calculations

Body condition was calculated based on DiBattista et al. (2007) as:

$$Relative\ Body\ Condition\ =\ 10{,}000 \times (\frac{Weight}{PCL^{-b}})$$

With b = 2.99 and PCL being the pre-caudal body length of the shark, measured from the tip of the nose to the base of the caudal fin. 2.99 was based on the slope of the regression line of the $\log_{10}$ weight-length relationship as determined by Dibattista et al. (2007). Body condition was used as a measure of fitness, with values greater than 1 indicating greater relative fitness while values lower than 1 indicated lower relative fitness (LeCren, 1951). When using body condition as a response variable, only body condition estimates for age-1 sharks were used, as these individuals would have spent at least a year in their nursery habitat, and thus their body condition was expected to be more determined

by the present habitat and not by any maternal influence (Bernardo, 1996; Weideli et al., 2019).

3.2.5 Predictor variables

Ecologically relevant predictor variables were used to model impacts on both survival and body condition. Seagrass and mangrove spatial extent were measured via imagery from the NASA Landsat suite of satellites (Cormier et al., in review; Chapter 2). A random forest model and Automatic Adaptive Signature Generalisation algorithm (AASG) was used to calculate total hectares of habitats such as seagrass, non-seagrass/bare, terrestrial vegetation, and bare/urban areas in North Bimini and the North Sound and Shark Land nurseries (Fig. 3.1; Dannenberg et al., 2016). These AASG models showed a high overall accuracy in determining seagrass vs. non-seagrass extent (82%) and vegetated vs. non-vegetated terrestrial habitat (99%). Satellite images were captured in February or January of each year depending on image availability; these months coincide with the time of lowest annual extent of seagrass (and are thus a conservative estimate of habitat extent) and provide a comparable proxy for annual seagrass extent across time (Fourquorean et al., 2012). Seagrass and terrestrial vegetation extent was measured for each year and averaged from $year_i$ to $year_{i+1}$ to create metrics of habitat availability during each shark's year of life, referred to herein as seagrass extent and mangrove extent.

Metrics of habitat change, to understand the amount or impacts of coastal development in a specific year, were also calculated. A metric of disturbance/coastal development was calculated by subtracting the extent of barren terrestrial habitat of $year_i$ from $year_{i+1}$. This metric is referred to herein as barren change, with a greater positive value indicating increased mangrove removal, disturbance and/or sediment deposition in that

year. Any year with a negative value for barren change was adjusted to 0, as decreases in barren extent were more likely due to small amounts of terrestrial vegetation re-growth in disturbed areas, and thus were not expected to affect juvenile survival. A metric of aquatic habitat change was also calculated for seagrass extent, with seagrass extent from $year_i$ subtracted from $year_{i+1}$. This metric is referred to herein as seagrass change, with high positive values indicating years of seagrass regrowth whereas years with negative values indicating seagrass loss or burial by sediment.

Nursery was included as a categorical predictor for both survival and body condition, with sharks categorized as either belonging to the North Sound (NS) or Shark Land (SL) nursery depending on where they were captured during annual sampling. A small number of sharks were caught in both nurseries between years and these individuals were excluded from analysis. Age classes included in this model have been shown to have small home ranges and high site fidelity to the nursery they are born in and thus are expected to remain in that nursery during the time periods of this study (Morrisey and Gruber, 1993a). Survival is expected to vary by nursery, as the two nurseries contain varying abiotic and biotic conditions, with NS having shallower water depth and more variability in salinity and water temperature, possibly resulting in lower survival (DiBattista et al., 2007; Stump, 2013).

Air temperature was gathered as a proxy for water temperature from the online historical weather database Weather Underground from the Bailey Town Bimini station (The Weather Company, 2024). The air temperature for the days of PIT sampling for both nurseries per year was averaged to create an average temperature per year. Temperature

was included as it has been shown to affect shark metabolism and movement in past studies, and thus may also impact shark survival and body condition (Guttridge et al., 2012).

As a proxy for intra-specific competition, the total number of juvenile sharks caught per year was added to the model, known herein as number of sharks caught. Additionally, as a metric of demographics, the proportion of caught age-0 sharks was calculated as the number of age-0 sharks divided by the total number of sharks caught that year. This metric is herein referred to as proportion of age-0s, with a higher proportion indicating a possibly higher number of sharks born in that year or less survival of age-0 sharks from the year previous, reducing the number of age-1s in the population.

In the survival model, metrics of shark fitness were also included: body length (measured in PCL), age (as a categorical variable of either 0 or 1) and body condition, and these variables were calculated as described above. These predictors were not included in the body condition model, where body condition was the response variable. Body condition was calculated based on a weight ~ length relationship and thus any relationship in the body condition model between these two metrics would not be ecologically meaningful. Additionally, for the body condition model, only data from age-1 sharks was used and so age was not included as a predictor.

3.2.6. Generalized linear mixed model - survival

To effectively understand the relationship between survival and the variables above, grouped effects such as year and shark ID had to be accounted for, as observations within any year are likely to be more similar than between years, and would have the same annual values for habitat metrics and population demographics. Also, an individual shark ID could

be included more than once in the model when the shark is re-caught and thus measurements of body length and body condition across years for the same ID would not be fully independent (Dean & Nielsen, 2007). Given the focus on survival, Shark ID and year could also be considered as 'random effects' *sensu* variables which are not a core research focus, but which need to be accounted for. For this reason, a generalised linear mixed model (GLMM) was used. The generalised component of a GLMM means that the model does not need to meet the assumption of normally distributed response variables (McCullagh & Nelder, 1989), while a mixed model approach allows the model to account for heterogeneity and clustered variables in a dataset (Dean & Nielsen, 2007). For the GLMM, a binomial model with logit link function was used, as survival was a binary response variable of either lived (=1) or died (=0) (McCullagh & Nelder, 1989).

In total, 11 predictor variables were included in the initial model, including metrics of abiotic factors (temperature), habitat extent (mangrove extent, seagrass extent), habitat change (barren change, seagrass change), individual shark fitness (body length, body condition, age) and population factors (nursery, number of sharks caught, proportion of age-0s). Since seagrass and coastal habitat extent vary spatially between years, interactions were fitted between habitat variables and nursery, as each nursery was expected to show a different relationship to habitat availability and change. For example, in a year where more habitat change occurred in NS, the NS nursery was expected to exhibit greater change in shark survival with barren change than in the SL nursery.

All statistical tests and analyses were conducted in R (R Core Team, 2022 v.4.2.2), using the dplyr package for pre-processing of datasets for analysis (Wickham et al., 2023) and the package glmmTMB for creation of GLMM models (Brooks et al., 2017). The

original model was first tested for normality of residuals using the simulate residuals function in the Dharma package in R (Hartig, 2022). Collinearity of model variables was then tested with the variance inflation factor (VIF) using the 'car' package (Fox & Weisberg, 2019). VIF measures multicollinearity, or the amount of collinearity one variable has with all other variables (Zuur et al., 2010). Variables are sequentially dropped based on greatest VIF, until no variable has a VIF greater than ~3, as suggested by Zuur et al. (2010) for studies where weak ecological trends may be present. The first variable to be dropped was the interaction between seagrass extent and nursery (VIF = 554) and thus seagrass extent was included without the interaction term. The next greatest VIF was found for the interaction between mangrove extent and nursery (VIF = 186) and thus this interaction was also removed so that only mangrove extent was included. Once these interactions were removed, no single variable had a VIF greater than 3, and all other variables and interactions were retained (Zuur et al., 2010). Due to the existence of clustering within the dataset of both year and shark ID, these two variables were included as random intercepts in the model (Dean & Nielsen, 2007).

3.2.7 Generalised linear mixed model – body condition

To also analyze the impacts of development on the sharks' body condition, a second GLMM, with year as a random intercept, was created. For this GLMM I used a gaussian distribution due to body condition being a continuous positive variable (McCullagh & Nelder, 1983). Body condition of age-1 sharks was used as the response variable and habitat variables (extent and change) from the year previous were used as predictors along with population factors (nursery, number of sharks caught, proportion of age-0s). As mentioned above, individual shark fitness factors, such as age and body length, were

excluded from this model. Additionally, unlike in the survival model, shark ID was not included as a random variable as each shark was only caught once as an age-1 individual and thus would only be included once in the model. Interaction terms were again included between habitat variables and nursery. The same process was followed as above for testing normality of residuals as well as collinearity amongst variables, resulting in the interaction terms being removed between nursery and mangrove and nursery and seagrass extent, as well as the proportion of age-0 sharks being removed due to a high VIF value (VIF = 4.3).

3.3. Results

3.3.1 Annual survival rate estimates

This study allowed for the calculation of annual survival rates from 1999 to 2017, based on the proportion of all sharks caught from one year to the next. Average survival rates across all years in the NS nursery from age-0 to age-1 were 0.38 +/- 0.07 with a maximum of 0.54 in 2012 and a minimum of 0.22 in 2000. Survival rates in SL for age-0 to age- 1 were 0.40 +/- 0.11 with a maximum of 0.63 in 2014 and a minimum of 0.19 in 2001. Survival rate estimates showed slightly lower estimates compared to survival rates from other studies prior to 2012 (DiBattista et al., 2007; Gruber et al., 2001; Stump, 2013) and greater variability in estimates with a larger range of values and a greater standard deviation, especially for the SL nursery (Table 3.1). During times of greatest coastal development, survival rate from age-0 to age-1 varied between the two nurseries (Fig. 3.2). In both nurseries, survival rate fluctuated from year to year between 2003 to 2007, but survival rate showed an overall positive trend in the NS, increasing from 0.35 to 0.45 with a dip in survival in 2004 during peak barren change (0.31), while survival rate initially decreased to 0.28 in 2003 from 0.60 in 2002 and then varied between 0.31 and 0.43 up to

2007 in SL. From 2015 to 2017, survival rate decreased in both nurseries: from 0.45 to 0.32 in NS and from 0.55 to 0.35 in SL.
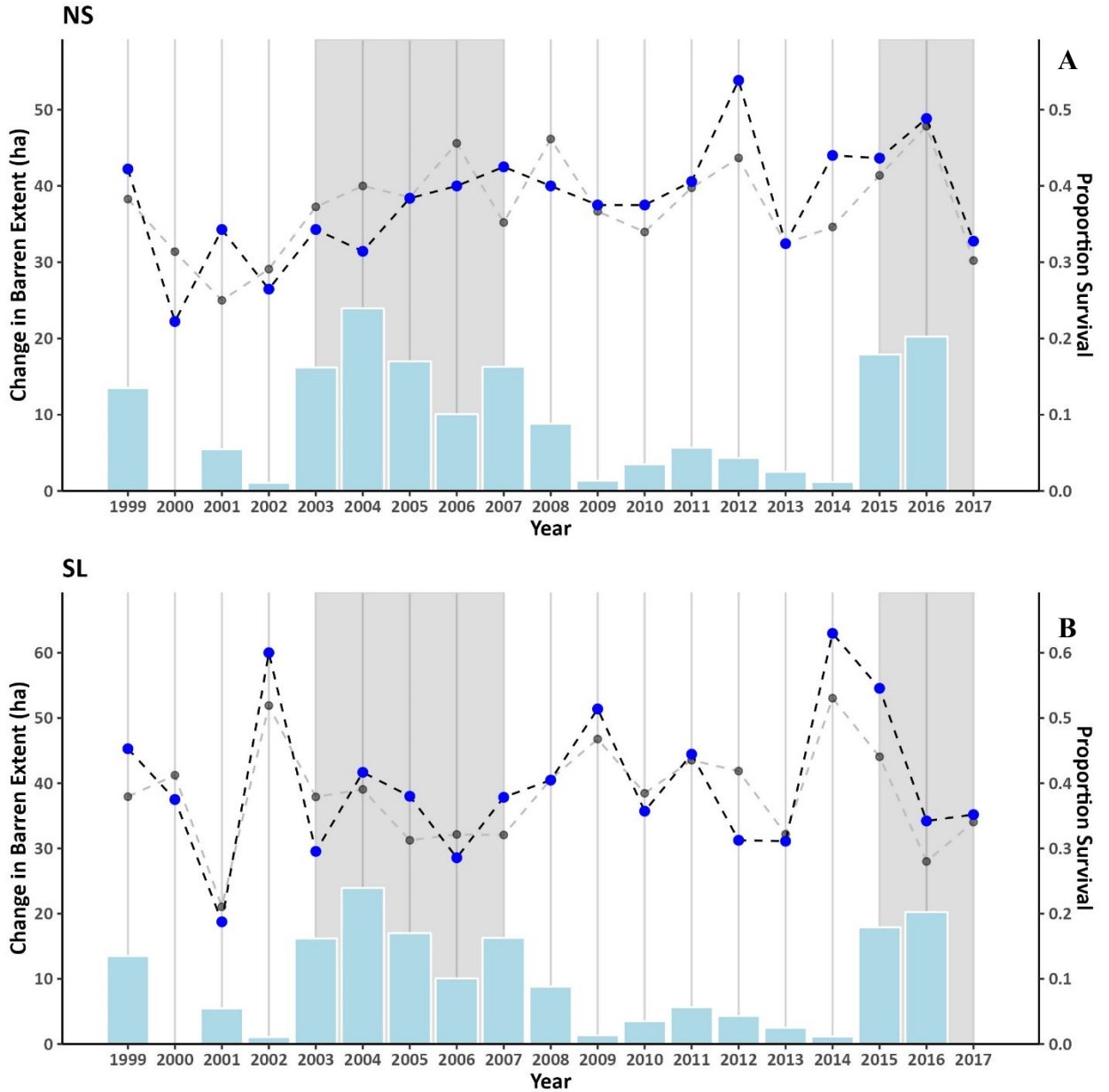
Fig. 3.2. Time-series plot of annual survival rates (proportion survival, right y-axis) for all age classes included in the model (grey dots) and survival rates for only age-0 to age-1 (blue dots) for NS (A, top) and SL (B, bottom). The amount of increase in barren extent in North Bimini from the year the sharks were caught to the following year (blue bars, left y-axis) is plotted for each year (x-axis). Grey areas highlight years of greatest coastal development.

