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SPATIAL PATTERNS OF COEXISTENCE AND SEPARATION IN A LARGE-BODIED MARINE PREDATOR COMMUNITY

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Maurits P. M. van Zinnicq Bergmann

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To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Maurits P. M. van Zinnicq Bergmann, and entitled Spatial Patterns of Coexistence and Separation in a Large-bodied Marine Predator Community, having been approved in respect to style and intellectual content, is referred to you for judgment.

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

Michael R. Heithaus

James W. Forqurean

Dean Whitman

Geert M. Aarts

Yannis P. Papastamatiou, Major Professor

Date of Defense: March 8, 2023

The dissertation of Maurits P. M. van Zinnicq Bergmann is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2023

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DEDICATION

Dedicated to the loving memories of my father, Philippe J. W. G. M. van Zinnicq Bergmann, and grandparents, Elisabeth A. van der Staay – van Berkel, and Jan van der Staay, whose love and support carried me to pursue my dreams since my early childhood.

"The Future belongs to those who believe in the beauty of their dreams"

– Eleanor Roosevelt

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ABSTRACT OF THE DISSERTATION

SPATIAL PATTERNS OF COEXISTENCE AND SEPARATION IN A LARGE-BODIED MARINE PREDATOR COMMUNITY

by

Maurits P. M. van Zinnicq Bergmann

Florida International University, 2023

Miami, Florida

Professor Yannis P. Papastamatiou, Major Professor

Species coexistence includes various diet, space, and/or habitat selection mechanisms. Species comprising predator communities should vary in spatial overlap to maximize their fitness. Elucidating how interspecific interactions affect space use and habitat selection in large-bodied marine predators, however, is challenging due to the infeasibility of conducting manipulative experiments. Consequently, the mechanisms enabling coexistence of constituent species remain generally poorly understood. Individual-based models of a predator community incorporating competition, predation, and asymmetrical intraguild predation (IGP) predicted that mesopredators should generally separate from apex predators in safe habitat, with stronger spatial separation occurring among species with strong interference (predator/prey), which becomes weaker as interference intensity decreases (e.g., IGP). Spatial overlap patterns within an elasmobranch (sharks and rays) community in Bimini, The Bahamas, based on biotelemetry with resource selection functions and movement models, generally matched theoretical predictions. For example, predator/prey (e.g., great hammerhead sharks versus southern stingrays) showed the clearest spatial separation, followed by $IG_{predator}/IG_{prey}$

(e.g., great hammerhead versus blacktip sharks). A lack of specific diet data, however, impedes the functional inferences that could be made. Quantifying trophic relationships for many elasmobranchs is difficult because directly observing foraging behavior is challenging and stomach contents analysis is not always feasible. The development of a minimally invasive and efficient tool using DNA metabarcoding from cloacal swabs, validated in a controlled feeding experiment and in the field, has promise for elucidating diets in and interspecific interactions among elasmobranchs.

Understanding space use is also important for designing marine protected areas (MPAs). In The Bahamas, an MPA in North Bimini has been proposed, although it is unclear how this MPA would benefit elasmobranchs if implemented. Integrating elasmobranch movement models with systematic conservation planning revealed that although the NBMPA would improve conservation, adding an additional MPA southwest of Bimini would be necessary to protect important habitats.

Altogether, integrating ecological modeling, field data, and new DNA-based diet reconstruction tools will help to resolve space use and community organization drivers, by providing insights into whether interspecific interactions might drive habitat selection and elucidating species-specific trophic pathways and dietary partitioning, that can also provide the foundation of effective and adaptive management.

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CHAPTER I

GENERAL INTRODUCTION

Variations in the level of spatial partitioning among species is common within predator communities (Lovari et al. 2013, López-Bao et al. 2016, Swanson et al. 2016, Lea et al. 2020). Species within predator communities often vary greatly in body sizes, with the potential for multiple interspecific interactions to exist, including competition, predation, and intraguild predation (where competing predators are also locked in predator-prey relationships; IGP) (Lourenço et al. 2014, Lesmeister et al. 2015, Gompper et al. 2016, Dröge et al. 2017). Spatial distribution patterns may arise from, in addition to interspecific interactions among predators, memory-based foraging, diverse habitat preferences, preferences or intolerances to abiotic conditions (Schlaff et al. 2014, Lesmeister et al. 2015, Dröge et al. 2017, Aarts et al. 2021). The wide variety of potential underlying causes for habitat selection makes the connection between interspecific interactions and distribution patterns obscure and difficult to discern from other potential drivers. Investigating this relationship is important, however, because it provides insight into the patterns and drivers of space use, and therefore coexistence among co-occurring predator species (Steinmetz et al. 2013, Vanak et al. 2013, López-Bao et al. 2016). In marine predator communities, such as elasmobranch, interactions have commonly been inferred from patterns of spatial partitioning (White and Potter 2004, Papastamatiou et al. 2006, Heupel et al. 2018, 2019, Lea et al. 2020), but possible drivers have rarely been identified (Papastamatiou et al. 2018). As a result, we still know very little of the effects of competition, predation, and IGP on the degree of spatial separation within elasmobranch communities and therefore how coexistence is achieved.

We also still know very little on the diets of elasmobranch species, so that interaction types and strengths among species remain poorly understood. While broad inferences on interaction type may be correctly made, interaction strengths differ among species, and vary in space and time, and with fluctuations in prey landscape (Vanak et al. 2013, Morosinotto et al. 2017, Tallian et al. 2022). The reason is that direct elasmobranch foraging behavior is difficult to observe (Nelson et al. 1977), and accurate and efficient methods for elasmobranch diet assessment are lacking. Conventional methods generally include visual or molecular stomach content analysis, obtained via invasive methods including stomach lavage, stomach eversion, or lethal sampling (Papastamatiou et al. 2006, Barnett et al. 2010, Dunn et al. 2010, Matich et al. 2020), but are undesirable for species of conservation concern (Heupel and Simpfendorfer 2010, Hammerschlag and Sulikowski 2011).Therefore, the development of a minimally invasive, high-resolution and efficient tool to reconstruct elasmobranch diets will bridge an important knowledge gap for this diverse taxonomic group.

Overexploitation and habitat destruction have been identified as the two biggest causes of elasmobranch population decline worldwide (MacNeil et al. 2020, Pacoureau et al. 2021, Dulvy et al. 2021). Marine protected areas (MPAs), aimed to restrict or prevent extractive and/or destructive practices, have been increasingly implemented for the regulation and protection of elasmobranchs (MacKeracher et al. 2019). However, due to increasing international pressure to meet international conservation goals (e.g., the protection of 10% of the world’s oceans discussed in the 2020 Aichi Biodiversity Target 11 (UNEP-WCMC 2021), the 20% biodiversity target stipulated by some governments such as The Bahamas (The Nature Conservancy 2017), or the call for the protection of

30% of marine and coastal waters by international organizations including International Union for the Conservation of Nature and Convention on Biological Diversity (IUCN 2016, Convention on Biological Diversity 2020)), many MPAs have been implemented hastily and opportunistically, without explicit conservation objectives so that MPAs have high chance for failure (Agardy 2018). Information on elasmobranch space use is important to help guide MPA design, or evaluate MPAs once established (Carlisle et al. 2019, Birkmanis et al. 2020). Unfortunately, such data is often unavailable, which makes their effectiveness uncertain (Oh et al. 2017).

The goals of this dissertation are threefold, namely to 1) understand spatial coexistence within an elasmobranch predator community, 2) develop a minimally invasive and efficient shark diet assessment method, and 3) design MPAs that protect 30% of important elasmobranch areas. To work towards my first goal, I used passive acoustic telemetry with applied resource selection functions, implemented via random forest machine learning algorithms, and movement models to quantify mechanisms and drivers of space use among eight species of elasmobranch, including apex (bull *Carcharhinus leucas*, great hammerhead *Sphyrna mokarran*, and tiger sharks *Galeocerdo cuvier*), dominant (Caribbean reef *C. perezi*, lemon *Negaprion brevirostris*, and nurse *Ginglymostoma cirratum* sharks), and subordinate (blacktip *C. limbatus* sharks and southern stingrays *Hypanus americanus*) mesopredators in Bimini, The Bahamas. Furthermore, by developing custom-made individual-based models based on behavioral mechanisms including competition, predation, and IGP, I am able to generate theoretical predictions of distribution patterns that will tell me, after comparing to observed distributions, whether these interspecific interactions are indeed assisting in driving observed elasmobranch space use patterns. To work towards my second goal, I first designed a controlled feeding experiment where wild-caught juvenile lemon sharks were fed a known non-natural teleost prey species diet to investigate whether this prey species can reliably be detected by fecal DNA metabarcoding and without incurring DNA contamination from the surrounding seawater (environmental DNA). Then, after validation of the method, I am able to test this method in the field by sampling wild juvenile bull sharks caught in the Florida Everglades National Park with the hope that I will be able to at least identify prey species that are known prey items for this species and size range in this area. Lastly, to achieve my third goal, I combined movement models from the same eight investigated elasmobranch species and a systematic conservation planning framework to evaluate how MPA designs should look like that consider the full implementation of the proposed North Bimini MPA. Moreover, to investigate the MPA efficacy, these designs were compared to designs that 1) were aimed at meeting the conservation target previously determined by the Bahamian government (20% of important coastal and marine resources by 2020), and 2) did not consider the establishment of the proposed North Bimini MPA. Finally, considering that some elasmobranch species (e.g., bull, great hammerhead, and tiger sharks) are seasonal residents to Bimini, I investigated whether the effectiveness of permanent MPAs could be improved by considering them as seasonal time-area closures.

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CHAPTER II

SPACE WARS: INTERSPECIFIC COMPETITION, PREDATION, AND INTRAGUILD PREDATION STRUCTURE A MARINE PREDATOR COMMUNITY

Abstract

Variations in the degree of spatial partitioning within predator communities can reflect interspecific interactions among constituent species. However, relating interspecific interactions to drivers of predator distribution patterns is challenging and predator communities often include a variety of interactions including competition, predation, and intraguild predation. Consequently, understanding how space use mechanisms among sympatric predator species contribute to coexistence remain poorly understood, especially in marine predator communities. Furthermore, while theoretical models predict the existence of stronger spatial separation when interactions consist of either strong interference (including predation and intraguild predation) or competitive advantages that are habitat-specific, their combined effect on the extent of spatial separation remains unclear. Here, I used passive acoustic telemetry with applied resource selection functions and movement models for eight elasmobranch species to quantify patterns and drivers of space use in Bimini, The Bahamas. Additionally, I built individual-based models to predict distribution patterns based on concurrent mechanisms of competition, predation, and intraguild predation. Individual-based models predicted stronger spatial separation with strong interference (predator/prey), which becomes weaker as interference decreases in intensity (e.g., intraguild predation). Elasmobranch space use patterns matched these predictions, as predator/prey (e.g., southern stingrays versus great hammerhead sharks) and intraguild predation among apex and subordinate mesopredators (e.g., blacktip versus great hammerhead sharks) showed the clearest spatial separation, followed by intraguild predation among apex and dominant mesopredators (e.g., Caribbean reef versus tiger sharks). Competitors (e.g., bull versus tiger sharks) showed more spatial overlap although there were smaller-scale differences in microhabitat use. Our study suggests that stronger spatial separation is found among elasmobranch species when interference is strong. For competitors, stronger spatial separation may require habitat-specific competitive advantages.

Introduction

Sympatric predators vary their degrees of spatial partitioning, ranging from high spatial overlap to complete spatial separation (Papastamatiou et al. 2006, Dröge et al. 2017). Spatial separation may be related to various processes such as competitive interactions, predator avoidance, territoriality, memory-based foraging, diet specialization, and foraging tactics (Baird 2001, Wakefield et al. 2013, Pottss and Lewis 2014, Dröge et al. 2017, Aarts et al. 2021). Adjustments of space use among co-occurring species may relieve or intensify interspecific interactions, including competition, predation, and intraguild predation (IGP; i.e., predation among competing predators) (Arias-Del Razo et al. 2012, Lourenço et al. 2014, Morosinotto et al. 2017). Despite the possibility of such interactions shaping community structure and dynamics, quantifying how they drive habitat selection decisions and patterns in large-bodied predators is challenging (Vanak et al. 2013, Vaudo and Heithaus 2013, Papastamatiou et al. 2018, Rodriguez Curras et al. 2021, Kachel et al. 2022). Spatial segregation alone is not proof of interspecific interactions because this pattern may also emerge from differing preferences or requirements related to habitat and physiology (Schlaff et al. 2014, Lesmeister et al. 2015, Kachel et al. 2022). Additionally, manipulation experiments (e.g., removal of one or more species) are impractical and unethical (Chase et al. 2002, Salo et al. 2010, Anderson and Semlitsch 2016). Studies that investigated the effects following apex predator recovery, arrival to a novel area, recolonization of, or reintroduction to, areas from which they have disappeared, and those that investigated the effect of one species by comparing two similar ecosystems, one with and one without that species, suggest that these interactions may be quite important (Doak et al. 2008, Mueller et al. 2016, Papastamatiou et al. 2018, Curveira-Santos et al. 2021, Towner et al. 2022, Avrin et al. 2023).

The ideal free distribution (IFD) has been foundational to predicting the distribution of animals among habitats (Menezes and Kotler 2019). The original IFD model predicts that, absent interference competition and predation, individuals will optimize their fitness by distributing themselves proportionally to patch quality (Fretwell and Lucas 1969). While proven insightful, underlying assumptions are often not met in nature (Menezes and Kotler 2019). For example, individuals are unlikely to be equal competitors and models that consider interference predict a range of distributions based on the nature of interference (e.g., dominance, prey search efficiency, and handling time) and species population sizes (Holmgren 1995, Brown 1998). Overall, these models predict that in order for spatial separation to exist among competing species, there needs to be either strong interference, or species must have an advantage over competitors in certain microhabitats (Brown 1989, Holmgren 1995, Papastamatiou et al. 2018). However, models that simultaneously consider differences in patch quality (e.g., prey density/distribution and refuge) are currently lacking, especially for marine systems (Papastamatiou et al. 2018).

Predictions of habitat distribution also change when considering predation, where habitats may differ in their risk to prey, or IGP. The IFD model has additionally been extended to investigate trade-offs between food and safety in a tritrophic food chain under simultaneous habitat selection by predators and prey, and immobile basal resources. Game-theoretic models predict that patch riskiness should be the main driver of prey distribution, with prey avoiding riskier patches regardless of resource distribution (safety matching) while resource productivity should determine predator distribution (resource matching; Hugie and Dill 1994, Luttbeg and Sih 2004). Contrary to model predictions, empirical experiments that tested this prediction found that while prey indeed favored safer patches, resource distribution also significantly affected prey distribution (Dupuch et al. 2009). Fitness often depends on body mass, and when prey optimally balance foraging and risk, they should prefer more resource-rich patches regardless of patch riskiness under low predation risk, while prey should be relatively uniformly distributed across patches when predation risk is high (Luttbeg and Sih 2004, Dupuch et al. 2009). The general predictions of the above predator-prey game are qualitatively similar to those of an asymmetrical IGP game (Heithaus 2001). This model predicts that at broad scales (among patches) $\mathrm{IG}_{\mathrm{predators}}$ should resource-match while $\mathrm{IG}_{\mathrm{prey}}$ should safety-match, which promotes coexistence. When avoidance and vigilance of both $\mathrm{IG}_{\mathrm{prey}}$ and resources are considered, IGP theory further suggests that $\mathrm{IG}_{\mathrm{prey}}$ may coexist at fine scales (within patches) with $\mathrm{IG}_{\mathrm{predators}}$, likely by balancing foraging and risk to secure enough resources (Heithaus 2001, Kimbrell et al. 2007). Overall, these models predict that for species where interactions consist of strong interference (i.e., one animal kills another) or IGP, prey may try to spatially avoid predators. Supporting predictions of IGP theory, within terrestrial predator communities where subordinate predators risk death by dominants, space use mechanisms are complex but commonly involve large-scale spatial segregation and/or fine-scale spatiotemporal avoidance (Mills and Gorman 1997, Steinmetz et al. 2013, Vanak et al. 2013, Dröge et al. 2017, Karanth et al. 2017, Lonsinger et al. 2017).

Elasmobranchs (rays and sharks) are generally apex and meso-trophic level predators that, in nearshore environments, typically occur in multi-species communities. As such, many species vary in their degree of spatial overlap (Compagno 1990, Munroe et al. 2014). Partitioning of space among co-occurring nearshore elasmobranchs has been extensively documented (Heupel et al. 2018, Papastamatiou et al. 2018, Lea et al. 2020), suggesting interspecific interactions in coastal ecosystems are prevalent. However, drivers behind such processes have rarely been investigated due to the challenges in obtaining *in situ* data and making behavioral observations. No study has yet investigated the magnitude of effect of interspecific competition, predation, and IGP in simultaneously driving space use patterns within diverse multi-species elasmobranch communities.

Bimini, The Bahamas, supports a diverse elasmobranch community for which the space use mechanisms that facilitate the coexistence among constituent species remain poorly understood (Jennings et al. 2012, Hansell et al. 2018, Smukall et al. 2021). Here, I employed biotelemetry to quantify resource selection and space use within and space use overlap between eight sympatric species of elasmobranch i.e., southern stingrays (*Hypanus americanus*), blacktip (*Carcharhinus perezi*), bull (*C. leucas*), Caribbean reef (*C. perezi*), great hammerhead (*Sphyrna mokarran*), adult and subadult lemon

(*Negaprion brevirostris*), nurse (*Ginglymostoma cirratum*), and tiger (*Galeocerdo cuvier*) sharks in Bimini, The Bahamas. Bull, great hammerhead, and tiger sharks are considered apex predators (Clark and von Schmidt 1965, Strong et al. 1990, Lowe et al. 1996, Doan and Kajiura 2020, Gallagher et al. 2021), while Caribbean reef, adult lemon, and nurse sharks can be classified as large mesopredators (Morrissey and Gruber 1993, Castro 2000, Tavares 2009), and southern stingrays, blacktip and subadult lemon sharks as small mesopredators (Snelson and Williams 1981, Matich et al. 2020, O'Shea et al. 2020). I predict that 1) those species for which intense interference (including predation and IGP) is possible, spatially segregate (stingrays, juvenile lemon, blacktip, and Caribbean reef sharks from bull, great hammerhead, and tiger sharks), and 2) for competitors (bull, great hammerhead, and tiger sharks), spatial overlap may be higher but there species may show preference for certain microhabitats (e.g., seagrass). To provide additional theoretical support to our predictions, I then built a series of custom-made individual-based models (IBMs) to predict distribution patterns among qualitatively different habitats based on the simultaneous mechanisms of competition, predation, and IGP.

Materials and methods

Site description

Bimini (25° 44′N, 79° 16′W) comprises a small subtropical cluster of islands, rocks and cays located on the northwestern margin of the Great Bahama Bank in The Bahamas archipelago. The two main islands, North Bimini and South Bimini, form a triangle shape that semi-envelope a shallow (<2 m depth) lagoon (~21 km^2). Their peripheries are tapestried with red mangroves (*Rhizophora mangle*) with the exception of the western sides, which are edged with sandy and rocky beaches. Shallow sand flats and seagrass meadows with scattered rocks, sponges and/or macrophytes can be found extending north, east, and south on the bank, whereas fringing coral reef and deeper sand and seagrass microhabitats slope along the western edge into the Florida Strait (Trave and Sheaves 2014). Regular wildlife tourism provisioning has taken place off southwest Bimini since 2012, attracting both target species (great hammerheads; Guttridge et al., 2017; Heim et al., 2021) and non-target species (bull and nurse sharks) to the provisioning site. Caribbean reef shark tourism provisioning has occurred occasionally further southwest along the drop off during the course of this study.

Acoustic tagging and monitoring

Acoustic transmitters (InnovaSea, Nova Scotia, Canada; V16; battery life 2,435 days to 10 years; transmission interval: 90 – 150 sec) were surgically implanted into the coelom of southern stingrays, blacktip, bull, Caribbean reef, great hammerhead, lemon, nurse and tiger sharks following capture, or attached externally to the base of the first dorsal fin via freediving for some great hammerheads, between April 2014 – July 2018 (Guttridge et al. 2017, van Zinnicq Bergmann et al. 2022, Smukall et al. 2022b). Sex and morphometrics (precaudal length, PCL) were recorded for each transmitter-equipped elasmobranch via direct measurement or estimated via laser-photogrammetry for some great hammerheads instrumented during freediving (Guttridge et al. 2017). Tagged elasmobranchs (individuals of all species were sexually mature except lemon sharks, which included a mix of sexually immature and mature individuals) were monitored for 2.5 years, between 1 October 2016 – 30 April 2019, using an acoustic receiver array

(VR2W, InnovaSea; n = 56) in locations so that all major marine biotopes were covered and movements from/to the lagoon could be detected (Figure 1). Each time a transmitter-equipped elasmobranch swims within the detection range of an acoustic receiver (500 m at minimum; van Zinnicq Bergmann et al. 2022), the unique tag ID code, along with the date and time of detection, are recorded and stored in the memory of that receiver. Receivers were retrieved, downloaded, serviced (e.g., biofouling cleaned off which can reduce performance (Heupel et al. 2008) and batteries replaced), and redeployed at least once per year.

Data analyses

All acoustic data analyses were performed in R version 4.2.0 (R Core Team, 2022) implemented using RStudio version 2022-02-3 (RStudio Team 2022).

Data preparation

Acoustic data cleaning is described in detail elsewhere (Kessel et al. 2014, Guttridge et al. 2017, van Zinnicq Bergmann et al. 2022). To summarize, I removed false positive detections that may arise when a transmitter is detected only once within a 1 h time bin on a single receiver. Double detections, simultaneously recorded detections from a single transmitter by multiple receivers with overlapping detection ranges, were also removed. To avoid incorporating any potential bias in the animal movement analysis resulting from stress related to the acoustic tagging event, any detections within the first 24 hr post-tagging were also discarded. To analyze species-specific temporal trends in the number of transmitter-equipped elasmobranchs detected on the receiver array, I calculated the proportion of tagged individuals detected per month and year (i.e., the number of detected elasmobranchs divided by the cumulative sum at liberty, and therefore possible to be detected), and subsequently aggregated monthly proportions across years.

Application of resource selection functions via random forests

Available resource units and presence/background points generation

Resource selection functions (RSFs) are statistical models used to quantify and predict animal spatial resource-use patterns, by yielding probability estimates of proportional use of particular resources (i.e., selected area units) relative to their availability in the environment (Boyce et al. 2002, Manly et al. 2007). Essentially, these predictive models assess relationships between resource use and resource variables (i.e., abiotic and/or biotic features/predictors present within respective resources) and by extension, enable the characterization of specific predictor value ranges and areas that an animal may select or avoid (Shoemaker et al. 2018). To predict relative habitat selection by investigated elasmobranchs, RSFs were implemented using random forest (RF; Breiman, 2001) machine learning algorithms (Shoemaker et al. 2018). The RF algorithm grows numerous decision trees using recursive binary splitting to create a forest, whereby different random data and predictor subsets for each tree are generated, after which predictions are aggregated (Breiman 2001). The implementation of RSFs via RF applied to passive acoustic telemetry data followed the protocol in Griffin et al., (2021).

I first used a mean-position algorithm (Simpfendorfer et al. 2002) to compute centers of activity (COA) from detection data, binned into 90-min segments (Griffin et al.

2021), implemented using the *VTrack* package version 2.10 (Campbell et al. 2012). I then defined available resource units by drawing 700 m buffers around each receiver location (Figure 2); as the minimum detection range at our study site was previously estimated to be 500 m (van Zinnicq Bergmann et al., 2022), COAs are able to interpolate approximate locations among receiver locations regardless of detection range. Next, I restricted both COAs (presences) and randomly distributed background points (theoretically available locations) to the defined available resource units to implement RSFs within a use/availability framework (Griffin et al. 2021). Individuals that yielded ≤50 COAs in total were discarded. Per remaining individual, an equal number of background points to COAs was generated across all available resource units and subsequently collapsed into 200 x 200 m raster grid cells (Griffin et al. 2021).

Environmental information aggregation

A microhabitat classification satellite map, commissioned by Save Our Seas Foundation (n+p, 2015), was converted into a raster with 200 x 200 m grid cells. Under-represented/sampled microhabitat class pixels (e.g., ‘high density Thalassia and Halodule, ‘large sponge’, and ‘mangrove edges, ponds and other inlets’) were merged or replaced with the most representative class present nearby: pixels classified as ‘Thalassia and Halodule (medium density)’ were merged with ‘Thalassia and Halodule (high density)’, whereas ‘large sponge’ and ‘mangrove edges, ponds and other inlets’ pixels were replaced with ‘Thalassia and Halodule (low density)’ and ‘Thalassia and Halodule (medium/high density)’, respectively (Figure 2). Furthermore, I collated depth data from the acoustic receiver array with depth data from previous baited underwater video surveys (Driscoll 2021, van Zinnicq Bergmann et al. 2022) and local snorkeling/diving sites (www.divebuddy.com; www.geoffschultz.org) to generate a depth (m) raster for the study site via ordinary Kriging (geospatial interpolation), using the automap package version 1.0-16 (Hiemstra et al. 2009) (Figure 3). A habitat raster was also generated by dividing the study site into habitats (i.e. bank, bank edge, lagoon, shelf) to increase spatial resolution (Figure 4).

Finally, I generated a water temperature raster for both summer (June 1 – Nov 30) and winter (Dec 1 – May 31) periods due to the observed seasonal residency to the acoustic array of several investigated elasmobranch species (e.g., blacktip, bull, great hammerhead, nurse, and tiger sharks; Guttridge et al., 2017; Smukall et al., 2022; van Zinnicq Bergmann et al., 2022, van Zinnicq Bergmann, unpubl.). Water temperature loggers (HOBO® Pro V2, Onset Computer Corporation) were deployed at a subset of receiver locations (n = 28). Due to failure/loss of several loggers, I first predicted (imputed) missing values at those same locations using a RF regression model, implemented via the packages *ranger* version 0.14.1 (Wright and Ziegler 2017) and *mlr* version 2.19.0 (Bischl et al. 2016). This model included logged water temperature (°C), averaged in 3-h bins, as the target variable, and a suite of temporal, spatial and environmental predictors (Table 1). For days and hours of day for which no value was logged, the target variable contained no data. Tuning and training of the model followed the steps described in section 2.3.2.3 in the main text. I used the 'performance' function in the *mlr* package and calculated a root mean squared error (RMSE) of 0.87, which indicated high model performance and means that the average error per estimate is 0.87 °C off the actual water temperature. Receiver locations for which loggers were unavailable inherited water temperature values from the closest receiver location with a logger that shared similar microhabitat and depth characteristics. Next, water temperature values were extracted for one representative date per season (seasonal bin midpoint i.e. 1 September 00:00 h for summer, 1 March 00:00 h for winter) (Hightower et al. 2022). I then used ordinary Kriging to generate summer and winter temperature rasters. Spatial variation in water temperature was minimal, resulting in an approximate uniform distribution of values for both summer (~30 °C) and winter (~25 °C) rasters.

All rasters were processed to have the same spatial resolution and extent as the microhabitat map. The microhabitat, depth, and habitat rasters were categorical, whereas those for water temperature were continuous. Subsequently, corresponding (micro)habitat and depth rasters were overlaid on top of the COA and background points, after which these points were assigned raster information extracted from corresponding grid cells (Griffin et al. 2021). Water temperature values, before being extracted, were matched to COA and background points according to their proximity in space and time with a match only occurring between a point and its nearest receiver location for which the time difference between that same point and recorded water temperature was minimal.

Relative habitat selection models

Species models were implemented via the packages *ranger* version 0.14.1 (Wright and Ziegler 2017) and *mlr* version 2.19.0 (Bischl et al. 2016), using presence/background points as the response variable and (micro)habitat, depth, and matched water temperature as predictors. To enhance model performance, prior to running the model I tuned hyperparameters by having the ‘tuneParams’ function in the *mlr* package select the optimal combination of hyperparameter values across 50 random search iterations (Griffin et al. 2021). Hyperparameters determine the extent of randomness across trees via specification of how many predictors each tree should contain (mtry), and how many observations each tree (sample.fraction) and terminal node at minimum (min.node.size) should include (Lovelace et al. 2019). Using tuned hyperparameter settings, the model was trained using 500 trees, replacement and 60% of the data (training data set). The trained model was subsequently used to predict across the remaining 40% of the data (holdout data set) to assess performance (Griffin et al. 2021). Overall and class (present vs background point) accuracy, error rate, and performance were assessed by applying the 'calculateROCMeasures' function within the *mlr* package to the holdout data set (Griffin et al. 2021). Evaluation measures included overall accuracy, sensitivity (true positive rate), specificity (true negative rate), fall-out (false positive rate), miss rate (false negative rate), and precision (positive predictive value). These values were derived from an absolute confusion matrix that compared true observations versus model predictions. Models were run separately for adult (>175 and 185 cm PCL for males and females, respectively) and subadult lemon sharks because of their more restricted home ranges during the subadult life stage (Feldheim et al. 2014).

Predictor marginal effects on the predicted outcome ($\hat{y}$) were assessed via construction of univariate partial dependency plots, using the *pdp* package (Greenwell 2017), for the three most important predictors as assessed by the permutation importance method (Breiman 2001). Continuous predictors were visualized with confidence intervals using a generalized additive model or loess smoother through the *ggplot2* package (Wickham 2016).

Two-way interactions were assessed by first using the ‘Interaction’ function within the *iml* package (Molnar 2018) to produce H-statistics that inform which three predictors generated the greatest strengths (Friedman and Popescu 2008). This was done using 25% of the training data set to reduce computation time (Griffin et al. 2021). This step was then repeated using the original model and full training set to identify the other predictors with which each top predictor interacted (Griffin et al. 2021). Interactions were visualized using bivariate partial dependency plots.

Finally, I extrapolated model predictions across the study site using trained RF models and all environmental rasters (separately for each water temperature raster) to derive seasonal relative habitat selection patterns, which were constrained to the maximum depth at which each species was detected by the acoustic array.

Random forest model evaluations

To evaluate robustness of model outcomes to varying parameter inputs, I conducted sensitivity analyses following Griffin et al., (2021). First, models were constructed as described above (sections 2.3.2.2) but using COA data binned in 60-min time steps. Second, models were re-ran using a buffer of either 500 or 900 m to assess the effect of available resources. All sensitivity analyses used original model hyperparameter settings.

I also investigated and mapped extrapolation reliability to evaluate whether predictive models unintentionally extrapolated in novel covariate space (Mesgaran et al. 2014, Griffin et al. 2021). Using the *dsmextra* package (Bouchet et al. 2020), I evaluated whether the presence/background points and their associated depth and water temperature values fell within (analogous extrapolation) or outside (univariate extrapolation) the sampled covariate space (see Griffin et al., 2021 for details).

Movement models

Dynamic Brownian bridge movement models (dBBMM, Kranstauber et al., 2012) were calculated for each species and lemon shark life stage to evaluate the representativeness of extrapolated relative habitat selection values and to quantify space use overlap. First, individual-level models were calculated using the *move* package version 4.1.8 (Kranstauber et al. 2022) and scaled up to the group-level using the *movegroup* package (Dedman and van Zinnicq Bergmann 2023) following van Zinnicq Bergmann et al. (2022). Subsequently, core (50%) and general use (95%) utilization distribution (UD) isopleths were calculated. Our movement models used a spatial resolution of 200 m^2, a location error of 500 m, and sliding window size of 23 locations. Individuals that were detected less frequently than the sliding window size or where all detections were at a single receiver were discarded. Movement models were based on detections recorded only at receiver locations ($n = 43$) that had corresponding microhabitat classifications from satellite imagery (Figure 1).

Among-species spatial comparisons

As a measure of space use overlap among species, I calculated dissimilarity in UDs for each possible species pair using the earth mover's distance algorithm (FastEMD). The FastEMD is a spatially explicit measure of similarity that quantifies the minimal effort needed to transform, for example, one UD 'seascape' into another

(Kranstauber et al. 2017). I used a threshold distance of 15,000 m which represents the maximum Euclidean distance among acoustic receivers in the array. I restricted UDs to 99.5% isopleths to increase processing speed (Kranstauber et al. 2017). The FastEMD 'effort' values were standardized to range between 0 and 1, whereby a 0 or 1 denote two identical, or completely dissimilar, UDs respectively.

I used the resource selection functions to calculate the difference in preferred depth (m) for each possible species pair. Specifically, I took the absolute difference between the preferred depth values (i.e., the minimal depth at which the marginal effect is maximal) of every species pair. I also used these functions to identify which habitat was predicted to be selected the most by each species, indicated by the habitat for which the $\hat{y}$ value was maximal.

Finally, I used these three metrics as axes (UD dissimilarity, preferred depth, and habitat) along which to investigate the extent of spatial overlap among species pairs for which particular interactions may be expected. Bull, great hammerhead, and tiger sharks were broadly classified as potential competitors. Southern stingrays, juvenile lemon, blacktip, and Caribbean reef sharks were categorized as either prey or IG_{prey}, while bull, great hammerhead, and tiger sharks were grouped as either predator or $IG_{predator}$. The degree of spatial overlap was assessed for both summer and winter.