Table 3.1. Comparison between survival rate estimates from this study to previous studies. Mean survival rate estimates are shown for age-0 to age-1 sharks in NS and SL (standard deviation in brackets) and maximum and minimum survival rate values per nursery. DiBattista et al., (2007) estimates were calculated for both nursery populations combined.

Years Assessed	NS Mean Survival (SD)	SL Mean Survival (SD)	Max – Min Annual Survival NS	Max – Min Annual Survival SL	Reference
1995 - 1999	0.52 (0.01)	NA	0.65 - 0.38	NA	Gruber et al., 2001
1995 - 2001	0.57 (0.05)		0.64 - 0.48		DiBattista et al., 2007
1995 - 2012	0.34 (0.03)	0.50 (0.02)	NA	NA	Stump, 2013
1999 - 2017	0.38 (0.07)	0.40 (0.11)	0.54 - 0.22	0.63 - 0.19	Current Study

3.3.2 Generalised linear mixed model – survival

The final GLMM for survival contained 8 fixed effects and 2 interaction terms, as well as two random intercept terms, one each for year and shark ID (Table 3.2).

Final model formula:

$$Survival_i \sim Condition_i + Body\ Length_i + Mangrove\ Extent$$
$$+\ Seagrass\ Extent + Temperature + Age_i + \#\ of\ Sharks\ Caught$$
$$+\ Prop.of\ Age0s + BarrenChange(ha) * Nursery + SGChange$$
$$* Nursery + (1|Year) + (1|SharkID)$$

The two random effects, Year and Shark ID, showed very small effects on the overall model (Odds ratios of 1.00 and 1.006, respectively, Table S4) indicating little variation in model results between years or individuals when all other variables were considered.

Overall, 5 of the 12 variables included in the model significantly affected survival: body length ($p < 0.001$), barren change ($p = 0.03$), nursery ($p < 0.001$), age ($p = 0.03$), number of sharks caught ($p = 0.04$) and the interaction between nursery and barren change ($p = 0.001$) (Table 3.2). While barren change was significant as well as the interaction between barren change and nursery, mangrove extent did not significantly affect survival ($p = 0.48$). Additionally, no significant effects were found for body condition, temperature, seagrass extent, seagrass change or proportion of age-0 sharks (p-values > 0.1, Table 3.2).

The coefficients for a GLMM fixed effects model with a binomial response are calculated in log-odds, which are not ecologically interpretable (Dunn & Smyth, 2018). Log-odds were thus transformed into odds ratios (OR) (Dunn & Smyth, 2018). For continuous variables, odds ratios report the impact that a one unit increase in a variable would have on the odds that the model would result in a positive outcome, or in this case a shark surviving. For example, if the odds ratio for barren change was reported as 1.02, an individual shark would have a 2% increased chance of survival per every hectare increase in barren change (Dunn & Smyth, 2018). On the other hand, an odds ratio was less than 1 indicates a reduced chance of survival with a one unit increase in the variable; for example, if the odds ratio was 0.98, the shark would have a 2% decreased chance of survival for every one-unit increase of the variable. For categorical variables, the odds ratios report the difference in chance of survival between one category of a variable and the 'baseline' category. Odds ratios from an interaction between a continuous and categorical variable represent the difference in the relationship between the continuous variable and the 'baseline' category and the continuous variable and the other category. Since an interaction was present between nursery and barren change, and the baseline

category for nursery was NS, the relationship between barren change and sharks born in SL was calculated by adding the log odds of the barren change variable to the log odds from the barren change and nursery interaction and subsequently converting to an odds ratio, resulting in an odds ratio of 0.982.

Of the significant variables in the model, an increase in barren change, a shark being age-1, or a shark being born in SL resulted in increased odds of survival (OR = 1.02, 1.58, 1.35 respectively), while sharks with larger body lengths, born in years with greater number of sharks caught, or sharks born in SL and in years with increased barren change, had decreased odds of survival (OR = 0.921, 0.996, 0.982) (Table 3.2). Boxplots were created to visualise the relationships of significant variables (Fig. 3.3). For the significant interaction between barren change and nursery, sharks born in NS which survived had a slightly higher mean barren change than sharks which had died, while in SL the opposite relationship was shown, though boxplots showed a high degree of overlap in both NS and SL (Fig. 3.3, left). For individual shark variables, sharks of age-1 showed much higher mean survival rates than sharks of age-0, while sharks which had survived in either age class had slightly smaller body length than sharks which had died (Fig. 3.3, right).

Table 3.2. Coefficient estimates of variables within the juvenile shark survival model (GLMM), with estimates reported as log odds and odds ratio, lower and upper 95% confidence intervals of odds ratios (LCI, UCI). Significant variables (p < 0.05) are shown in bold.

Variable	Log Odds Ratio	Std. Error	Odds Ratio	LCI Odds Ratio	UCI Odds Ratio	P-Value
Intercept	4.198	3.968	NA	NA	NA	0.290
Body Condition	-0.295	0.242	0.744	0.463	1.195	0.220
Body Length	**-0.082**	**0.019**	**0.921**	**0.887**	**0.957**	**2.13e-5**
BarrenChange	**0.019**	**0.008**	**1.019**	**1.002**	**1.035**	**0.026**
Nursery (SL)	**0.455**	**0.137**	**1.577**	**1.206**	**2.062**	**8.68e-4**
Seagrass (SG)Change	-0.001	0.002	0.999	0.994	1.004	0.792
Mangrove extent	-0.000	0.002	1.000	0.995	1.005	0.966
Seagrass extent	-0.003	0.003	0.997	0.991	1.002	0.213
Temp	0.016	0.037	1.016	0.945	1.093	0.667
Age (1)	**0.301**	**0.143**	**1.351**	**1.022**	**1.787**	**0.034**
# of Sharks Caught	**-0.004**	**0.002**	**0.996**	**0.992**	**1.000**	**0.049**
Prop. Age-0s	1.038	0.723	2.817	0.683	11.162	0.150
BarrenChange: Nursery (SL)	**-0.037**	**0.011**	**0.964**	**0.943**	**0.985**	**0.001**
Nursery SL: SGChange	-0.001	0.003	0.999	0.993	1.006	0.802
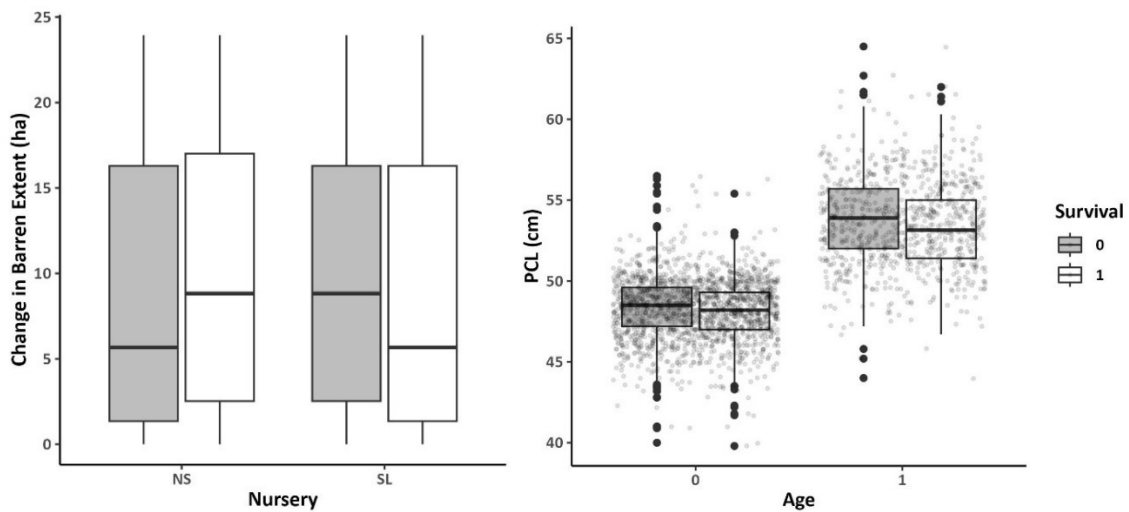
Fig. 3.3. Boxplots of variables which showed significant p-values in the survival model. On the left, the barren change during the year after a shark's capture is plotted for the NS and SL nursery and categorized into individuals which survived to the following year (1) and individuals which were never re-caught (0), with a significant interaction between barren change and nursery. On the right, body length measured at pre-caudal length (PCL)

is plotted for age-0 and age-1 sharks and again categorized into individuals which survived to the following year (1) and individuals which were never re-caught (0).

3.3.3 Generalised linear mixed model - body condition

The final model for body condition included 4 fixed effects with 2 interaction terms, and 1 random intercept term (Table 3.3).

Final model formula:

$$Condition_i \sim \ Mangrove\ Extent + Seagrass\ Extent + \ Temperature$$
$$+ \#\ of\ Sharks\ Caught + \ BarrenChange(ha) * Nursery$$
$$+ SGChange * Nursery + \ (1|Year)$$

The random effect, year, did not show large variance (5.11e-4, Table S5) in intercepts between clusters of different years, indicating a relatively small effect of years on body condition once other variables had been accounted for. Overall, two of the variables included in the model significantly affected body condition based on a nominal p-value of 0.05, and both showed a negative relationship to survival: the number of sharks caught and the interaction between seagrass change and nursery (p = 0.007 and 0.056, coefficient estimates of -9.56e-4 and -0.002, respectively, Table 3.3). In addition, seagrass extent showed a marginally non-significant and positive relationship to body condition (p = 0.065, coefficient estimate = 0.0008); Table 3.3). The remaining variables did not significantly affect body condition (p > 0.1; Table 3.3).

Table 3.3. Coefficient estimates of variables within body condition model (GLMM). Significant variables are shown in bold and marginally significant variables in grey.

Variable	Coeff. Estimate	LCI (95%)	UCI (95%)	Std. Error	P-Value
Intercept	0.598	-0.732	1.928	0.678	0.378
Seagrass Change	4.55e-4	-0.001	2.19e-4	3.44e-4	0.186
Nursery (NS)	0.013	-0.019	0.044	0.016	0.420
BarrenChange	0.002	-8.61e-4	0.005	0.001	0.170
Mangrove extent	-1.08e-4	-8.94e-4	6.76e-4	4.00e-4	0.786
Seagrass extent	8.80e-4	-5.62e-5	0.002	4.78e-4	0.065
Temp	0.002	-0.011	0.014	0.006	0.725
# Sharks Caught	**-8.33e-4**	**-0.0014**	**-2.22-4**	**3.11e-4**	**0.007**
SGChange: Nursery (NS)	-6.62e-4	-0.0013	-1.92e-5	3.47e-4	0.056
BarrenChange: Nursery (NS)	3.33e-4	-2.97e-3	0.002	0.001	0.792

Body condition was plotted against seagrass change per nursery, to further understand this interaction (Fig. 3.5), and showed that body condition decreased when seagrass extent increased more in a year (greater seagrass change) in the NS, but no relationship existed for SL (Fig. 3.5).
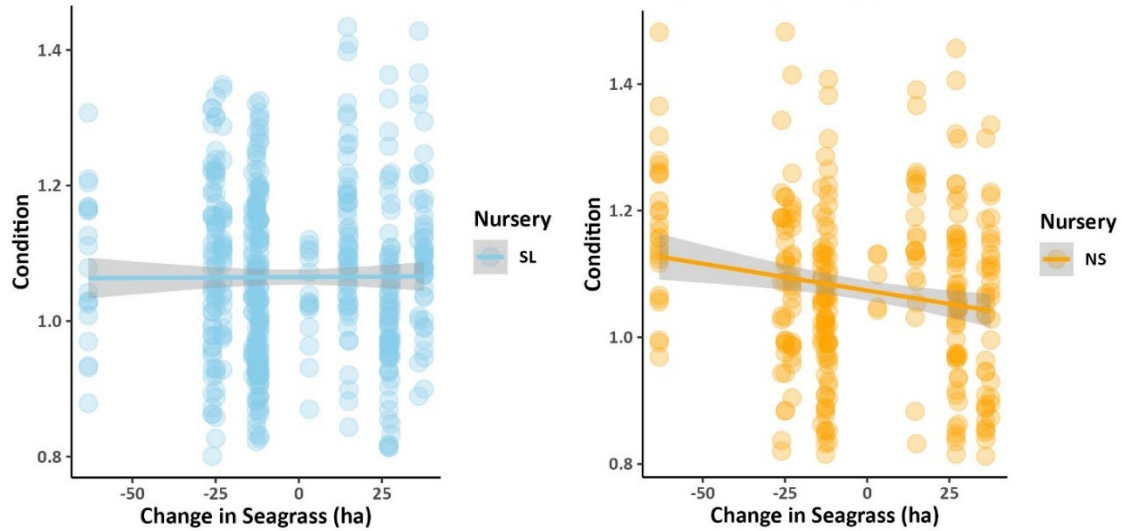
Fig. 3.5. Body condition of age-1 sharks caught in SL (left) and NS (right) nurseries compared to change in seagrass extent during the year prior to the shark's capture, with negative values indicating a decrease in seagrass extent and positive values indicating an increase in seagrass extent. Lines represent linear model lines of best fit for the relationship between condition and change in seagrass for each nursery, with 95% confidence intervals (grey shading).

3.4. Discussion

In total, 18 years of mark-recapture data of juvenile lemon sharks were analysed, resulting in estimates of individual survival from age-0 to age-1 and age-1 to age-2 for both the North Sound (NS) and Shark Land (SL) nursery areas from 1999 to 2017. During this time, extensive coastal development occurred from 2003 to 2007 and again from 2015 to 2017 (Fig. 3.2). To understand impacts of coastal development on juvenile shark survival, individual survival estimates were related to a range of abiotic and biotic variables in a binomial GLMM to determine which factors affected the probability of survival. These variables included metrics of habitat extent (mangrove and seagrass extent), habitat change (barren change, seagrass change), individual shark fitness (body length, body condition, age) and population factors (nursery, number of sharks caught, proportion of age-0 sharks).