Individual-based models

To investigate the potential interspecific drivers on distribution patterns within predator communities, I developed custom-built IBMs to examine the simultaneous effects of competition, predation, and IGP on the extent of spatial separation among apex predator, dominant and subordinate mesopredator ‘sharks’ outside of abiotic context i.e., physical environment and oceanography (Papastamatiou et al. 2018). I also used this modeling approach to predict how habitat occupancy could be influenced by variations in resource abundance (low/intermediate/high). All simulations were executed in the multi-agent programmable modeling environment NetLogo version 6.3.0 (Wilensky 1999).

The simplified modeling world comprised three equally-sized patches representing lagoon, shallow bank, and shelf within which simulated sharks moved and foraged (Papastamatiou et al. 2018). Each patch contained a fixed number of randomly distributed resource ‘prey shoals’ (50, 100, or 150 depending on the specific resource abundance simulation set) comprising two types, A and B (e.g., large and small reef fishes), but their ratios varied. Shoals of type A were more abundant in the shelf (ratio 3:2), less abundant in the lagoon (2:3), and equally abundant in the bank (1:1) habitat compared to shoals of type B. The shape of the virtual world was an unbounded torus, enabling free predator movement among accessible habitats (Papastamatiou et al. 2018). The initial number of predators was fixed (total of 1110, ratio 1:10:100 for apex, dominant, and subordinate, respectively) and represented the carrying capacity for each species. Simulated sharks started with 800 energy units and were initially randomly distributed across accessible model space, with the restriction that the lagoon was inaccessible to apex predators to reflect a spatial refuge for mesopredators, and because apex shark species were rarely observed in the Bimini lagoon which becomes very shallow during low tide.

Basic model mechanics can be found elsewhere (Papastamatiou et al. 2018). Briefly, sharks moved continuously through model space at a constant speed of 0.8 m s^{-1}

for apex, 0.6 m s^{-1} for large mesopredators, and 0.5 m s^{-1} for small mesopredators, which mimic the cruising speeds of species that fall in these trophic levels, respectively (Watanabe et al. 2015, Payne et al. 2016). Individuals lost energy each time step, died if their energy got depleted, but gained energy if they successfully captured prey (175 and 125 energy units for shoals of type A and B, respectively). Upon discovering a shoal, sharks switched from a naïve random search pattern to area-restricted searching, characterized by a tighter distribution of turn angles. Shoals moved using short random walks constrained around their initial starting locations, but with rare leaps in model space that increased in likelihood in response to the presence of foraging sharks. Foraging sharks detected undiscovered shoals close by (i.e., private information) and shoals discovered by others at a fourfold greater distance (i.e., social information; Papastamatiou et al., 2018). Mesopredators were detectable by apex predators at 1.5 units away and attacked if they were within 0.3 units of each other. The likelihood of predation or IGP (an apex predator successfully foraging on a subordinate or dominant mesopredator, respectively) was based on a random draw, whereby an apex had a higher probability of success in relation to a subordinate than a dominant (40 versus 25%, respectively). Otherwise, if a foraging attempt was unsuccessful, the targeted mesopredator escaped, modeled via a random leap in model space. Interference competition was modeled via a subordinate giving way to an approaching dominant at a shoal resource (Papastamatiou et al. 2018).

The consumption of a dominant or subordinate yielded a ~13- or ~5-fold increase in energy gain for the apex compared to a shoal, respectively, and are based on realistic energetic gains by apex predators. The energy content of large and small mesopredators was determined by calculating the energy contents of a common local reef fish species and of a mesopredator shark, taken as a ratio and multiplied by the average energy content of both fish prey patches. For reef fish, I used the stoplight parrotfish (*Sparisoma viride*), which has a tissue energy density of ~28 kJ g^{-1} (Van Rooij et al. 1995, 1998). This value was multiplied by the weight (~0.93 kg), converted from length using FishBase (www.fishbase.de), of an adult fish (35.9 cm fork length; Van Rooij et al., 1995), resulting in a calorific value of ~25.9 MJ. For a small mesopredator, I used an average size blacktip shark measuring 1.5 m total length with a converted weight from length of ~22 kg. This weight was multiplied by the tissue energy density of a shark species for which this information is known i.e. scalloped hammerhead pups (*Sphyrna lewini*; 6.07 kJ g^{-1} [Lowe, 2002]), yielding a calorific value of ~133 MJ. Similarly, for a large mesopredator, I calculated a calorific value of ~395 MJ for a Caribbean reef shark with an average size of ~2.06 m total length and weight of ~65 kg (Talwar et al. 2022); absent species-specific data to convert length to weight, I used available data from the genus to derive a weight estimate.

If an energy threshold (2.5 times starting energy level) was exceeded, a shark became satiated and did not interact with potential prey during any time steps where this condition was met. If an energy threshold (1.25 times starting energy level) was exceeded and the model carrying capacity was not reached for that guild, sharks had the potential to reproduce a single offspring based on a random draw from a log-normal distribution (5% chance, which imitates the low reproductive rates of these sharks) (Papastamatiou et al. 2018). Each model iteration was run for 5,000 time steps, for a total of 100 repetitions for any resource abundance scenario, with the number of individuals per species per habitat recorded at the end of each simulation. A 1,000-tick burn-in period was prepended to each simulation to ensure all simulated individuals were not completely naïve to their environment, and were excluded from reporting (Papastamatiou et al. 2018).

Results

A total of 85 elasmobranchs comprising eight species were included in the analyses (Table 2). Some species (e.g., bull, great hammerhead, adult lemon, and tiger sharks) were seasonally detected on the array, with the proportion of detected tags getting close to or reaching zero between June – September. Blacktip, Caribbean reef, subadult lemon, nurse sharks and southern stingrays, on the other hand, were more year-round residential, highlighted by the proportion of detected tags rarely dropping below 0.5 and never lower than 0.3 (Figure 5).

Relative habitat selection

A total of 122,851 COAs were calculated from the compiled data set (Table 2). Overall, model accuracy and performance varied across species but was consistently high (Table 3). Accuracy (86.6 ± 6.3, mean ± SD) ranged from 76 to 98%, whereas sensitivity (90.1 ± 7.8) ranged from 78 to 99%. Predictor importance/rank varied across elasmobranch species (Figures 6, 7). Depth was the most important predictor for all species. Marginal effect values decreased sharply with increasing depth for blacktip sharks, subadult lemon sharks, and southern stingrays, moderately for adult lemon sharks, remained constant for Caribbean reef sharks, and were higher at greater depths for bull, great hammerhead, nurse, and tiger sharks. The second and third most important predictors were either habitat or microhabitat class with the exception of Caribbean reef and tiger sharks, for which water temperature appeared to be more important. For both these species, higher water temperature coincided with higher ŷ values (Figures 7c, 7i).

Blacktip sharks were more likely to select for low density seagrass and deep-water located in shelf and bank interior habitats (Figure 7a). Bivariate interactions highlighted high ŷ values in the shallow (0–5 m depth) bank interior containing low density seagrass, as well as in deep-water shelf habitat (Figure 8a). Bull, great hammerhead, and nurse sharks exhibited the highest ŷ values in deep water and sandy benthos microhabitats located in the shelf habitat (Figures 7, 8). Notably, bull sharks preferred shelf habitat between 10–25 m but did not seem to have a strong preference for any particular water temperature range in this habitat (Figure 8b). Great hammerheads seemed to select for sandy benthos and deep water between 10–25 m, and while ŷ values were not particularly high for any temperature range over sandy benthos, they were highest in deep water between 28–32 °C (Figure 8d). Nurse shark ŷ values, on the other hand, were the highest in sand and deep-water shelf habitat >15m depth (Figure 8g). In contrast, Caribbean reef sharks only selected for deep water (Figure 7c). Specifically, bivariate interactions showed high ŷ values between 10–15 m in this shelf habitat and between 28–30 °C (Figure 8). Lemon sharks did not seem to prefer one habitat strongly over another, and while adults strongly preferred sandy benthos, sargassum and deep-water microhabitats, subadults exhibited a moderate selection for low density seagrass microhabitat (Figures 7e, 7f). For adults, bivariate interactions reflected a lack of strong preference for any particular habitat but instead showed a strong preference for 0–5 m depths and water temperatures between 28–32 °C (Figure 8e). Subadult lemon sharks revealed no clear preference patterns (Figure 8f). Stingrays showed similar univariate selection patterns to those of subadult lemon sharks (Figure 7h). Interactions, in contrast, revealed high selection values for stingrays in bank edge habitat containing sargassum and seagrass microhabitats in depths <10 m and with water temperatures between 30–32 °C, and deep water <15 m (Figure 8h). Finally, tiger sharks exhibited high ŷ values for sand and deep-water shelf habitat between 24–30 °C, and preferring depths between 5 – 15 m (Figures 7i, 7i).

Sensitivity of relative habitat selection models

Evaluations of RF models showed that model outcomes were robust to input parameter variations i.e., COA time-bin and available resource buffer sizes. Specifically, using 60-min time bins for COA calculation produced overall similar results from RF models compared to those using 90-min bins (Figure 9). Depth remained unchanged as the most important predictor for all species but tiger sharks, for which habitat became more important. The positions of second and third most important predictor was switched only for blacktip sharks, whereas for nurse sharks water temperature replaced habitat as third most important predictor (Figures 9, 10). Additionally, associated ŷ values only changed slightly.

Accuracy metrics were similar for all species regardless of bin size (~1–2% differences; Tables 3, 4). Using a 60-min bins accuracy was slightly increased for blacktip (86–87%), subadult (76–78%) and adult (87–89%) lemon, and tiger (80–81%) sharks, but slightly decreased for bull sharks (88–87%). Subsequently, model predictions and extrapolations in Bimini during both seasons led to minimal differences in species relative habitat selection patterns, except for adult lemon sharks for which selection for the bank and lagoon increased (Figures 6, 11).

Using 500m buffers for available habitat construction had no effect on overall accuracy measurements of RF models and predictions across Bimini looked very similar (Figure 12, Table 5). Likewise, using 900m buffers did not change overall accuracy measurements, however, increased by 5% for the tiger shark RF model (Table 6). This is reflected in the spatial predictions, which showed higher resolution in relative selection along the western shelf (Figure 13).

Extrapolation reliability

Evaluation of extrapolation reliability across Bimini revealed that extrapolation space became increasingly unreliable (univariate extrapolation) with increasing depth off the shelf (Figure 14). Additionally, extrapolations were slightly unreliable in areas <1 m deep, located adjacent to shorelines in South Bimini and the lagoon. Contrastingly, areas between 1–30 m depth fell within existing covariate space (analogue extrapolation) as measured by depth and water temperature, providing support that limiting extrapolations to the maximum observed depth was warranted.

Extrapolated relative habitat selection and space use

While extrapolated areas of high relative selection for bull, Caribbean reef, great hammerhead, nurse, and tiger sharks mainly occurred only in one habitat, those for others (blacktip, adult and sub-adult lemon sharks, stingray) were distributed across several habitats (Figure 15). The former species group showed a strong affinity to the shelf habitat off the west coast, containing fringing and artificial coral reef, sand, and seagrass microhabitats, bordering deep water (>30 m), and exhibited low selection everywhere else within the study site, regardless of the season considered (Figures 15b–d, g, i, k–m, p, r). In contrast, blacktip summer and winter densest clusters of higher values were primarily located on the bank interior close to the shoreline and adjacent to the lagoon in shallow low-density seagrass microhabitat, but areas of high selection value were also identified along the shelf (Figures 15a, j). Similar to blacktip sharks, adult lemon sharks also exhibited high selection values extrapolated to the shelf habitat, but their densest clusters of higher values occurred in the shelf edge habitat, covered with sargassum and mostly low-density seagrass. These patterns were similar for both seasons considered, with an additional large area of higher values identified northeast of Bimini in the bank interior during winter (Figures 15e, n). Finally, subadult lemon sharks and stingrays exhibited dense clusters of high relative selection located in the bank edge and interior habitats south and east of Bimini, as well as in the lagoon, characterized by a mix of low and medium/high seagrass densities. For both species, extrapolated values of selection in the lagoon were higher for winter than for summer (Figures 15f, h, o, q).

Space use patterns across seasons were broadly similar to those from extrapolated relative habitat selection. For both seasons, core and general use areas of bull, Caribbean reef, great hammerhead, nurse, and tiger sharks were mainly or solely located along the deeper western shelf habitat, with only tiger sharks exhibiting core areas off North Bimini while those of the remaining species were located southwest (Figures 16b–d, g, i, k–m, p, r). In contrast, blacktip shark space use was scattered around the study site during summer, while during winter core and general use areas were located mainly on the shallow bank away from deep water (Figures 16a, j). Adult lemon sharks primarily used the shallow waters south of Bimini during summer but expanded their space use to the lagoon during winter (Figures 16e, n). Subadult lemon sharks exhibited the greatest space use, with core and general use areas covering much of the lagoon and bank towards the south and east. The largest core area shifted from the lagoon in summer to southwest Bimini during winter (Figures 16f, o). Finally, southern stingrays space use did not differ much across seasons, although became slightly more concentrated along the shoreline of South Bimini in winter (Figure 16h, q).

Patterns in extrapolated relative selection values and those in estimated UDs for the different seasons were largely consistent, although area covered by each of the methods differed (Figures 15, 16). Specifically, core areas for all species largely coincided with extrapolated areas of high relative selection, with the only exception being adult lemon sharks in winter where the only core area was located in extrapolated areas of low relative selection. Additionally, for all species and both seasons, extrapolated areas of high relative selection extended beyond core UD areas. For example, while core areas for all species except for subadult lemon sharks that were located along the western shelf covered only small areas, RF models extrapolated high relative selection values along the whole western shelf or greater parts thereof. Similarly, for stingrays, blacktip and subadult lemon sharks extrapolated areas of high relative selection off South Bimini and the lagoon extended beyond identified core areas to adjacent areas of similar microhabitat.

Among-species spatial comparisons

Dissimilarity in UDs among species was highly variable within seasons, with standardized values ranging from 0.05–0.57 (0.25 ± 0.16, mean ± SD) for summer and 0.04–0.3 (0.25 ± 0.09) for winter (Table 7). The lowest dissimilarity values were found between bull, great hammerhead, and nurse sharks. Highest dissimilarity occurred between tiger sharks and all other species.

Differences in minimum depth at which $\hat{y}$ values were greatest ranged from 0–16 m (7.53 ± 5.33; Table 8). Largest differences were found between nurse sharks and all other mesopredators but Caribbean reef sharks, whereas smallest differences were found between apex predators (bull vs great hammerhead) and between small mesopredators (blacktip vs subadult lemon shark and southern stingray, and stingray vs subadult lemon shark).

Overlap or separation of preferred habitat depended on the species pairs considered (Table 9). The primary habitat for blacktips (bank interior) was different from any other species investigated. However, the primary habitat for all apex predators and some large mesopredators (i.e., Caribbean reef and nurse sharks) was the shelf. Finally, stingrays, adult and subadult lemon sharks preferred the bank edge habitat.

When considering possible intraguild interactions, those species pairs for which either strong interference, predation, or IGP can be expected, tended to segregate spatially (Figure 17). For example, stingrays potentially competing with nurse sharks, or Caribbean reef with subadult lemon sharks, showed differences in preferred habitat, a large difference in preferred depth, and moderate/high UD dissimilarity. Likewise, subadult lemon and blacktip sharks (IG prey) used different preferred habitats from those selected by bull, great hammerhead, and tiger sharks (IG predators), and had moderate to large differences in preferred depth and high UD dissimilarity. Stingrays (prey) similarly spatially segregated from apex predators. However, the apex predators themselves showed reasonably high spatial overlap despite the potential for competitive interactions among these species. Bull, great hammerhead, and tiger sharks all preferred the same shelf habitat with small differences in preferred depth, and bull and great hammerhead sharks showed moderate to low dissimilarity in UD.

Individual-based model predictions

The IBMs showed that the concurrent effects of competition, predation, and IGP caused spatial separation between apex and mesopredators among habitats, whereby subordinate mesopredators exhibited a higher degree of preference for the safer habitat than dominant mesopredators (Figure 18). Specifically, the abundance of subordinates in the lagoon (spatial refuge) was ~1.5 times higher than in other patches, while differences between bank and shelf were minimal (lagoon: 270.0 ± 1.2, bank: 185.8 ± 0.9, shelf: 173.1 ± 0.2); in contrast, the abundance of dominants was only ~1.2 times higher in the lagoon compared to the other patches, for which abundances were also similar (lagoon: 37.3 ± 0.3, bank: 31.8 ± 0.1, shelf: 30.9 ± 0.3). Low resource levels resulted in a higher abundance of subordinates in the lagoon compared to lagoon abundances at higher resource levels (low: 283.7 ± 13.6, intermediate: 265.7 ± 14.2, high: 260.6 ± 15.8), while resource level variations had marginal effects on dominant abundances in the lagoon (low: 36.3 ± 5.5, intermediate: 36.8 ± 5.0, high: 38.7 ± 5.2). Furthermore, abundances of subordinates and dominants in bank and shelf patches were similar regardless of resource level except for subordinates at intermediate resources, for which abundances were higher in the bank (192.3 ± 17.7) than in the shelf patch (163.5 ±16.6). Apex predators were distributed equally among bank and shelf patches, with minimal effect of resource levels on their spatial distribution.

Discussion and Conclusions

In this study, I explored space use mechanisms for coexistence employed in a marine predator community by investigating the simultaneous effects of competition, predation, and IGP on the degree of spatial partitioning among multiple sympatric elasmobranch species and comparing to theoretical predictions. Biotelemetry results support our first prediction that spatial segregation occurred among species pairs linked via strong interference (i.e., one may kill the other, predator/prey, or IGP). I also found stronger spatial overlap among competing species but with some evidence that species prefer certain microhabitats. Finally, I predicted that the degree of preference for safer habitat would be higher for subordinate versus dominant mesopredators, which was mostly upheld.

Coexistence mechanisms within predator communities may include partitioning of diet, temporal activity and/or space (Vanak et al. 2013, Karanth et al. 2017). Within terrestrial predator communities characterized by strong interference or IGP, subordinate competitors frequently employ spatial partitioning from dominants to minimize encounter rates (Steinmetz et al. 2013, Dröge et al. 2017, Lonsinger et al. 2017), which conforms to predictions of IGP theory (Heithaus 2001). Similarly, I found that southern stingrays, blacktip, Caribbean reef, and subadult lemon sharks (prey or IG_{prey}) spatially segregated from bull, great hammerhead, and/or tiger sharks by varying in their preferred depth range, region, and/or exhibiting high UD dissimilarity (or low space use overlap). Our results further suggest that the greater the difference in body sizes between mesopredators and apex predators, the stronger the spatial partitioning employed, which align with predictions of our IBMs. For example, while Caribbean reef sharks differed from tiger sharks only in space use overlap (i.e. species exhibited high UD dissimilarity), southern stingrays, blacktip, and subadult lemon sharks differed from bull, great hammerhead, and tiger sharks not only in space use overlap, but also in preferred depth range, and region. Likewise, previous empirical observations from terrestrial carnivore communities have shown that while subordinate mesopredators largely spatially segregated from apex predators, dominant mesopredators mostly spatially overlapped with apex predators, achieving coexistence presumably via fine-scale behavioral avoidance (Steinmetz et al. 2013, Dröge et al. 2017). Although I did not investigate possible fine-scale avoidance by dominant mesopredators toward apex, this coexistence mechanisms may play an important role in preventing the loss of access to valuable resources (Heithaus 2001, Kimbrell et al. 2007, Gallagher et al. 2021). Our IBMs further predict that subordinate mesopredators should increase their spatial separation from apex under low resource levels. This is not surprising, as previous studies and theory suggest that the potential for interference increases when available prey decreases, resulting in the displacement of mesopredators to less risky or safer habitats (Polis et al. 1989, Steinmetz et al. 2013).

Potentially competing apex predatory sharks in Bimini showed some patterns of spatial partitioning. Specifically, bull and great hammerhead sharks exhibited high UD dissimilarity with tiger sharks (bull and great hammerhead core areas overlapped off southwest Bimini, whereas the core area of tiger sharks was located off North Bimini), while showing the same depth and region preferences. These results may suggest that this apex shark community is structured by behavioral interference competition, with tiger sharks being dominant over bull sharks, and great hammerheads being the least dominant (O'Shea et al. 2015). In line with predictions of the IFD with unequal competitors that differ in dominance, I indeed found a broader distribution for bull sharks than for tiger sharks; their space use covered the majority of available theoretically good habitat. However, contrary to expectations, I did not observe great hammerheads to have the broadest distribution among all three species. This species occupied a comparatively small fraction of available theoretically good habitat, which suggests that suitable habitat did not limit its distribution. This discrepancy may result from the presence of ecotourism provisioning conducted off southwest Bimini during the study period (Heim et al. 2021), which is also where great hammerheads were acoustically tagged and where their core area is located. Indeed, preliminary data analysis investigating the effects of provisioning on the space use of great hammerheads showed that provisioned sharks exhibited a constrained distribution centered around the provisioning dive site, a pattern that was enhanced during the provisioning season, while naïve individuals (i.e., sharks that were never visually or acoustically observed during provisioning events) exhibited a broader distribution that was markedly different in shape with their core area located away from the provisioning site (Heim et al., *in prep*).

Theory also predicts that coexistence among sympatric predators would require each species to maintain a competitive advantage in specific microhabitats (Brown 1989, 1998). Habitat-specific competitive advantages may lead to rapid spatial separation among competing species, and have been found in both marine and terrestrial ecosystems (Cresswell et al. 2001, Papastamatiou et al. 2018, Sabando et al. 2020). Tiger sharks exhibit greater affinities to seagrass microhabitats (Nowicki et al. 2021, Gallagher et al. 2021, 2022), which function as important feeding grounds for known tiger shark prey, including marine turtles (Short et al. 2007, Christianen et al. 2014, Fourqurean et al. 2019). Their cryptic coloration may enhance tiger shark camouflage over seagrass beds, leading to increased foraging success for tiger sharks in this microhabitat type (Heithaus and Dill 2002). Furthermore, adult tiger sharks may also be better suited for preying on turtles due to their dentition (Randall 1992, Heithaus et al. 2008), which may make them more likely to stalk seagrass microhabitats. Seagrass beds are more abundant on the northern side of North Bimini, hence may cause tiger sharks to largely exclude bull and great hammerheads from this available theoretically good habitat. Competing blacktip reef and grey reef sharks at a Pacific atoll show strong spatial separation across habitats, which may partially be due to the coloration of blacktip reef sharks giving them a cryptic advantage on sandflat and lagoon habitat (Papastamatiou et al. 2018).

Second, theory on two-species density-dependent habitat selection predicts that if the density of dominant tiger sharks is low compared to that of subordinate bull or great hammerhead sharks, then tiger sharks can be expected to be more specialist to seagrass beds (distribution more spatially constrained), and bull or great hammerheads more generalist (more broadly distributed) (Brown 1998). In Bimini, tiger sharks are reliably caught throughout the year but appear highly transient (Hansell et al. 2018, Smukall et al. 2022a, 2022b). In contrast, accurate local abundance estimates for bull and great hammerhead sharks are lacking. All three species show higher detection rates during the cooler winter months, however, bull and great hammerheads showed higher residency than tiger sharks at any one time (van Zinnicq Bergmann, unpubl.) and generally appear in relatively high abundances at local provisioning sites (Guttridge et al. 2017, Heim et al. 2021, van Zinnicq Bergmann, pers. obs.).

Finally, apex shark species may simply match the distribution of particular prey resources. For example, bull and great hammerhead distributions overlap with, in addition to the provisioning site, natural and artificial coral reef habitat off southwest through northwest Bimini where large reef fish are generally seen. The seagrass beds and sand flats off North Bimini are important foraging areas for turtles and dolphins (Melillo et al. 2009, Melillo-Sweeting et al. 2022), which are known prey items for large tiger sharks (Lowe et al. 1996, Aines et al. 2018).

Our approach, combining diverse analytical methodologies, provides novel insight in the space use mechanisms driving coexistence among marine predator communities. However, several caveats should be considered. Aside from the low sample size for some species (e.g., tiger sharks, n = 3) and locations where individuals were acoustically tagged (van Zinnicq Bergmann et al. 2022), our suppositions of possible ecological interactions among elasmobranch species were based on limited dietary data. Detailed and accurate local dietary information is important for understanding trophic relationships, providing insights in interaction type and strength. While our interaction classifications were likely broadly accurate, interaction strengths are likely to vary among species and in space and time, mediated by fluctuations in their prey ‘landscape’ (abundance and distribution) (Vanak et al. 2013, Karanth et al. 2017, Morosinotto et al. 2017). Incorporating novel, minimally invasive, and efficient shark dietary assessment methods (e.g., DNA metabarcoding from cloacal swabs; van Zinnicq Bergmann et al. 2021) and underwater video surveys of primary prey items (Lester et al. 2021) will provide a valuable next step to better understand the relative impacts of interspecific interactions on the space use mechanisms employed within marine predator communities.

The dependence on simulation models makes the assessment of space use mechanisms for coexistence within large-bodied predator communities challenging (Papastamatiou et al. 2018). Nevertheless, our study provides convincing evidence that competitive interactions and predator avoidance concurrently help promote spatial separation among co-occurring elasmobranch species. Furthermore, being able to forecast how the distributions within multi-species predator communities are affected by the presence of a constituent species has important ramifications for conservation. The loss of apex sharks in particular may lead to cascades with substantial changes in the distribution of mesopredators within multi-species predator communities (e.g., Towner et al. 2022).

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Tables

Table 1. Variables considered for the random forest regression model used for predicting missing water temperature values at all receiver locations simultaneously

Type of variable	Variable name	Unit	Source
Target	Logged water temperature	°C	1
Input	Air temperature	°C	2
	Atmospheric pressure	mb	2
	Cloud cover	%	2
	Day of year		1
	Hour of day		1
	Lunar illumination	%	3
	Precipitation	mm	2
	Receiver location		4
	Sea surface temperature	°C	5
	Sun angle	° from horizon	6
	Tidal phase	Ebbing/flooding	7
	Wind direction	° (0-360)	2
	Wind speed	km/h	2

Sources: 1) Water temperature loggers, 2) www.worldweatheronline.com, 3) Lunar R package[a];

4) Metadata; 5) www.seatemperature.info; 6) oce R package[b]; 7) www.noaa.com

[a] Lazaridis, E., 2022. lunar: Lunar Phase & Distance, Seasons and Other Environmental Factors. R package version 0.2-01. Available from CRAN

[b] Kelley, D., Richards, C., 2022. oce: Analysis of Oceanographic Data. R package version 1.7-6, https://CRAN.R-project.org/package=oce

Table 2. Acoustic detection data for elasmobranch species, including subadult lemon shark subset in Bimini, The Bahamas.

Species	n	Average size (cm)	Total COAs	Avg COAs	Average day at liberty
Blacktip shark	9	109.6 ± 9.7	12,522	1,391.3	646.1 ± 283
Bull shark	15	184.3 ± 11.1	9,967	664.5	592.1 ± 306.1
Caribbean reef shark	7	141.6 ± 13.9	23,132	3,304.6	744.7 ± 315.2
Great hammerhead shark	12	234.7 ± 16.6	13,280	1,106.7	586.4 ± 356.6
Lemon shark (adult)	2	199.5 ± 0.7	1,093	546.5	832.2 ± 154.3
Lemon shark (subadult)	6	162.2 ± 19.3	4,544	757.3	653.1 ± 187.1
Nurse shark	15	166.4 ± 20.8	46,457	3,097.1	825.5 ± 177.0
Southern stingray	16	70.8 ± 21.8	10,856	678.5	395.2 ± 308.2
Tiger shark	3	280 ± 5.0	368	122.7	633.5 ± 291.2

Size is precaudal length for sharks and curved disk width for stingrays.

Table 3. Confusion-matrix derived performance metrics of the trained random forest model applied to the holdout data set

Species	Accuracy	Sensitivity (true positive rate)	Specificity (true negative rate)	Fall-out (false positive rate)	Miss rate (false negative rate)	Precision (positive predictive value)
Blacktip shark	0.86	0.84	0.88	0.12	0.16	0.87
Bull shark	0.88	0.97	0.79	0.21	0.03	0.82
Caribbean reef shark	0.98	0.99	0.97	0.03	0.01	0.97
Great hammerhead shark	0.91	0.98	0.84	0.16	0.02	0.86
Lemon shark (adult)	0.87	0.88	0.86	0.14	0.12	0.86
Lemon shark (subadult)	0.76	0.78	0.74	0.26	0.22	0.75
Nurse shark	0.89	0.95	0.82	0.18	0.05	0.84
Southern stingray	0.84	0.91	0.77	0.23	0.09	0.79
Tiger shark	0.80	0.81	0.79	0.21	0.19	0.79

Accuracy (i.e. the number of correctly classified predictions over the total number of predictions), sensitivity, specificity, fall-out, miss rate and precision per species and different ontogenetic stage, monitored within Bimini

Table 4. Confusion-matrix derived performance metrics of the trained random forest model applied to the holdout data set. Values are based on COAs calculated using 60-min time bins.

Species	**Accuracy**	**Sensitivity (true positive rate)**	**Specificity (true negative rate)**	**Fall-out (false positive rate)**	**Miss rate (false negative rate)**	**Precision (positive predictive value)**
Blacktip shark	0.87	0.85	0.89	0.11	0.15	0.88
Bull shark	0.87	0.96	0.78	0.22	0.04	0.82
Caribbean reef shark	0.98	0.99	0.97	0.03	0.01	0.97
Great hammerhead shark	0.91	0.98	0.84	0.16	0.02	0.86
Lemon shark (adult)	0.89	0.89	0.89	0.11	0.11	0.88
Lemon shark (subadult)	0.78	0.83	0.74	0.26	0.17	0.76
Nurse shark	0.89	0.95	0.82	0.18	0.05	0.84
Southern stingray	0.84	0.92	0.76	0.24	0.08	0.79
Tiger shark	0.81	0.81	0.8	0.2	0.19	0.82

Accuracy (i.e. the number of correctly classified predictions over the total number of predictions), sensitivity, specificity, fall-out, miss rate and precision per species and different ontogenetic stage monitored within Bimini.

Table 5. Confusion-matrix derived performance metrics the of trained random forest model applied to the holdout data set. Values are based on COAs calculated with 500 m buffers around receivers.

Species	Accuracy	Sensitivity (true positive rate)	Specificity (true negative rate)	Fall-out (false positive rate)	Miss rate (false negative rate)	Precision (positive predictive value)
Blacktip shark	0.87	0.83	0.91	0.09	0.17	0.9
Bull shark	0.87	0.97	0.78	0.22	0.03	0.81
Caribbean reef shark	0.98	0.99	0.97	0.03	0.01	0.97
Great hammerhead shark	0.91	0.98	0.84	0.16	0.02	0.86
Lemon shark (adult)	0.86	0.87	0.84	0.16	0.13	0.85
Lemon shark (subadult)	0.75	0.82	0.66	0.34	0.18	0.72
Nurse shark	0.88	0.93	0.84	0.16	0.07	0.85
Southern stingray	0.83	0.9	0.76	0.24	0.1	0.79
Tiger shark	0.85	0.85	0.86	0.14	0.15	0.86

Accuracy (i.e. the number of correctly classified predictions over the total number of predictions), sensitivity, specificity, fall-out, miss rate and precision per species and different ontogenetic stage monitored within Bimini.

Table 6. Confusion-matrix derived performance metrics of the trained random forest model applied to the holdout data set. Values are based on COAs calculated with 900 m buffers around receivers.

Species	**Accuracy**	**Sensitivity (true positive rate)**	**Specificity (true negative rate)**	**Fall-out (false positive rate)**	**Miss rate (false negative rate)**	**Precision (positive predictive value)**
Blacktip shark	0.87	0.83	0.91	0.09	0.17	0.9
Bull shark	0.87	0.97	0.78	0.22	0.03	0.81
Caribbean reef shark	0.98	0.99	0.97	0.03	0.01	0.97
Great hammerhead shark	0.91	0.98	0.84	0.16	0.02	0.86
Lemon shark (adult)	0.86	0.87	0.84	0.16	0.13	0.85
Lemon shark (subadult)	0.75	0.82	0.66	0.34	0.18	0.72
Nurse shark	0.88	0.93	0.84	0.16	0.07	0.85
Southern stingray	0.83	0.9	0.76	0.24	0.1	0.79
Tiger shark	0.85	0.85	0.86	0.14	0.15	0.86

Accuracy (i.e. the number of correctly classified predictions over the total number of predictions), sensitivity, specificity, fall-out, miss rate and precision per species and different ontogenetic stage monitored within Bimini.

Table 7. Seasonal standardized values of dissimilarity in spatial utilization distributions among elasmobranch species quantified using the earth mover's distance (FastEMD) algorithm.