Additionally, to understand impacts of coastal development on juvenile lemon shark fitness, individual body condition estimates from age-1 sharks were related to habitat extent, habitat change, as well as the population factors listed above. Overall, seagrass and mangrove extent did not significantly affect juvenile lemon shark survival while increased seagrass extent marginally increase body condition. However, the amount of habitat change in a year showed significant effects on both survival and body condition, with greater increases in barren extent in a year increasing survival in the NS and decreasing survival in SL while a greater increase in seagrass extent in a year decreased body condition in NS sharks and had no effect on body condition for SL sharks. Other variables also showed significant effects on survival and body condition, with survival impacted by age, nursery and body length and both survival and body condition being reduced in years when more sharks were caught. These results highlight the intricate relationship of juvenile lemon sharks to their environment, showing that habitat changes can influence survival and body condition in complex ways.

3.4.1 Lemon shark survival estimates and trends

To understand the impacts of long-term habitat change on juvenile lemon shark survival, I used a mark-recapture dataset spanning over 20 years. This dataset allowed me to estimate annual survival rates of Bimini lemon sharks in the NS and SL from 1999 up to 2017 and then match it with created habitat maps over the same time span from Chapter 2 (Fig. 2.2). During this time-span, significant changes have occurred in North Bimini. Beginning in 2004, large areas of mangrove and other coastal vegetation were removed, and sediment infilling occurred to stabilize land for construction. Beginning in 2015, more coastal vegetation was removed in the Western side of the NS nursery, along with dredging

for the extension of previously existing boating channels and subsequent creation of new islands with dredged sediment, resulting in a total loss of 46 ha of vegetation and a 103 ha increase in barren/ urban areas (Fig. 3.1, right). These two time periods of coastal vegetation removal and infilling had impacts on the adjacent marine environments, resulting in changes in seagrass extent and density (Chapter 2). When analyzing estimated lemon shark survival rates in the two nursery populations over this same period, impacts of coastal development were not as clear. Counter-intuitively, the NS population, which has been closer to the development, showed slightly increasing survival rates through time (Fig. 3.2, top). However, in 2017, survival showed a decrease from the year previous (~0.5 to ~0.3). This decrease may indicate that dredging and island creation since 2016 have resulted in a possible tipping point in habitat quality in the NS for lemon sharks, leading to future low survival rates of juveniles living in and born into this area, however, it may also be a due to natural variability in the population. In the SL nursery population, estimated survival rates showed greater variability than in the NS population from 1999 to 2004. Then beginning in 2003, when coastal development began to increase, survival rate decreased to 0.28 from 0.60 in 2002 and then varied between 0.31 and 0.43 up to 2007. By 2007 near the end of a development period, survival rates increased again. The survival rate in SL continued to show high variability between years, reaching a peak in 2014, but subsequently steadily decreased up to 2017. Based on these trends, it is possible that SL sharks showed negative response to both major development events, however high variability in survival rate between years makes this relationship difficult to disentangle (Fig 3.2., bottom).

While previous studies in Bimini using mark-recapture data have assessed annual survival rates over shorter time periods (DiBattista et al., 2007; Gruber et al., 2001) or as grouped survival rates by age, nursery, and years of disturbance (Stump, 2013) this study has calculated annual survival rates over an 18-year period from 1999 to 2017. Calculating survival rates per year has both benefits and disadvantages. On the one hand, calculating survival rate per year allows for assessment of inter-annual variability and impacts of annual environmental effects. Consequently, estimating survival rate per year may also reduce some of the robustness of survival estimates as less data is available for the calculation of each year's survival rate as compared to when survival is averaged for one age class over several years (eg. DiBattista et al., 2007; Stump et al., 2013). Additionally, variability may be introduced through differences in sampling crew, effort, timing of sampling and weather conditions from year to year. Despite this, survival rate estimates calculated in this study yielded similar magnitudes to previous studies in the two Bimini nurseries, but with slightly lower calculated averages and greater standard deviations, especially for the SL population. Average survival rates from age-0 to age-1 were 0.38 +/- 0.07 in the NS and 0.4 +/- 0.11 in SL, as compared to previous estimates of 0.34 +/- 0.03 and 0.50 +/- 0.02, respectively, as calculated by Stump (2013) from 1995-2012, or 0.57 +/- 0.05 for both nurseries as calculated by DiBattista et al. (2007) from 1995-2000 and 0.52 +/- 0.01 by Gruber et al. (2001) from 1995-1999 (Table 3.1). Survival estimates may be lower due to the longer time covered by this study, which is at least 5 years more than previous assessments (Table 3.1) and covers two periods of expansive coastal development, from 2003-2007 with removal of vegetation and dredging and from 2015-2017 with the creation of new islands in the NS (Chapter 2).

This study also estimated greater range between maximum and minimum annual survival rates in SL compared to NS and compared to previous studies. In NS, annual survival rates ranged from 0.54 to 0.22, while survival in SL varied from 0.63 to 0.19. In previous studies of annual survival rate, survival rates ranged from 0.60 to 0.38 in NS (Gruber et al., 2001) and 0.64 to 0.48 for both nurseries combined (DiBattista et al., 2007). The variability captured in this study may indicate some impacts of development, as this study contains at least 17 more years of data as compared to the studies above. This variation in survival between nurseries may also be partly due to the different sampling and recapture efficiency for these two nurseries, with SL having a greater potential for emigration due to it being less enclosed than NS (Franks, 2007). It is possible, therefore, that age-0 individuals moved out of the SL nursery to other nearby mangrove areas to the east of SL which are not included in annual sampling, especially during more recent years of high disturbance; this would result in lower recapture rates of these lemon sharks and thus reduced survival estimates as compared to studies prior to disturbance from 1995 to 2000 and compared to NS (Guttridge et al., 2012).

3.4.2 Survival model

Using a binomial GLMM approach with a range of potential abiotic and biotic variables influencing juvenile lemon shark survival, this study found that neither mangrove nor seagrass extent measured in hectares significantly impacted juvenile shark survival (p-value = 0.48) when all other variables were considered (Table 3.2). There are several possibilities as to why mangrove extent as measured in this study did not impact survival. Firstly, due to the limitations of satellite image analysis over such a long period with limited availability of ground-truthing data, vegetation extent could not be mapped to species, and

thus 'mangrove extent' is only a proxy for actual mangrove habitat and included other vegetation (Chapter 2). While we know that a large portion of mangroves was removed during vegetation removal for development, making vegetation loss an effective proxy for mangrove removal (Gruber and Parks, 2002), it is not possible to quantify the exact proportion of this calculated vegetation extent that provided juvenile lemon shark habitat before its removal. Additionally, while the entire extent of mangrove was removed from Mosquito Point during development in 2005, a large area of mangroves continues to exist in the eastern part of Bimini, known as East Wells (Fig. 3.1). This large habitat area possibly allows for lemon sharks, which have been shown to exert habitat selection, to move to more preferable areas within their nursery for protection from predators (Franks, 2007; Gruber and Morrisey, 1993b; Guttridge et al., 2012; Weatherby et al., 2007). The considerable extent of mangroves in East Wells, therefore, likely still provides adequate habitat for lemon sharks in both NS and SL.

In addition to the above, seagrass extent may also not have significantly influenced juvenile shark survival due to underlying resiliency in the population. It was hypothesized that in years with less seagrass extent, foraging ability would be impacted due to cascading trophic changes, leading to lower shark health, and ultimately decreased survival probability (Jennings et al., 2008; Newman et al., 2010). However, juvenile lemon sharks may show some resiliency to decrease in their preferred prey from loss of seagrass. Previous studies have shown that compared to sharks in the South Bimini nursery, sharks in the NS have adapted to eating a greater variety of prey species, due to lower availability of their preferred prey, mojarra spp. (*Eucinostomus spp.*), and this trend may also be true for SL (Franks, 2007; Newman et al., 2010). These baseline sub-optimal foraging

conditions may mean that development and decrease in seagrass extent did not have a great enough effect to cause survival rates varying from pre-existing conditions. It is also possible that seagrass does not play an important role in providing prey for the age classes and sizes included in this study, with the smallest and youngest sharks tending to remain close to mangrove fringes for protection from predators, meaning that loss or change in seagrass may not impact their overall survival (Hussey et al., 2017; Jennings et al., 2008). Juvenile lemon sharks have also shown some behavioural plasticity and thus may have been shifted their foraging strategies to more mangrove associated species when seagrass extent had decreased or had shifted to other available seagrass patches within their nursery (Dhellemmes et al., 2021; Hussey et al., 2017).

Interestingly, while total habitat extents did not significantly affect survival, the amount of coastal development in a year, measured as 'barren change' from year to year, or the increase in barren habitat including sediment deposition and island creation, was shown to significantly impact overall survival of juvenile lemon sharks ($p = 0.03$; Table 3.2). However, the resulting trend did not match our expected hypothesis that increased barren change in a year would result in decreased survival. In fact, in years when more barren change occurred, sharks had a slightly higher chance of survival, although to only a small extent which may not be biologically significant (1% greater chance per hectare increase; Table 3.2). As the interaction between nursery and barren change was also significant ($p < 0.001$; Table 3.2), the relationship of barren change to survival varied by nursery, with the SL population showing a negative relationship to habitat change as compared to the NS population (2% lower chance of survival per hectare increase in barren change Table 3.2; Fig. 3.3). It is important to consider the difference in size of effects

between these two relationships. The largest change in barren extent measured by satellite maps during this study was ~23 ha. Based on odds ratios calculated from the GLMM, this would result in a 23% increased chance of survival in NS, but a 46% decreased chance of survival in SL, indicating that barren change is having an overall negative impact on sharks in the Bimini lagoon, especially considering the larger number of sharks caught in SL compared to NS, an average of 97 vs.74 sharks.

There could be several reasons why sharks captured in SL had a negative relationship to changes in barren extent while NS sharks did not (Fig. 3.3). Firstly, population sizes in SL tend to be greater than NS, with an average of 74 sharks caught in NS per year and 97 caught in SL, this may indicate increased baseline competition in SL and thus decreased resilience to a possible reduction in resource availability with changes in habitat. Additionally, when evaluating survival rates over time in SL, survival decreased during years of high barren change from 2003-2007, when most development was occurring in the southwestern portion of North Bimini near Mosquito Point, but importantly also during a period of extensive channel dredging. These newly dredged channels may have allowed for greater movement of predators into the SL nursery, increasing predation (Jennings et al., 2008). However, the SL population also showed a decrease in survival from 2015 to 2017, when the greatest development occurred quite far from the SL nursery, within a well-established part of NS (Morrisey and Gruber, 1993a). Therefore, another hypothesis for a decrease in SL and not NS shark survival is that SL competition may have increased due to movement of individual sharks from the NS nursery away from development. Lemon sharks in Bimini have been shown to execute degrees of habitat selection, explicitly avoiding certain bottom types, and NS sharks have been shown

to exhibit greater exploratory behaviour while SL sharks are more often found close to shore (Dhellemmes et al., 2021; Hussey et al., 2017; Gruber and Morrisey, 1993b). It is possible that older juvenile (> age-2) sharks from NS (not included in this study due to reduced recapture rates for older individuals, DiBattista at el., 2007) shifted their distribution from the western edge of the NS nursery/ Mosquito Point to the Eastern edge of NS and even towards SL, increasing competition among sharks during years of greater development. Older juveniles up to age 5 have been caught previously in NS and SL, and older and larger juveniles will exhibit larger daily movement ranges as their risk of predation decreases, allowing them to preferentially select more suitable habitat (Franks 2007; Guttridge et al., 2012). This hypothesis is further supported by recent results from acoustic monitoring studies which show that juvenile sharks may have shifted their core use area further east towards SL as compared to previous studies (Gruber & Morrisey, 1993a; Kressler, in press).

The positive relationship of juvenile shark survival to coastal development in the NS is more perplexing, if we assume that statistical significance in this model suggests biological significance. One plausible reason for higher survival rates in NS during years of high development is the naturally occurring resource limitations in this region (Newman et al., 2007). In a resource limited habitat, it is possible that the dredging for the creation of islands between 2015 to 2017 temporarily increased available nutrients through the uplifting of buried material, which may have also resulted in greater seagrass extent and associated species serving as prey (Nayar, 2007; Chapter 2). Such a trophic cascade may provide a short-term benefit to lemon sharks through an increase in prey availability, leading to greater survival rates. However, this short-term benefit may also result in

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eutrophication and increased turbidity, eventually reducing overall productivity (Marotta et al., 2009; Windom & Stickney, 2009). Additionally, pollution from construction may introduce chemicals and other toxins which may reduce juvenile survival in the future (Gelsleichter, 2005). Such a future reduction in survival may already be evident in a 20% decrease in survival rates from 2016 (~0.5) to 2017(~0.3).

In addition to the relationships between survival and habitat change, which were the focus of this study, results from the GLMM also reflected previously assessed relationships between survival and morphological and population level variables. Firstly, survival rate was higher overall in SL than in NS. This is expected as NS is more resource limited and contains higher abiotic variability (Newman et al., 2010; Franks, 2007; Stump, 2013). Survival was also shown to be higher from age-1 to age-2 than age-0 to age-1; this reflects lemon shark's life history strategy of high number of pups with low parental care, resulting in low survival rates of juvenile sharks in the first year of birth (Manire & Gruber, 1993). Additionally, as found by DiBattista et al. (2007), larger sharks with greater body length exhibited lower survival rates, possibly due to larger individuals showing greater exploration and thus a greater risk of predation (Dhellemmes et al., 2021). Increased number of sharks caught also resulted in lower survival rates, which matched with a previous hypothesis by Morrisey and Gruber (1993a) that increased competition would decrease chance of survival in Bimini nurseries. Since competition is limiting survival in both the NS and SL, this also suggests that the habitat is resource limited, further supporting hypotheses above that influx of nutrients from dredging in NS may increase survival, or that increased competition from NS sharks moving to SL would decrease SL survival (Ward et al., 2006).

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Several other variables which were expected to impact survival were not found to be significant in the binomial survival GLMM, including temperature, proportion of age-0s and body condition. Temperature may have had minimal impact due to air temperature being used as a proxy for water temperature, and temperature data not being collected for the entire year, but rather only during the time of shark sampling, which also limited the range in temperature between years to only 6 degrees Fahrenheit (2 degrees Celsius). Water temperature has been shown to have varying effects on body condition and growth of sharks, with elevated temperature increasing metabolism but also increasing movement as more prey is needed to meet energy demands (Guttridge et al., 2012). This intricate relationship of sharks to water temperature may not be captured in changes in survival rate. Proportion of age-0s was expected to either increase survival through lower chance of predation on each individual shark when born in a larger cohort or decrease survival through increase in competition during the first year of life (Gruber et al., 2001). However, the difference in population age structures between years may not have been different enough to elicit a statistically significant relationship to survival. Finally, body condition did not impact survival probability of individuals. While past studies have found that increased condition decreased survival, these studies also found that body length of sharks may have a greater impact as faster growing individuals, regardless of weight, show a clear relationship to greater range and thus increased predation (DiBattista et al., 2007).

3.4.3 Body condition model results

Body condition is a measure of the weight to length relationship of fish, with fish exhibiting higher weight-length ratios having assumed greater fitness based on the assumption that they are better able to acquire food while limiting energy expenditure

(Tesch & Ricker, 1968). Body condition may be reduced during years of decreased prey availability or quality as well as during years of increased movement due to difficulty of finding prey or avoiding predators (Le Cren, 1951). Trophic changes in Bimini due to coastal development were expected to result in lower lemon shark prey availability, based on changes in seagrass extent found during years of high development (Chapter 2). In fact, previous studies have found that 2 years after mangrove removal from 2003 to 2007 there was lower fish species richness and a decline in mojarra spp. abundance in the NS, lemon shark's preferred prey (Newman et al., 2010; Stump, 2013). In addition to changes in prey availability, loss of mangrove refugia was expected to increase movement of sharks as they would spend more time in predator avoidance, thus causing a decrease in body condition as they use more resources in daily movement.

When using body condition as a response rather than a predictor in a Gaussian distribution GLMM, I found no significant relationship between body condition and mangrove extent, but did find a marginally significant relationship between seagrass extent and body condition, though with a small coefficient (p=0.065, Coeff =0.0008). This indicates that greater seagrass extent may indeed be related to greater prey availability. However, body condition, like survival, was also affected by habitat change, specifically the interaction between nursery and seagrass change, with a slight decrease in body condition during years of high increase in seagrass extent in the NS (p = 0.056, Coeff Est. = -0.0006, Table 3.3) but not in SL (Fig. 3.3). As discussed above, an increase in seagrass extent as measured by satellite imagery may also be an indication of increased nutrient availability, possibly reaching a point of eutrophication (Chapter 2). This may result in more prey availability, but also in deleterious health effects for lemon sharks, as prey

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quality and nutrition may decrease (de Sousa Rangel, 2020). This could be one reason why high seagrass extent would increase body condition while a large increase in extent in a year may decrease body condition; a high increase in seagrass may be an indication of algae growth or eutrophication. Additionally, in past studies of lemon shark habitat use, juvenile sharks in the NS have been shown to avoid dense seagrass areas, potentially due to the difficulty of capturing prey, meaning an increase in seagrass during a year may also hinder a lemon shark's ability to hunt and find high quality prey, especially if that increase in seagrass is due to higher nutrient levels and thus possibly higher turbidity (Brown et al., 2018; Morrisey & Gruber, 1993b). Alternatively, seagrass change could also be used as a proxy for the impacts of coastal development on aquatic habitats, as change in seagrass lagged the change in terrestrial habitat extent (Chapter 2). Considering seagrass as this proxy, NS sharks may then have a greater reduction in body condition with increase in seagrass density as they reside in closer proximity to disturbance than SL sharks (Jennings et al., 2008). This hypothesis would also match with the hypothesis above (Section 4.2) that increased development in a year resulted in increased movement of NS sharks to preferable areas, decreasing their body condition as they use more energy to move. Of course, it is important to again consider the biological significance these variables and not only the statistical significance. Both seagrass change and seagrass extent represent relatively small changes in the body condition; for example in a year with a 25 ha increase in seagrass, this would only lead to a 0.015 decrease in body condition, where as a year with 25 hectares more seagrass extent, this would to a 0.02 increase in body condition.

In addition to habitat variables, a significant relationship was found between the number of sharks caught and body condition; when more sharks were caught during

sampling in that year, body condition decreased, although marginally ($p = 0.02$, Coeff Est. $= -0.003$, Table 3.3). Increased competition for resources has been shown to decrease body condition among many shark and fish species, so my results match this expected relationship (Rueda et al., 2015; Kamimura et al., 2021; Weideli et al., 2019). Additionally, since number of sharks caught also decreased survival, this suggests that increased competition for resources may be leading to decreased body condition and decreased survival, even if body condition was not found to be a significant predictor in the survival model.

As in the survival model, temperature as measured for this study did not significantly impact body condition, possibly either because air temperature was not an effective proxy for water temperature, or the relationship between temperature and body condition may be too intricate to perceive on a population level and such a long-term analysis such as this one (Guttridge et al., 2012). Nursery was also not found to affect body condition of sharks, contrary to survival, indicating that predation pressure may be driving difference in survival between the two nurseries rather than availability of resources.

3.5. Conclusions

Through this study, coastal development since 1999 was found to significantly affect juvenile shark survival, with change in habitat in a year being more important than overall habitat availability. This may show that enough mangrove and seagrass habitat continue to exist in other areas of the Bimini lagoon, such as East Wells, to provide protection from predators and adequate foraging areas to maintain survival, but that lemon sharks are still susceptible to the secondary effects of ongoing coastal development and construction. Nutrient loading from dredging during the development from 2015 to 2017,

for example, may lead to short-term increased survival in the closer NS nursery. However, it may also lower body condition during years of high seagrass and possibly algae growth, with excess nutrient loading lowering quality of prey. On the other hand, juvenile lemon sharks in SL may experience increased competition during years of greater change due to movement of older juveniles out of the NS nursery and into SL where less development occurred.

While many questions remain in the relationship between shark survival and coastal development, this study provides a baseline for answering further questions. Some aspects of lemon shark biology could not yet be included in this analysis, such as parental genotype, and changes in genetic diversity from year to year in response to biennial birth cycles should be included as future model variables. Predator density has also been shown to be a driver in shark movements and survival (Hussey et al., 2017) and if possible, should be included in future studies of long-term survival trends. Additionally, as survival rates in 2017 were lower than both 2015 and 2016 in the NS, it is also possible that NS survival rates at the time of this study have not yet been impacted by island creation but may be as lagged effects in the future. Therefore, it would be important to continue lemon shark mark-recapture studies to assess if the continued presence of coastal development in the NS and future construction could reach a 'tipping point' in habitat viability with stronger impacts on shark survival. It is also critical to consider that even though this study did not detect strong negative impacts of seagrass and mangrove loss on shark survival, this does not mean that these habitats are not essential to long-term lemon shark survival. It is more likely that the threshold of required habitat extent is still met by other larger mangrove areas in Bimini, such as in East Wells, which is still largely untouched by development.

Since future developments are planned for East Wells, this study highlights the importance

of ongoing protection of this important habitat to ensure long-term lemon shark resilience.

Chapter 4: General Discussion

In my thesis, I created the first long-term record of annual coastal and aquatic vegetation maps for Bimini, using readily available satellite imagery. My thesis provides not only baseline information on annual habitat extent and distribution that can be used to provide context for future, or past studies, but also proves the feasibility of mapping habitat change over the long-term with the automatic adaptive signature generalisation (AASG) algorithm in Bimini. Using created habitat maps along with available long-term mark-recapture data from the Bimini Biological Field Station Foundation (BBFSF), I showed that juvenile lemon sharks (*Negaprion brevirostris*) are impacted by coastal development in both annual survival and body condition, though impacts of development vary between the two nurseries, North Sound (NS) and Shark Land (SL)

4.1 Impacts of coastal development on lemon sharks

Results of this thesis slightly contrast past studies which showed a reduction of juvenile lemon shark survival in NS post mangrove removal in 2005 (Stump, 2013). My results did not show this same reduction in NS juvenile survival, instead showing that survival in the SL population was more affected by this event and that shark survival in SL had a negative relationship to increased barren terrestrial extent (Chapter 3, Fig. 3.4). Differences between these results could be possibly due to natural inter-annual variation in NS lemon shark survival rates, which may be better accounted for in this study's longer-term dataset, at least 5 years longer than previous assessments (Stump, 2013). In studies outside of Bimini, lemon sharks have been shown to exist in relatively barren habitat with little mangrove vegetation, instead using shallow areas as protection from predators (Garla et al., 2009). It is possible, therefore, that the shallow waters in the NS provide enough

protection from predators for survival to remain relatively high even when mangroves are removed. On the other hand, SL has relatively deep water and higher predator abundance as compared to NS, resulting in SL sharks being less exploratory and staying closer to shore (Dhellemmes et al., 2021). The SL population may thus be more effected by changes in mangrove extent, as mangrove roots may be their primary protection from predation. Due to their less exploratory nature, SL sharks may also be less able to move to areas of more suitable habitat, or to move to areas with lower competition when NS sharks possibly move further south and east during years of high development. Based on satellite-derived habitat maps, the largest influx of new sediment for creation of islands occurred between 2015 and 2017 in the NS, coinciding with the last couple of years of available mark-recapture data. Survival rates in both SL and NS decreased in 2017 compared to 2015 and 2016, and so it is possible that development will have future impacts on survival which have not yet been detected. Additionally, increase in seagrass extent was related to a lower body condition for sharks pointing to possible eutrophication or algae growth during years of high 'seagrass' growth, lowering the quality of prey for lemon sharks.

4.2 Assumptions and limitations

There are some caveats to consider when using satellite imagery for mapping habitat changes. The first is the availability of ground-truthing data. For my thesis, the availability of only 1 year of *in-situ* seagrass data for the training of satellite maps (Chapter 2) meant that the variety of habitats mapped in the aquatic zone had to be limited to seagrass vs. non-seagrass areas. Other studies have reported the presence of other vegetation types in Bimini, including corals reefs, *Sargassum* and sponge beds, though these habitats exist in mostly isolated patches and were not expected to influence overall habitat changes

through time (Hussey, 2003; Pellet et al., 2015). Additionally, because satellite imagery derived maps are based on light reflectance, and free satellite imagery from Landsat satellites use large bandwidths to categorize light, some vegetation which are of similar spectral reflectance may be categorized incorrectly (Pettorelli et al., 2014). For example, in my thesis, it is possible that some areas of seagrass may instead be macroalgae. This may be possible for some areas of the NS in 2018 to 2020, where seagrass extent seemed to increase past its extent found pre-development in 1999. It is possible that dredging for boating channels introduced sediments and nutrients into the water column, increasing turbidity and nutrient availability and allowing for increased algal growth (Johansson, 2000). The created maps and the implications of coastal development on changes in seagrass beds have to be approached with some caution, as both natural variation and map inaccuracies could be leading to observed changes. However, in my thesis, timing of seagrass extent reductions in the NS closely mirror the timing of changes in terrestrial vegetation extent in North Bimini, despite aquatic and terrestrial maps being created completely independently of each other. This suggests that changes in the aquatic zone did in fact occur at least in part due to coastal deforestation, dredging and sedimentation.

In future, to further assess accuracy of habitat maps and reliability of habitat estimates, more *in-situ* aquatic habitat sampling should be performed to identify seagrass and non-seagrass areas. Additionally, since this thesis only created maps up to 2020, these maps could be updated to incorporate more recent years and allow for continued monitoring of habitat changes. Furthermore, further cross-validation could be applied to the creation of habitat maps with the AASG algorithm, similar to Wilson et al., (2020) allowing for model averaging and improving the accuracy of created maps.

Some considerations should also be made when assessing annual survival rate estimates. While calculating survival rates per year allows for investigation of impacts of annual habitat changes, accuracy of survival rate estimates may be decreased compared to those averaged over multiple years and across ages classes and nurseries as completed by DiBattista et al. (2007) and Stump (2013). Additionally, survival rates in this study do not include an estimate of sampling efficiency. To account for this limitation this study used individual survival as a response variable in the GLMM rather than annual survival rates. DiBattista et al., (2007) estimated that, at least for the NS nursery, there is a 99% chance of recapturing a shark which is alive at the time of sampling, indicating that survival estimates on an individual level should be fairly robust to a difference in re-capture rate and sampling efficiency between years. Still, my results showed greater variability of survival estimates across time as compared to previous estimates of annual survival (Gruber et al., 2001). This greater range between minimum and maximum annual survival rates is expected to be due to the longer time span of study from 1999 to 2017, which included several coastal development events. In comparison, previous annual estimates were calculated prior to the majority of habitat change in the NS and SL from 1995 to 2000, which may have resulted in more consistent survival rates. Due to the long-term nature of my study, considerations should also be made for the accuracy of body condition estimates as difference in sampling efficiency or techniques may have varied between sampling crews. However, these variations in crew should not provide a consistent reduction or increase in body condition estimates through time, as crews changed on a consistent basis.

Some challenges exist when relating spatial environmental data to species level changes across time. For my thesis, it was necessary to determine at what distance from a

shark's capture location would habitat no longer impact that shark. Ultimately, the entire seagrass extent of the Bimini lagoon was used as a predictor variable for shark survival and body condition as this would ensure that changes in seagrass extent would be adequately captured for each year. While a small spatial range of only 0.68 km^2 was previously found for juvenile sharks less than 54cm in Bimini (Morrisey & Gruber, 1993a), other studies have found large variation in exploration and space use between individual lemon sharks in Bimini, and so a larger spatial scale was used to ensure potential habitat was adequately captured (Dhellemmes et al., 2020), However, in future studies, the area of seagrass habitat used as a predictor for each individual shark could be reduced to include only the habitat present around the specific net in which the shark was captured, though this would require assessing whether the shark had remained at the same net in the following year.