Species	**Blacktip**	**Bull**	**Caribbean reef**	**Great hammerhead**	**Lemon (adult)**	**Lemon (subadult)**	**Nurse**	**Southern stingray**	**Tiger**
Blacktip		0.27	0.29	0.3	0.27	*0.17*	0.31	0.21	0.39
Bull	0.37		*0.12*	**0.06**	*0.11*	0.24	**0.08**	*0.13*	0.51
Caribbean reef	0.31	0.22		*0.16*	*0.14*	0.25	*0.17*	*0.18*	0.56
Great hammerhead	0.39	**0.04**	0.26		*0.1*	0.24	**0.05**	*0.14*	0.53
Lemon (adult)	0.24	0.25	0.24	0.27		*0.18*	*0.12*	*0.12*	0.57
Lemon (subadult)	*0.18*	0.25	0.2	0.27	0.22		0.27	*0.14*	0.51
Nurse	0.36	**0.08**	0.24	**0.07**	0.24	0.24		*0.17*	0.55
Southern stingray	0.21	0.23	*0.16*	0.25	*0.19*	**0.08**	0.22		0.5
Tiger	0.33	0.36	0.33	0.39	0.25	0.35	0.38	0.33	

Summer and winter values are shown above and below the black-filled diagonal cells, respectively. Boldfaced, italicized, and default type style values denote low, moderate, and high UD dissimilarity, respectively.

Table 8. Differences in preferred depth (m) among elasmobranch species pairs. Preferred depth was assessed using resource selection functions, implemented via random forest machine learning algorithms (see Figure 7).

Species	Blacktip	Bull	Caribbean reef	Great hammerhead	Lemon (adult)	Lemon (subadult)	Nurse	Southern stingray	Tiger
Blacktip									
Bull	12.5								
Caribbean reef	10	2.5							
Great hammerhead	12.5	0	2.5						
Lemon (adult)	1	11.5	9	11.5					
Lemon (subadult)	0	12.5	10	12.5	1				
Nurse	16	3.5	6	3.5	15	16			
Southern stingray	0	12.5	10	12.5	1	0	16		
Tiger	9	3.5	1	3.5	8	9	7	9	

Table 9. Preferred region comparisons among elasmobranch species pairs; 0: different, 1: identical. Preferred region was assessed using resource selection functions, implemented via random forest machine learning algorithms. Based on Figure 8.

Species	**Blacktip**	**Bull**	**Caribbean reef**	**Great hammerhead**	**Lemon (adult)**	**Lemon (subadult)**	**Nurse**	**Southern stingray**	**Tiger**
Blacktip									
Bull	0								
Caribbean reef	0	1							
Great hammerhead	0	1	1						
Lemon (adult)	0	0	0	0					
Lemon (subadult)	0	0	0	0	1				
Nurse	0	1	1	1	0	0			
Southern stingray	0	0	0	0	1	1	0		
Tiger	0	1	1	1	0	0	1	0	

Figures

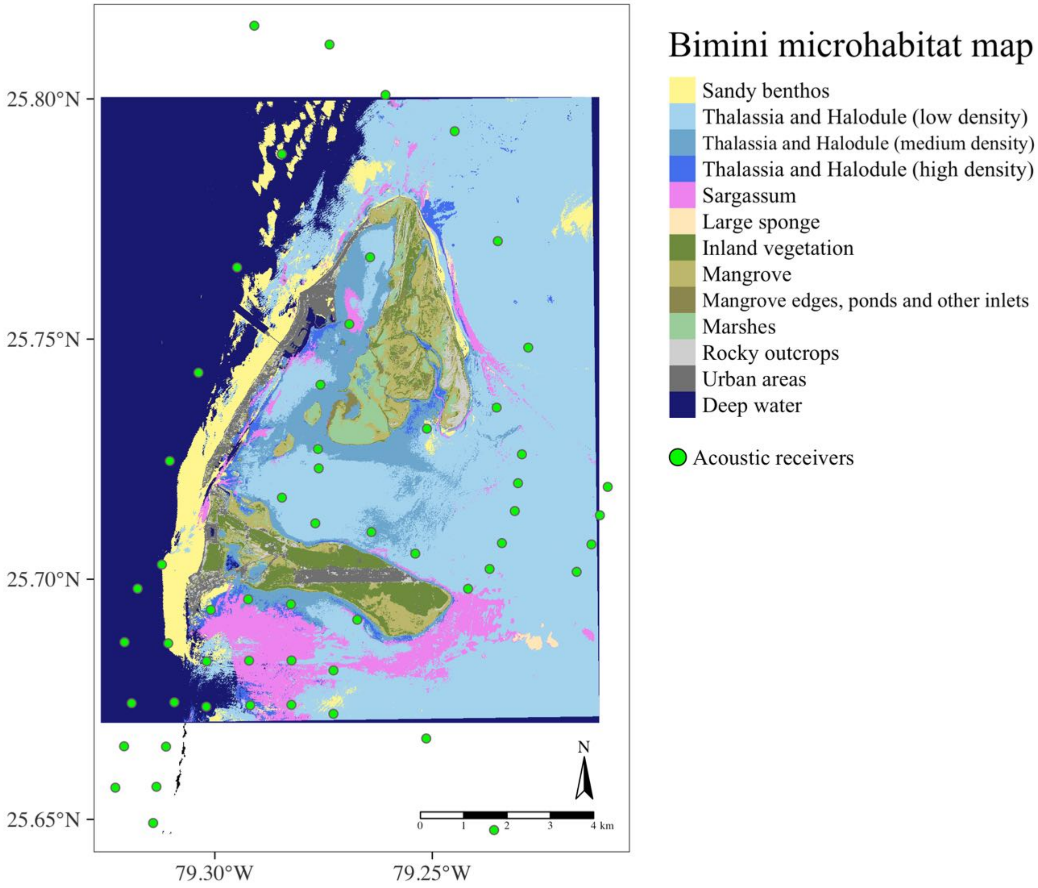

Figure 1. Bimini microhabitat classification raster overlaid with locations of acoustic receivers (green dots).

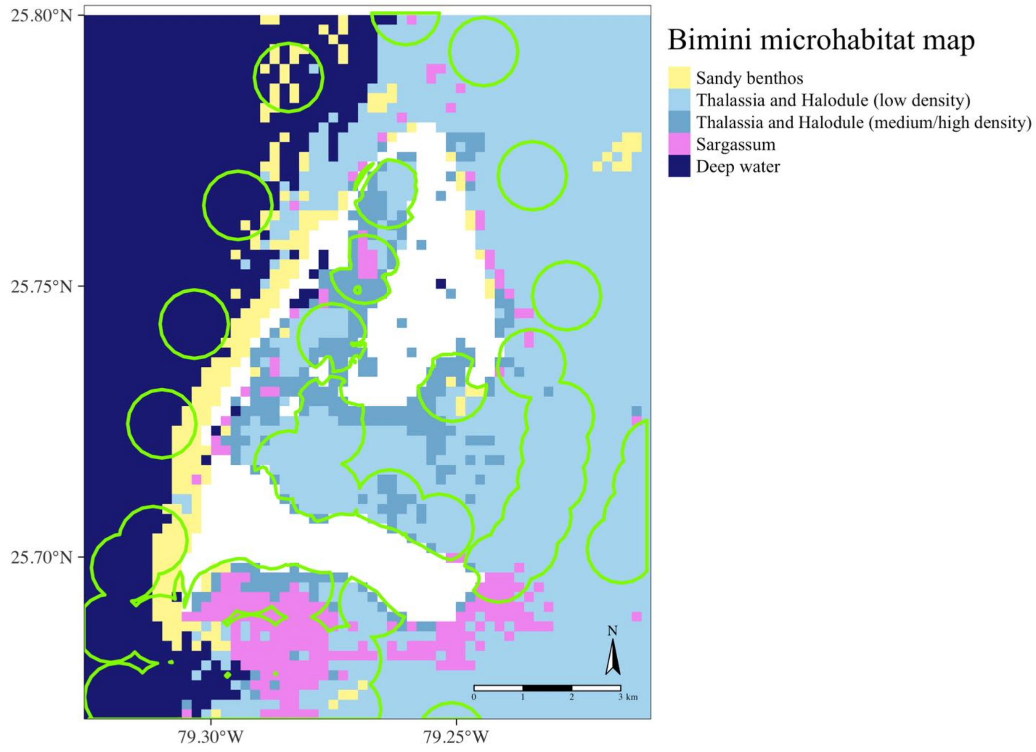

Figure 2. Bimini microhabitat classification raster drawn at 200 m pixel resolution, overlaid with available resource units, which represent 700 m buffers around each acoustic receiver location, shown as green lines.

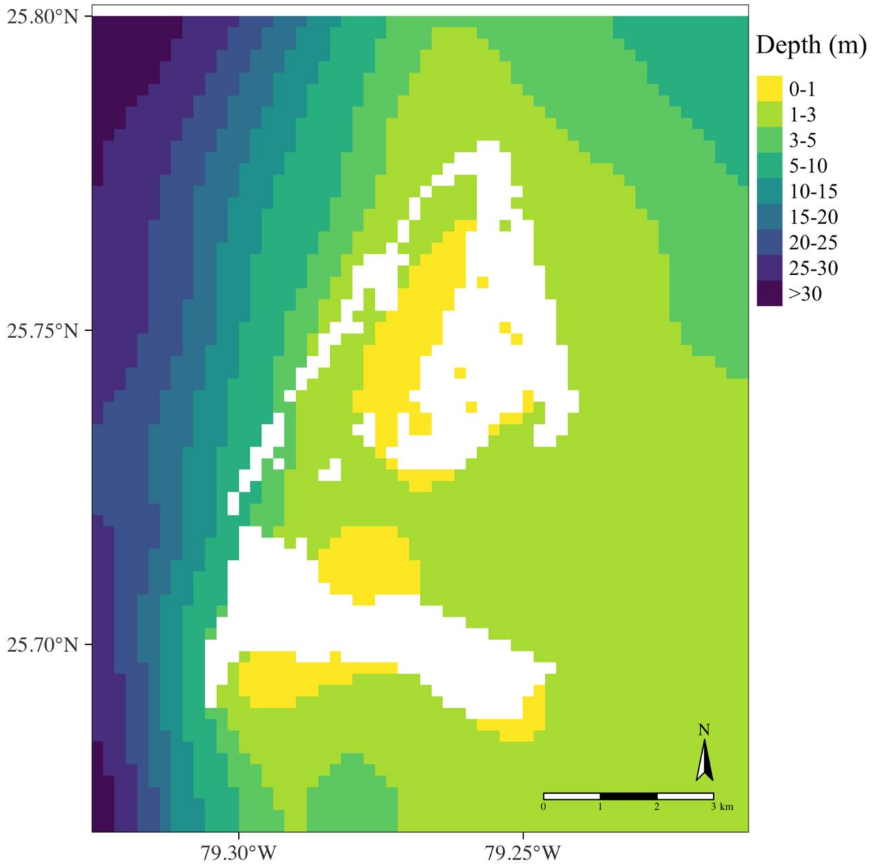

Figure 3. Bimini depth raster generated via ordinary Kriging, drawn at 200 m pixel resolution.

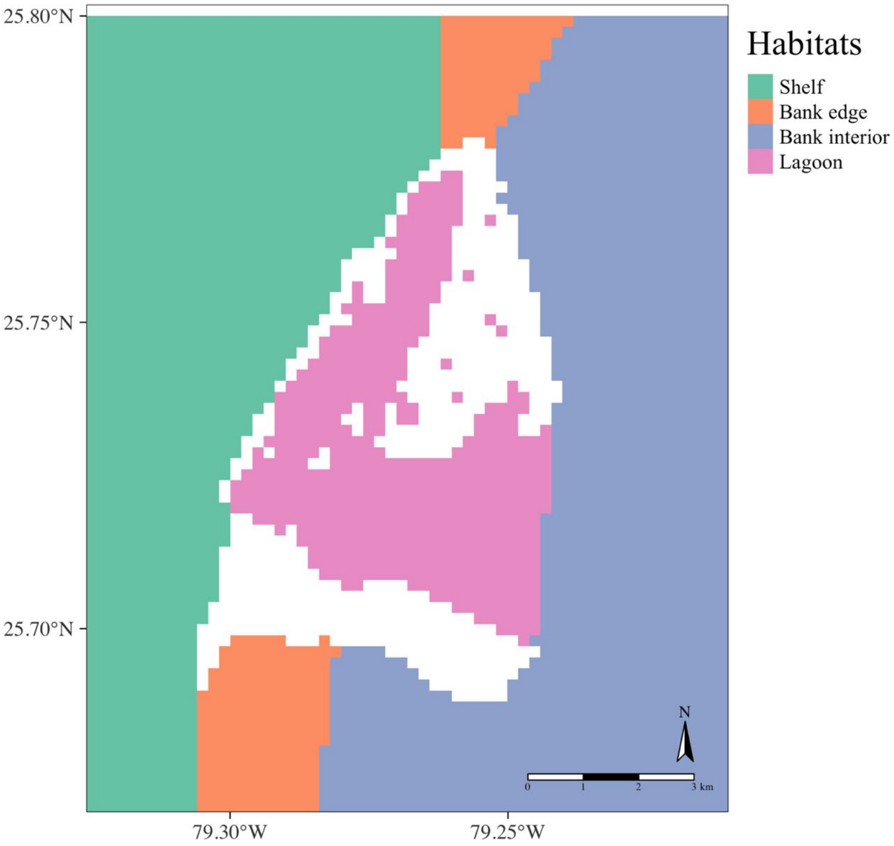

Figure 4. Bimini raster whereby the marine environment is split up in habitats, drawn at 200 m pixel resolution.

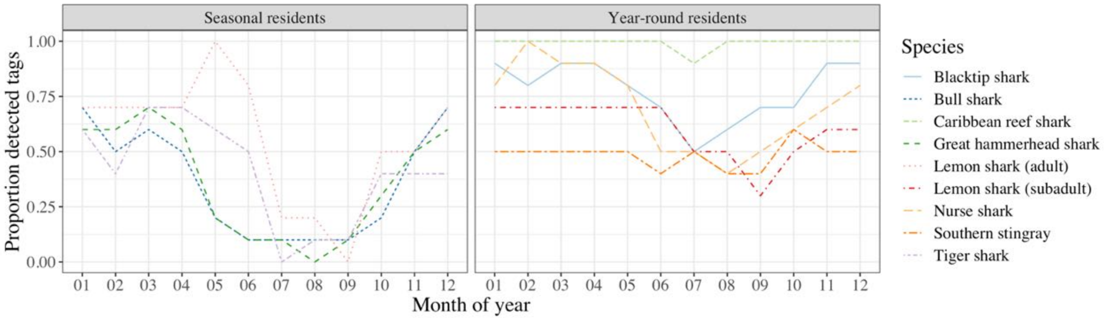

Figure 5. Proportional tags detected (number of tags detected divided by the number of tags deployed) on the acoustic receiver array per species, aggregated per month and across years.

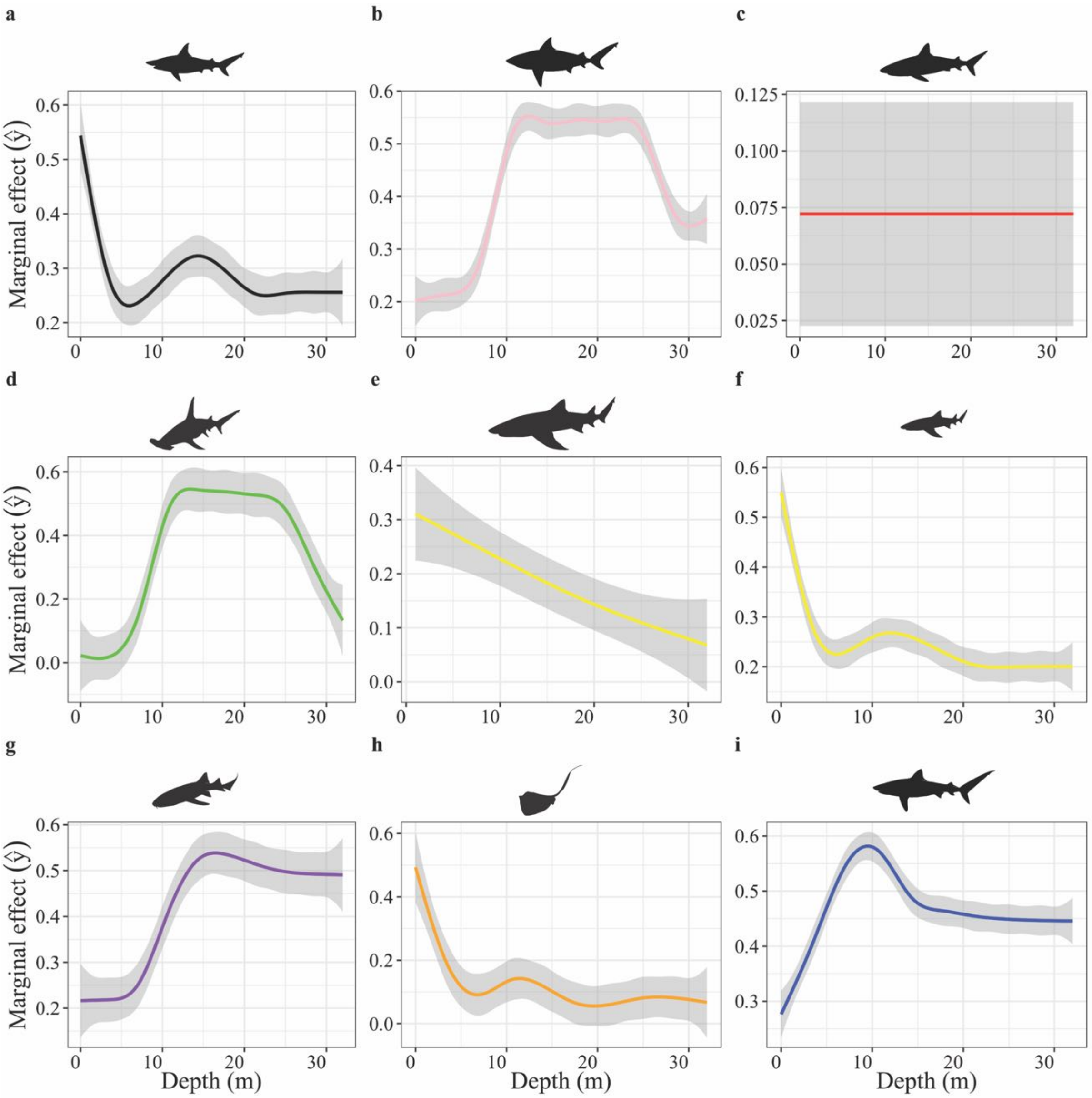

Figure 6. Preferred depth use for a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sharks, h) southern stingrays, i) tiger sharks. Preferred depth use was determined using resource selection functions, implemented via random forest machine learning algorithms.

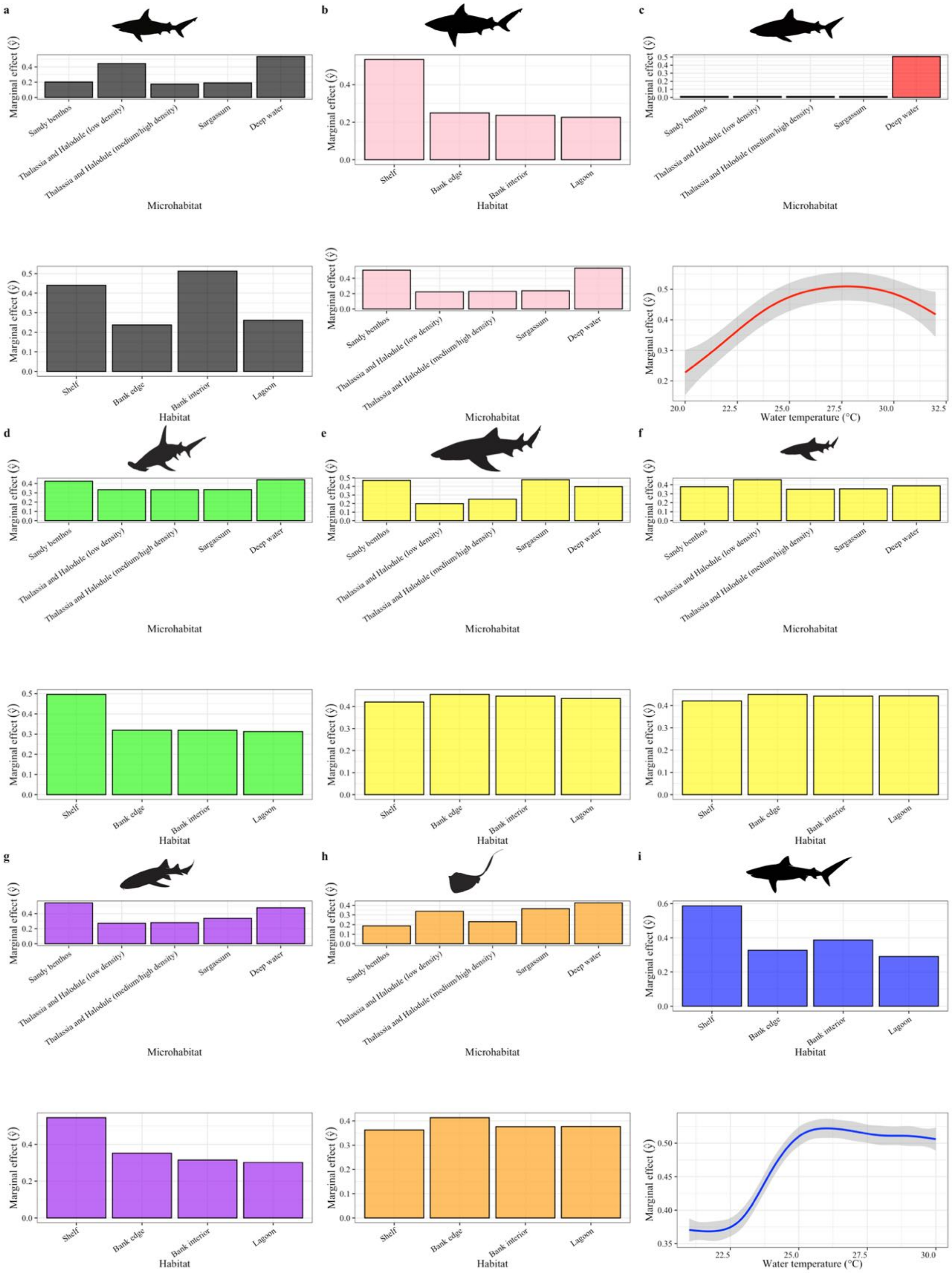

Figure 7. Univariate partial dependency plots for second and third most important predictors. a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sarks, h) southern stingrays, i) tiger sharks.

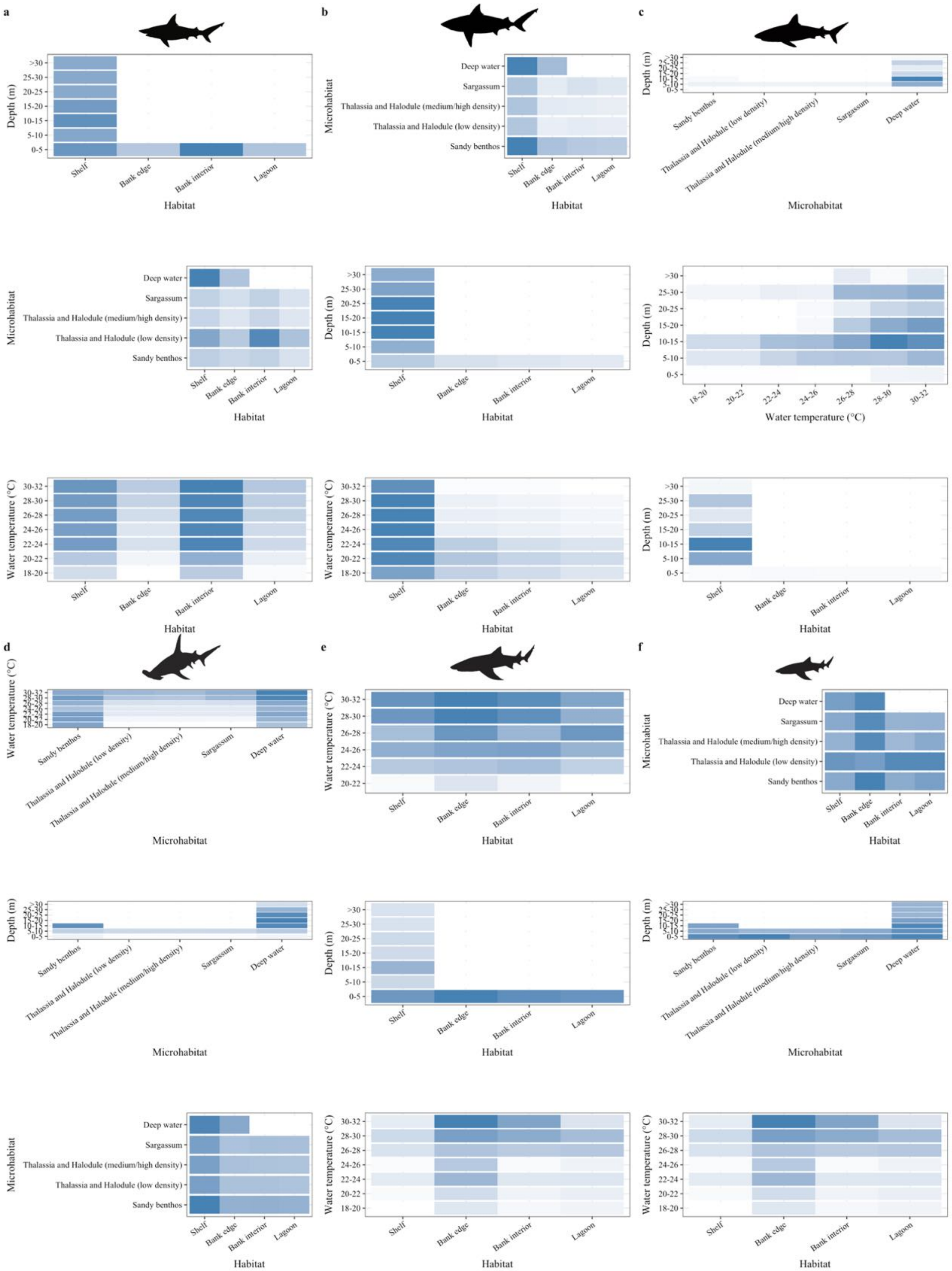

Figure 8. Bivariate interaction partial dependency plots ranked by most important (top) interaction to least important (bottom). a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sharks, h) southern stingrays, i) tiger sharks.

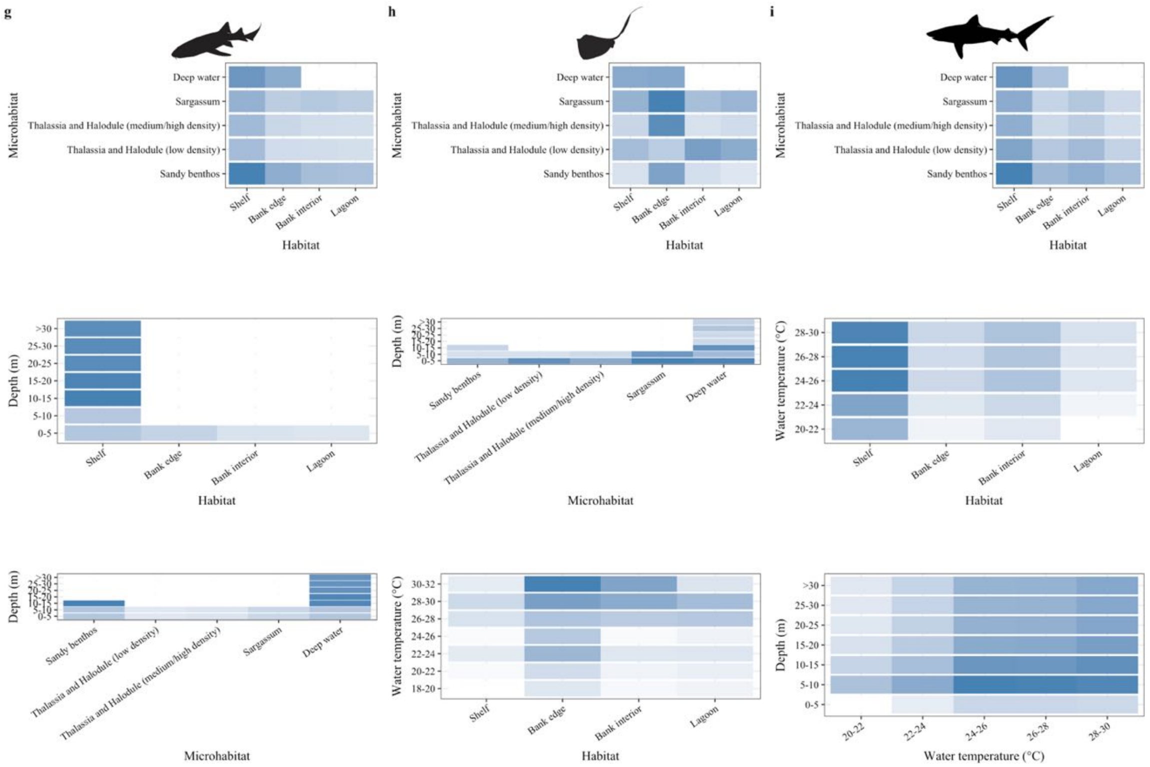

Figure 8 (continued). Bivariate interaction partial dependency plots ranked by most important (top) interaction to least important (bottom). a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sharks, h) southern stingrays, i) tiger sharks.

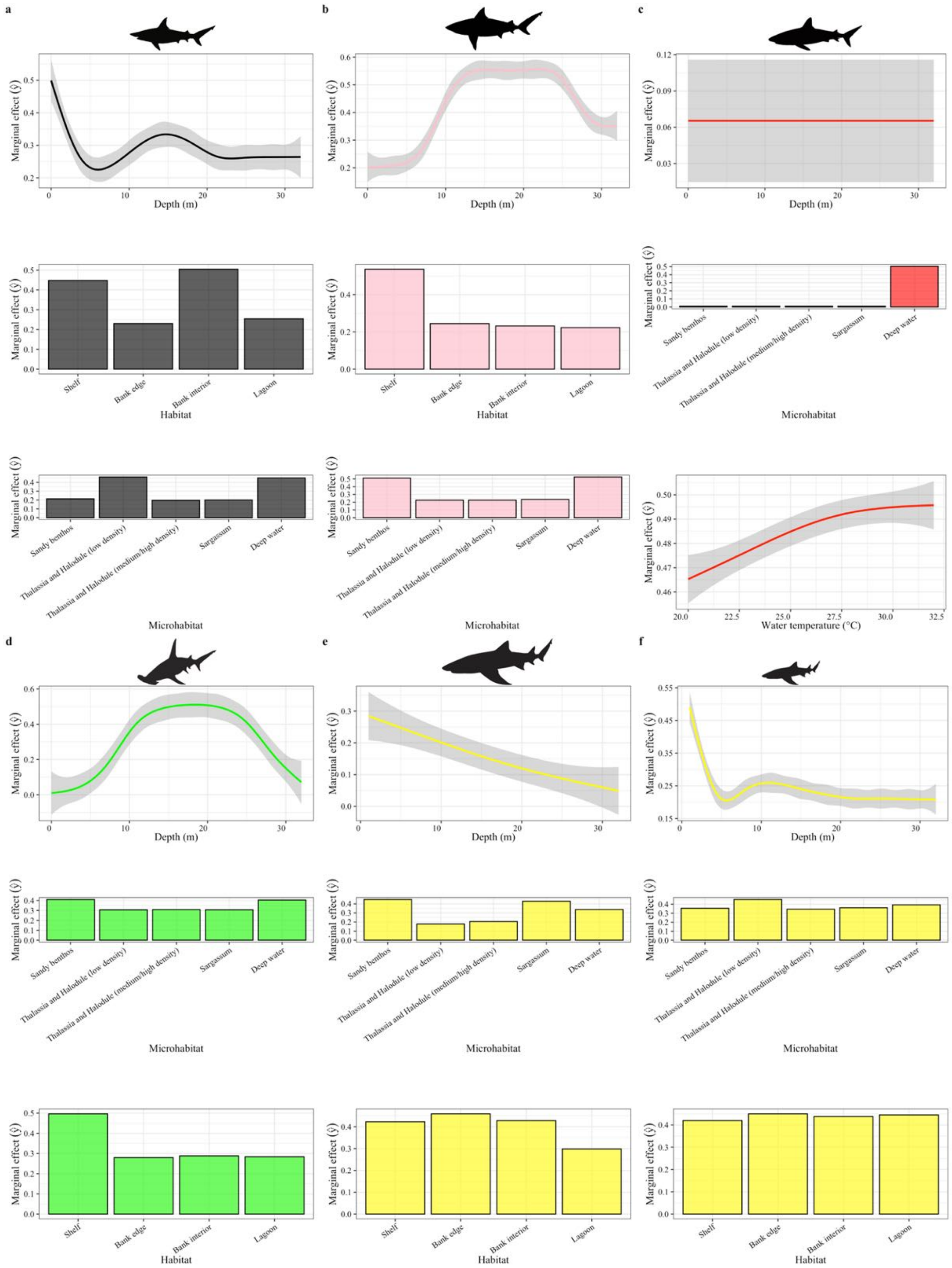

Figure 9. Univariate partial dependency plots of the top three most important predictors for a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sharks, h) southern stingrays, i) tiger sharks. Based on COA calculation time-bin segments of 60 min.

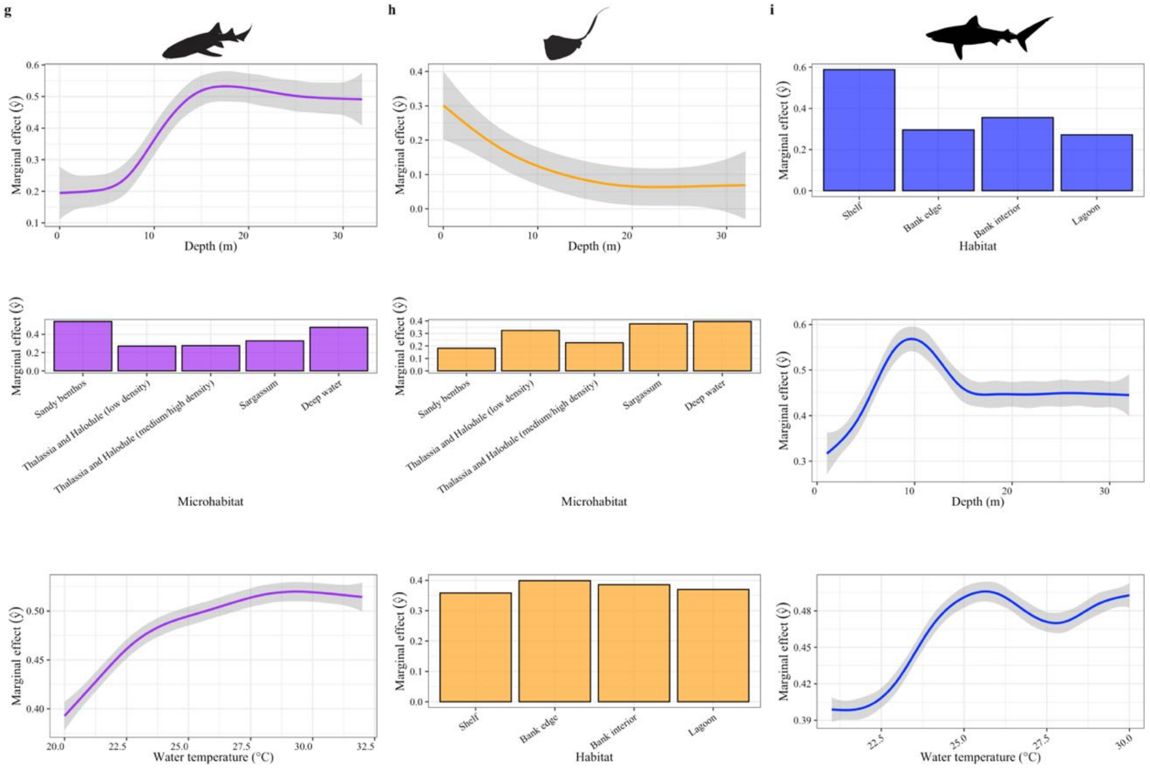

Figure 9 (continued). Univariate partial dependency plots of the top three most important predictors for a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sharks, h) southern stingrays, i) tiger sharks. Based on COA calculation time-bin segments of 60 min.

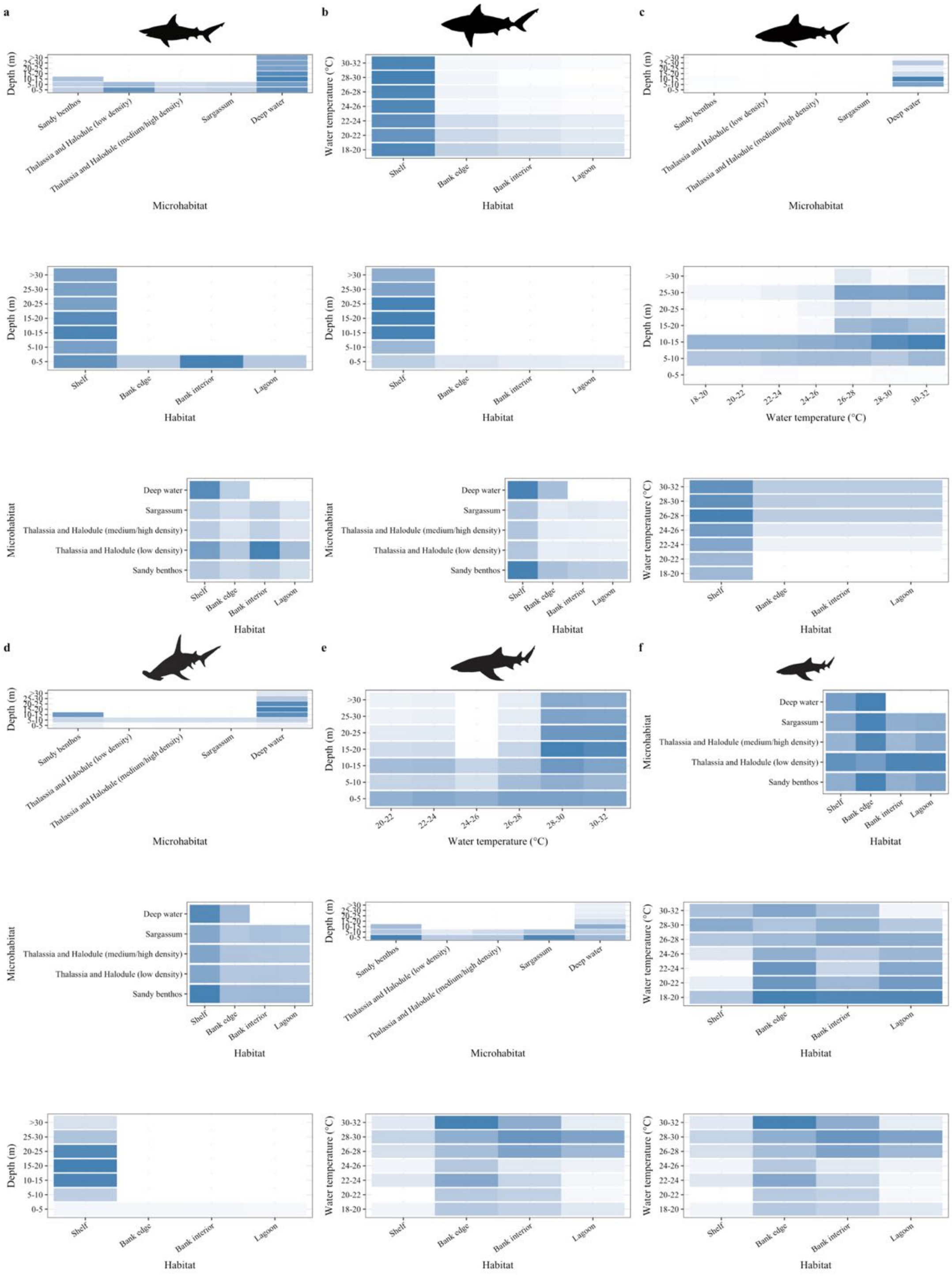

Figure 10. Bivariate interaction partial dependency plots ranked by most important (top) interaction to least important (bottom). a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sharks, h) southern stingrays, i) tiger sharks. Based on COA calculation time-bin segments of 60 min.

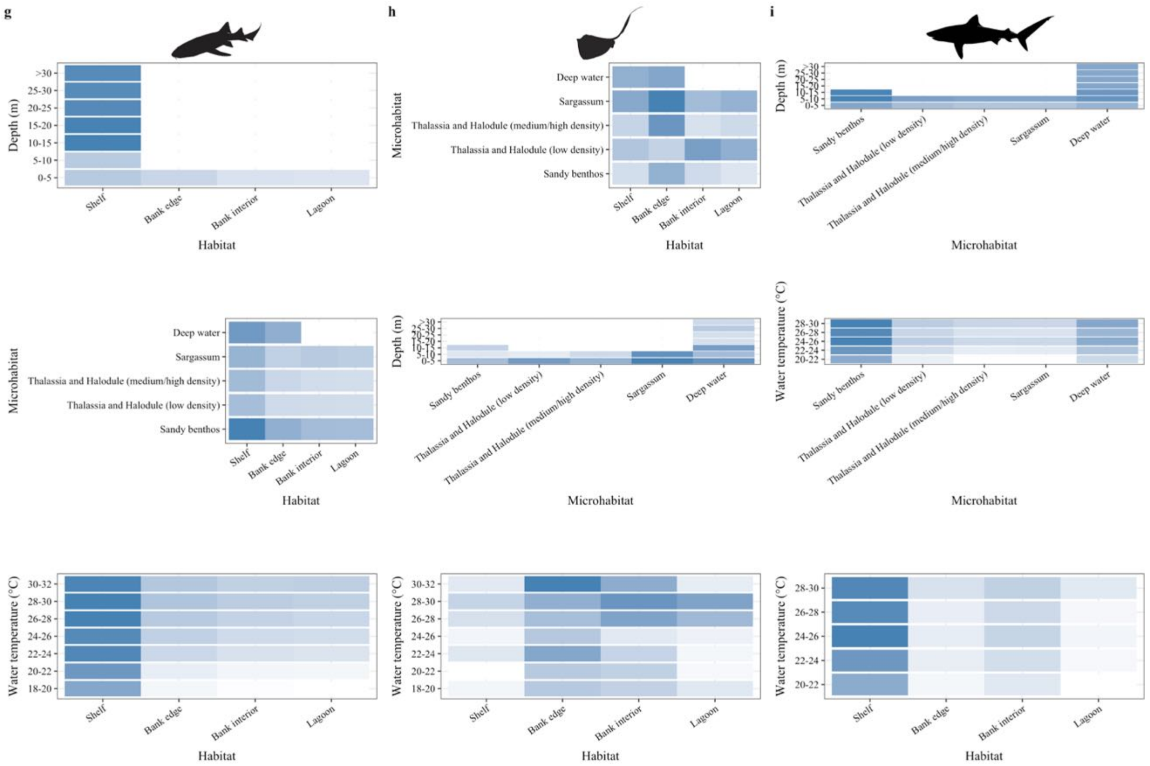

Figure 10 (continued). Bivariate interaction partial dependency plots ranked by most important (top) interaction to least important (bottom). a) blacktip sharks, b) bull sharks, c) Caribbean reef sharks, d) great hammerhead sharks, e) adult lemon sharks, f) subadult lemon sharks, g) nurse sharks, h) southern stingrays, i) tiger sharks. Based on COA calculation time-bin segments of 60 min.

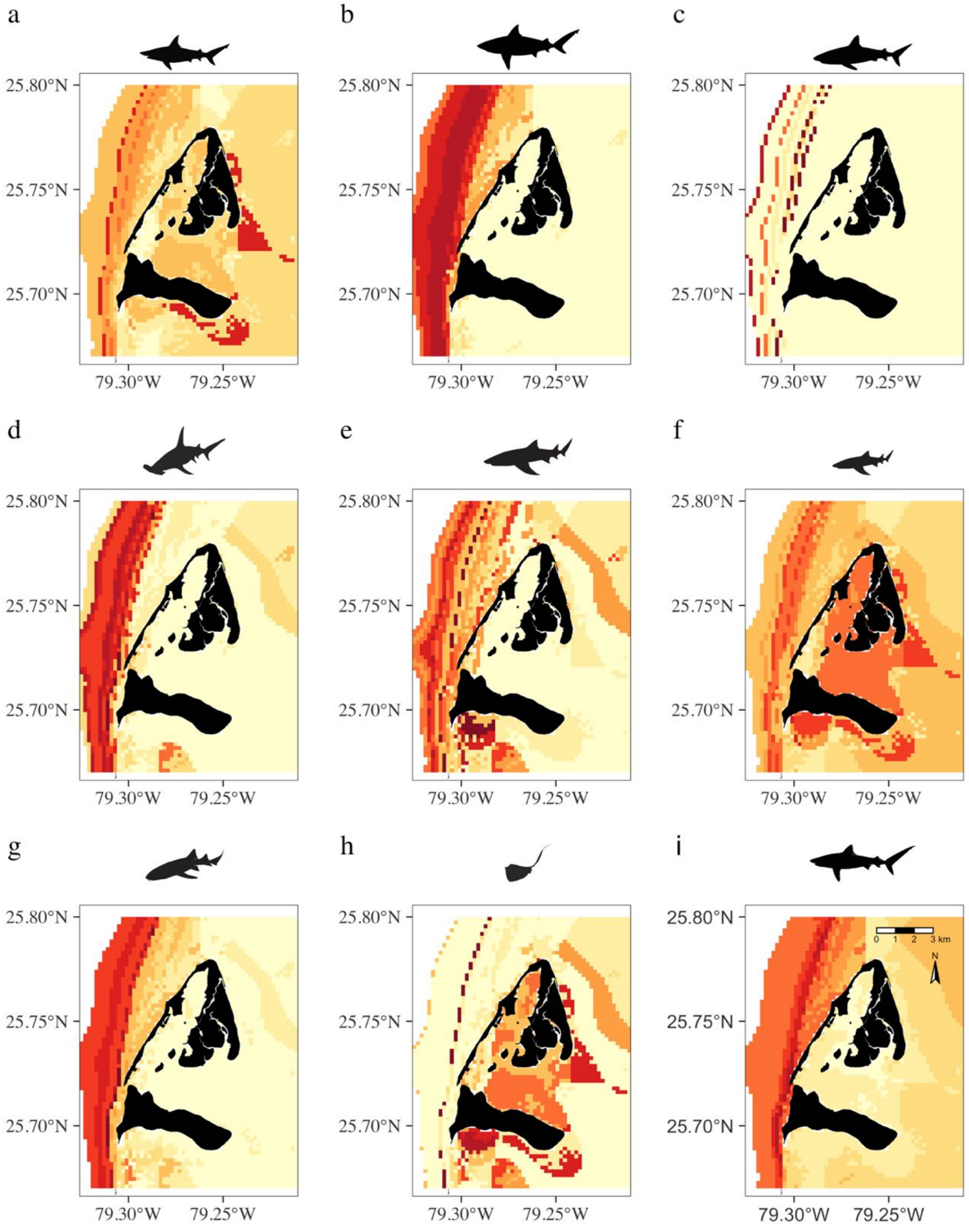

Figure 11. Seasonal predicted and extrapolated probability of relative selection. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k, bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Based on COA calculation time-bin segments of 60 min.

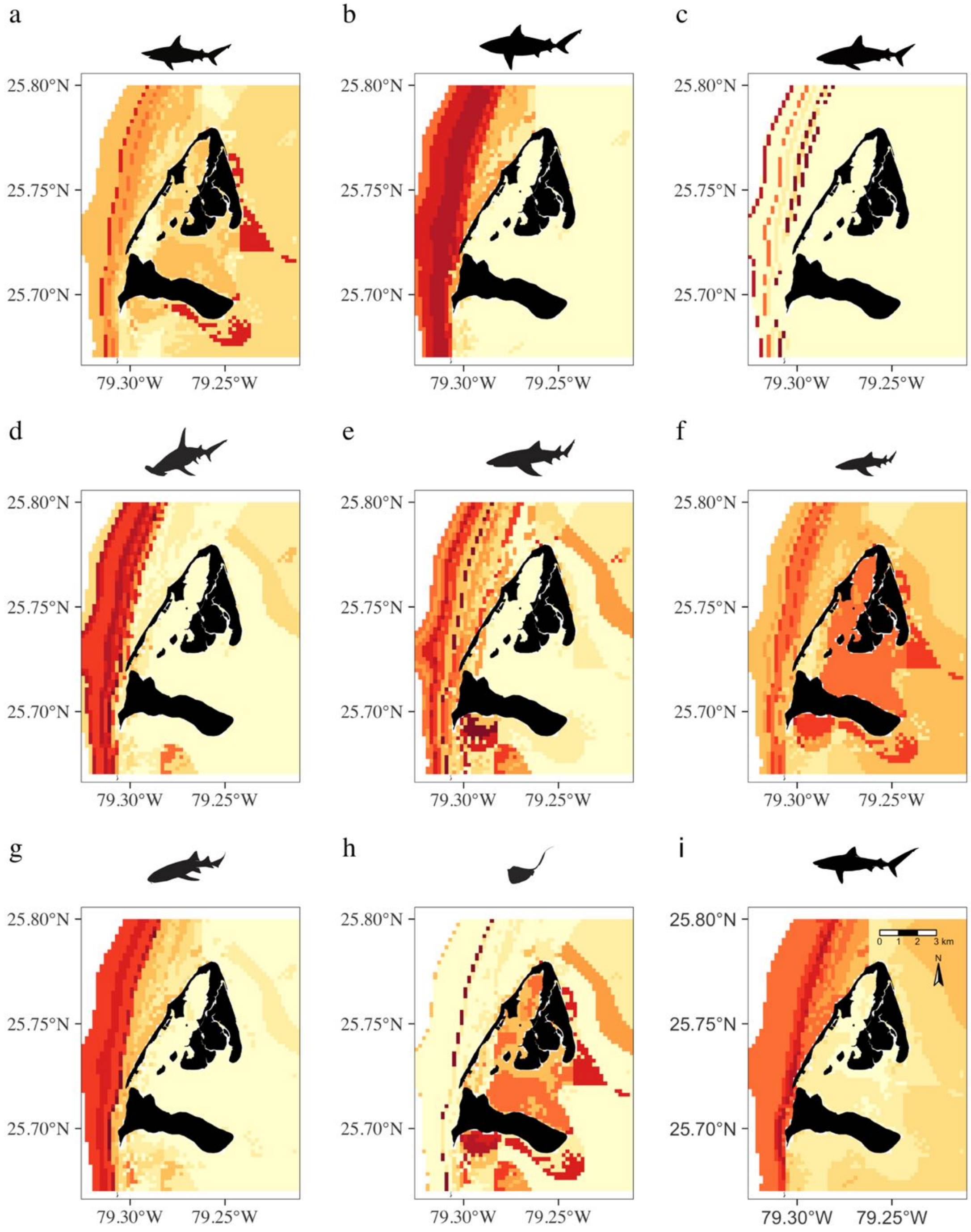

Figure 11 (continued). Seasonal predicted and extrapolated probability of relative selection. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k, bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Based on COA calculation time-bin segments of 60 min.

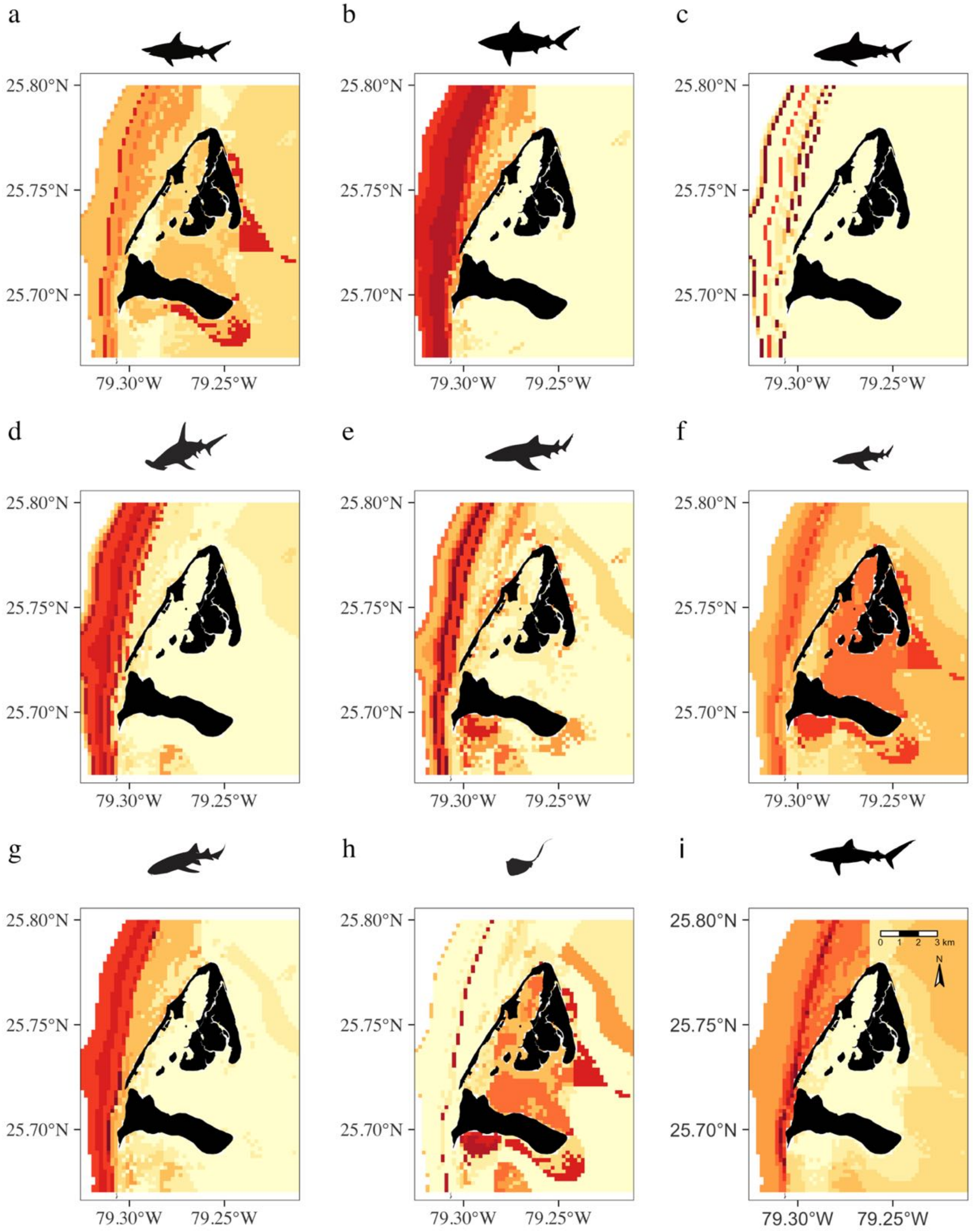

Figure 12. Seasonal predicted and extrapolated probability of relative selection. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k, bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Based on available resource use buffers of 500.

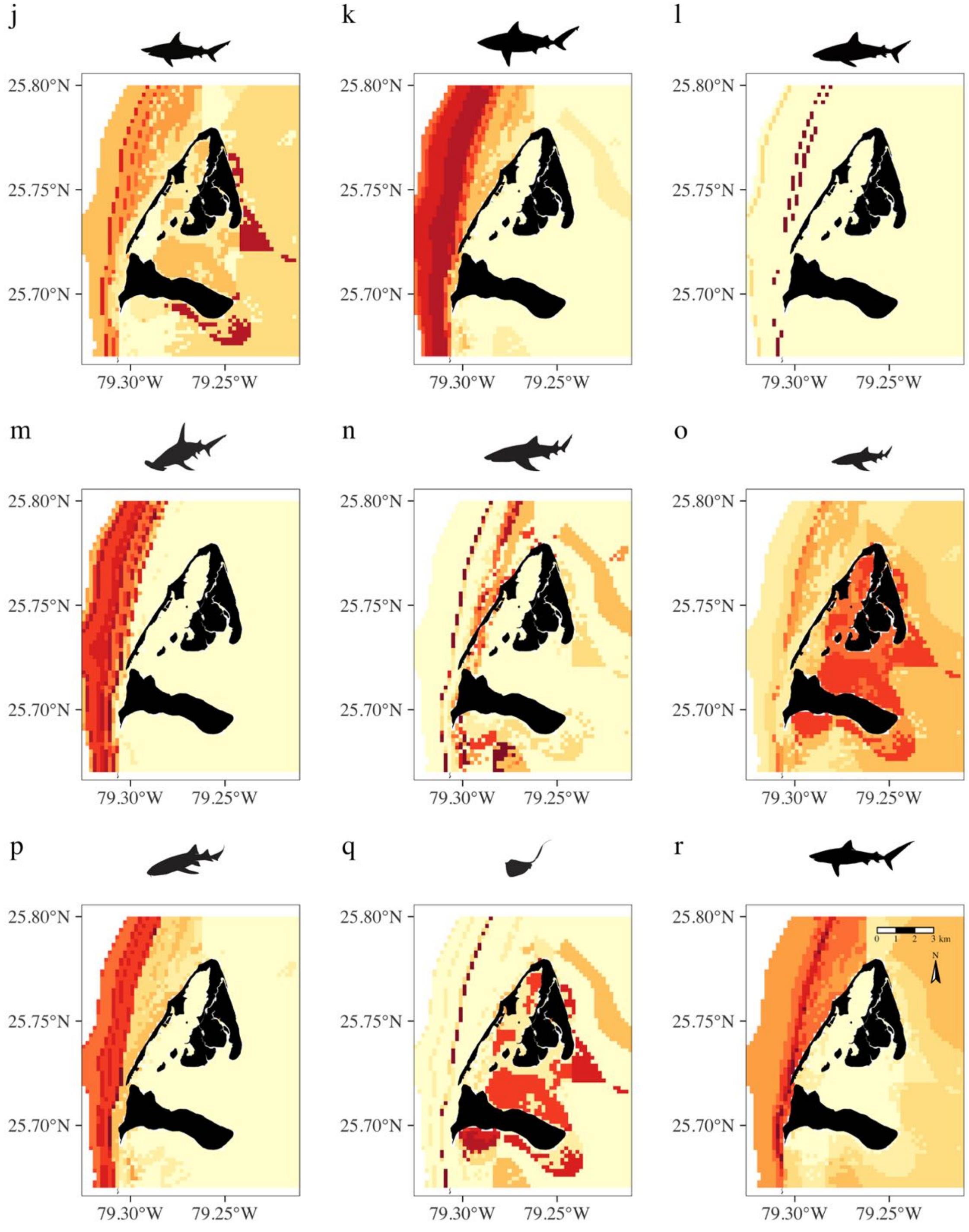

Figure 12 (continued). Seasonal predicted and extrapolated probability of relative selection. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k, bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Based on available resource use buffers of 500 m.

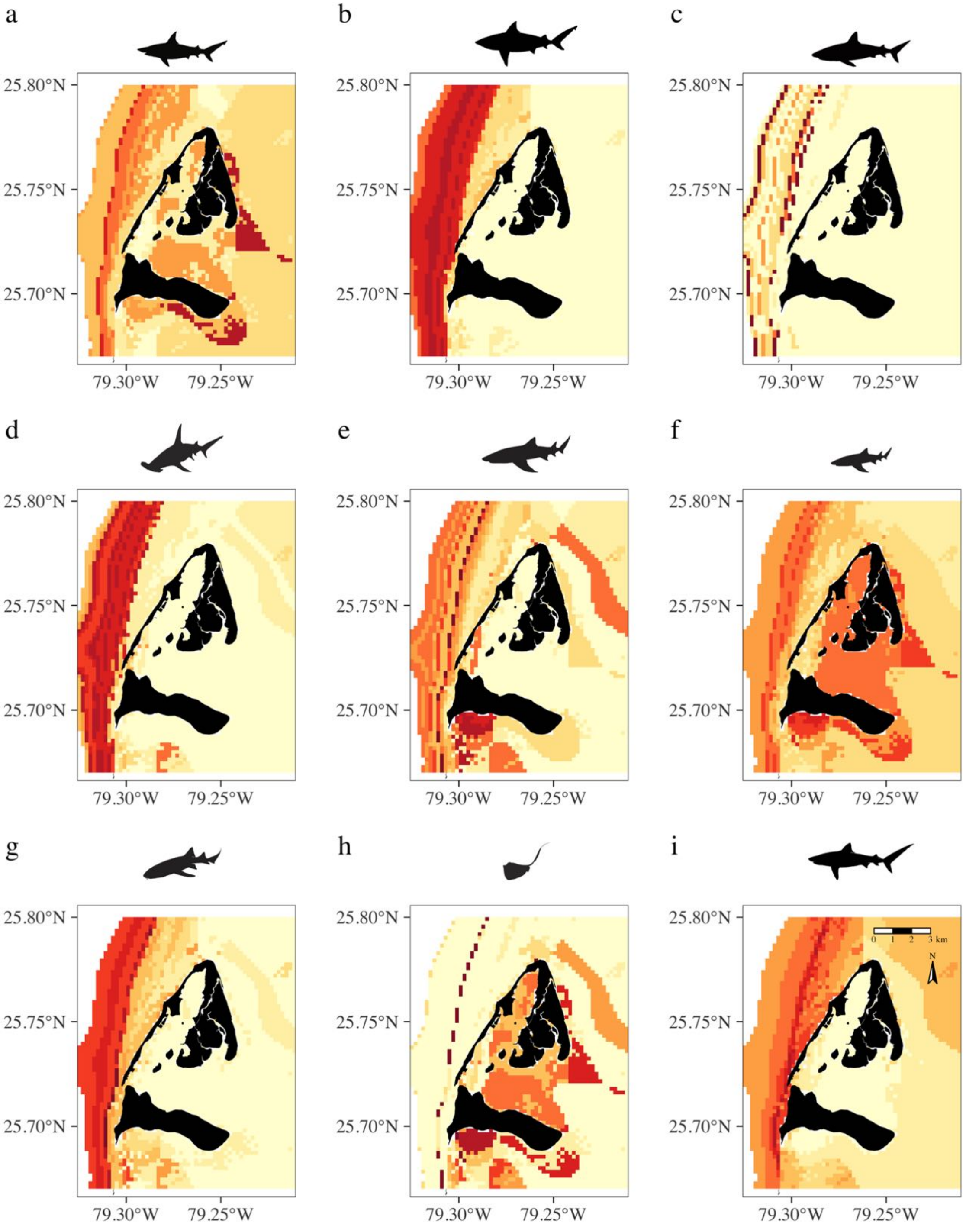

Figure 13. Seasonal predicted and extrapolated probability of relative selection. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k, bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Based on available resource use buffers of 900 m.

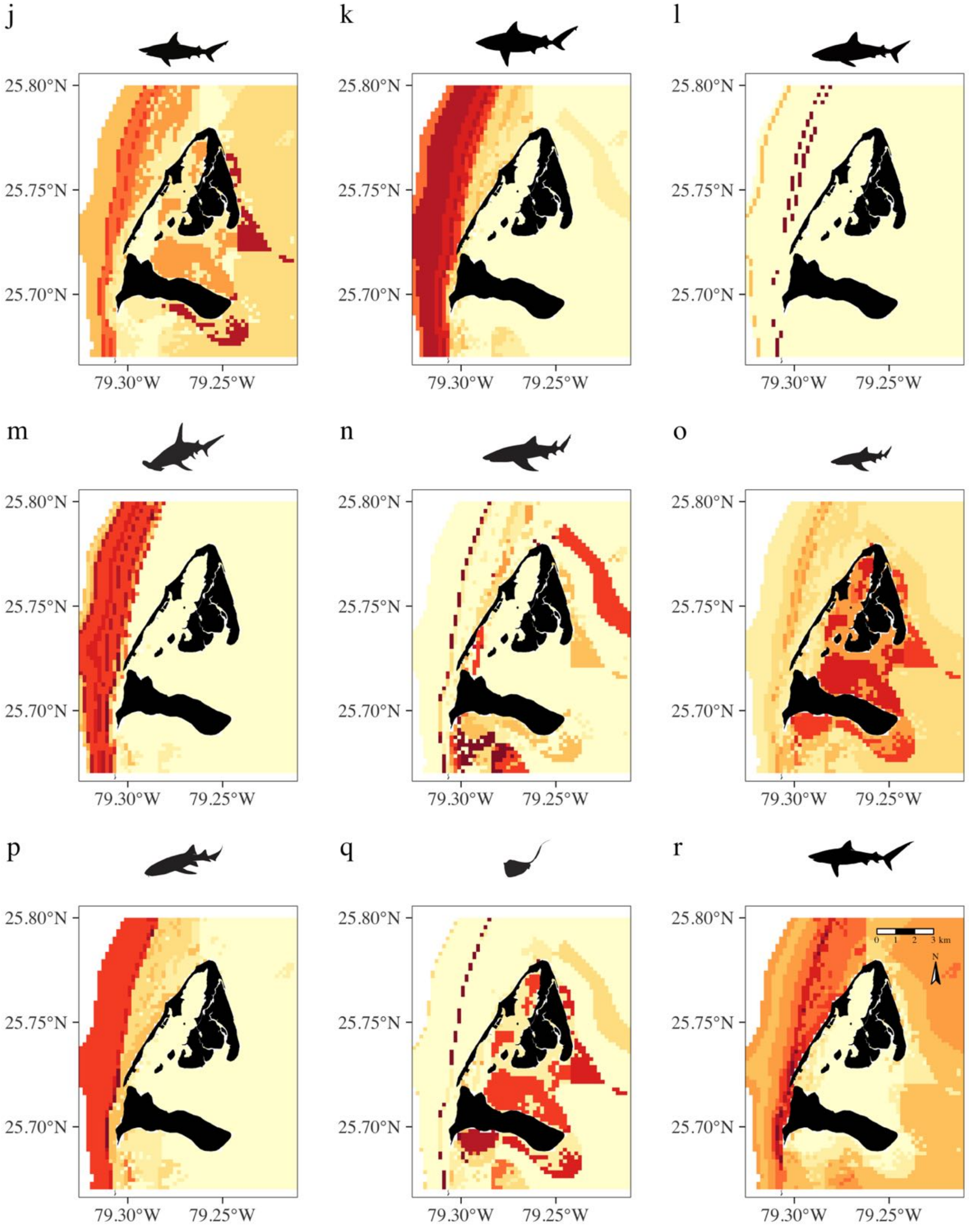

Figure 13 (continued). Seasonal predicted and extrapolated probability of relative selection. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k, bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Based on available resource use buffers of 900 m.