It is important to consider that ecological relationships of species to their environment are extremely complex and difficult to disentangle (Thrush et al., 2005; Schlaff et al., 2014). Despite this, both body condition and survival were found to be significantly affected by habitat factors, signifying the important influence that habitat quantity and quality have on the lemon shark population of Bimini.

4.3. Scientific Contribution and Future Recommendations

While anthropogenic pressures through habitat loss are expected to be a primary driver of extinction risk for some shark species, it is often difficult to directly associate habitat loss with changes in shark survival (Dulvy et al., 2021; Sievers et al., 2019). This study is one of the first to directly relate vegetation extent and change to the survival of a coastal shark species, using AASG to map vegetated habitat extent over several decades to a high accuracy with little *in-situ* data availability. Using the AASG algorithm allows for

consistent classifications across time and comparable annual measurements of habitat extent which are essential for assessing long-term change and its impacts on local ecologies (Dannenberg et al., 2015). This thesis, therefore, provides a framework for future studies of coastal vegetation change in other locations where coastal development is occurring or has occurred in close proximity to known shark use areas. Using satellite mapping along with the AASG algorithm may be especially useful for tracking studies of coastal species, to pair species movements with vegetation presence, and could be applied with higher resolution imagery, where cost allows, for mapping of vegetation to species (Willaimson et al., 2019). By completing similar studies in other areas, the relationship between sharks and their habitat can be further elucidated to increase scientific understanding of how coastal habitat is important to shark species and what protections should be put in place to ensure future habitat viability.

4.4 Conclusion

The clear takeaway from this thesis is that coastal development is affecting the Bimini lagoon ecosystem. Since 1999, a total of 46 hectares of terrestrial vegetation, including mangroves, has been removed and 103 hectares of barren sediment/ urban development have been created. Compounding effects of vegetation removal, sediment deposition, and channel dredging resulted in clear reductions in seagrass extent and density, with seagrass extent rebounding within 2 to 5 years, but with a possible species composition change (Chapter 2). These changes in seagrass and coastal habitats are occurring in an important habitat for juvenile lemon sharks, a habitat that continues to be used for pupping by female lemon sharks which show natal philopatry to the area. While sharks continue to be born in both NS and SL, their body condition and survival is being

affected by development, with years of intensive development reducing survival in SL and a reduction in seagrass extent post development reducing body condition in both SL and NS sharks. While the NS population shows some resiliency to habitat loss, further reduction in survival may occur as some of the greatest habitat change has occurred in the NS near the end of available mark-recapture data in 2017, and NS survival rate estimates have already decreased from 2015 to 2017 (Chapter 3). It is also important to consider the large expanse of mangroves which continues to exist in East Wells. This area may provide enough habitat for continued viability of the lemon shark nursery and is also one of the only areas which has shown consistent seagrass extent since 1999, potentially providing consistent habitat for prey species (Chapter 2; Figure 2.5). Since East Wells has been slated for both further development as well as a potential marine protected area, it is important to continue to focus on this area for protection. Additionally, since continued development is expected in the NS of Bimini, it is important to apply mitigation measures, such as the effective use of silt curtains, to reduce impacts of ongoing construction. These mitigation measures have been suggested in the past (Black & Veatch, 2008) but not effectively applied based on the sedimentation which was observed during periods of dredging in this study. This one simple mitigation measure would drastically reduce impacts on adjacent seagrass beds and potentially juvenile lemon shark nurseries.

Literature Cited

Aggarwal, S. (2003). Principles of remote sensing. In *Satellite remote sensing and GIS applications in agricultural meteorology* (Vol. 23, pp. 23–28). World Meteorological Organisation. https://www.preventionweb.net/files/1682_9970.pdf#page=28

Akar, Ö., & Güngör, O. (2012). Classification of multispectral images using Random Forest algorithm (Ö. Akar, Trans.). *Journal of Geodesy and Geoinformation*, *1*(2), 139–146. https://doi.org/10.9733/jgg.241212.1t

Atwood, T. B., Connolly, R. M., Ritchie, E. G., Lovelock, C. E., Heithaus, M. R., Hays, G. C., Fourqurean, J. W., & Macreadie, P. I. (2015). Predators help protect carbon stocks in blue carbon ecosystems. In *Nature Climate Change* (Vol. 5, Issue 12, pp. 1038–1045). Nature Publishing Group. https://doi.org/10.1038/nclimate2763

Bahamas Department of Meteorology. (2020). *Climate of the Bahamas*. Bahamas Weather. http://www.bahamasweather.org.bs/

Banskota, A., Kayastha, N., Falkowski, M. J., Wulder, M. A., Froese, R. E., & White, J. C. (2014). Forest Monitoring using Landsat time series data: A review. *Canadian Journal of Remote Sensing*, *40*(5), 362–384. https://doi.org/10.1080/07038992.2014.987376

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193. https://doi.org/10.1890/10-1510.1

Barker, M. J., Gruber, S. H., Newman, S. P., & Schluessel, V. (2005). Spatial and ontogenetic variation in growth of nursery-bound juvenile lemon sharks, Negaprion brevirostris: A comparison of two age-assigning techniques. *Environmental Biology of Fishes*, *72*(3), 343–355. https://doi.org/10.1007/s10641-004-2584-3

Barley, S. C., Meekan, M. G., & Meeuwig, J. J. (2017). Species diversity, abundance, biomass, size andtrophic structure of fish on coral reefs in relation to shark abundance. *Marine Ecology Progress Series*, *565*, 163–179.

Bernardo, J. (1996). Maternal Effects in Animal Ecology1. *American Zoologist*, *36*(2), 83–105. https://doi.org/10.1093/icb/36.2.83

Black & Veatch International. (2008). *Bimini Bay project report*. http://www.depp.gov.bs/Documents/Bimini_Bay_Resort_report.pdf

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug J, Maechler M, Bolker BM (2017). Glmmtmb balances speed and Flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*. *9*(2), 378-400. doi:10.32614/RJ-2017-066.

Brown, C. J., Broadley, A., Adame, M. F., Branch, T. A., Turschwell, M. P., & Connolly, R. M. (2019). The assessment of fishery status depends on fish habitats. *Fish and Fisheries*, *20*(1), 1–14. https://doi.org/10.1111/faf.12318

Brown, E. J., Vasconcelos, R. P., Wennhage, H., Bergström, U., Støttrup, J. G., van de Wolfshaar, K., Millisenda, G., Colloca, F., & Le Pape, O. (2018). Conflicts in the coastal zone: Human impacts on commercially important fish species utilizing coastal habitat. *ICES Journal of Marine Science*, *75*(4), 1203–1213. https://doi.org/10.1093/icesjms/fsx237

Castro, J. I. (2011). *The Sharks of North America* (Illustrated edition). Oxford University Press.

Carbalo, J. (2006). Effect of natural sedimentation on the structure of tropical rocky sponge assemblages: Écoscience: Vol 13, No 1. *Ecscience*, *13*(1), 119–130. https://doi.org/10.2980/1195-6860(2006)13[119:EONSOT]2.0.CO;2

Carlson, J. K., Kroetz, Andrea, Hoover, Angie, Blake, Hamilton, Gardiner, Jayne M., & Wiley, Tonya R. (2022). *Shark nursery grounds and essential fish habitat studies: Report on 2021 field activities in the Gulf of Mexico shark pupping and nursery survey*. Southeast Fisheries Science Center (U.S.). https://repository.library.noaa.gov/view/noaa/49034

Chander, G., Markham, B. L., & Helder, D. L. (2009). Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sensing of Environment*, *113*(5), 893–903. https://doi.org/10.1016/j.rse.2009.01.007

Chapman, D. D., Babcock, E. A., Gruber, S. H., DiBattista, J. D., Franks, B. R., Kessel, S. A., Guttridge, T., Pikitch, E. K., & Feldheim, K. A. (2009). Long-term natal site-fidelity by immature lemon sharks Negaprion brevirostris at a subtropical island. *Molecular Ecology*, *18*(16), 3500–3507. https://doi.org/10.1111/j.1365-294X.2009.04289.x

Chen, N. (2020). Mapping mangrove in Dongzhaigang, China using Sentinel-2 imagery. *Journal of Applied Remote Sensing*, *14*(01), 1. https://doi.org/10.1117/1.jrs.14.014508

Cisneros-Montemayor, A. M., Barnes-Mauthe, M., Al-Abdulrazzak, D., Navarro-Holm, E., & Sumaila, U. R. (2013). Global economic value of shark ecotourism: Implications for conservation. *ORYX*, *47*(3), 381–388. https://doi.org/10.1017/S0030605312001718

Dannenberg, M. P., Hakkenberg, C. R., & Song, C. (2016). Consistent classification of landsat time series with an improved automatic adaptive signature generalization algorithm. *Remote Sensing*, *8*(8). https://doi.org/10.3390/rs8080691

Dannenberg, M. P., Song, C., Hakkenberg, C. R., & AAG, R. S. S. G. (2018). A long-term, consistent land cover history of the Southeastern United States. *Photogrammetric Engineering and Remote Sensing*, *84*(9), 559–568. Scopus. https://doi.org/10.14358/PERS.84.9.559

Darweesh, K. F., Hellal, Ahmed M., Saber, Amy A., EL-Kafrawy, Sameh B., Adbelsalam, Ali A.H., & EL-Naggar, Hussein A. (2021). Three decades of remote sensing habitat mapping, along the Egyptian Coast of Aqaba Gulf, Red Sea. *Egyptian Journal of Aquatic Biology and Fisheries*, *25*(6), 467–487. https://doi.org/10.21608/ejabf.2021.214042

de Vincenzi, G., Micarelli, P., Viola, S., Buffa, G., Sciacca, V., Maccarrone, V., Corrias, V., Reinero, F. R., Giacoma, C., & Filiciotto, F. (2021). Biological Sound vs. Anthropogenic Noise: Assessment of Behavioural Changes in Scyliorhinus canicula Exposed to Boats Noise. *Animals*, *11*(1). https://doi.org/10.3390/ani11010174

Dean, C. B., & Nielsen, J. D. (2007). Generalized linear mixed models: A review and some extensions. *Lifetime Data Analysis*, *13*(4), 497–512. https://doi.org/10.1007/s10985-007-9065-x

Dhellemmes, F., Finger, J.-S., Smukall, M. J., Gruber, S. H., Guttridge, T. L., Laskowski, K. L., & Krause, J. (2021a). Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators. *Journal of Animal Ecology*, *90*(1), 260–272. https://doi.org/10.1111/1365-2656.13283

Dhellemmes, F., Finger, J.-S., Smukall, M. J., Gruber, S. H., Guttridge, T. L., Laskowski, K. L., & Krause, J. (2021b). Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators. *Journal of Animal Ecology*, *90*(1), 260–272. https://doi.org/10.1111/1365-2656.13283

Dhellemmes, F., Smukall, M. J., Guttridge, T. L., Krause, J., & Hussey, N. E. (2021). Predator abundance drives the association between exploratory personality and foraging habitat risk in a wild marine meso-predator. *Functional Ecology*, *35*(9), 1972–1984. https://doi.org/10.1111/1365-2435.13874

Dibattista, J. D., Feldheim, K. A., Gruber, S. H., & Hendry, A. P. (2007). When bigger is not better: Selection against large size, high condition and fast growth in juvenile lemon sharks. *Journal of Evolutionary Biology*, *20*(1), 201–212. https://doi.org/10.1111/j.1420-9101.2006.01210.x

Diehl, S. (1992). Fish Predation and benthic community structure: The role of omnivory and habitat complexity. *Ecology*, *73*(5), 1646–1661. https://doi.org/10.2307/1940017

Dogan, O. K., Akyurek, Z., & Beklioglu, M. (2009). Identification and mapping of submerged plants in a shallow lake using quickbird satellite data. *Journal of Environmental Management*, *90*, 2138–2143.

Donato, D. C., Kauffman, J. B., Murdiyarso, D., Kurnianto, S., Stidham, M., & Kanninen, M. (2011). Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, *4*(5), Article 5. https://doi.org/10.1038/ngeo1123

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci, B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, K. B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., … Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, *31*(21), 4773-4787.e8. https://doi.org/10.1016/j.cub.2021.08.062

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LN, Fordham SV, Francis MP, Pollock CM, Simpfendorfer CA, Burgess GH, Carpenter KE, Compagno LJ, Ebert DA, Gibson C, Heupel MR, Livingstone SR, … White WT. (2014). Extinction risk and conservation of the world's sharks and rays—PubMed. *Elife*, *3*. https://pubmed.ncbi.nlm.nih.gov/24448405/

Dunn, P. K., & Smyth, G. K. (2018). Chapter 9: Models for Proportions: Binomial GLMs. In P. K. Dunn & G. K. Smyth (Eds.), *Generalized Linear Models With Examples in R* (pp. 333–369). Springer. https://doi.org/10.1007/978-1-4419-0118-7_9

Durako, M., Hall, M., & Merello, M. (2001). *Patterns of change in the seagrass-dominated Florida Bay hydroscape*. https://doi.org/10.1201/9781420039412-23

Edrén, S. M. C., & Gruber, S. H. (2005). Homing ability of young lemon sharks, Negaprion brevirostris. *Environmental Biology of Fishes*, *72*(3), 267–281. https://doi.org/10.1007/s10641-004-2583-4

Ellegaard, M., Nguyen, N. T. G., Andersen, T. J., Michelsen, A., Nguyen, N. L., Doan, N. H., Kristensen, E., Weckström, K., Son, T. P. H., & Lund-Hansen, L. C. (2014). Temporal changes in physical, chemical and biological sediment parameters in a tropical estuary after mangrove deforestation. *Estuarine, Coastal and Shelf Science*, *142*, 32–40. https://doi.org/10.1016/j.ecss.2014.03.007

Erftemeijer, P. L. A., Semesi, A. K., & Ochieng, C. A. (2001). Challenges for marine botanical research in East Africa: Results of a bibliometric survey. *South African Journal of Botany*, *67*(3), 411–419. https://doi.org/10.1016/S0254-6299(15)31157-1

Esri Inc. (2020). *ArcGIS Pro* (2.7.0) [Computer software]. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview

European Space Agency. (2021). *Sentinel Applications Platform (SNAP)* (8.0.9) [Computer software]. European Space Agency.