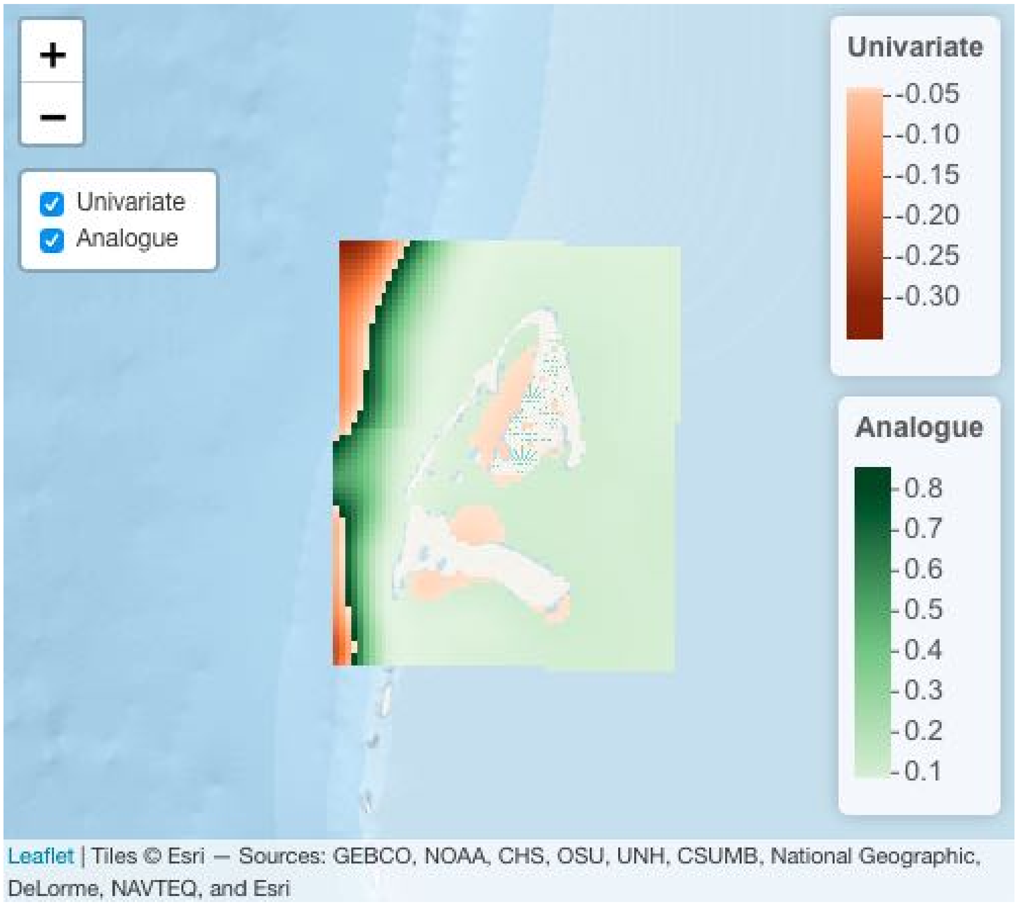

Figure 14. Extrapolation reliability around Bimini. Areas where predictions were considered outside of the covariate space are highlighted in red color gradient, whereas the green color gradient highlights areas where predictions fell within the sampled covariate space.

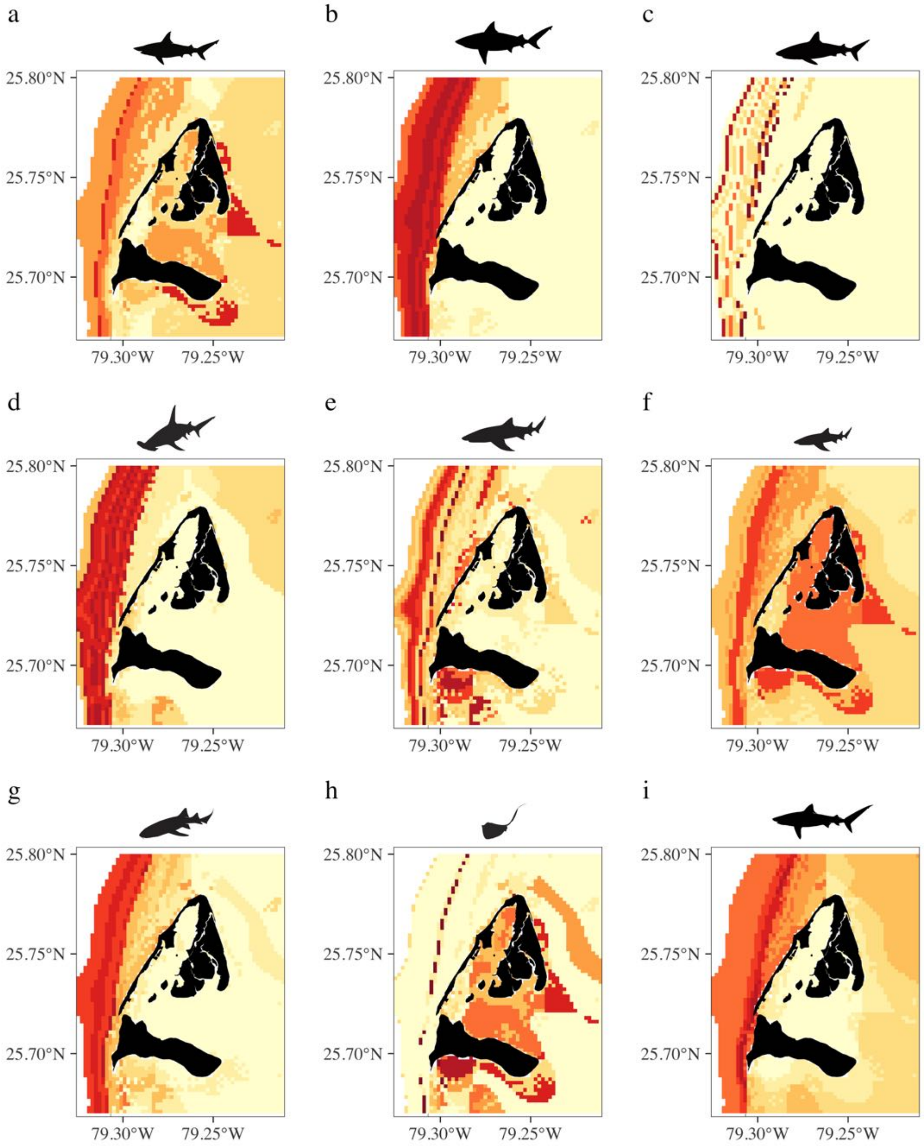

Figure 15. Seasonal predicted and extrapolated probability of relative selection derived from random forest models. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k), bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q), southern stingrays, i/r) tiger sharks.

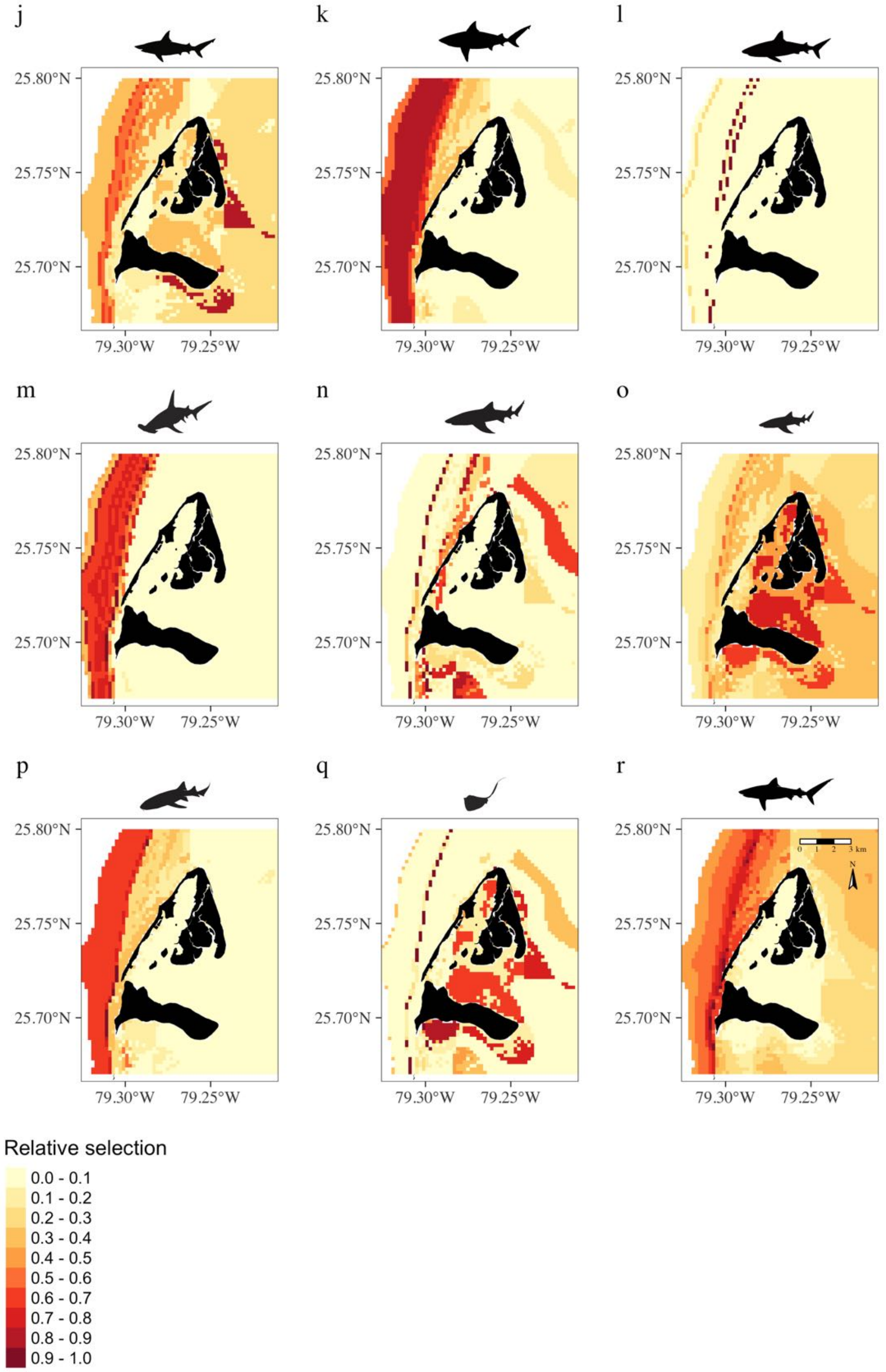

Figure 15 (continued). Seasonal predicted and extrapolated probability of relative selection derived from random forest models. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k), bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q), southern stingrays, i/r) tiger sharks.

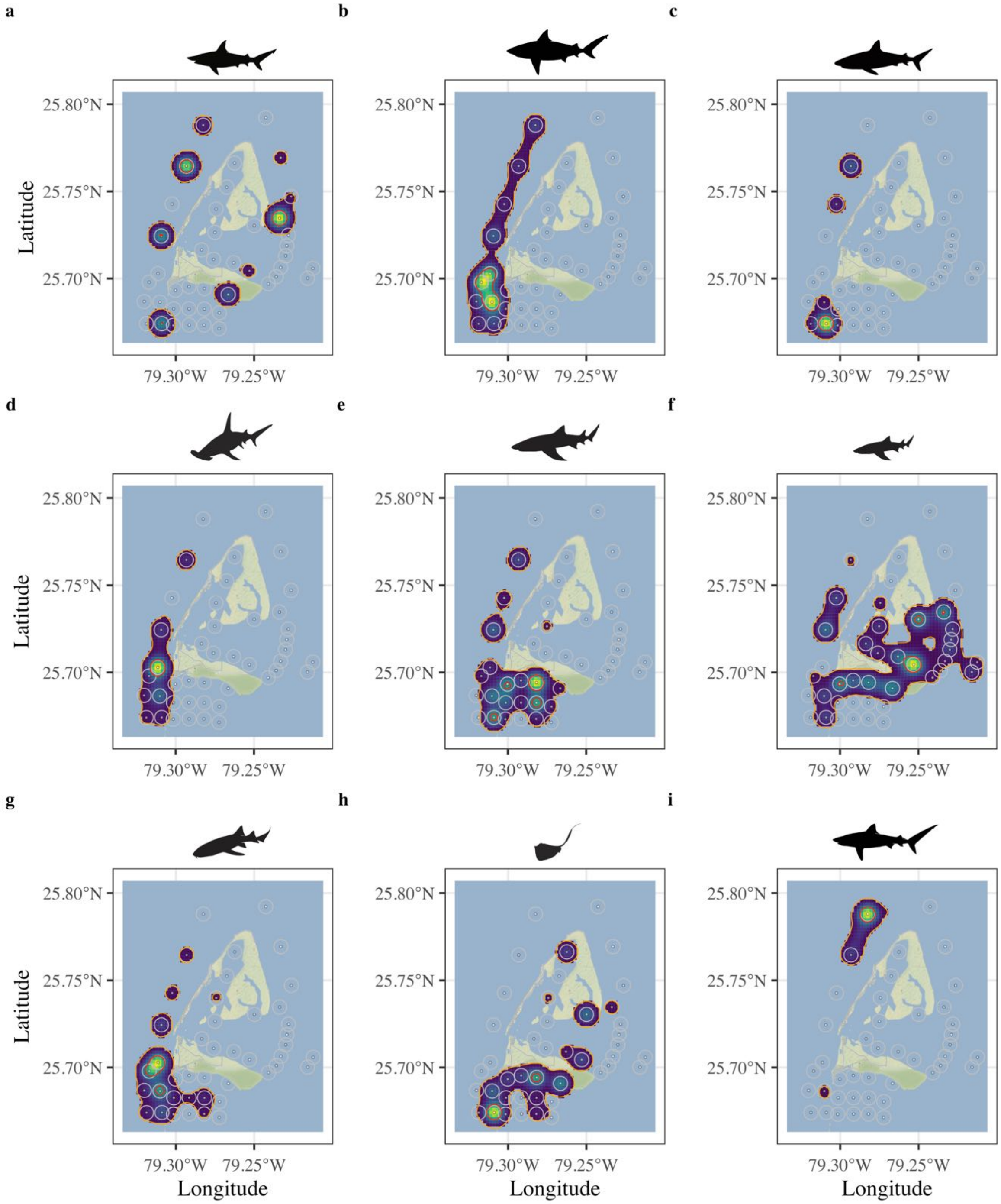

Figure 16. Seasonal utilization distributions. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k), bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Red and orange lines indicate 50% and 95% UD isopleths, respectively. White dots and grey circles denote acoustic receiver locations with their respective detection ranges (500 m).

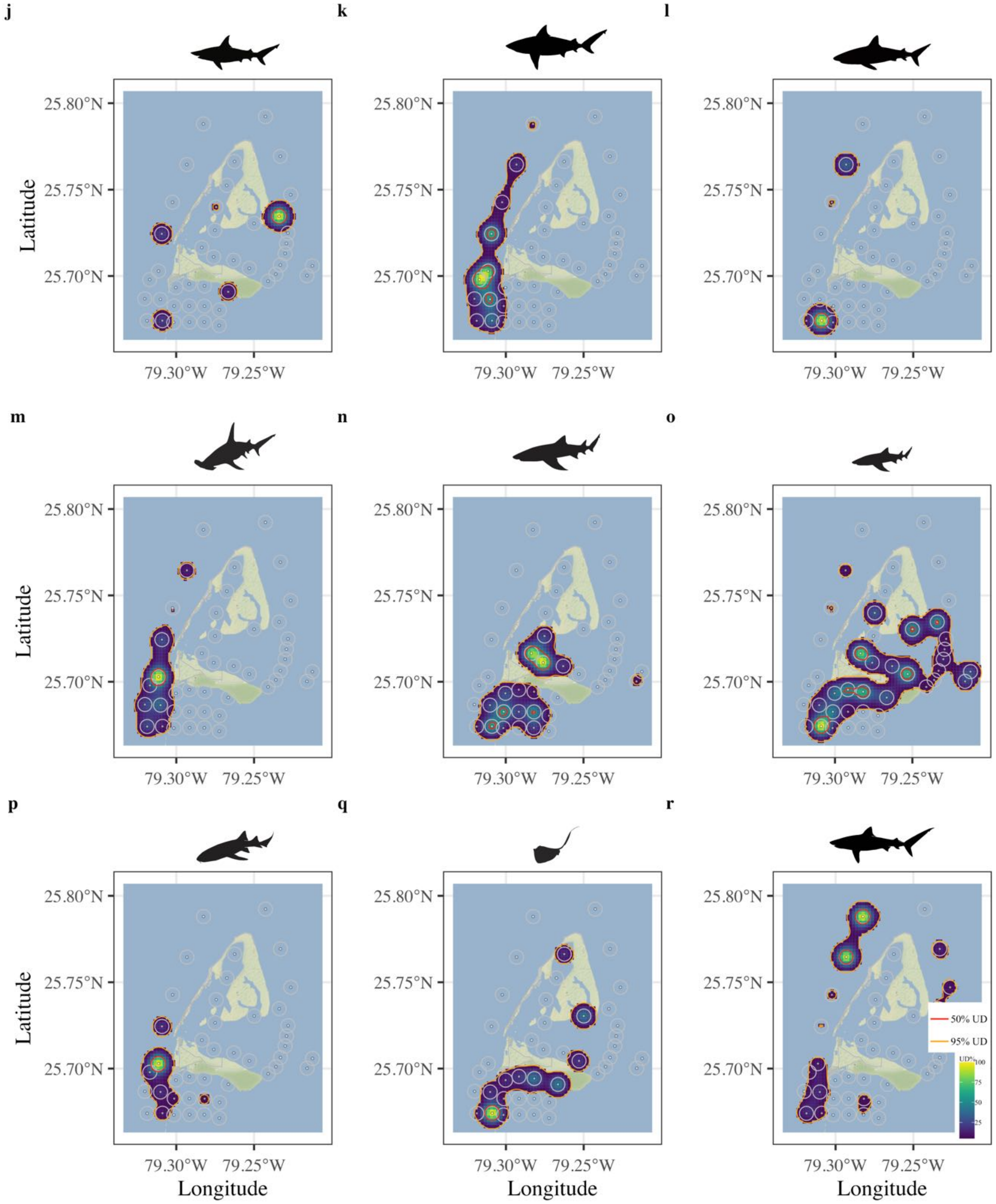

Figure 16 (continued). Seasonal utilization distributions. a–i: summer, j–r: winter. a/j) blacktip sharks, b/k), bull sharks, c/l) Caribbean reef sharks, d/m) great hammerhead sharks, e/n) adult lemon sharks, f/o) subadult lemon sharks, g/p) nurse sharks, h/q) southern stingrays, i/r) tiger sharks. Red and orange lines indicate 50% and 95% UD isopleths, respectively. White dots and grey circles denote acoustic receiver locations with their respective detection ranges (500 m).

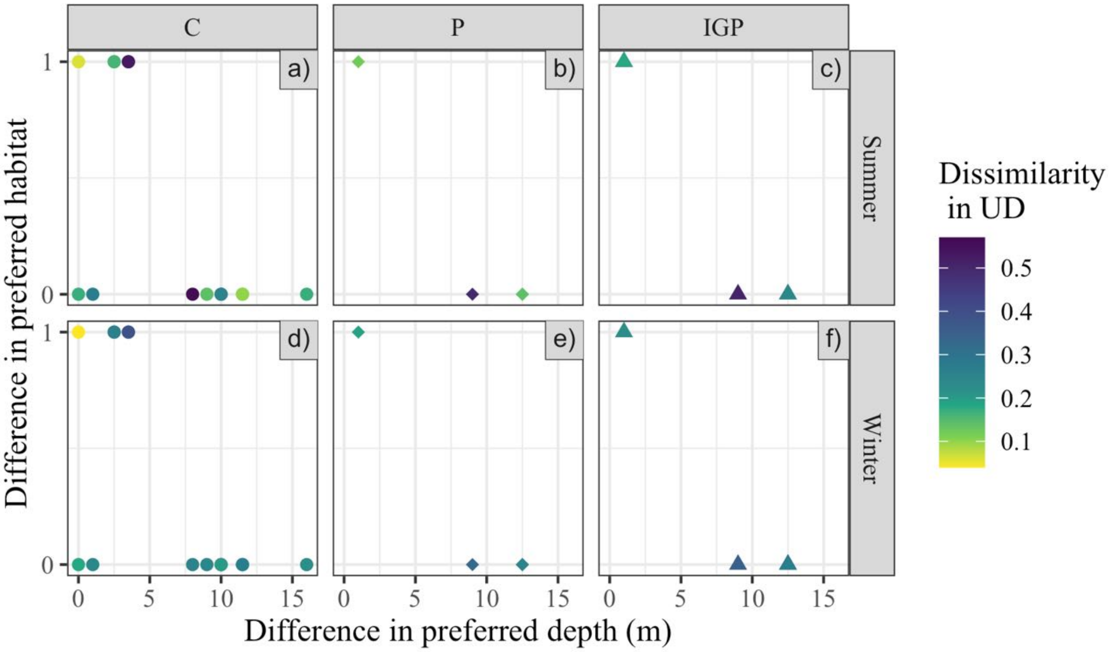

Figure 17. Summer and winter scatter plots showing the relationships between UD dissimilarity, difference in preferred depth and difference (0) or similarity (1) in most preferred region for potential competitors (C), intraguild predator and intraguild prey (IGP), and predator and prey (P).

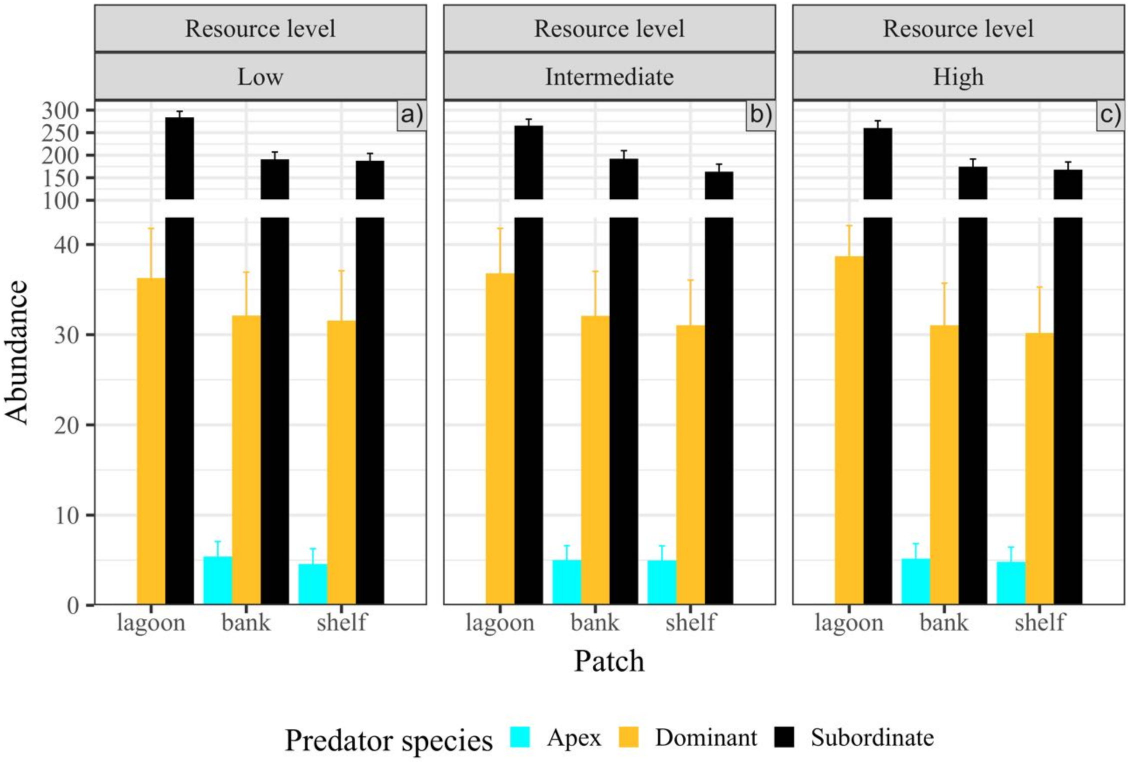

Figure 18. Individual-based model simulations predicting habitat distributions of apex predators, and dominant and subordinate mesopredators, based on differences in shoal resource levels: a) low, b) intermediate, c) high. In all panels, bars represent mean counts by species within each habitat type with standard errors, calculated over all 100 iterations at each resource level.

CHAPTER III

ELUCIDATING SHARK DIETS WITH DNA METABARCODING FROM CLOACAL SWABS

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Abstract

Animal dietary information provides the foundation for understanding trophic relationships, which is essential for ecosystem management. Yet, in marine systems, high-resolution diet reconstruction tools are currently under-developed. This is particularly pertinent for large marine vertebrates, for which direct foraging behaviour is difficult or impossible to observe and, due to their conservation status, the collection of stomach contents at adequate sample sizes is frequently impossible. Consequently, the diets of many groups, such as sharks, have largely remained unresolved. To address this knowledge gap, I applied metabarcoding to prey DNA in faecal residues (fDNA) collected on cotton swabs from the inside of a shark's cloaca. I used a previously published primer set targeting a small section of the 12S rRNA mitochondrial gene to amplify teleost prey species DNA. I tested the utility of this method in a controlled feeding experiment with captive juvenile lemon sharks (*Negaprion brevirostris*) and on free-ranging juvenile bull sharks (*Carcharhinus leucas*). In the captive trial, I successfully isolated and correctly identified teleost prey DNA without incurring environmental DNA (eDNA) contamination from the surrounding sea water. In the field, I was able to reconstruct high resolution teleost dietary information from juvenile *C. leucas* fDNA that was generally consistent with expectations based on published diet studies of this species. While further investigation is needed to validate the method for larger sharks and other species, it is expected to be broadly

applicable to aquatic vertebrates and provides an opportunity to advance our understanding of trophic interactions in marine and freshwater systems.

Introduction

Ecological network analysis and ecosystem-based fisheries management are contingent on a holistic understanding of the diet of constituent species (Casey et al., 2019; Pikitch et al, 2004; Shabtay, Portman, Ofir, Carmel, & Gal 2018). However, accurate and efficient methods to assess diet composition are currently lacking for many large-bodied aquatic predators such as sharks, whose feeding behaviour is difficult to observe directly. Shark diet assessment and reconstruction generally rely on morphological stomach content analysis, obtained through invasive methods such as stomach eversion and gastric lavage, or lethal sampling (Barnett, Redd, Frusher, Stevens, & Semmens, 2010; Bornatowski, Braga, Abilhoa, & Corrêa, 2014; Cortés & Gruber, 1990; Matich, Plumlee, Weideli, & Fisher, 2020; Papastamatiou, Wetherbee, Lowe, & Crow, 2006; Rosende-Pereiro, Flores-Ortega, González-Sansón, & Corgos, 2019; Trystram, Rogers, Soria, & Jaquemet, 2017). These methods are necessary but undesirable for threatened and/or protected species (Hammerschlag & Sulikowski, 2011; Heupel & Simpfendorfer, 2010). Moreover, morphological stomach content analysis is labour intensive, requires extensive taxonomic knowledge and lacks resolution as prey items are often digested, making them difficult or impossible to identify. This also introduces a bias towards prey that are slower to digest (Baker, Buckland, & Sheaves, 2014; Gosselin, Lonsinger, & Waits, 2017). Alternatively, obtaining gross information on diet through the non-lethal and less invasive analysis of biochemical tracers that integrate consumed prey information in consumer tissues over a large time span (weeks to months), such as bulk and compound-specific stable isotopes and fatty acids, is limited in that both methods require intensive sampling of both predator and prey species (Munroe, Meyer, Heithaus, 2018; Nielsen, Clare, Hayden, Brett, & Kratina, 2018). They also rely on well-resolved trophic discrimination factors or calibration coefficients to make gross dietary inferences that are rarely resolved to constituent species (Hussey et al., 2012; Meyer, Pethybridge, Nichols, Beckmann, & Huveneers, 2019; Nielsen et al., 2018). Indeed, for generalist predators that feed across multiple trophic levels, such as many shark species, species-level resolution of prey often remains uncertain when using chemical tracers (Layman et al., 2012; Nielsen et al., 2018).

There is a growing momentum in the application of high throughput sequencing (HTS) technology in conjunction with DNA metabarcoding in diet reconstruction studies, which allows for the large-scale, high-resolution characterization of species composition in stomach contents and faecal samples (Brassea-Pérez, Schramm, Heckel, Chong-Robles, & Lago-Lestón, 2019; Carroll et al., 2019; Dunn, Szabo, McVeagh, & Smith, 2010; Finucci, Bustamante, Jones, & Dunn, 2016; Gordon et al., 2019; Monterroso et al., 2019). However, the collection of shark faeces is challenging because defecation events are rarely observed and typically result in faecal particles suspended in seawater, making them difficult to collect. Moreover, once faeces have been released into the water, or on skin or other surfaces, environmental DNA (eDNA) contamination may be introduced (Meekan, Jarman, McLean, & Schultz, 2009; Poulakis et al., 2017). Consequently, even in the rare instance of sampling faecal matter during a defecation event, it becomes difficult to determine whether detected prey DNA originates from the faecal matter or from eDNA present in the surrounding seawater. The development of an accurate, efficient, and minimally invasive method for the collection and metabarcoding of faecal DNA (fDNA) that concurrently reduces or eliminates eDNA contamination could bridge a major part of the current knowledge gap concerning the diets of different shark species. Sharks expel both urinary and solid waste through the cloaca, which may create an opportunity to sample fDNA directly from a shark sometime around a defecation event instead of opportunistically collecting a faecal sample released by the animal during a capture and tagging event (Hancock, Poulakis, Scharer, 2019; Poulakis et al., 2017).

Here, I aimed to assess the applicability of the collection of traces of faecal material from a shark's cloaca using cotton swabs, and subsequently metabarcoding of fDNA extracted from these samples, in order to assess the animals' diet. My first objective was to ground truth the method by performing a controlled feeding experiment with captive juvenile lemon sharks (*Negaprion brevirostris*, Poey 1868) to determine whether a known diet can reliably be identified by fDNA metabarcoding and if eDNA contamination from surrounding seawater can be excluded. I focus on a single primer set targeting a small fragment of the 12S rRNA region to identify a teleost prey species that is not part of the natural diet of *N. brevirostris* in this size class. My second objective was to test the utility of the method on free-ranging juvenile bull sharks (*Carcharhinus leucas*, Müller and Henle 1839) using the same primer set to determine whether the method could reliably be used to obtain prey signatures that are consistent with previously published diet studies and locally available prey.

Materials and methods

Experimental study

Negaprion brevirostris capture and husbandry

Three male juvenile *N. brevirostris* (Table S1) were collected from a tidal creek system in Cape Eleuthera, The Bahamas (24°49′46.43″N, 76°19′41.49″W), on 15 and 16 October 2018. All individuals were caught using either seine netting or rod and reel fishing, followed by transportation to the Cape Eleuthera Institute's covered, open-sided outdoor wet-laboratory facility. Sharks were individually housed in 13,000 L (3.7 m diameter x 1.3 m depth) continuous flow-through sea water tanks and exposed to ambient water conditions and a natural photoperiod (latitude 25°N) (Bouyoucos et al., 2017). Fresh aerated seawater (flow rate: 1 L/s; time to fill a holding tank: 2 h 41 min) was supplied from an intake at 1.5 m depth, located approximately 200 m offshore in a hard-bottom mangrove creek habitat with nearby patch reefs.

Controlled feeding experiment and fDNA collection

Following capture, the sharks were housed for 14 or 15 days between 15-29 October 2018. Once daily between 7:30-8:00 h, from the day after capture until the day of release, individual sharks were offered 6% of their body weight (instead of the recommended 2%) in *Euthynnus alletteratus* (little tunny) filets in order to reduce food retention time, accelerate the onset of faecal production, and to extend the time period during which faeces would be produced (Cortés & Gruber, 1990; Wetherbee & Gruber, 1990) (Table S1). This pelagic teleost species is not a natural prey item of juvenile *N. brevirostris*, whose diet has previously been linked to mangrove communities (Cortés &

Gruber, 1990; Newman, Handy, & Gruber, 2010). Consequently, it is highly unlikely that *E. alletteratus* would have been consumed under natural conditions, and therefore be detected prior to the onset of the feeding experiment. Offered prey that was not consumed was removed from the tank within 60 min. Cloacal swab samples were collected for 13 days starting on the day of capture. All three sharks were sampled daily between 11:00-14:00 h for fDNA. The sharks were placed in a cooler partially filled with seawater from their tank, held upside down in tonic immobility (a temporal state of paralysis; Kessel & Hussey, 2015), and pelvic fins were spread apart while the posterior half of the shark was held out of the water. This enabled clear access to the cloaca and prevented contact between the swab and the exterior skin and surrounding water. In order to further reduce the risk of contamination from fish eDNA that might be present in the tank water, the external cloacal area was dabbed dry with a paper towel (discarded after single use) prior to sample collection. A sterile, individually packaged cotton tipped swab with wood handle (Puritan 25-806 1WC FDNA; length 15.2 cm, tip diameter 0.48 cm) was inserted ~1 cm into the cloaca and rotated against the inside wall for ~5 s. Following removal, the tip was cut off from the excess handle using sterilized scissors (leaving ~2 cm of the handle for handling the swab in the laboratory) and stored for further processing (as described under 'fDNA and eDNA processing and extraction'). Upon completion of the experiment, the sharks were released in good condition at the same location as where they were captured.

eDNA controls

In order to test for potential contamination of the cloacal swabs with teleost eDNA from the surrounding seawater in the controlled feeding experiment, I characterized the eDNA species composition of four water samples from the tanks in which the sharks were housed. Water samples (2 L each) were collected with sterile collection bottles, from two tanks, on two consecutive days concurrently with the cloacal swab sample collection (i.e. between 3.5-6.5 h after the sharks had been fed). Vacuum filtration was carried out directly on site with a peristaltic pump, filtering the water through hydrophilic polyethersulfone (PES) filters (Pall Corporation; 47 mm diameter; 0.45 µm pore size). After filtration, filters were stored at -20°C until further processing as described under 'fDNA and eDNA processing and extraction'.

Field application

Field trials were conducted on a well-studied population of juvenile *Carcharhinus leucas* in the Shark River Estuary in the Florida Everglades National Park (ENP), USA, in the 2019 wet season (April-November) (Table S2). Sharks were caught using 500 m longlines, fitted with 50 15/0 circle hooks baited with mullet (*Mugil spp*), attached by 2 m gangions of 400 kg test monofilament line (as described by Heithaus, Delius, Wirsing, & Dunphy-Daly, 2009). Sharks were brought onboard and placed inside a cooler partially filled with water collected directly from the sampling site. The water was changed prior to the start of the workup of each shark. Sex was determined and length measurements were taken to the nearest cm for each animal, and weight was measured to the nearest half kg. Cohort and age class were estimated based on size at capture (Matich & Heithaus

2015). Subsequently, a cloacal swab sample was collected as described above, after which the sharks were released.

fDNA and eDNA processing and extraction

The fDNA cotton swab samples and the filters containing eDNA sample filtrates, were stored in sterile 5.0 ml cryogenic screw cap vials containing silica beads. The silica beads function as a desiccant, drying out the swabs and filters, preventing the DNA from degrading (Bakker et al., 2017). Subsequently, all samples were initially preserved in a cooler filled with ice and then stored at -20°C until extraction. Sterile tweezers and pliers were used to handle all samples. Prior to extraction, the wooden ends were removed from the cotton swabs and filters were cut in half. Filter and swab samples were processed on separate occasions. Genomic DNA was extracted using the DNeasy PowerSoil Kit (www.qiagen.com), following the manufacturer's protocol. DNA was eluted into 100 µl and frozen at -20°C until further processing. At all stages of sample collection and laboratory procedures single-use disposable gloves were used. All surfaces, field sampling, and filtration and laboratory equipment were cleaned with a 50% bleach solution and all laboratory work was carried out inside a laminar flow hood. Swab and filter DNA extraction and library preparation were performed at Jonah Ventures, Boulder, CO, USA (www.jonahventures.com) in dedicated controlled eDNA laboratories.

Library preparation and sequencing

Concentrations of a subset of extracted genomic DNA were measured using a Qubit 4 Fluorometer (Thermo Fisher Scientific), prior to PCR amplification. The MiFish-U primer set (Miya et al., 2015), targeting a ~171 bp fragment of the mitochondrial 12S rRNA region, was used for the amplification of fDNA and eDNA from cloacal swabs and water filters, respectively. This primer set was specifically designed for the amplification of fish DNA (thus inherently it will also amplify the DNA of a number of elasmobranch species) and was chosen for this study because both *N. brevirostris* and *C. leucas* are primarily piscivorous (Newman et al., 2010; Poulakis et al., 2017; Snelson & Williams, 1981; Snelson, Mulligan, & Williams, 1984). The MiFish-U primer set is known to be highly specific for the amplification of teleost DNA, with very little cross-amplification of other groups of animals (except for some elasmobranchs) (Collins et al., 2019; Miya et al., 2015). Therefore, I expected that using this particular set would maximize the number of fDNA sequence reads that could be obtained using a single primer set. Both forward (5'-GTCGGTAAAACTCGTGCCAGC-3') and reverse (5'-CATAGTGGGGTATCTAATCCCAGTTTG-3') primers contained a 5' adaptor sequence to allow for subsequent indexing and Illumina sequencing. Each 25 µl PCR reaction was prepared according to Promega (Madison, WI) PCR Master Mix specifications, which included 12.5 µl Master Mix, 0.5 µM of each primer, 1.0 µl of gDNA, and 10.5 µl DNase/RNase-free water. All PCR amplifications were done in triplicate reactions using the following PCR profile: initial denaturation at 95°C for 3 min, followed by 45 cycles of 20 s at 98°C, 30 s at 60°C, and 30 s at 72°C, and a final elongation at 72°C for 10 min. In order to determine amplicon size and PCR efficiency, each reaction was assessed by electrophoresis, running the products through a 2% agarose gel and visualized on a UV light platform. Amplicons were subsequently cleaned by incubation with Exo1/SAP for 30 min at 37°C, followed by inactivation at 95°C for 5 min. A second PCR was performed on the cleaned amplicons from the first stage PCR reaction in order to give each sample a unique 12 nucleotide index sequence, yielding a total length of 346 bp. The indexing PCR included Promega Master mix, 0.5 µM of each primer and 2 µl of template DNA. The PCR profile included an initial denaturation of 95°C for 3 min, followed by 8 cycles of 95°C for 30 s, 55°C for 30 s and 72°C for 30 s. To test for successful barcoding, the indexed PCR products were visualized on a 2% agarose gel. As the samples were collected on separate sampling campaigns, two Illumina libraries containing the swab samples from the two different species were built on separate occasions. All samples were run alongside other libraries from unrelated projects, equalizing the sequencing depth across all samples by pooling an equal number of samples for each run. Sample library pools were sequenced on an Illumina MiSeq platform at the CU Boulder BioFrontiers Sequencing Center using the v2 500-cycle kit. Necessary quality control measures were performed at the sequencing center prior to sequencing.

Bioinformatic processing and statistical analysis

Sequences were processed using the JAMP pipeline (https://github.com/VascoElbrecht/JAMP). Raw reads were demultiplexed with "iu-demultiplex' v2.3 (https://github.com/merenlab/illumina-utils). Forward and reverse reads from each sample were paired end merged with Usearch v11.0.667 (Edgar, 2010).

Forward and reverse primers were trimmed and reads with sequence length 130-210 bp were retained using Cutadapt v1.18 (Martin 2011). Quality filtering was carried out using expected error filtering (max ee = 0.5) as implemented in Usearch (Edgar & Flyvbjerg, 2015). Subsequently, instead of OTU clustering, reads affected by sequencing and PCR errors were removed using the unoise3 algorithm with an alpha value of 5 (Edgar, 2016). Denoising was applied to each individual sample and Exact Sequence Variants (ESV) compiled in an ESV table including sequences and read counts for each sample. Taxonomy assignment was performed by mapping each ESV against the MitoFish database (http://mitofish.aori.u-tokyo.ac.jp/) containing complete and partial mtDNA reference data, using Usearch_global with maxaccepts 0 and -maxrejects 0 to ensure mapping accuracy. A value of 0 ensures all potentially matching sequences are aligned and the best one is selected. With the default settings, only the top potential hits would be compared, leading to less accurate results if many similar sequences are in the reference database. Consensus taxonomy is generated from the hit tables, by first considering 100% matches followed by going down in 1% steps until hits are present for each ESV. In the respective 1% bracket, taxonomy present in at least 90% of the hits is reported. An NA is reported if several taxa match the ESV. To reduce errors caused by misidentified taxa, the bracket is increased to 2% if matches of 97% or higher are present, and no family level taxonomy is returned. All resulting prey sequences where subsequently blasted in GenBank to ensure that potential prey species were not missed because some western Atlantic teleost 12S sequences that are deposited in GenBank, are not yet available in the MitoFish database. Where an ESV could subsequently not be assigned to genus and/or species level, the vernacular name of the family was recorded where possible, based on the genus or species known to occur in my study site (Kline et al., 2014; Trexler & Goss, 2009). All statistical analyses were performed in R v3.4.0 (https://www.R-project.org/). The vegan package v. 2.4–081 in R was used for the calculation of the sample-based prey species accumulation curve. A regression analysis was performed to examine if the cloacal swab sample size was large enough to adequately describe the diet of the juvenile *C. leucas* in this system.

Results

Controlled feeding experiment

While cloacal swab collection was initiated on the first day of capture, the sharks did not start feeding until the third or fourth day, after which feeding continued daily until the end of the trial (Figure 1; Table S1). *Negaprion brevirostris* DNA (1,060,112 total sequence reads) was recovered from every sample from all individuals across the entire trial indicating that sampling, sample storage, and DNA processing workflows were successful. No teleost DNA was detected in the swab samples in the days prior to the initiation of feeding, providing a negative control for the experiment, indicating that no teleost eDNA contamination from the water had occurred. Once the sharks started feeding, teleost DNA was detected, and all teleost sequence reads were assigned to *Euthynnus alletteratus* (53,619 sequence reads total across all positive swabs, see Table S3 for summaries of bioinformatics stats). The first appearance of *E. alletteratus* reads on swabs varied between 3.5-6.5 h (shark 1 and 2) and 2 days (shark 3) after feeding. *E. alletteratus* reads were present in swab samples intermittently thereafter, from days four or five to the end of the feeding trial (Table S4.A). Once feeding commenced, 5/10 swabs from shark 1, 2/10 from shark 2, and 3/11 swabs from shark 3 contained *E. alletteratus* sequences. The number of sequence reads per individual and per sample was variable but increased towards the end of the experiment for all three individuals. The proportion of recovered *N. brevirostris* reads relative to those recovered from *E. alletteratus*, averaged across individuals and samples, was 0.84 (range, 0.72 – 0.97) (Table 4.A). Four water samples from the tanks housing the sharks were collected, filtered, extracted and sequenced (6,292 total sequence reads) in order to profile potential eDNA contamination in the swabs. One eDNA sample contained no teleost eDNA, one contained only *E. alletteratus* and 2 contained *E. alleratus* with up to three other local teleost species (*Halichoeres bivittatus* [748 reads], *Atherinomorus stipes* [112 reads], *Stegastes sp*. [451 reads]) (Table S4.B).

Carcharhinus leucas fDNA

A total of 21 juvenile *C. leucas* (110.2 2 ± 14.8 cm stretched total length [STL], mean ± SD; 90 – 132 cm, range) were caught and sampled for fDNA (see Table S2 for catch data). All swabs contained host and/or prey DNA (Figure 2 and Table S5). A total of 1,850,298 sequence reads, distributed over 37 ESVs (i.e., prey species) were recovered from the 21 swabs (Figure 3, Table S5; See Table S3 for summaries of bioinformatics stats). Host DNA was present in 18 out of the 21 cloacal swabs and accounted for only 0.65% (11,972 sequence reads) of the total number of recovered sequence reads. Similarly, prey DNA was recovered from 18 cloacal swabs (Figure 2). The three swab samples that did not contain prey DNA, did contain host DNA. The 37 different ESVs consisted of 20 orders comprising 26 families of which seven could be identified down to species level. DNA from one elasmobranch prey species (family *Dasyatidae*) was also detected (Table S5).

The majority of the detected teleost prey families/species of the sampled juvenile *C. leucas* (Table S5) were native to the Everglades National Park (ENP) and/or the Gulf of Mexico, while three species are invasive to the ENP (*Naso lituratus, Hypophthalmichthys nobilis, Cyprinus carpio*). The majority of prey sequence reads was assigned to *Ariidae* (catfishes: 56.8%, present in 15 samples that contained teleost prey DNA) (Figure 2 & 3, Table S5). The second most abundant prey family was *Mugilidae* (mullets: 20.6%, present in six samples) followed by *Serranidae* (sea basses: 7.2%, present in six samples). Combined these three families made up the bulk of the recovered diet (84.6%), while the other unique ESVs (spread over 12 samples) individually made up <3% of all sequence reads (Figure 2 & 3, Table S5), with the lowest read count (119 sequence reads) belonging to a species from the family *Serranidae*. Three samples contained only catfish DNA (sharks 1, 5, and 11), whereas the recovered diet from three other sharks (12, 13, and 15) consisted of multiple prey species (n = 26, n = 19, and n = 24, respectively) from fresh, estuarine and marine environments (Figure 3, Table S5). A diet species accumulation curve (Figure 4) shows that 21 samples is not yet sufficient to fully capture the species richness of juvenile *C. leucas* diets in the system because the curve has yet to reach a plateau and the slope of the regression line through the last four data points is greater than 0 ($p = 0.002$). A total of 11 negative extraction controls per each run were sequenced in parallel with the swab samples and none of these negative controls contained any teleost or elasmobranch reads.

Discussion

Here I show that cloacal swabs for the collection of faecal matter, and subsequent analysis by metabarcoding of fDNA, can be used to reconstruct shark diets. By first conducting a controlled feeding experiment with captive juvenile *Negaprion brevirostris* that were fed a known diet, I show that fDNA can detect prey items without incurring contamination from teleost eDNA that may be present in the surrounding seawater. I then show that cloacal swabs collected from juvenile *Carcharhinus leucas* in the field identified prey species that are a well-known dietary component for this species, highlighting the potential applicability of fDNA swab metabarcoding as a diet reconstruction method.

Validating cloacal swab fDNA metabarcoding under controlled conditions

The predictions of the controlled feeding experiment were that (1) the only DNA recovered from cloacal swab samples would be that of the host species and its known prey, (2) that prey DNA would be detected only after the onset of feeding, and (3) that eDNA contamination was not the source of prey DNA detected on the swabs. The results confirm these expectations. All cloacal swabs collected in the juvenile *N. brevirostris* controlled-feeding experiment contained either only host DNA or both host DNA and known prey DNA. It is most likely that host DNA originates from epithelial cells that are unavoidably collected during swabbing because they were recovered from 100% of the swab samples. In the days before the sharks started eating the offered filets, no teleost DNA was detected in swabs, but the consistent presence of host DNA provided a positive control for the workflow. Once the sharks started feeding, *Euthynnus alletteratus* was the only teleost species that was detected in the swab samples in addition to the host DNA. It is highly unlikely that eDNA contamination from the surrounding water was the source of these DNA sequence reads. If *E. alletteratus* DNA on the cloacal swabs originated from the surrounding tank water rather than from the ingested food, it would most likely have been detected in most, if not all, swab samples collected during the experiment instead of only on ~33% of them. This is further supported by the characterization of the eDNA profile of the tank water in which three reef-associated teleost species were found across four water samples. If eDNA contamination from the water had been the source of *E. alletteratus* rather than faecal material inside the cloaca, the DNA of the additional three teleost species recovered from the eDNA water samples would almost certainly have been detected on the swab samples as well (and others given that they originate from outside sea water pumped through the tanks), especially given the relatively high contributions observed in some of the eDNA samples. These results indicate that the precautions implemented to avoid eDNA contamination during sampling (holding the posterior part of the shark out of the water and drying the cloacal area with paper tissue) are sufficiently rigorous to avoid such contamination.

Minimum food transit time in juvenile *N. brevirostris*, defined as the time it takes to observe faeces for the first time following a meal, has previously been indicated to be ~12 h (Wetherbee & Gruber, 1990). Yet, in my study the onset of prey DNA detection in cloacal swabs ranged from 3.5 to 48 h after the sharks accepted the offered filets for the first time. These differences may be indicative of variability in food retention and digestion times between individuals, but it may also be a result of the type of sampling method used, i.e. the collection of expelled faecal matter as opposed to fDNA collection using a cloacal swab. In Wetherbee & Gruber (1990) faecal production was detected only after defecation took place, whereas cloacal swabs have potentially detected *E. alletteratus* DNA either prior to defecation or sometime after. However, only ~32.3% of the swabs contained *E. alletteratus* DNA, with variable numbers of sequence reads among swabs and individuals. *N. brevirostris* do not defecate continuously. Instead, faecal matter builds up behind the cloaca prior to defecation and there is considerable individual variability in defecation frequency (Wetherbee & Gruber, 1990). Accordingly, while traces of fDNA are left behind, the temporal window to collect fDNA with cloacal swabs is likely to be relatively small.

Testing the method under field conditions

My study in the coastal Everglades was not designed to be a comprehensive investigation of the diet of juvenile *C. leucas*, rather it was to assess the execution of the sampling approach in a field setting, and with the expectation that, at least, prey items known *a priori* to occur in the diet of this species would be detected. The cloacal swab sampling approach was successful in the field in that I was able to recover teleost sequence reads from most of the sharks. The metabarcoding results were generally consistent with previously published diet data for this species and size range in similar systems. The four predominant ESVs (84.6% of all sequence reads) obtained from 18 out of the 21 cloacal swabs were assigned to two species of catfish (*Ariidae*), white mullet (*Mugil curema*), and a species from the family *Serranidae*, which are all abundant in the Shark River Estuary and are known prey items for juvenile *C. leucas* (O'Connell, Shepherd, O'Connell, & Myers, 2007; Poulakis et al., 2017; Snelson & Williams, 1981;

Snelson et al., 1984). Stomach content analyses have previously shown that *C. leucas* consume a wide variety of prey species including teleosts, molluscs, crustaceans, and other elasmobranchs. In estuarine systems, such as the Everglades, juvenile *C. leucas* may feed in freshwater, brackish and/or coastal marine habitat types (Cliff & Dudley, 1991; Matich & Heithaus, 2015; Snelson & Williams, 1981; Snelson et al., 1984; Trystram et al., 2017). Additionally, within the Shark River Estuary, stable isotope and acoustic tracking analyses have revealed ontogenetic niche shifts, as well as relatively high levels of individual dietary specialization for foraging from particular food webs (i.e. marine vs freshwater/estuarine) among juvenile *C. leucas* (Matich et al., 2017; Matich, Heithaus, & Layman, 2011; Matich & Heithaus, 2015). Such behaviours may be consistent with the relatively large number of rarer ESVs (n = 33) that were infrequently detected in the cloacal swabs of the juvenile *C. leucas*, relative to the dominant ESVs. These included a variety of prey families/species (ranging from freshwater to marine species), including known invasive species and some teleost prey items that were not specifically known to be part of the juvenile *C. leucas*' diet.

While the diversity of ESVs detected in a minority of swabbed *C. leucas* was higher than expected from previous stomach content analyses, results like these are not unprecedented. Consumer diets from highly diverse communities are often equally diverse, resulting in a large number of rare dietary prey ESVs (Casey et al., 2019; Leray et al., 2013). Generally, molecular analysis of faecal matter results in higher taxonomic resolution compared to traditional methods such as morphological stomach content analysis, and consequently, reveals a higher prey diversity (Berry et al., 2015; Bessey et al., 2019; Jeanniard-Du-Dot, Thomas, Cherel, Trites, & Guinet, 2017; Sousa, Silva, &

Xavier, 2019; Thomas, Nelson, Lance, Deagle, & Trites, 2017). In sharks, DNA metabarcoding of stomach contents previously showed a prey species richness accumulation at nearly double the rate compared to morphological stomach content analysis of the same samples (Barnett et al., 2010; Dunn et al., 2010). Such studies have led to a number of unexpected new ecological findings (Bessey et al., 2019; Granquist, Esparza-Salas, Hauksson, Karlsson, & Angerbjörn, 2018; Leray, Meyer, & Mills, 2015; Riemann et al., 2010; Sousa et al., 2019) . For example, DNA from mesopelagic fishes (family Myctophidae) was unexpectedly detected in the stomachs of three mobula ray species (Bessey et al., 2019). Similarly, in this study, DNA of a myctophid species was detected, among other marine teleost species, in the swab samples from five different *C. leucas*, with a total of 11,365 sequence reads (sharks 6, 9, 12, 13, and 15, Table S5). The recovered sequence matches a species from the genus *Diaphus* with a maximum percentage identity of 96%. Regardless, it cannot currently be determined whether the sequence reads from this family originated from ingestion or contamination. While more work is needed to properly interpret these results, such as using statistical modelling approaches to quantify and correct for the abundance of false positive samples (Ficetola, Taberlet, & Coissac, 2016; Lahoz-Monfort, Guillera-Arroita, & Tingley, 2016), improvement of reference sequence databases for teleost prey species will certainly provide more clarity.

Methodological considerations

DNA metabarcoding from cloacal swabs for the investigation of dietary composition holds great potential for resolving trophic relationships in ecological communities, offering several advantages relative to other methods. The collection of cloacal swabs, in contrast to other methods, is minimally invasive. Moreover, the collection of a cloacal swab is generally much less time-consuming than collecting stomach contents and faster than collecting most tissues for stable isotope or fatty acid analysis, which is advantageous when dealing with stress-sensitive species. In such instances, the application of cloacal swabs may present the only viable alternative to the more invasive procedures without imposing extra risk to the animal. I recovered prey DNA from ~33% of sampling events in *N. brevirostris* known to have fed recently in an experimental setting, and ~86% of *C. leucas* sampled in the field. This success rate is comparable to or exceeds other approaches for diet sampling involving stomach contents because sharks with empty stomachs (a large fraction of specimens collected by baited hook-and-line) and those that evert their stomach during capture may still provide dietary information by applying this method (Brunnschweiler, Nielsen, & Motta, 2011; Joyce et al., 2002; Lowe et al., 1996). While biochemical tracers generally can be used on 100% of sampled individuals, diets can only be reconstructed with very low taxonomic resolution, if at all, using these methods.

However, like any other diet analysis method available, cloacal swab fDNA metabarcoding does have its limitations (Alberdi et al., 2019; Sousa et al., 2019). One of the caveats is that secondary predation (prey consumed by prey), or incidentally ingested items that are present in the water column, cannot be distinguished from intentionally ingested prey items (Bessey et al., 2019). Cannibalism will be obscured by host DNA, which is an issue for resolving diet for any species where this is common (Pompanon et al., 2012). Nor does the method allow for the determination of the prey’s size or life stage, or the quantitative analysis of consumed items beyond relative abundances, although progress toward this goal is expected (Deagle et al., 2019; Monterroso et al., 2019). Furthermore, additional specialized primer sets are needed to target different prey groups (e.g., teleosts, crustaceans, and/or mammals) in shark cloacal swab samples. Importantly, cloacal swab fDNA metabarcoding is inherently sensitive to the time of defecation, meaning that it may only pick up fDNA within a limited time frame prior to, and after defecation. Finally, it is important to note that digestion rate plays a crucial role in prey detection of tissue-based extractions, often leading to an under-representation of those taxa whose tissue is more rapidly digested (Sousa et al., 2016). Without knowledge on specific digestion rates, it remains difficult to pinpoint over what exact time frame a prey item is consumed and for how long its signal remains detectable. However, correction factors can be estimated to account for differential digestibility rates, and derived results have been shown to be more robust when compared to morphological methods (Sousa et al., 2019).

Future outlook

The controlled feeding experiment with captive juvenile *N. brevirostris* was successful in the detection of known prey items without incurring eDNA contamination. However, experiments to further our understanding of the obtained results are recommended. For example, experiments designed to better understand the relationship between food retention time and fDNA signal decay are vital to improve the interpretation of results obtained from future field applications of this method. In addition, the method would benefit from experiments that investigate the effects of mixed diets on fDNA recovery and composition, and from those that examine the relationship between prey biomass and sequence read abundance. While the method was successfully field-tested on juvenile *C. leucas* with only ~14% (3/21) swabs containing no detectable prey DNA, future studies should explore whether cloacal swab fDNA metabarcoding applied to larger sharks and other large vertebrate species can also recover prey DNA sequences successfully. Finally, due to the temporal differences with biochemical tracer data, it will be important to verify the correlation between short-term feeding and the biochemical tracer values of slow-turnover tissues by applying both types of method to the same individuals (Thomson et al., 2012).

The accuracy of the method presented here is contingent on the availability of well stocked and curated reference databases (Cristescu, 2014; Devloo-Delva et al., 2019). My study is an excellent example of the need for local sequence libraries. The 12S primer set used in this study offers very high specificity for teleosts (and a number of elasmobranchs), but lacks adequate references (Collins et al., 2019; Miya et al., 2015), in particular for the western Atlantic Ocean and the Gulf of Mexico. This became apparent from the relatively low number of ESVs assigned to the species level (Table 1). When comparing the prey ESVs against the available 12S teleost reference databases, due to a lack of teleost 12S barcodes, many sequences were assigned to a species not native to the study area. Because 12S sequences are evolutionary conserved, these matches represent local sister species (or potentially another species for which the short barcode is (almost) identical) that do have a 12S barcode sequence deposited in the reference database. Consequently, results from metabarcoding-based diet studies must be interpreted with caution until more comprehensive databases become available. Accordingly, region-specific fish barcode databases will significantly improve the resolution of molecular diet studies.

Conclusion

Feeding ecology is a cornerstone for understanding not only predator biology, but also the functions of predators in ecosystems. Here, I introduce a minimally invasive, and efficient tool for helping to elucidate the diets of sharks. Crucially, the use of this tool is not limited to small sharks and after further investigation, may also be applied to larger sharks and other large vertebrate taxa (e.g., teleosts, reptiles and birds) for which direct observation of foraging behaviour is limited or impossible. Furthermore, additional primer sets targeting different taxonomic groups may also successfully be employed to amplify fDNA, depending on the research question, target species and geographic location. The method thus carves the way for addressing hypothesis-driven research questions related to high-resolution foraging behaviour and prey selection patterns of free-ranging animals that are difficult to observe directly. In contrast to other minimally invasive methods, fDNA analysis provides diet information that is both short-term (days) and high in taxonomic resolution. Consequently, fDNA may be used to identify species-specific trophic pathways and intra- and interspecific dietary partitioning. Ultimately, combining fDNA analysis with complementary methods to answer ecological questions will offer significant advancements from conventional investigations, and may further our understanding of trophic linkages.

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Figures

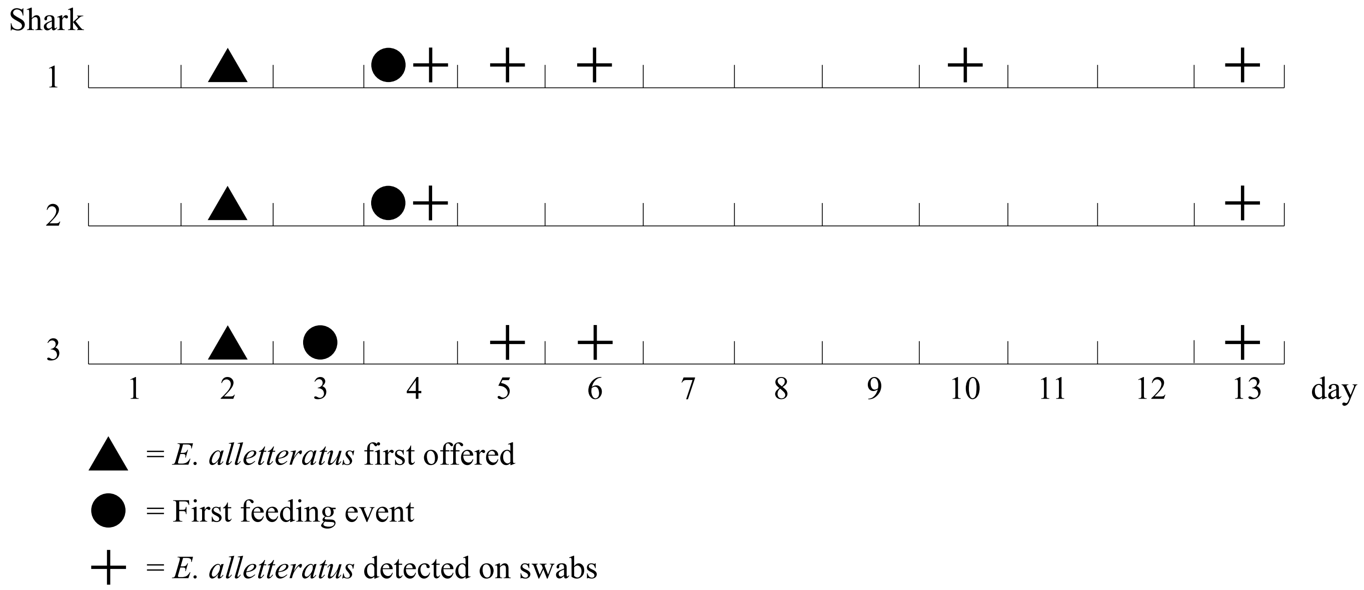

Figure 1. Schematic overview of the results of the controlled feeding experiment for three juvenile lemon sharks, *Negaprion brevirostris*, held in captivity. Day 1 denotes the day of capture.

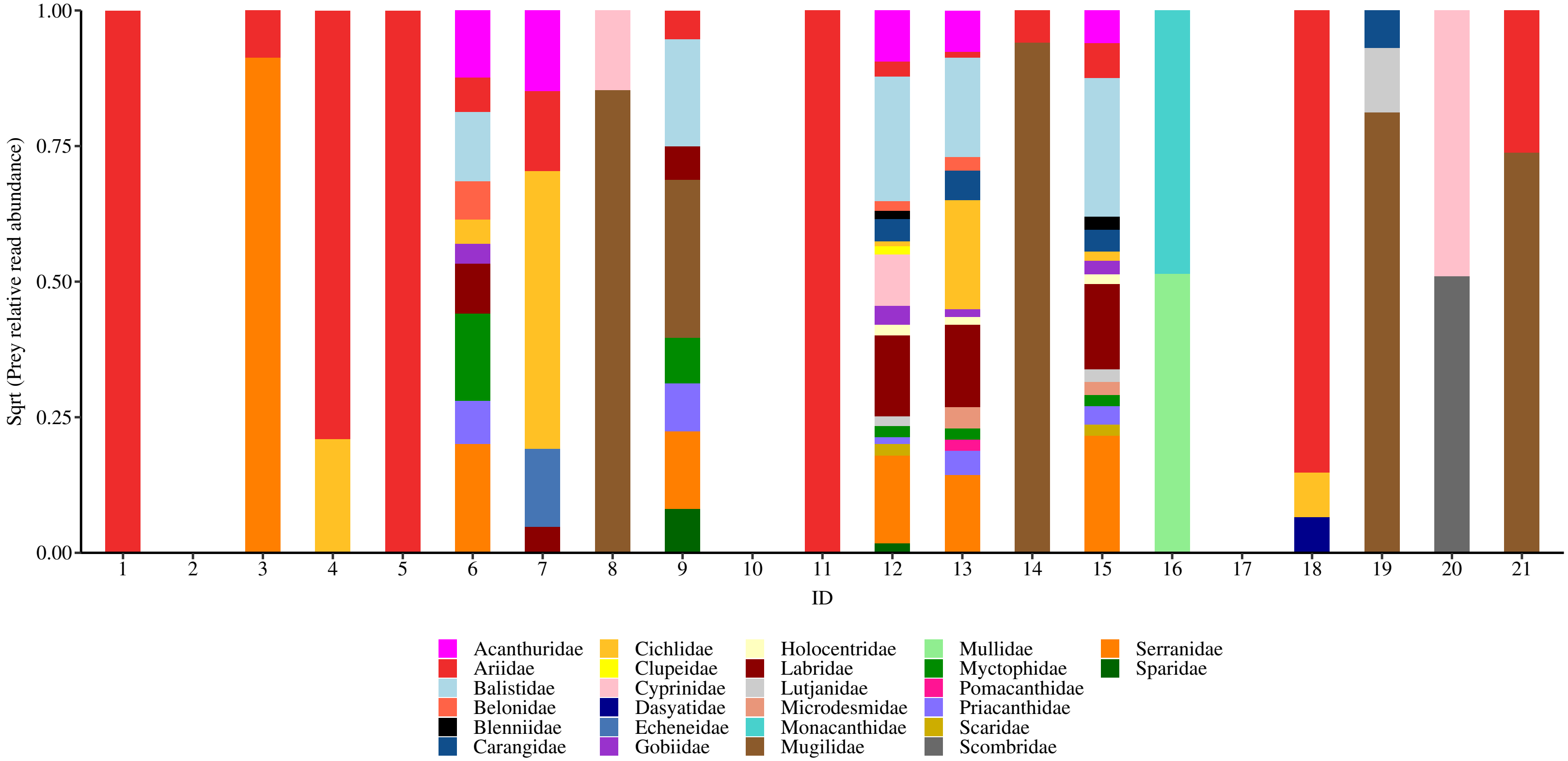

Figure 2. Cloacal swab sample results showing the prey diversity (family taxonomic level) for each individual juvenile bull shark, *Carcharhinus leucas*, sampled within the Shark River estuary in the Florida Everglades National Park, FL, USA. In shark samples #2, 10 and 17 no fDNA was detected and therefore are not shown in the graph.