Feldheim, K. A., Gruber, S. H., & Ashley, M. V. (2002). The breeding biology of lemon sharks at a tropical nursery lagoon. *Proceedings of the Royal Society B: Biological Sciences*, *269*(1501), 1655–1661. https://doi.org/10.1098/rspb.2002.2051

Feldheim, K. A., Gruber, S. H., DiBattista, J. D., Babcock, E. A., Kessel, S. T., Hendry, A. P., Pikitch, E. K., Ashley, M. V., & Chapman, D. D. (2014). Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. *Molecular Ecology*, *23*(1), 110–117. https://doi.org/10.1111/mec.12583

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, *13*(8), 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x

Field, I. C., Meekan, M. G., Buckworth, R. C., & Bradshaw, C. J. A. (2009). Susceptibility of sharks, rays and chimaeras to global extinction. In *Advances in Marine Biology* (Vol. 56, pp. 275–363). Academic Press. https://doi.org/10.1016/S0065-2881(09)56004-X

Fourqurean, J. W., Willsie, A., Rose, C. D., & Rutten, L. M. (2001). Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology*, *138*(2), 341–354. https://doi.org/10.1007/s002270000448

Fox J, Weisberg S (2019). An R companion to applied regression. Third Edition. *Sage,* Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Franks, B. (2007). The spatial ecology and resource selection of juvenile Lemon sharks (Negaprion brevirostris) in their primary nursery areas. *Drexel* University

Fraser, M. W., Short, J., Kendrick, G., McLean, D., Keesing, J., Byrne, M., Caley, M. J., Clarke, D., Davis, A. R., Erftemeijer, P. L. A., Field, S., Gustin-Craig, S., Huisman, J., Keough, M., Lavery, P. S., Masini, R., McMahon, K., Mengersen, K., Rasheed, M., … Wu, P. (2017). Effects of dredging on critical ecological processes for marine invertebrates, seagrasses and macroalgae, and the potential for management with environmental windows using Western Australia as a case study. *Ecological Indicators*, *78*, 229–242. https://doi.org/10.1016/j.ecolind.2017.03.026

Fuentes, M. M. P. B., Gillis, A. J., Ceriani, S. A., Guttridge, T. L., Van Zinnicq Bergmann, M. P. M., Smukall, M., Gruber, S. H., & Wildermann, N. (2019). Informing marine protected areas in Bimini, Bahamas by considering hotspots for green turtles (Chelonia mydas). *Biodiversity and Conservation*, *28*(1), 197–211. https://doi.org/10.1007/s10531-018-1647-2

Garla, R. C., Garcia, J., Veras, L. B., & Lopes, N. P. (2009). Fernando de Noronha as an insular nursery area for lemon sharks, Negaprion brevirostris, and nurse sharks, Ginglymostoma cirratum, in the equatorial western Atlantic Ocean. *Marine Biodiversity Records*, *2*, e109. https://doi.org/10.1017/S1755267209000670

Gelsleichter, J., Manire, C. A., Szabo, N. J., Cortés, E., Carlson, J., & Lombardi-Carlson, L. (2005). Organochlorine concentrations in bonnethead sharks (Sphyrna tiburo) from four Florida estuaries. *Archives of Environmental Contamination and Toxicology*, *48*(4), 474–483. https://doi.org/10.1007/s00244-003-0275-2

Gruber, S. H., & Parks, W. (2002). Mega-Resort Development on Bimini: Sound Economics or Environmental Disaster. *Bahamas Journal of Science*, *9*(2), 2–18.

Gruber, S. H., de Marignac, J. R. C., & Hoenig, J. M. (2001). Survival of Juvenile Lemon Sharks at Bimini, Bahamas, Estimated by Mark–Depletion Experiments. *Transactions of the American Fisheries Society*, *130*(3), 376–384. https://doi.org/10.1577/1548-8659(2001)130<0376:SOJLSA>2.0.CO;2

Gupta, K., Mukhopadhyay, A., Giri, S., Chanda, A., Datta Majumdar, S., Samanta, S., Mitra, D., Samal, R. N., Pattnaik, A. K., & Hazra, S. (2018). An index for discrimination of mangroves from non-mangroves using Landsat 8 OLI imagery. *MethodsX*, *5*, 1129–1139. https://doi.org/10.1016/j.mex.2018.09.011

Guttridge, T. L., Gruber, S. H., DiBattista, J. D., Feldheim, K. A., Croft, D. P., Krause, S., & Krause, J. (2011). Assortative interactions and leadership in a free-ranging population of juvenile lemon shark Negaprion brevirostris. *Marine Ecology Progress Series*, *423*, 235–245. https://doi.org/10.3354/meps08929

Guttridge, T., Gruber, S., Franks, B., Kessel, S., Gledhill, K., Uphill, J., Krause, J., & Sims, D. (2012a). Deep danger: Intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks Negaprion brevirostris. *Marine Ecology Progress Series*, *445*, 279–291. https://doi.org/10.3354/meps09423

Ha, N. T., Manley-Harris, M., Pham, T. D., & Hawes, I. (2020). A Comparative assessment of ensemble-based machine learning and maximum likelihood methods for mapping seagrass using sentinel-2 imagery in tauranga harbor, New Zealand. *Remote Sensing*, *12*(3), Article 3. https://doi.org/10.3390/rs12030355

Hakkenberg, C. R., Dannenberg, M. P., Song, C., & Vinci, G. (2020). Automated Continuous Fields Prediction from Landsat Time Series: Application to Fractional Impervious Cover. *IEEE Geoscience and Remote Sensing Letters*, *17*(1), 132–136. Scopus. https://doi.org/10.1109/LGRS.2019.2915320

Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., Gallagher, A. J., Irschick, D. J., Skubel, R., & Cooke, S. J. (2019). Ecosystem Function and Services of Aquatic Predators in the Anthropocene. In *Trends in Ecology and Evolution* (Vol. 34, Issue 4, pp. 369–383). Elsevier Ltd. https://doi.org/10.1016/j.tree.2019.01.005

Hansell, A. C., Curtis, T. H., Carlson, J., Cortés, E., Fay, G., & Cadrin, S. X. (2021). Stock Assessment of the Lemon Shark off the Southeast United States. *North American Journal of Fisheries Management*, *41*(1), 35–48. https://doi.org/10.1002/nafm.10518

Hansen, M. C., & Loveland, T. R. (2012). A review of large area monitoring of land cover change using Landsat data. *Remote Sensing of Environment*, *122*, 66–74. https://doi.org/10.1016/j.rse.2011.08.024

Hartig F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6. https://CRAN.Rproject.org/package=DHARMa.

Henseler, C., Nordström, M. C., Törnroos, A., Snickars, M., Pecuchet, L., Lindegren, M., & Bonsdorff, E. (2019). Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach. *Estuarine, Coastal and Shelf Science*, *226*, 106272. https://doi.org/10.1016/j.ecss.2019.106272

Heupel, M. R., Carlson, J. K., & Simpfendorfer, C. A. (2007). Shark nursery areas: Concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, *337*, 287–297. https://doi.org/10.3354/meps337287

Hussey, N. E., DiBattista, J. D., Moore, J. W., Ward, E. J., Fisk, A. T., Kessel, S., Guttridge, T. L., Feldheim, K. A., Franks, B. R., Gruber, S. H., Weideli, O. C., & Chapman, D. D. (2017). Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1852), 20170166. https://doi.org/10.1098/rspb.2017.0166

Hussey, N.R. (2003). *An evaluation of Landsat 7 ETM+ satellite imagery for quantitative biotope mapping of the Bimini islands, Bahamas including two known lemon shark (Negaprion brevirostris) nursery grounds.* [MSc]. University of Wales.

Huxham, M., Whitlock, D., Githaiga, M., & Dencer-Brown, A. (2018). Carbon in the coastal seascape: How interactions between mangrove forests, seagrass meadows and tidal marshes influence carbon storage. *Current Forestry Reports*, *4*(2), 101–110. https://doi.org/10.1007/s40725-018-0077-4

Irons, J. R., Dwyer, J. L., & Barsi, J. A. (2012). The next Landsat satellite: The landsat data continuity mission. *Remote Sensing of Environment*, *122*, 11–21. https://doi.org/10.1016/j.rse.2011.08.026

Jennings, D. E., DiBattista, J. D., Stump, K. L., Hussey, N. E., Franks, B. R., Grubbs, R. D., & Gruber, S. H. (2012). Assessment of the aquatic biodiversity of a threatened coastal lagoon at Bimini, Bahamas. *Journal of Coastal Conservation*, *16*(3), 405–428. https://doi.org/10.1007/s11852-012-0211-6

Jennings, D. E., Gruber, S. H., Franks, B. R., Kessel, S. T., & Robertson, A. L. (2008a). Effects of large-scale anthropogenic development on juvenile lemon shark (Negaprion brevirostris) populations of Bimini, Bahamas. *Environmental Biology of Fishes*, *83*(4), 369–377. https://doi.org/10.1007/s10641-008-9357-3

Johansson, J. O. R. (2000). Historical overview of Tampa Bay water quality and seagrass: Issues and trends. *Seagrass Management: It's Not Just Nutrients Proceedings of a Symposium St. Petersburg, Florida*, 1.

Kamimura, Y., Taga, M., Yukami, R., Watanabe, C., & Furuichi, S. (2021). Intra- and inter-specific density dependence of body condition, growth, and habitat temperature in chub mackerel (Scomber japonicus). *ICES Journal of Marine Science*, *78*(9), 3254–3264. https://doi.org/10.1093/icesjms/fsab191

Kauffman, J. B., Adame, M. F., Arifanti, V. B., Schile-Beers, L. M., Bernardino, A. F., Bhomia, R. K., Donato, D. C., Feller, I. C., Ferreira, T. O., Jesus Garcia, M. del C., MacKenzie, R. A., Megonigal, J. P., Murdiyarso, D., Simpson, L., & Hernández Trejo, H. (2020). Total ecosystem carbon stocks of mangroves across broad global environmental and physical gradients. *Ecological Monographs*, *90*(2), e01405. https://doi.org/10.1002/ecm.1405

Kemp, W. M., Boynton, W. R., Adolf, J. E., Boesch, D. F., Boicourt, W. C., Brush, G., Cornwell, J. C., Fisher, T. R., Glibert, P. M., Hagy, J. D., Harding, L. W., Houde, E. D., Kimmel, D. G., Miller, W. D., Newell, R. I. E., Roman, M. R., Smith, E. M., & Stevenson, J. C. (2005). Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. *Marine Ecology Progress Series*, *303*, 1–29. https://doi.org/10.3354/meps303001

Kessel, Steve T. (2004). *Spatial Variations in nursery bound juvenile lemon shark (Negaprion brevoristris) prey items, Bimini, Bahamas.* [BSc]. Cardiff University.

Kilminster, K., McMahon, K., Waycott, M., Kendrick, G. A., Scanes, P., McKenzie, L., O'Brien, K. R., Lyons, M., Ferguson, A., Maxwell, P., Glasby, T., & Udy, J. (2015). Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of The Total Environment*, *534*, 97–109. https://doi.org/10.1016/j.scitotenv.2015.04.061

Kinney, M. J., & Simpfendorfer, C. A. (2009). Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters*, *2*(2), 53–60. https://doi.org/10.1111/j.1755-263X.2008.00046.x

Klemas, V. V. (2016). Remote sensing of submerged aquatic vegetation. In C. W. Finkl & C. Makowski (Eds.), *Seafloor Mapping along Continental Shelves: Research and Techniques for Visualizing Benthic Environments* (pp. 125–140). Springer International Publishing. https://doi.org/10.1007/978-3-319-25121-9_5

Kuhn, M. (2008). Building Predictive Models in R Using the caret Package. *Journal of Statistical Software*, *28*, 1–26. https://doi.org/10.18637/jss.v028.i05

Le Cren, E. D. (1951). The Length-Weight Relationship and Seasonal Cycle in Gonad Weight and Condition in the Perch (Perca fluviatilis). *Journal of Animal Ecology*, *20*(2), 201–219. https://doi.org/10.2307/1540

Leblanc, M.-L., LaRocque, A., Leblon, B., Hanson, A., & Humphries, M. M. (2021). Using Landsat Time-Series to monitor and inform seagrass dynamics: A case study in the Tabusintac estuary, New Brunswick, Canada. *Canadian Journal of Remote Sensing*, *47*(1), 65–82. https://doi.org/10.1080/07038992.2021.1893672

Lewis, R.R., (1976). Impact of dredging in the Tampa Bay estuary, 1876-1976. Presented at the time-stressed coastal environments: assessment and future action, the coastal society, Arlington, Virginia, pp. 31–55.

Liang, H., Wang, L., Wang, S., Sun, D., Li, J., Xu, Y., & Zhang, H. (2023). Remote sensing detection of seagrass distribution in a marine lagoon (Swan Lake), China. *Optics Express*, *31*(17), 27677. https://doi.org/10.1364/OE.498901

Lyons, M. B., Phinn, S. R., & Roelfsema, C. M. (2012). Long term land cover and seagrass mapping using Landsat and object-based image analysis from 1972 to 2010 in the coastal environment of South East Queensland, Australia. *ISPRS Journal of Photogrammetry and Remote Sensing*, *71*, 34–46. https://doi.org/10.1016/j.isprsjprs.2012.05.002

Lyzenga, D. R. (1978). Passive remote sensing techniques for mapping water depth and bottom features. *Applied Optics*, *17*(3), 379–383. https://doi.org/10.1364/AO.17.000379

Manire, C. A., & Gruber, S. H. (1993). A preliminary estimate of natural mortality of age-0 lemon sharks, Negaprion brevirostris. *NOAA Technical Report NMFS*, *115*, 65–71.