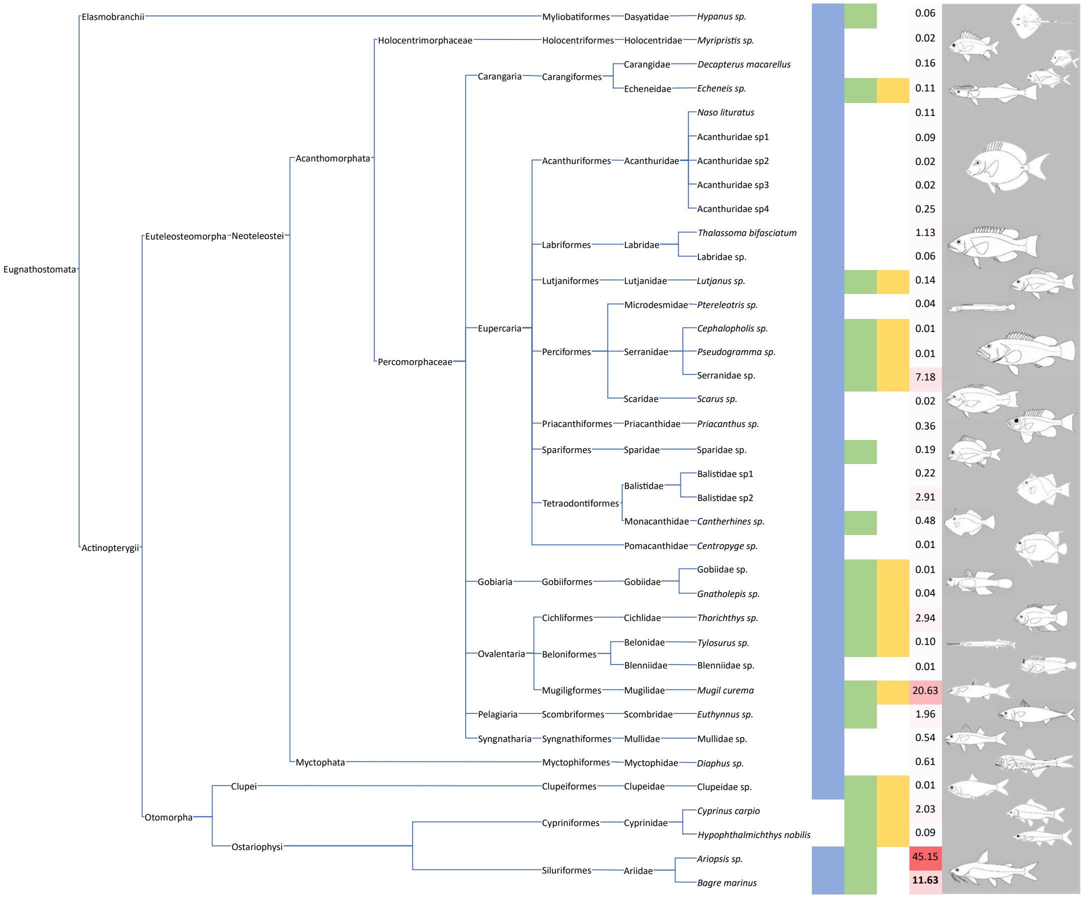

Figure 3. Cladogram showing the prey diversity (unique Exact Sequence Variants (ESV)) and their frequencies (relative read abundance) over all collected bull shark cloacal swabs. Colors denote the environment in which the prey species can be found (blue = marine, green = brackish, yellow = freshwater), as well as their relative importance in the diet of the bull sharks (darkest red = most important). Image attributions: FishBase (www.fishbase.org). Taxonomic denominations were extracted from The Fish Tree of Life (www.fishtreeoflife.org).

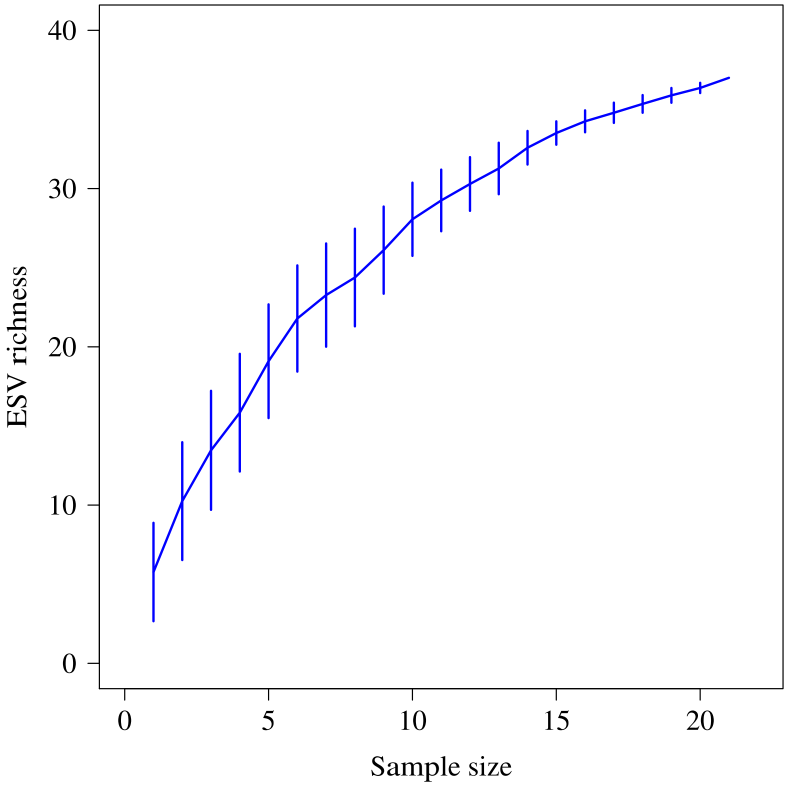

Figure 4. Species accumulation curve showing prey richness (unique Exact Sequence Variants (ESV)) as a function of the number of juvenile bull sharks, *Carcharhinus leucas*, sampled. Error bars indicate standard errors after 100 permutations.

CHAPTER IV

USING MOVEMENT MODELS AND SYSTEMATIC CONSERVATION PLANNING TO INFORM MARINE PROTECTED AREA DESIGN FOR A MULTI-SPECIES PREDATOR COMMUNITY

This chapter is based in full on the previously published article listed below:

van Zinnicq Bergmann, M.P.M., Guttridge, T.L., Smukall, M.J., Adams, V.M., Bond, M.E., Burke, P.J., Fuentes, M.M.P.B., Heinrich, D.D.U., Huveneers, C., Gruber, S.H., Papastamatiou, Y.P, 2022. Using movement models and systematic conservation planning to inform marine protected area design for a multi-species predator community. Biological Conservation 266, 109469. https://doi.org/10.1016/j.biocon.2022.109469

Abstract

Marine protected areas (MPAs) are increasingly applied to regulate fishing and conserve marine biodiversity. Yet, MPAs are often designed without sufficient ecological knowledge of the species they are intended to protect. This is particularly relevant to large and wide-ranging marine predators including many elasmobranchs (sharks and rays), for which region-specific space-use information is limited. Further, uncertainty remains in how to integrate movement datasets with systematic conservation planning frameworks to meet explicit conservation objectives. I addressed these knowledge gaps by combining movement models, constructed from passive acoustic telemetry data for eight elasmobranch species, and systematic conservation planning to investigate the design and adequacy of MPAs in Bimini, The Bahamas. Currently, there is a proposal for a no-take MPA in North Bimini (NBMPA), although it is unclear how this MPA would benefit elasmobranch communities if or when implemented. My results show that although the NBMPA would contribute to elasmobranch conservation, the supplementation with an additional MPA southwest of Bimini would be necessary to protect important habitats for multiple elasmobranch species. This southwestern area was highlighted as a conservation priority area of both permanent MPA designs as well as seasonal time-area closures, regardless of NBMPA implementation status and

conservation targets considered in this study. My integrative approach also demonstrates its ability to optimize MPA designs for marine predator communities, combining multi-species movement models, constructed from acoustic telemetry datasets that include space-use estimates over multiple years, with MPA optimization tools.

Introduction

Overexploitation and habitat destruction are primary drivers of marine megafauna population decline and range contraction, which have already led to regional extirpation in many species (Dulvy et al., 2021; MacNeil et al., 2020; Pacoureau et al., 2021; Yan et al., 2021). Marine protected areas (MPAs), which limit or prohibit extractive and/or destructive practices, are a widely applied tool with the broad objective of contributing to the conservation of marine biodiversity (Davidson and Dulvy, 2017; Edgar et al., 2014; Grorud-Colvert et al., 2021). The 2020 Aichi Biodiversity Target 11 to conserve 10% of coastal and marine areas by 2020 drove a rapid expansion of MPAs globally, with a near 12-fold increase in the area covered from 0.67% of the world's ocean in 2000 to 7.92% at the time of this writing (UNEP-WCMC, 2021). The need to meet this target has given rise to MPAs that are opportunistically – rather than systematically – designed (Baldi et al., 2017; MacKeracher et al., 2019). This has led to ambiguous conservation objectives that often fail due to hasty planning processes (Agardy, 2018). Fundamentally, MPAs should be informed by long-term ecological data of target species, which can, in turn, help evaluate MPA performance once established (Birkmanis et al., 2020; Carlisle et al., 2019; Dwyer et al., 2020). However, the necessary empirical data are not always available when designing MPAs, making them less likely to meet their intended goals (Oh et al., 2017; Santos et al., 2021).

Advances in biotelemetry technology and analytical tools have led to increases in information on species movement and distribution (Griffin et al., 2021; Hussey et al., 2015). In particular, passive acoustic telemetry has provided valuable fine-scale and long-term information on residency, habitat use, and home range that has informed conservation policy and management (Hays et al., 2019; Lennox et al., 2019; Matley et al., 2021). Information on animal space use is critical for long-term MPA effectiveness, which is a function of the extent of spatial overlap between animal space use and MPA boundaries (Kramer and Chapman, 1999; Villegas-Ríos et al., 2021). Although passive acoustic telemetry has previously been used to evaluate and improve MPA effectiveness (Bond et al., 2012; Chapman et al., 2005; Gallagher et al., 2021; Lea et al., 2016; Lee et al., 2014; Meyer et al., 2010), integrating these data with a systematic conservation planning framework that guides the design and location of reserves to meet explicit biodiversity objectives, could potentially further optimize MPA performance (Dwyer et al., 2019; Fuentes et al., 2019; Margules and Pressey, 2000). However, a lack of certainty in how to integrate these two components hampers the widespread application of such integration (Dwyer et al., 2019). To date, only one study has taken such an approach to inform protection for elasmobranchs (herafter: sharks and rays), but this was limited to a single species (Dwyer et al. 2019). However, it is imperative to adopt a more holistic, multi-species approach to improve ecosystem-based management (Matley et al., 2021).

The Bahamas hosts diverse shark communities, which are regionally significant for conservation efforts (MacNeil et al., 2020; Talwar et al., 2020; Ward-Paige and

Worm, 2017). This is mainly by virtue of bans on commercial gillnet and longline fishing implemented in the early 1990s (Clementi et al., 2021; Haas et al., 2017; Ward-Paige and Worm, 2017) and to a lesser extent the declaration of the economic exclusive zone as a shark sanctuary in 2011, which banned shark retention and trade (Ward-Paige, 2017). Nevertheless, sharks at various life stages remain vulnerable to non-fishing related anthropogenic threats such as habitat degradation and loss. Indeed, destruction of essential shark habitats, often overlooked by sanctuary regulations (Ward-Paige and Worm, 2017), is a significant threat in The Bahamas, driven predominantly by ongoing coastal development (Sherman et al., 2018). While MPAs already exist in The Bahamas, expansions of existing MPAs and new MPAs have been proposed (Bahamas National Trust, 2018). However, shark habitat was not considered in the planning process due to limited information available (The Nature Conservancy, 2017). Consequently, the extent to which essential shark habitats (e.g., used for foraging or reproduction purposes) are protected remains uncertain. Similarly, rays and their habitats were not considered a conservation priority despite rays being ecologically – and economically – important (Flowers et al., 2020; Haas et al., 2017). This is particularly concerning given the high extinction risk of many ray species globally (Dulvy et al., 2017, 2016; Kyne et al., 2020; Yan et al., 2021).

Bimini is the only subtropical islands and cays cluster located on the northwestern Great Bahama Bank that hosts extensive and interconnected mangrove, seagrass, and coral reef habitats (Trave and Sheaves, 2014). Its coastal marine ecosystem supports high biodiversity via the provisioning of critical nursery, refuge, and foraging habitats for many species, including a diverse elasmobranch community (Hansell et al., 2018;

Jennings et al., 2012; Smukall et al., 2021). However, since 1997 channel dredging, land reclamation, and mangrove deforestation for the large-scale development at North Bimini has increasingly changed the morphology of the island, detrimentally affecting local habitats and elasmobranchs (Beal et al., 2021; Dibattista et al., 2011; Gruber and Parks, 2002; Jennings et al., 2008). Indeed, analyses on the health status of this ecosystem indicated that approximately 18% of seagrass meadows and 39% of mangroves have disappeared due to development, reducing the survival rate of newborn lemon sharks (*Negaprion brevirostris*), which use mangrove habitat as nursery areas, by ~24% (Jennings et al., 2012, 2008). These most likely have become underestimates as unsustainable development has since expanded and is still ongoing (first author, pers. obs.).

To protect at least 20% of its marine and coastal environment by 2020 under the Caribbean Challenge Initiative (Broad and Sanchirico, 2008; The Nature Conservancy, 2017), The Bahamas Department of Fisheries proposed the North Bimini MPA (NBMPA; ~24 km^2) to be one of five new, top-priority and no-take sites to become legally established under the Network of Marine Reserves (Dahlgren, 2004; Gruber and Parks, 2002; Wise, 2014). Its boundaries were chosen to protect valuable habitats (e.g., sand/mud flats, mangroves, and seagrass) and local biodiversity from unsustainable development, sedimentation and climate change impacts (Bahamas National Trust, 2018). However, despite efforts to have this MPA implemented in 2001, this has not yet occurred (Wise, 2014). Meanwhile, many global organizations including International Union for the Conservation of Nature (IUCN, 2016) and Convention on Biological Diversity (CBD, 2020) called for the full protection of 30% of ocean biodiversity by

2030. It is therefore timely to develop methods to plan and design MPAs contributing toward meeting this biodiversity target and implement these methods for the proposed NBMPA in relation to elasmobranch communities.

Here, I used animal movement models integrated with a systematic conservation planning framework to design MPAs that protect 30% of important areas for a multi-species elasmobranch community, assuming the full implementation of the proposed NBMPA. I then investigated the effectiveness of these MPAs by comparing them to designs that (1) were aimed to meet the 20% conservation target previously communicated by the Bahamian government and (2) did not include the proposed NBMPA. Further, I also compared designs between summer and winter to investigate the effectiveness of permanent MPAs versus seasonal time-area closures.

Materials and methods

Study site

Bimini, The Bahamas, (25°44'N, 79°16'W) is located ~86 km due east of Miami, Florida (Figure 1). A shallow (<2 m) triangular-shaped central lagoon (~21 km^2) separates the two main islands North Bimini and South Bimini. Red mangroves (*Rhizophora mangle*) fringe the islands' peripheries with the exception of the western sides, which are bordered by white sand beaches. On their western sides, fringing coral reefs, sand flats and seagrass meadows descend to the deep pelagic zone and Gulf Stream. Extending east onto the bank are shallow sand and seagrass habitats, interspersed with various densities of rocks, sponges and/or macrophytes. Wildlife tourism provisioning of great hammerhead sharks (*Sphyrna mokarran*) is conducted regularly off the west side of South Bimini from January through April since 2014 (Heim et al., 2021).

Elasmobranch species movements

Between April 2014 – July 2018, southern stingrays (*Hypanus americanus*), blacktip (*Carcharhinus limbatus*), bull (*C. leucas*), Caribbean reef (*C. perezi*), great hammerhead (*S. mokarran*), lemon (*N. brevirostris*), nurse (*Ginglymostoma cirratum*), and tiger (*Galeocerdo cuvier*) sharks were tagged with acoustic transmitters (V16, Innovasea®), either via surgical implantation in the abdominal body cavity following capture, or via freediving and external dart tagging at the base of the first dorsal fin (i.e. great hammerhead) (Feldheim et al., 2014; Guttridge et al., 2017; Hansell et al., 2018; Heinrich et al., 2021; Smukall et al., 2021; Wood et al., 2016). These species were selected because they occur in relatively high abundances in Bimini, and exhibit varying ecological functions (Guttridge et al., 2017; Hansell et al., 2018). Elasmobranchs were sexed and had their morphometrics measured, or were estimated while free-swimming through the use of laser-photogrammetry (i.e. great hammerhead; Guttridge et al. 2017).

Transmitter-equipped elasmobranchs were monitored using an acoustic receiver array between 1 October 2016 – 30 April 2019 (VR2W, Innovasea®; n = 52; Figure 1). Range tests conducted during the same period revealed a detection range of 500 m and 958 m for receivers deployed in coral reef and sand habitats, respectively (Figures S1 and S2; Guttridge et al. [2017]). Receiver locations were chosen strategically to include all major putative elasmobranch habitats. Additionally, chosen locations allowed for the monitoring of elasmobranchs entering and exiting the lagoon.

Detections were filtered to exclude possible false-positives (Simpfendorfer et al., 2015), including signals that were detected only once within a 1-h time frame on a single receiver. Double detections arising from transmitters that were detected simultaneously by receivers with overlapping detection ranges were also removed. Finally, detections recorded within the first 24 h post-tagging were excluded from further analysis to account for potential bias arising from stress (Guttridge et al., 2017). A residency index score, calculated as the proportional number of days at liberty in which an elasmobranch was detected by the acoustic receiver array (Guttridge et al., 2017), was calculated.

Individual-level utilization distributions (UDs), which are the probability density distributions of animals at a given location over a period of time (Winkle, 1975), were estimated for each species using the dynamic Brownian bridge movement model (dBBMM) (Kranstauber et al., 2012) in the R *move* package version 3.2.2 (Kranstauber et al., 2019). The dBBMM is similar to the traditional BBMM (Horne et al., 2007) but better equipped for dealing with irregular sampling of tracks (Kranstauber et al., 2012). As such, dBBMMs are generally more appropriately applied to passive acoustic telemetry data. To estimate a UD, the dBBMM integrates the temporal component of detection data by explicitly modeling movements among consecutive locations (i.e., receiver stations). This is achieved by both accounting for the chronological order at which stations are visited, as well as the travel time among them. The model reconstructs the movement path by applying correlated random walks, creating a probability density distribution or "bridge" between two consecutive stations of where the animal could have been when it was not detected. A minimal time difference between stations is suggestive of a straight-line movement and therefore the variance in Brownian motion (σ^2_m, associated error of the movement path), calculated for a subsection of the trajectory determined by the sliding window size, would be small. Conversely, a larger time difference is suggestive of a tortuous movement path, which would result in a larger σ^2_m value (Kranstauber et al., 2012). In my models, I used a spatial resolution of 1 km^2 (see section 2.3). The location error was set to 500 m, the most conservative detection range estimate in my study.

To scale up to group-level UDs, individual-level UDs were scaled from 0 to 1 to facilitate interpretation as relative intensity of utilization, summed and rescaled again (Dröge et al., 2017; Papastamatiou et al., 2013). Juvenile lemon sharks were separated from subadult and adult conspecifics because they display highly restricted home ranges (Chapman et al., 2009; Morrissey and Gruber, 1993). To account for unequal spatial representation of stations in different areas, group-level UDs were weighted by estimating individual-level UDs per area, and by dividing group-level UDs by the number of grid cells containing receivers within the same area (south and southwest [n = 15], central lagoon and bank [n = 22], north [n = 7]; Figure 1), followed by another rescaling (Papastamatiou et al., 2013). Core (50% probability density) and general use (95% probability density) areas were then calculated. Finally, UD layers were reclassified to discrete space-use classes to enable the targeting of proportions of these ranges for the systematic conservation planning analysis (see section 2.3). The above protocol was repeated for summer (1 June – 30 November) and winter (1 December – 31 May) acoustic datasets, based on fluctuations in water temperature at the study site (Guttridge et al., 2017). All processing of UDs were performed in ArcMap® version 10.5.

A disadvantage of passive acoustic telemetry, apart from the frequent limited spatial coverage, is tagging location bias that may be introduced in studies that estimate animal space use (Hays et al., 2020; Papastamatiou et al., 2018). This is often an issue as tagging locations may be limited by logistics or budgetary constraints. To evaluate the potential bias introduced by passive acoustic tracking, I qualitatively compared the number of species and conspecifics detected at a subset of receiver stations to those observed using baited remote underwater video systems (BRUVS) surveys conducted near the same stations between 1 February 2017 – 29 November 2018 (Clementi et al., 2021). See supplementary materials for details on BRUVS surveys.

Conservation planning analysis – Marxan

To inform MPA design, I used the systematic decision-support tool Marxan, which aids in the selection of efficient, spatially compact and near-optimal reserve design solutions (Ball et al., 2011). Marxan provides near-optimal solutions to the minimum set problem (also known as the reserve design problem), which answers the question of how to meet targets at a minimum cost (Ball et al. 2011). To solve this problem, Marxan requires the user to define spatial planning units, conservation features, targets for each feature, and other design criteria such as clumping requirements. I divided my study site into 1 km^2 grid cells, for a total of 180 planning units. The choice of planning unit size was based on a previously executed planning exercise to maintain consistency in recommendations (Fuentes et al., 2019). For my planning region the conservation features of interest were benthic habitats (n+p, 2015) as surrogate for species habitats and diversity, elasmobranch species space-use classes, and lemon shark nurseries. Five nurseries have been identified in Bimini for newborn and small juvenile lemon sharks, which are characterized by mangrove-fringed shorelines (Figure S3; Chapman et al., 2009; see supplementary materials).

I defined four planning scenarios to investigate the design and robustness of MPAs at protecting 30% of defined conservation features, exploring two possible sets of conservation feature targets, and considered whether including the proposed NBMPA influenced spatial recommendations for future protection (Table 1; Fuentes et al., 2019). To investigate the potential effect of seasonal differences in elasmobranch space use on the reserve design solutions and determine whether seasonal time-area closures pose a better management strategy than permanent MPAs, I repeated these scenarios including the space use of elasmobranch species across the full year (scenarios 1 – 4), during summer only (scenarios 5 – 8), and during winter only (scenarios 9 – 12).

My two target sets considered for my scenarios were: 20% baseline targets (area protected for all features) to reflect the 20% biodiversity goals set out by the Bahamian government (Broad and Sanchirico, 2008); and 30% baseline targets for all features to reflect the 30% by 2030 goals as recommended by many global organizations (CBD, 2020; IUCN, 2016). Baseline targets were combined with retention targets (features with high intrinsic susceptibility to extinction e.g., species with vulnerable life history processes including reproduction areas, and threatened species; Haupt et al. [2017]). Retention targets ranged from 10% for small juvenile lemon sharks and lemon shark nurseries to 20% for Critically Endangered great hammerhead sharks (Table 2; Haupt et al. 2017, Rigby et al. 2019). Terrestrial habitats including rocky outcrops, urbanized areas and inland vegetation were not targeted for conservation and therefore had their targets set to 0% (for full list of targets by feature see Table 2).

Data on cost metrics relevant for users that would be impacted by increasing MPA size were not available for the context of my study. In particular, in my study region while MPAs would exclude further development activities (coastal) and fishing, only the former is directly relevant here and only in the context of southern stingrays and juvenile lemon sharks that rely on mangrove nursery areas for their survival. Nevertheless, I evaluated the suitability of an existing cost layer for the region (Fuentes et al., 2019), which was developed for costs associated with the implementation of an MPA to protect green turtles (*Chelonia mydas*) in the region, but determined that the stakeholders consulted for this cost layer were not adequate for elasmobranch communities. Additionally, this cost layer is also somewhat outdated (>4 years old) and might not be reflective of current stakeholder views and opinions. With this in mind, I framed the Marxan problems as focusing on minimizing area of protection and used the planning unit area as my cost metric. My expectation is that the recommended MPA design would be further refined through an implementation process using deliberative decision making and intensive stakeholder engagement, which would consist of eliciting costs and preferences.

To take into consideration design criteria such as clumping of planning units, I used the method by Stewart and Possingham (2005) to identify an optimal boundary length modifier, which minimizes trade-offs in costs and compactness. This resulted in a final boundary length modifier value of 215. Species penalty factors, which are used to distinguish the relative importance of different conservation features, were set to 20 to ensure that all conservation targets were met in each run. Each scenario was run 100 times (with 1 000 000 iterations per run) using the adaptive simulated annealing algorithm of Marxan ran within CLUZ (Conservation Land-Use Zoning Software; Smith, 2019).

For each scenario, I recorded total area selected for best solutions. I compared spatial maps of best solution (i.e. reserve design with the lowest value for the objective function that is therefore the most efficient and least costly to implement) and summed solution, or selection frequency (i.e. the frequency out of 100 runs in which a planning unit was selected to be part of a reserve design, resembling its irreplaceability; Carwardine et al. 2009).

The spatial similarity of solutions between sets of summer and winter scenarios were compared using two methods (Adams et al., 2010). First, pairwise comparisons were made for compiled single best solutions using the Cohen's kappa (κ) statistic, which measures the spatial agreement of solution sets after removing spatial overlap expected by chance (Richardson et al., 2006). Kappa can range between -1 and 1. The closer the statistic is to 1, the more the spatial configurations of solutions agree; conversely, the closer it is to -1 the stronger their disagreement. Second, pairwise comparisons were made for compiled summed solutions using the Spearman rank correlation (ρ) statistic. All statistical analyses were performed in R v3.5.1 (R Core Team, 2019) and the kappa statistic was calculated using the *caret* package (Kuhn, 2008).

Results

Elasmobranch species movements

Annual

A total of ~1.2 M detections were recorded from 99 elasmobranchs, comprising eight species (range across all individuals: 56 – 122 793 detections; Table S1). On average, animals were detected for 229.2 days (SD: 213.3; range: 2 – 842) and across 12.2 stations (SD: 7.2; range: 1 – 33). Residency index scores were highly variable across species. Some were transient (e.g., tiger: 0.07 ± 0.04, mean ± SD; bull: 0.21 ± 0.13; great hammerhead: 0.32 ± 0.15), whereas others were considered more residential (e.g., nurse: 0.48 ± 0.27; Caribbean reef: 0.48 ± 0.33).

The extent of elasmobranch space use that intersected with planning units was highly variable (31.8 ± 17.7 km^2). Group-level UD estimations identified core and general use areas of bull, Caribbean reef, great hammerhead, and tiger sharks located primarily off the west side of Bimini. Great hammerhead, and tiger sharks also used areas to the east with some of their space use overlapping with the proposed NBMPA (Figure 2). In contrast, the space use of southern stingrays, blacktip, nurse, subadult and adult lemon sharks were more widespread, with core and general use areas scattered throughout the study site and with comparatively higher overlap with the proposed NBMPA. The space use of juvenile lemon sharks fell completely within the boundaries of the NBMPA (Figure 2).

A total of 216 BRUVS were analyzed across six locations and observations compared to passive acoustic tracking data obtained from those same locations (Figure S3). Overall, elasmobranch hotspots were located toward the west and southwest of

Bimini with the number of species and individuals gradually declining toward the east, as identified by both methods. Additionally, across all sites, passive acoustic tracking detected more species and individuals than were observed by BRUVS surveys, which suggests that the acoustic tagging of elasmobranchs was representative of the actual species diversity and that no obvious group-level bias in elasmobranch space-use estimates existed in my study (Figure S4).

Seasonal

Extents of summer (29.1 ± 17.5 km^2) and winter (27.7 ± 15.8 km^2) space use were highly variable, whereas absolute differences among seasons and species were relatively small (9.9 ± 12.9 km^2). Seasonal differences in the locations of core and general use areas were relatively small for southern stingrays, blacktip, lemon and Caribbean reef sharks, with only the latter species showing a complete lack of spatial overlap with the proposed NBMPA (Figure S4). Conversely, bull and nurse sharks expanded their core and general use areas to include parts of the NBMPA and surrounding area during the summer. The opposite patterns were observed for great hammerhead and tiger sharks, which only used parts of the NBMPA in winter (Figure S5).

Priority conservation areas

Permanent MPAs

All four permanent scenarios (Table 1) met all targets and total area selected ranged from 34 km^2 (scenario 1) to 57 km^2 (scenario 4), with the spatial configuration of conservation priorities across the study site depending on the scenario being considered.

The best solutions across scenarios showed that selected planning units consistently included the southwest portion of Bimini. In scenario 1 and 2, best solutions included additional planning units to the central east (Figure 3a, b). When considering inclusion of the NBMPA (25 planning units total), selected planning units moved from locations to the east to locations adjacent to the proposed NBMPA (Figure 3c, d).

The best and summed solutions showed spatially similar patterns. Spatial conservation priorities were located southeast and southwest of Bimini as planning units in these areas displayed medium to high selection frequency (> 50%). One relatively large area located southwest of South Bimini was consistently identified as a highest priority conservation area (selection frequency > 90%), with an additional small area located in central-east Bimini (within the NBMPA boundaries). When the analysis assumed the implementation of the NBMPA, selection frequency in the central-east decreased, showing a shift in spatial priorities to within or adjacent to the locked-in NBMPA (Figure 4c, d).

Seasonal time-area closures

All targets were met for the seasonal scenarios, and reserve area ranged from 34 km^2 (scenario 5) to 57 km^2 (scenario 8) in summer and from 36 km^2 (scenario 9) to 58 km^2 (scenario 12) in winter. Best and summed solutions were similar across seasons, showing spatial consistency (Figures 5 and 6). The agreements in spatial similarity among sets of best solutions was fair to good ($\kappa = 0.63$, $p < 0.001$), following the classification proposed in Fleiss et al. (2003). In addition, there was a strong positive correlation among sets of summed solutions sets ($\rho = 0.88$, $p < 0.001$). While the inclusion of planning units varied with the scenario considered, best solutions again consistently showed that those areas are concentrated to the southwest of Bimini (Figures 5a, b, e, f). Similarly, the selection of planning units to the central east depended on whether the NBMPA was considered implemented or not (Figures 5c, d, g, h). Medium to high priority conservation sites (>50% selection frequency) were again concentrated in the southwest and southeast of the study site, with an additional high priority site located in the central-east. The shift of spatial priorities from the central-east area to within or adjacent to the proposed NBMPA was again observed when the MPA was considered implemented (Figures 6c, d, g, h).

Discussion

The design and adequacy of new and proposed MPAs in Bimini were evaluated to determine whether the 30% conservation target recommended by global organizations were met for elasmobranch communities. By constructing species-specific group-level UDs for tagged elasmobranchs and having quantitative conservation targets for each space-use class, benthic habitat and shark nursery feature (Table 2), I identified spatially explicit MPAs that maximize the protection of important elasmobranch areas at minimum MPA size. My results identified improvements that can be made to the proposed MPA design by complementing the NBMPA with an additional MPA that includes spatial priorities located in the southwestern planning region. This MPA design was the most consistently identified, regardless of the considered scenario, and when compared to seasonal time-area closures, and therefore robust to seasonal differences in elasmobranch space-use patterns.

The NBMPA would contribute to elasmobranch conservation if implemented because some feature targets are met in this area, especially for juvenile lemon sharks. However, most conservation priority areas for elasmobranchs are located outside of this proposed MPA, especially in the southwestern planning region. This matches other studies (Fuentes et al., 2019) that found the southern portion of Bimini as being generally more important for biodiversity, in this case juvenile green turtles and their habitats, than the area within the proposed NBMPA. Although the NBMPA would also include important mangrove and seagrass habitats on the central and east side of Bimini, it would not include fringing coral reefs located southwest of the islands, which were identified as important for all investigated species. Sloping into the deep pelagic zone, this shelf edge habitat is exposed to the productive Gulf Stream, and is functionally dependent on neighboring shallow-water coral reef, mangrove, and seagrass nursery habitats for their supply of coral reef fish and elasmobranch recruits (Franks, 2007; Mumby et al., 2004; Nagelkerken et al., 2002, 2000). These factors likely make this area an important foraging habitat for at least some of the focal elasmobranch species, and also for elasmobranchs not considered here, including spotted eagle rays (*Aetobatus narinari*; Silliman and Gruber, 1999). This habitat may also fulfill other important ecological functions for a host of other species. Large pelagic species (e.g., billfishes [class: Actinopterygii], wahoo [*Acanthocybium solandri*], dolphinfish [*Coryphaena hippurus*] and tunas [family: Scombridae]) use this shelf edge habitat as a movement or migration corridor (Buchan, 2000). For example, over a six-year period, 22 Endangered Atlantic bluefin tuna (*Thunnus thymnus*) (Collette et al., 2015), most of which were tagged in the Gulf of St. Lawrence, Canada (Block et al., 2019), were detected by acoustic receivers in this area (B. Block, pers. comm.). These individuals likely use Bimini as a migration corridor between their foraging habitat in Canadian waters and spawning grounds in the Gulf of Mexico (Wilson et al., 2015). The incorporation of this area in any MPA design for Bimini would therefore be beneficial for protecting wider marine biodiversity.