Marbà, N., Arias-Ortiz, A., Masqué, P., Kendrick, G. A., Mazarrasa, I., Bastyan, G. R., Garcia-Orellana, J., & Duarte, C. M. (2015). Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. *Journal of Ecology*, *103*(2), 296–302. https://doi.org/10.1111/1365-2745.12370

Marotta, H., Bento, L., Esteves, F. de A., & Enrich-Prast, A. (2009). Whole Ecosystem Evidence of Eutrophication Enhancement by Wetland Dredging in a Shallow Tropical Lake. *Estuaries and Coasts*, *32*(4), 654–660. https://doi.org/10.1007/s12237-009-9152-1

Masek, J. G., Wulder, M. A., Markham, B., McCorkel, J., Crawford, C. J., Storey, J., & Jenstrom, D. T. (2020). Landsat 9: Empowering open science and applications through continuity. *Remote Sensing of Environment*, *248*, 111968. https://doi.org/10.1016/j.rse.2020.111968

Maxar. (2022). *World Imagery* [Map]. Esri. https://www.arcgis.com/apps/mapviewer/index.html?webmap=c03a526d94704bfb839445e80de95495

McCullagh P, Nelder JA (1989). Generalized linear models. Chapman & Hall Ltd

McHugh, M. L. (2012). Interrater reliability: The kappa statistic. *Biochemia Medica*, *22*(3), 276–282.

Mcleod, E., Chmura, G., Bouillon, S., Salm, R., Björk, M., Duarte, C., Lovelock, C., Schlesinger, W., & Silliman, B. (2011). A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Frontiers in Ecology and the Environment*, *9*. https://doi.org/10.1890/110004

Morrissey, J. F., & Gruber, S. H. (1993a). Habitat selection by juvenile lemon sharks,Negaprion brevirostris. *Environmental Biology of Fishes*, *38*(4), 311–319. https://doi.org/10.1007/BF00007524

Morrissey, J. F., & Gruber, S. H. (1993b). Home range of juvenile lemon sharks, Negaprion brevirostris. *Copeia*, *1993*(2), 425–434. JSTOR. https://doi.org/10.2307/1447141

Murchie, K. J., Schwager, E., Cooke, S. J., Danylchuk, A. J., Danylchuk, S. E., Goldberg, T. L., Suski, C. D., & Philipp, D. P. (2010). Spatial ecology of juvenile lemon sharks (Negaprion brevirostris) in tidal creeks and coastal waters of Eleuthera, The Bahamas. *Environmental Biology of Fishes*, *89*(1), 95–104. https://doi.org/10.1007/s10641-010-9693-y

Murdiyarso, D., Purbopuspito, J., Kauffman, J. B., Warren, M. W., Sasmito, S. D., Donato, D. C., Manuri, S., Krisnawati, H., Taberima, S., & Kurnianto, S. (2015). The potential of Indonesian mangrove forests for global climate change mitigation. *Nature Climate Change*, *5*(12), Article 12. https://doi.org/10.1038/nclimate2734

National Oceanic and Atmospheric Administration (NOAA). (2005). *NOS Scanned Bathymetric & Fishing Map: Bimini* [dataset]. https://www.ngdc.noaa.gov/mgg/bathymetry/maps/finals/NG_17-9/

National Oceanic and Atmospheric Administration (NOAA). (2023). *Tide Predictions: TEC4617 North Bimini*. NOAA Tides and Currents. https://tidesandcurrents.noaa.gov/noaatidepredictions.html?id=TEC4617&units= metric&bdate=20200204&edate=20200226&timezone=LST/LDT&clock=24hour &datum=MLLW&interval=hilo&action=data

Nayar, S., Miller, D. J., Hunt, A., Goh, B. P. L., & Chou, L. M. (2007). Environmental effects of dredging on sediment nutrients, carbon and granulometry in a tropical estuary. *Environmental Monitoring and Assessment*, *127*(1), 1–13. https://doi.org/10.1007/s10661-006-9253-2

Newman, S. P., Handy, R. D., & Gruber, S. H. (2007). Spatial and temporal variations in mangrove and seagrass faunal communities at Bimini, Bahamas. *Bulletin of Marine Science*, *80*(3), 529–553.

Newman, S. P., Handy, R. D., & Gruber, S. H. (2010). Diet and prey preference of juvenile lemon sharks Negaprion brevirostris. *Marine Ecology Progress Series*, *398*, 221–234. https://doi.org/10.3354/meps08334

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., & Williams, S. L. (2006). A global crisis for seagrass ecosystems. *BioScience*, *56*(12), 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Palandro, D. A., Andréfouët, S., Hu, C., Hallock, P., Müller-Karger, F. E., Dustan, P., Callahan, M. K., Kranenburg, C., & Beaver, C. R. (2008). Quantification of two decades of shallow-water coral reef habitat decline in the Florida Keys National Marine Sanctuary using Landsat data (1984–2002). *Remote Sensing of Environment*, *112*(8), 3388–3399. https://doi.org/10.1016/j.rse.2008.02.015

Pellet, Jerome. (2015). *Bimini Islands Habitat Classification*. N+P.

Pettorelli, N., Laurance, W. F., O'Brien, T. G., Wegmann, M., Nagendra, H., & Turner, W. (2014). Satellite remote sensing for applied ecologists: Opportunities and challenges. *Journal of Applied Ecology*, *51*(4), 839–848. https://doi.org/10.1111/1365-2664.12261

Poursanidis, D., Traganos, D., Teixeira, L., Shapiro, A., & Muaves, L. (2021). Cloud-native seascape mapping of Mozambique's Quirimbas National Park with Sentinel-2. *Remote Sensing in Ecology and Conservation*, *7*(2), 275–291. https://doi.org/10.1002/rse2.187

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/

Rangel, B. de S., Hammerschlag, N., & Moreira, R. G. (2021). Urban living influences the nutritional quality of a juvenile shark species. *Science of The Total Environment*, *776*, 146025. https://doi.org/10.1016/j.scitotenv.2021.146025

Rasher, D. B., Hoey, A. S., & Hay, M. E. (2017). Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports*, *7*(15684), 1–10. https://doi.org/10.1038/s41598-017-15679-w

Rose, R. A., Byler, D., Eastman, J. R., Fleishman, E., Geller, G., Goetz, S., Guild, L., Hamilton, H., Hansen, M., Headley, R., Hewson, J., Horning, N., Kaplin, B. A., Laporte, N., Leidner, A., Leimgruber, P., Morisette, J., Musinsky, J., Pintea, L., … Wilson, C. (2015). Ten ways remote sensing can contribute to conservation. *Conservation Biology*, *29*(2), 350–359. https://doi.org/10.1111/cobi.12397

Rueda, L., Massutí, E., Alvarez-Berastegui, D., & Hidalgo, M. (2015). Effect of intra-specific competition, surface chlorophyll and fishing on spatial variation of gadoid's body condition. *Ecosphere*, *6*(10), art175. https://doi.org/10.1890/ES15-00087.1

Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2014). Influence of environmental factors on shark and ray movement, behaviour and habitat use: A review. *Reviews in Fish Biology and Fisheries*, *24*(4), 1089–1103. https://doi.org/10.1007/s11160-014-9364-8

Seitz, R. D., Wennhage, H., Bergström, U., Lipcius, R. N., & Ysebaert, T. (2014). Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science*, *71*(3), 648–665. https://doi.org/10.1093/icesjms/fst152

Serrano, O., Lovelock, C. E., B. Atwood, T., Macreadie, P. I., Canto, R., Phinn, S., Arias-Ortiz, A., Bai, L., Baldock, J., Bedulli, C., Carnell, P., Connolly, R. M., Donaldson, P., Esteban, A., Ewers Lewis, C. J., Eyre, B. D., Hayes, M. A., Horwitz, P., Hutley, L. B., … Duarte, C. M. (2019). Australian vegetated coastal ecosystems as global hotspots for climate change mitigation. *Nature Communications*, *10*(1), Article 1. https://doi.org/10.1038/s41467-019-12176-8

Short, F., & Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environmental Conservation*, *23*, 17–27. https://doi.org/10.1017/S0376892900038212

Sievers, M., Brown, C. J., Tulloch, V. J. D., Pearson, R. M., Haig, J. A., Turschwell, M. P., & Connolly, R. M. (2019). The Role of Vegetated Coastal Wetlands for Marine Megafauna Conservation. In *Trends in Ecology and Evolution* (Vol. 34, Issue 9, pp. 807–817). Elsevier Ltd. https://doi.org/10.1016/j.tree.2019.04.004

Silva, T. S. F., Costa, M. P. F., Melack, J. M., & Novo, E. M. L. M. (2008). Remote sensing of aquatic vegetation: Theory and applications. *Environmental Monitoring and Assessment*, *140*(1), 131–145. https://doi.org/10.1007/s10661-007-9855-3

Stump, K. L. (2013). *The Effects of Nursery Habitat Loss on Juvenile Lemon Sharks, Negaprion brevirostris* [PhD Thesis, University of Miami]. https://www.proquest.com/docview/1442548402?pq-origsite=gscholar&fromopenview=true

Tesch, FW & Ricker, WE. (1968). Methods for assessment of fish production in fresh waters. *Blackwell Scientific*, 93–123.

The Weather Company. (2024). *Bailey Town, Bimini, The Bahamas Weather History*. Weather Underground. https://www.wunderground.com/history/daily/bs/alice-town/MYBS

Thrush, S. F., Hewitt, J. E., Herman, P. M. J., & Ysebaert, T. (2005). Multi-scale analysis of species–environment relationships. *Marine Ecology Progress Series*, *302*, 13–26. https://doi.org/10.3354/meps302013

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Topouzelis, K., Makri, D., Stoupas, N., Papakonstantinou, A., & Katsanevakis, S. (2018). Seagrass mapping in Greek territorial waters using Landsat-8 satellite images. *International Journal of Applied Earth Observation and Geoinformation*, *67*(October 2017), 98–113. https://doi.org/10.1016/j.jag.2017.12.013

Turekian, K. K., & Newell, N. D. (1957). Salinity variations in sea water in the vicinity of Bimini, Bahamas, British West Indies. *American Museum of Natural History*, *1822*. http://hdl.handle.net/2246/4701

Tussenbroek, B. I. van, Cortés, J., Collin, R., Fonseca, A. C., Gayle, P. M. H., Guzmán, H. M., Jácome, G. E., Juman, R., Koltes, K. H., Oxenford, H. A., Rodríguez-Ramirez, A., Samper-Villarreal, J., Smith, S. R., Tschirky, J. J., & Weil, E. (2014). Caribbean-wide, long-term study of seagrass beds reveals local variations, shifts in community structure and occasional collapse. *PLOS ONE*, *9*(3), e90600. https://doi.org/10.1371/journal.pone.0090600

USGS. (2022). *Earth Explorer*. https://earthexplorer.usgs.gov/

Valiela, I., Bowen, J. L., & York, J. K. (2001). Mangrove Forests: One of the World's Threatened Major Tropical Environments. *BioScience*, *51*(10), 807–815. https://doi.org/10.1641/0006-3568(2001)051[0807:MFOOTW]2.0.CO;2

Wang, D., Wan, B., Qiu, P., Su, Y., Guo, Q., Wang, R., Sun, F., & Wu, X. (2018). Evaluating the performance of Sentinel-2, Landsat 8 and Pléiades-1 in mapping mangrove extent and species. *Remote Sensing*, *10*(9), Article 9. https://doi.org/10.3390/rs10091468

Ward, A. J. W., Webster, M. M., & Hart, P. J. B. (2006). Intraspecific food competition in fishes. *Fish and Fisheries*, *7*(4), 231–261. https://doi.org/10.1111/j.1467-2979.2006.00224.x

Ward-Paige, C. A., & Worm, B. (2017). Global evaluation of shark sanctuaries. *Global Environmental Change*, *47*, 174–189. https://doi.org/10.1016/j.gloenvcha.2017.09.005

Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, *106*(30), 12377–12381. https://doi.org/10.1073/pnas.0905620106

Weideli, O. C., Bouyoucos, I. A., Papastamatiou, Y. P., Mescam, G., Rummer, J. L., & Planes, S. (2019). Same species, different prerequisites: Investigating body condition and foraging success in young reef sharks between an atoll and an island system. *Scientific Reports*, *9*(1), 13447. https://doi.org/10.1038/s41598-019-49761-2

Weideli, O. C., Papastamatiou, Y. P., & Planes, S. (2019). Size frequency, dispersal distances and variable growth rates of young sharks in a multi-species aggregation. *Journal of Fish Biology*, *94*(5), 789–797. https://doi.org/10.1111/jfb.13968

Wetherbee, B. M., Gruber, S. H., & Rosa, R. S. (2007). Movement patterns of juvenile lemon sharks Negaprion brevirostris within Atol das Rocas, Brazil: A nursery characterized by tidal extremes. *Marine Ecology Progress Series*, *343*, 283–293. https://doi.org/10.3354/meps06920

Wheeler, C. R., Gervais, C. R., Johnson, M. S., Vance, S., Rosa, R., Mandelman, J. W., & Rummer, J. L. (2020). Anthropogenic stressors influence reproduction and development in elasmobranch fishes. *Reviews in Fish Biology and Fisheries*, *30*(2), 373–386. https://doi.org/10.1007/s11160-020-09604-0

White, E. R., Nagy, J. D., & Gruber, S. H. (2014). Modeling the population dynamics of lemon sharks. *Biology Direct*, *9*(1), 23. https://doi.org/10.1186/1745-6150-9-23

Whitfield, P., Kenworthy, W., Hammerstrom, K., & Fonseca, M. (2002). The role of a hurricane in the expansion of disturbances initiated by motor vessels on seagrass banks. *J Coast Res*, *37*, 86–99.

Wickham H (2016). Ggplot2: elegant graphics for data analysis. *Springer-Verlag New York*. ISBN 978-3-319-24277-4. https://ggplot2.tidyverse.org.

Wickham H, François R, Henry L, Müller K, Vaughan D. (2023). Dplyr: a grammar of data manipulation. R package version 1.1.4. https://CRAN.R-project.org/package=dplyr

Williams, J. J., Papastamatiou, Y. P., Caselle, J. E., Bradley, D., & Jacoby, D. M. P. (2018). Mobile marine predators: An understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1875). https://doi.org/10.1098/rspb.2017.2456

Wilson, K. L., Wong, M. C., & Devred, E. (2020). Branching algorithm to identify bottom habitat in the optically complex coastal waters of Atlantic Canada using sentinel-2 satellite imagery. *Frontiers in Environmental Science*, *8*(November). https://doi.org/10.3389/fenvs.2020.579856

Wise, S. P. (2014). Learning through experience: Non-implementation and the challenges of protected area conservation in The Bahamas. *Marine Policy*, *46*, 111–118. https://doi.org/10.1016/j.marpol.2014.01.010

Xie, Y., Sha, Z., & Yu, M. (2008). Remote sensing imagery in vegetation mapping: A review. *Journal of Plant Ecology*, *1*(1), 9–23. https://doi.org/10.1093/jpe/rtm005

Zhafarina, Z., & Wicaksono, P. (2019). Benthic habitat mapping on different coral reef types using random forest and support vector machine algorithm. *SPIE*, *11372*, 26. https://doi.org/10.1117/12.2540727

Zhang, C., Li, W., & Travis, D. (2007). Gaps-fill of SLC-off Landsat ETM+ satellite image using a geostatistical approach. *International Journal of Remote Sensing*, *28*(22), 5103–5122. https://doi.org/10.1080/01431160701250416

Zhang, T., Su, J., Xu, Z., Luo, Y., & Li, J. (2021). Sentinel-2 satellite imagery for urban land cover classification by optimized random forest classifier. *Applied Sciences*, *11*(2), Article 2. https://doi.org/10.3390/app11020543

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Appendix A: Chapter 2 Supplementary Tables and Figures

Table S1. Wavelength spectral ranges for the blue, green, red, and near-infrared bands for Landsat 5 (L5), 7(L7), 8(L8) satellites and years in which satellites were operational.

Bands	L5 TM	L7 ETM+	L8 OLI
Blue	0.452-0.518	0.450–0.515	0.450–0.515
Green	0.528-0.609	0.525–0.605	0.525–0.600
Red	0.626-0.693	0.630–0.690	0.630–0.680
Near-Infrared	0.776-0.904	0.775–0.900	0.845–0.885
Years in Operation	1984 - 2013	1999 – 2013*	2013 - Current

*While L7 is still in operation, due to a scan-line corrector malfunction, no usable

imagery of Bimini has been collected since 2013.

Table S2. Satellite images used for terrestrial and aquatic maps with day, year, month (YM) and time collected as well as Landsat Product Identifier. Tidal height recorded from NOAA (n.d.) historical tides and currents database recorded in North Bimini station TEC4617.

| YM	Day	Time (EST)	Satellite	Tidal Height (m)	Landsat Product Identifier L1
1999.03	23	1022	Landsat 5	0.40	LT05_L1TP_014042_19990323_20200908_02_T1
2000.02	14	1036	Landsat 7	0.61	LE07_L1TP_014042_20000214_20200918_02_T1
2001.02	08	1023	Landsat 5	0.46	LT05_L1TP_014042_20010208_20200906_02_T1
2002.02	27	1021	Landsat 5	0.38	LT05_L1TP_014042_20020227_20200905_02_T1
2003.02	22	1032	Landsat 7	0.58	LE07_L1TP_014042_20030222_20200916_02_T1
2004.01	16	1022	Landsat 5	0.12	LT05_L1TP_014042_20040116_20200904_02_T1
2006.02	06	1033	Landsat 5	0.12	LT05_L1TP_014042_20060206_20200901_02_T1
2007.02	09	1038	Landsat 5	0.52	LT05_L1TP_014042_20070209_20200831_02_T1
2009.02	14	1029	Landsat 5	0.64	LT05_L1TP_014042_20090214_20200827_02_T1
2011.02	20	1033	Landsat 5	0.76	LT05_L1TP_014042_20110220_20200823_02_T1
2014.01	11	1044	Landsat 8	0.05	LC08_L1TP_014042_20140111_20200912_02_T1
2010.02	10	1043	Landsat 8	0.00	LC08_L1TP_014042_20100210_20200909_02_T1
2015.02	18	1043	Landsat 8	0.00	LC08_L1TP_014042_20160218_20200907_02_T1
2016.05	08	1042	Landsat 8	0.81	LC08_L1TP_014042_20160508_20200907_02_T1
2017.02	04	1043	Landsat 8	0.27	LC08_L1TP_014042_20170204_20200905_02_T1
2018.02	22	1043	Landsat 8	0.69	LC08_L1TP_014042_20180122_20200902_02_T1
2020.02	13	1043	Landsat 8	0.79	LC08_L1TP_014042_20200213_20200823_02_T1
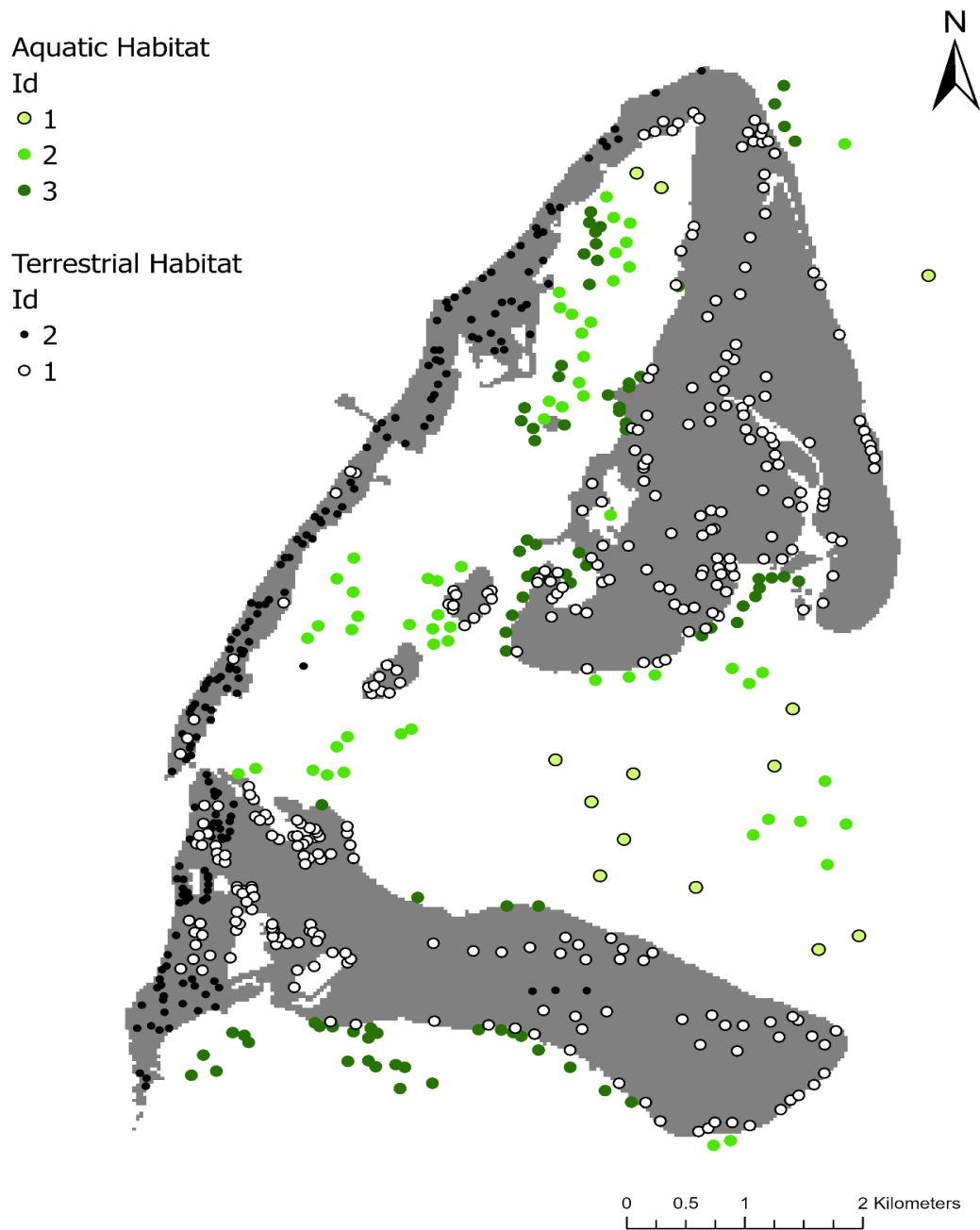
Fig. S1. Training data points used in random-forest models for terrestrial and aquatic 2016 reference maps. Aquatic habitats classified as LDSG/Bare (1), MDSG (2) and HDSG (3). Terrestrial habitats classified as bare (1) and vegetated (2).
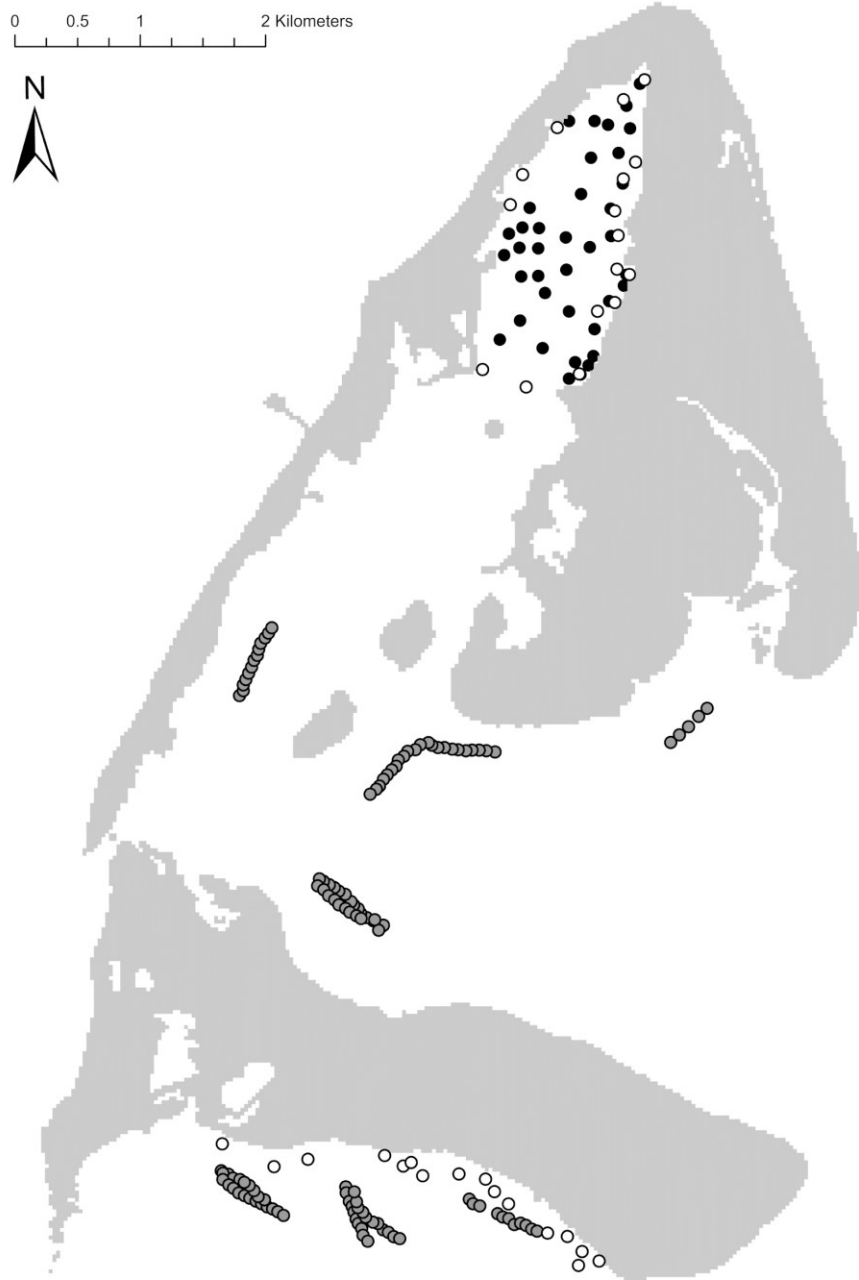
Fig. S2. Test data point locations for aquatic maps for 1999 image (black), 2003 image (white) and 2020 image (grey).

Fig. S3. Test data point locations for terrestrial maps for 1999 image (black), 2003 image (white) and 2020 image (grey).

Table S3. Confusion matrix for the AASG created terrestrial maps showing number of pixels classified as bare or vegetated compared to test data created in ArcGIS Pro through visualisation of a false colour satellite image from each year. Numbers in bold show the number of correctly identified points in each class.

Year: 1999		Test Data		
	Class	Bare	Vegetated	User's Accuracy
Classified Map	Bare	**45**	0	100%
	Vegetated	0	**70**	100%
	Producer's Accuracy	100%	100%	**Overall Accuracy: 100%** **Kappa Coefficient: 1.0**
Year: 2011		Test Data		
	Class	Bare	Vegetated	User's Accuracy
Classified Map	Bare	**64**	0	100%
	Vegetated	2	**74**	97%
	Producer's Accuracy	97%	100%	**Overall Accuracy: 98%** **Kappa Coefficient: 0.97**
Year: 2020		Test Data		
	Class	Bare	Vegetated	User's Accuracy
Classified Map	Bare	**58**	0	100%
	Vegetated	0	**86**	100%
	Producer's Accuracy	100%	100%	**Overall Accuracy: 100** **Kappa Coefficient: 1.0**

Appendix B: Chapter 3 Supplementary Tables and Figures

Table S4: The amount of variance between group intercepts and the standard deviation of that variance, measured for each of the random intercept variables in the survival GLMM

Variable	Variance	Odds Ratio	Std. Deviation	# of Groups
Year	6.259e-09	1.00	7.912e-05	19
Shark.ID	6.450e-02	1.006	2.540e-01	2065

Table S5: The amount of variance between group intercepts and the standard deviation of that variance, measured for the random intercept of year in the body condition GLMM

Variable	Variance	Std. Deviation	# of Groups
Year	0.001	0.037	18