Spatiotemporal variability in space use of marine megafauna species is important to consider when designing or evaluating MPAs (Dwyer et al., 2019; Lambert et al., 2017). By comparing the spatial similarity of Marxan solutions between summer and winter, I found that the replacement of permanent MPAs by seasonal time-area closures does not pose a better management strategy because all considered areas are important for conservation year-round. Time-area closures have often been implemented to exclude fishing practices during a specific time of year when a target species is at its most vulnerable (e.g., aggregation or spawning sites, and during critical movement phases) (Allen and Singh, 2016). Such management strategies are often tailored successfully to a single target species (e.g., Shillinger et al. 2008). Subsequently, this approach is unlikely to work for multiple species simultaneously, especially when they have different movement strategies (e.g., seasonal migration versus year-round residency). Given that the elasmobranchs monitored in this study exhibited a variety of space use and residency patterns to Bimini, important conservation areas were always occupied by individuals of at least one or more investigated species throughout the year.

Several caveats associated with my integrated approach should be acknowledged. First, my analyses focused on identifying conservation priorities purely on the spatial requirements of investigated species and thus sought to minimize reserve area but did not consider socio-economic cost. While this is appropriate for the purpose of answering my research questions and identifying spatial conservation priorities based on ecological values, inclusion of realistic socio-economic factors either as spatial data or through stakeholder engagement would be the necessary next step if moving from design of marine reserves to implementation (Adams et al., 2019; Ban and Klein, 2009). Notably, stakeholders in the region have been engaged in MPA design aspects in other research and planning processes (e.g., Fuentes et al., 2019), which provides an opportunity for returning to these groups to continue engagement and receive feedback on these new MPA design scenarios accounting for elasmobranchs. Previous engagement and elicitation processes have mapped areas important for wildlife tourism. These areas may in fact benefit from MPAs designed to protect elasmobranchs, as some species (e.g., Caribbean reef and great hammerhead sharks) are popular for snorkeling and dive tourism. I have chosen not to incorporate existing maps of stakeholder use (Fuentes et al., 2019) as a cost layer in this planning exercise given the potential complex relationships of both benefits and costs of the proposed MPAs with the stakeholders previously considered. Instead, further direct stakeholder engagement with these same stakeholder groups would be the critical next step in the planning process (Adams et al., 2019).

Second, the sample size per species may be insufficient to allow for population-level inferences in space use (Sequeira et al., 2019). While minimum sample sizes are likely to be specific to the study species, and the behavior and life stage of tagged individuals (Dwyer et al., 2019; Sequeira et al., 2019; Shimada et al., 2020), a sample size of >10 individuals is suggested to be appropriate for estimating population-level space use (Sequeira et al., 2019). Consequently, space-use estimates for blacktip, Caribbean reef, tiger, and juvenile lemon sharks (species-specific sample sizes <10 individuals) may not have fully captured population-level space use patterns, although previous studies corroborate restricted space use patterns found for small juvenile lemons in this study (e.g., Guttridge et al., 2012; Heinrich et al., 2021).

Finally, my elasmobranch space-use estimates may be biased by tagging location. For wide-ranging animals tagging locations will often be highlighted as high use areas, not necessarily because animals spend a lot of time there, but simply because they form the starting point from which the tracks radiate (Hays et al., 2020). Additionally, for animals with restricted movements, areas identified as low to no use may not reflect the unimportance of those same areas by the larger population if such areas are located within their range (Papastamatiou et al., 2018). Due to logistical constraints, most of my tagging efforts did not occur in the north side of Bimini. Consequently, my tagging was biased to individuals in the east, south and west sides that may be less likely to use the north region of Bimini. This bias could therefore underestimate shark space use in this northern area of my study site. My BRUVS data only partially addressed this issue because BRUVS deployments were similarly biased in their placement, with no sampling conducted north of Bimini. Specifically, BRUVS data support the passive acoustic tracking data, showing that elasmobranchs were most often sighted west and southwest of Bimini and that tagging location was unlikely to have affected observed distribution patterns. My telemetry and BRUVS results also corroborate previous fisheries-independent catch data showing that catches from east Bimini were dominated by blacktip, lemon, nurse, and tiger sharks, with low to no catches of bull, Caribbean reef and great hammerhead sharks (Hansell et al., 2018; Smukall et al., 2021). Future studies are encouraged to conduct visual surveys covering the full spatial extent of the planning region to better account for potential tagging location bias in space-use estimates (Fuentes et al., 2019; Papastamatiou et al., 2018).

To optimize MPA performance, areas important to animals of conservation concern require inclusion within MPA boundaries (Kramer and Chapman, 1999; Villegas-Ríos et al., 2021). Normally, analyses that include animal movement in spatial prioritization tend to be based on satellite or GPS telemetry data (Perrig et al., 2020; Santos et al., 2021). Acoustic data are often included directly or indirectly, via species distribution models, in systematic conservation planning to meet explicit biodiversity objectives (Abecasis et al., 2015; Dwyer et al., 2019). In contrast, my work demonstrates an integration of acoustic data through movement models, for both residential and migratory species, with a systematic conservation planning framework. My quantitative approach allows for space use estimation over multiple years, time spans that are rarely possible with satellite or GPS tracking, although this comes at the cost of reduced spatial resolution due to the often limited coverage of receiver arrays. I recommend that future planning of MPAs consider the use of such methods to identify important areas and account for conservation targets when designing MPAs.

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Tables

Table 1. Four defined planning scenarios considered for Marxan analyses (scenarios 1 – 4) that were repeated three times (annual: scenarios 1 – 4, summer: 5 – 8, winter: 9 – 12) to investigate spatial recommendations in MPA designs.

Proposed NBMPA status	**Targets**	
	20%	**30%**
Not implemented	Scenario 1: Baseline target of 20%, proposed NBMPA not implemented	Scenario 2: Baseline target of 30%, proposed NBMPA not implemented
Implemented	Scenario 3: Baseline target of 20%, proposed NBMPA implemented	Scenario 4: Baseline target of 30%, proposed NBMPA implemented

Table 2. Sums of baseline and retention target values per conservation feature and target scenario used in the Marxan analyses.

Conservation feature	**Targets**	
	20% baseline	**30% baseline**
Habitat		
Sandy benthos	20%	30%
Low density *Thalassia* and *Halodule*	20%	30%
Medium density *Thalassia* and *Halodule*	20%	30%
High density *Thalassia* and *Halodule*	20%	30%
Sargassum	20%	30%
Large sponge	20%	30%
Inland vegetation	0%	0%
Mangrove	20%	30%
Mangrove edges, ponds and other inlets	20%	30%
Marshes	20%	30%
Rocky outcrops	0%	0%
Urban areas	0%	0%
Unclassified deep water	20%	30%
Species space use (core and general use areas)		
Blacktip shark	20%	30%
Bull shark	20%	30%
Caribbean reef shark	20%	30%
Great hammerhead shark	40%	50%
Lemon shark (juvenile)	30%	40%
Lemon shark (subadult/adult)	20%	30%
Southern stingray	20%	30%
Tiger shark	20%	30%
Lemon shark nurseries		
Bonefish hole	30%	40%
North Sound	30%	40%
Pirate's Well	30%	40%
Sharkland	30%	40%
South Bimini	30%	40%

Figures

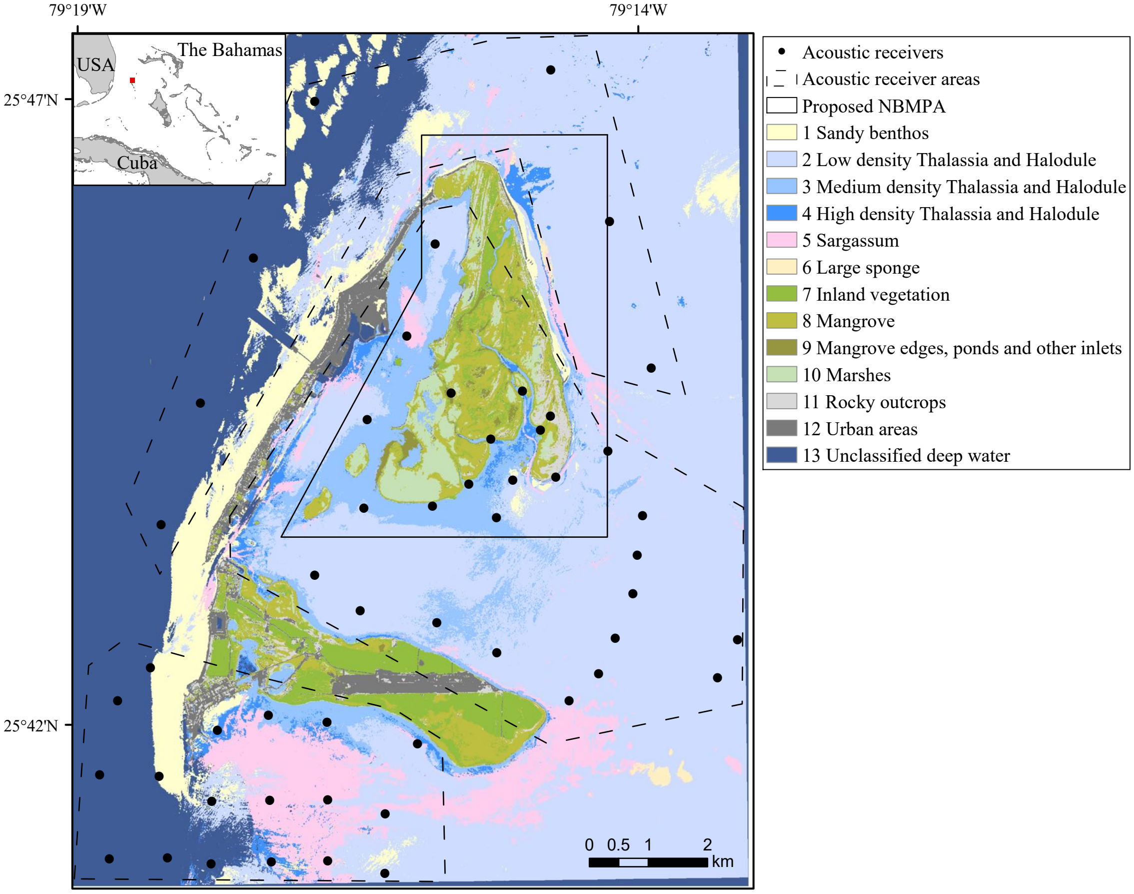

Figure 1. Bimini, The Bahamas. Filled black circles depict the acoustic receiver array that was active between 1 October 2016 – 30 April 2019, spanning a variety of habitats as conveyed by the different colors used (see figure legend). The solid black line depicts the boundaries of the proposed North Bimini Marine Protected Area and the dashed lines the three different clusters of receiver locations for which sub-area space use was estimated prior to the estimation of site-wide space use. *Image credit: LAND INFO Worldwide Mapping, LLC, includes material Copyright © DigitalGlobe-Longmont, Colorado. All rights reserved, through an Enterprice Licence.*

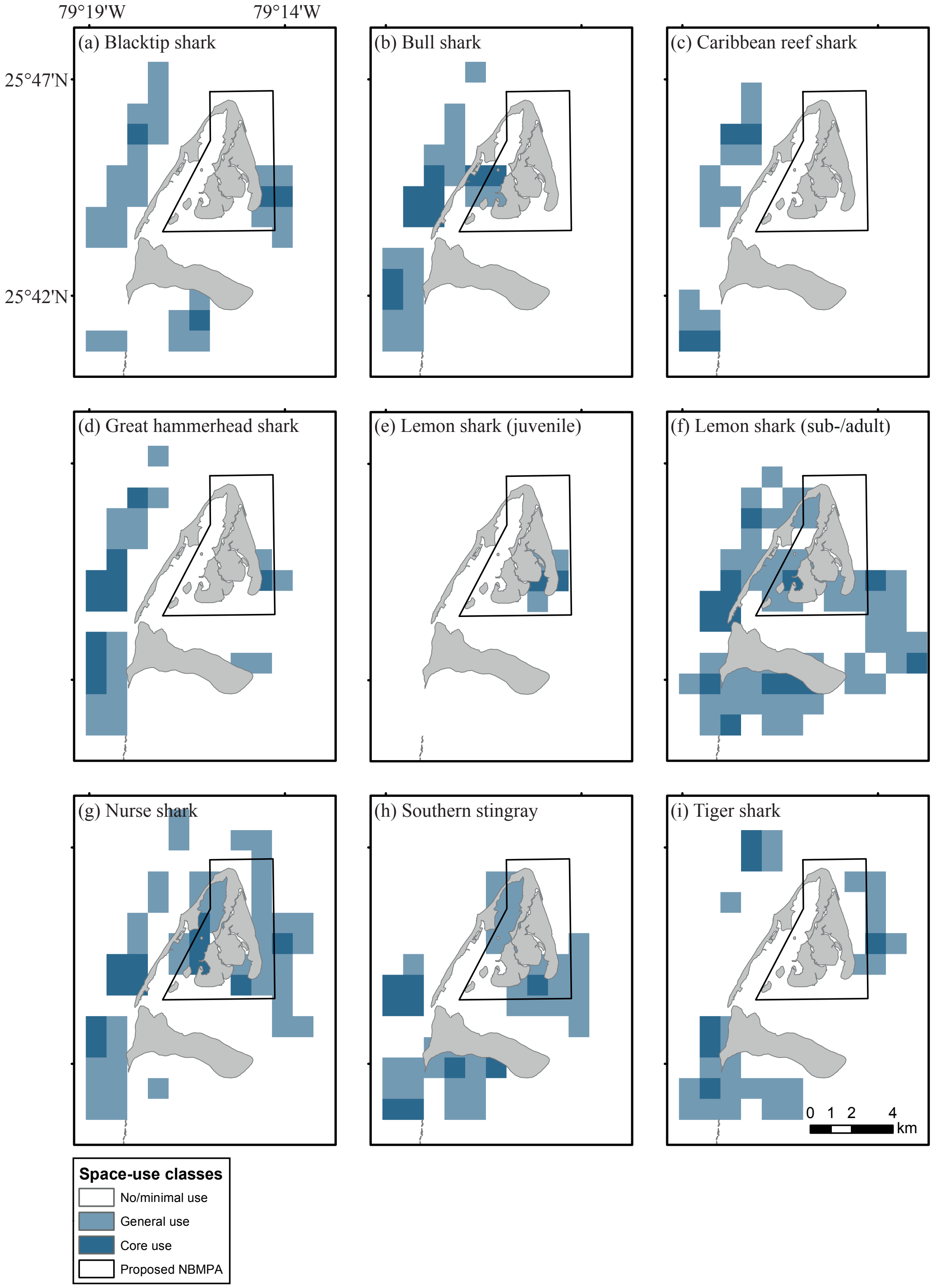

Figure 2. Estimated annual space use patterns for the elasmobranch species that were acoustically monitored around Bimini between Oct 2016 and April 2019. Colors represent no/limited use (white), general use (light blue), and core use (dark blue) areas. The solid black line indicates the boundaries of the proposed NBMPA.

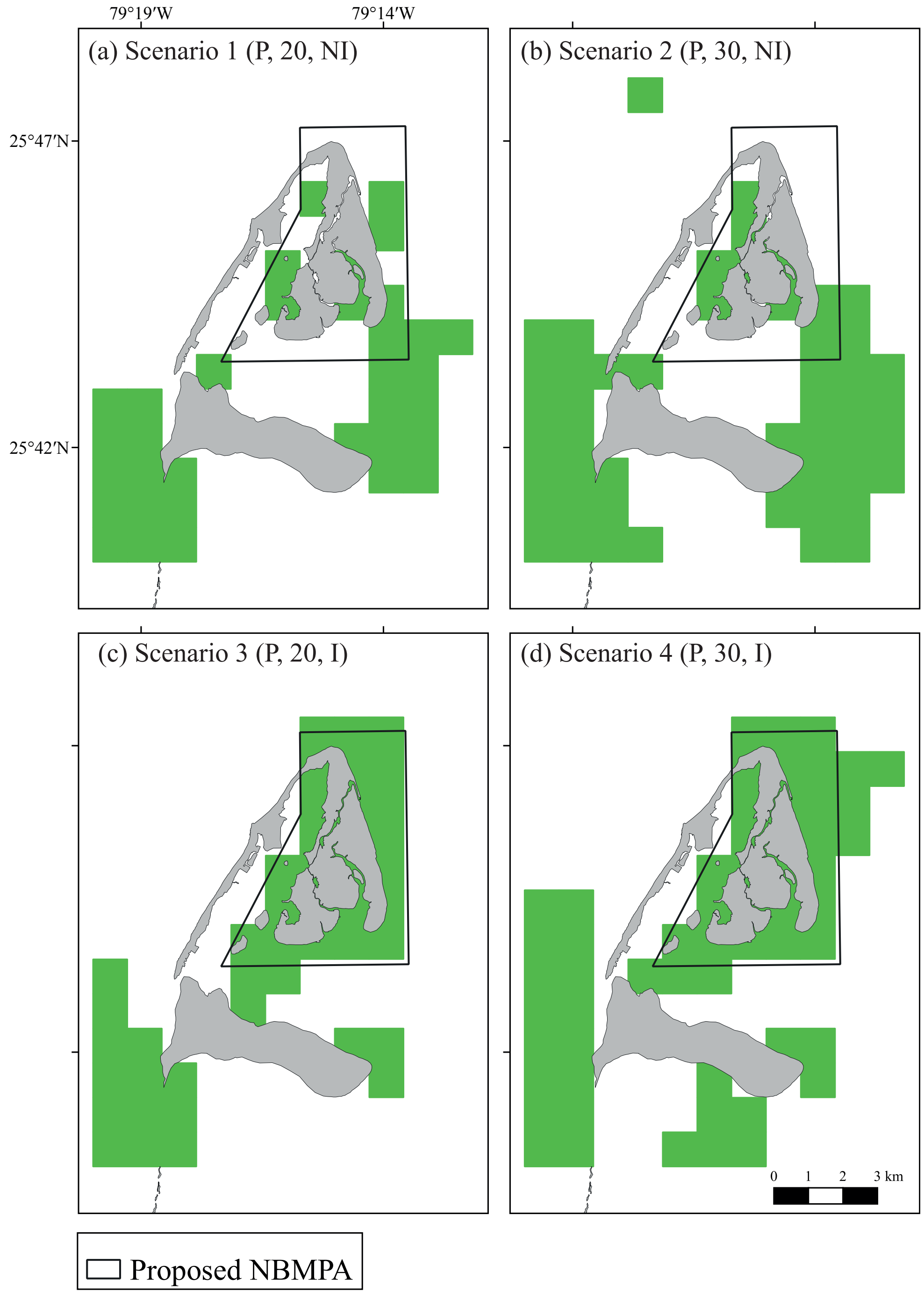

Figure 3. Marxan best solutions. P: permanent solutions, 20: 20% baseline target, 30: 30% baseline target, NI: proposed NBMPA not implemented, I: proposed NBMPA implemented. Scenario 4 is the preferred scenario. The boundaries of the proposed NBMPA are indicated by the solid black line.

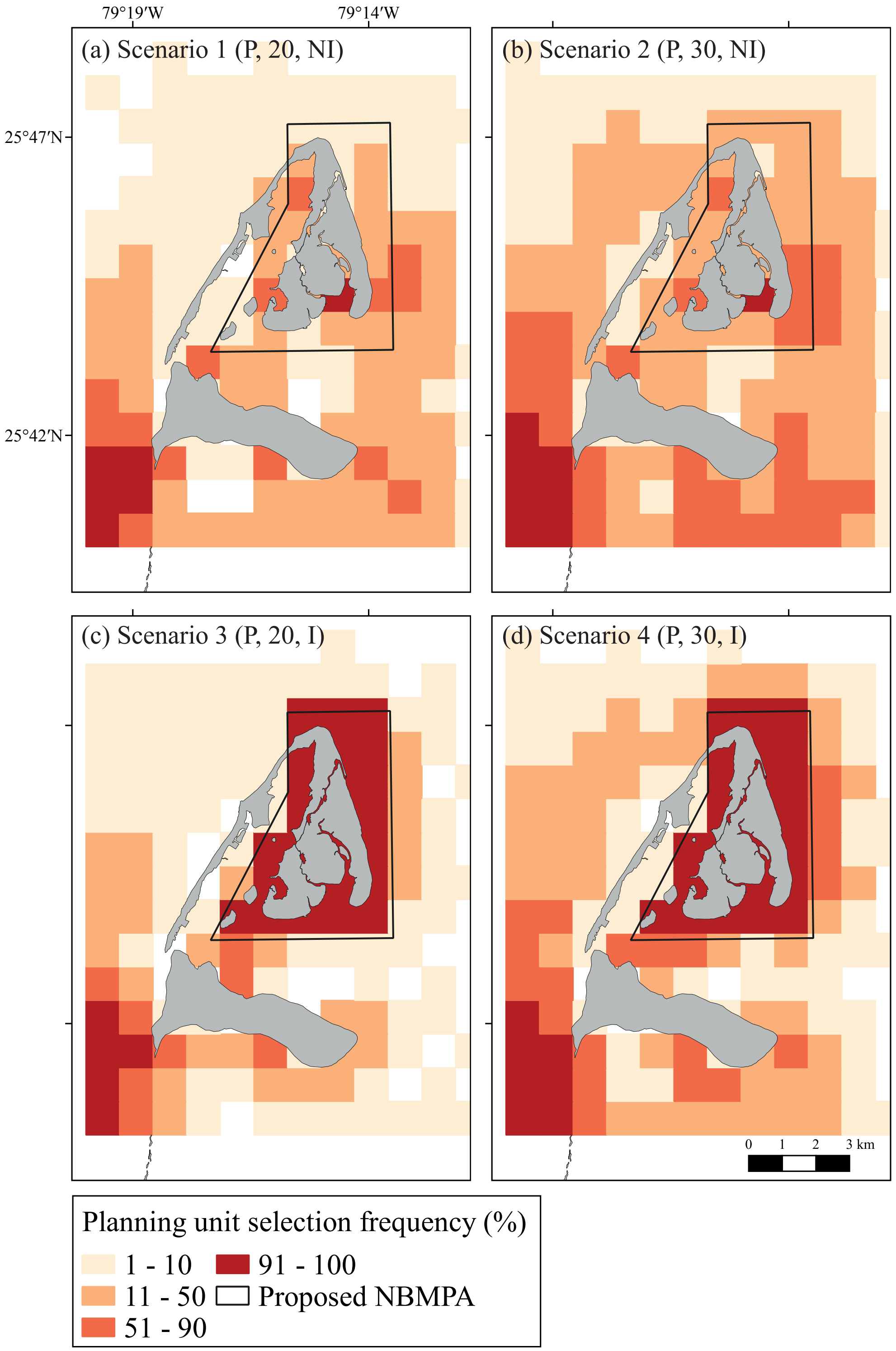

Figure 4. Marxan summed solutions. P: permanent solutions, 20: 20% baseline target, 30: 30% baseline target, NI: proposed NBMPA not implemented, I: proposed NBMPA implemented. Scenario 4 is the preferred scenario. The boundaries of the proposed NBMPA are indicated by the solid black line.

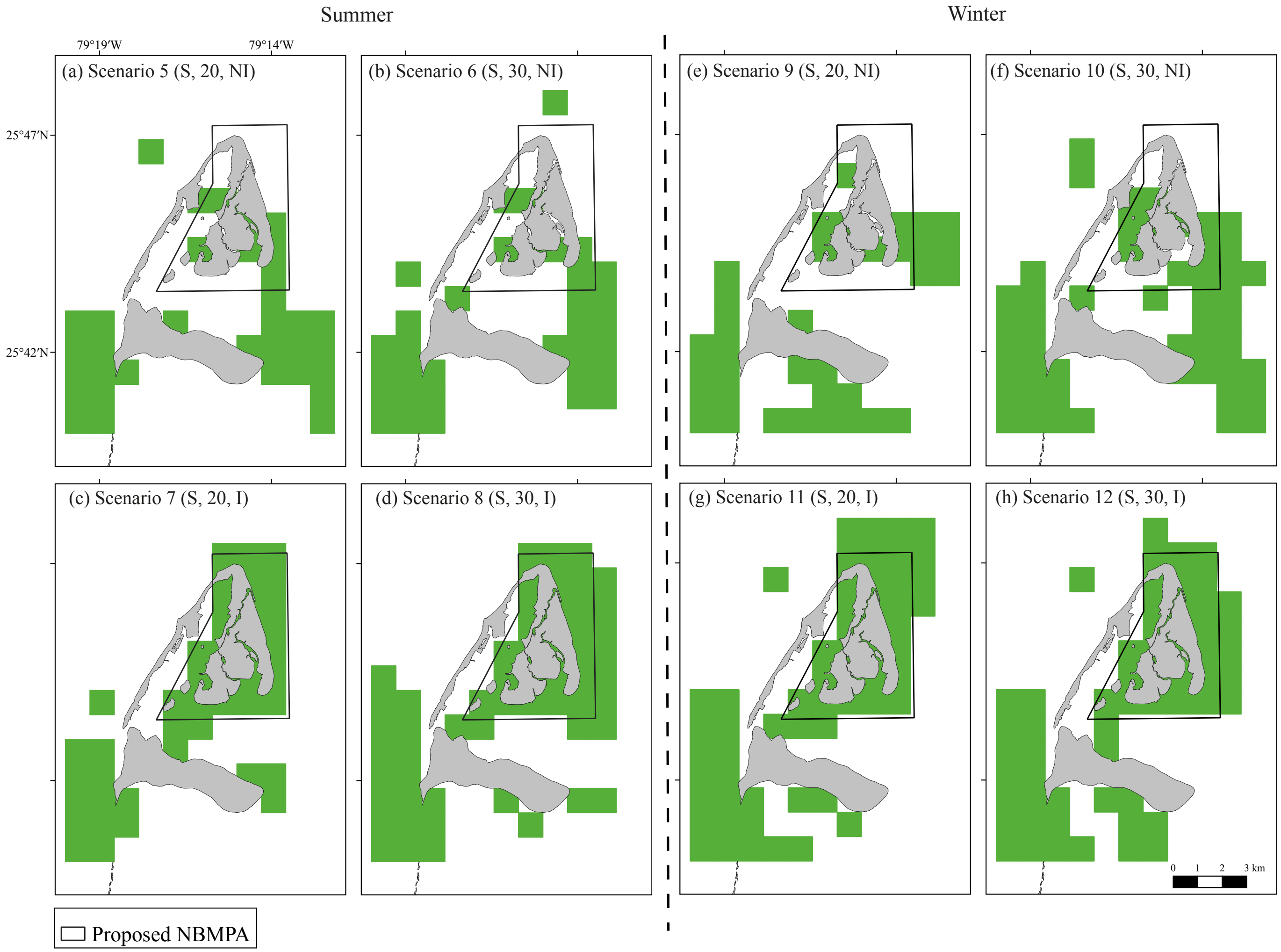

Figure 5. Marxan seasonal best solutions for time-area closures, separated by a vertical dashed line. S: seasonal, 20: 20% baseline target, 30: 30% baseline target, NI: proposed NBMPA not implemented, I: proposed NBMPA implemented. The boundaries of the proposed NBMPA are indicated by the solid black line.

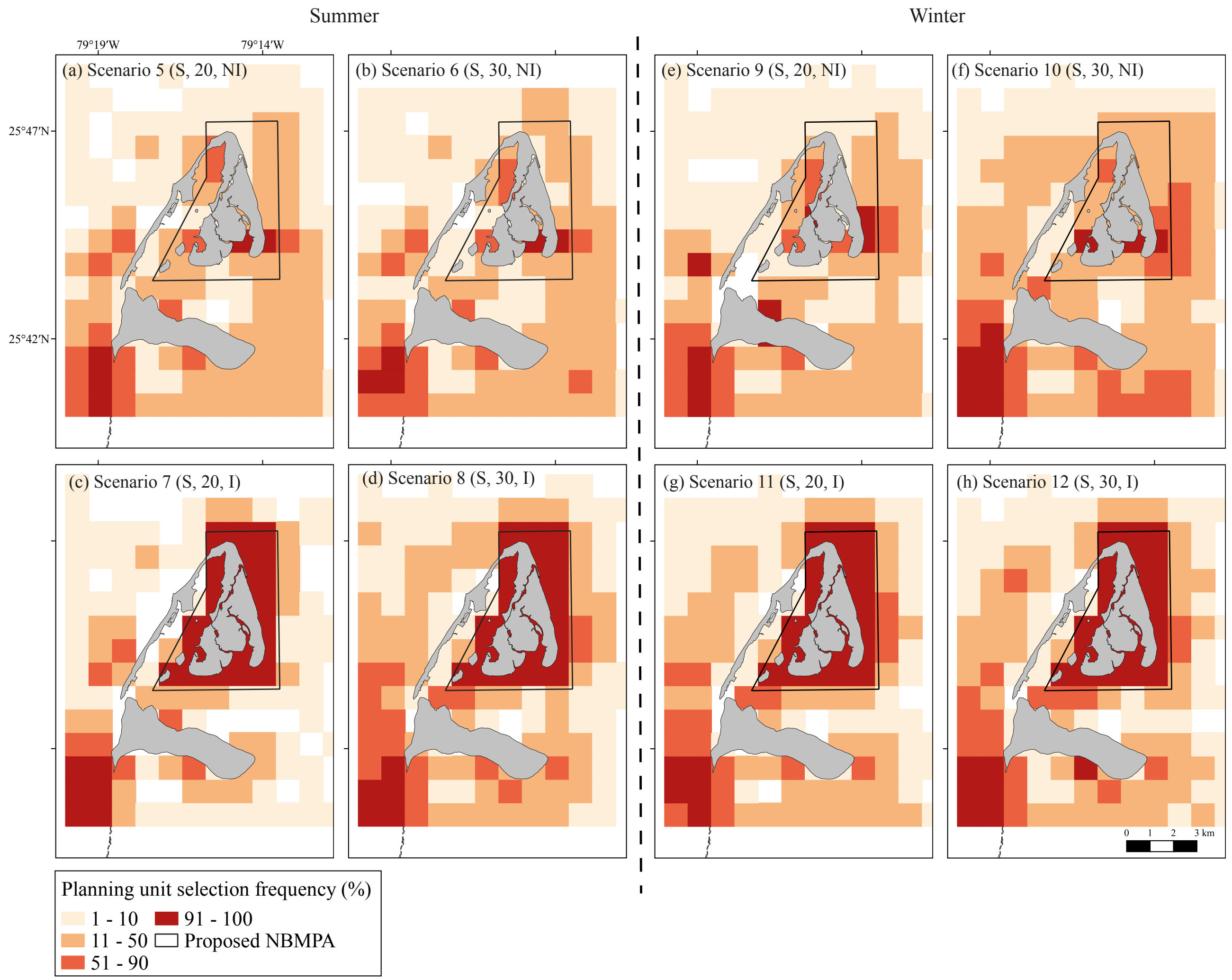

Figure 6. Marxan seasonal summed solutions, separated by a vertical dashed line. S: seasonal, 20: 20% baseline target, 30: 30% baseline target, NI: proposed NBMPA not implemented, I: proposed NBMPA implemented. The boundaries of the proposed NBMPA are indicated by the solid black line.

CHAPTER V

GENERAL CONCLUSIONS

Within predator communities, the quantification of space use patterns and drivers is imperative for understanding how constituent species can spatially coexist. However, for predator communities, which often combine multiple interspecific interactions (e.g., competition, predation, and intraguild predation), and marine predator communities in particular, ascribing interspecific interactions to observed habitat selection and distribution patterns is a non-straightforward approach and behavioral observations of interactions are challenging to make considering the concealing environment in which marine predators live. Furthermore, while predator diets underpin interspecific interactions, the challenges of documenting foraging behavior underwater mean that the diets of many marine predator species, including elasmobranchs (sharks and rays), remain poorly resolved, and high-resolution diet reconstruction tools are currently underdeveloped. Overcoming this limitation is important for developing a better understanding of the functions that elasmobranchs fulfil in marine ecosystems, and the development of minimally invasive and efficient diet assessment methods is desirable due to drastic declines of many elasmobranch species worldwide and the currently large reliance on lethal sampling to obtain dietary information. Overfishing and habitat destruction have been identified as the two biggest causes of elasmobranch population declines globally. Marine protected areas (MPAs) are an increasingly implemented tool to regulate fishing and conserve biodiversity to meet the 2020 Aichi Biodiversity Target 11 to conserve 10% of coastal and marine waters by 2020, with global organizations, including the Convention on Biological Diversity, going even further by calling the protection of 30% of marine areas by 2030. However, due to the often lack of elasmobranch movement and space use data, whether or not MPAs meet their intended goals after being implemented, remains uncertain.

In this dissertation, I first investigated elasmobranch spatial coexistence by employing passive acoustic telemetry with applied resource selection functions, implemented via random forest machine learning algorithms, and movement models to quantify patterns and drivers of space use among apex (bull *Carcharhinus leucas*, great hammerhead *Sphyrna mokarran*, and tiger sharks *Galeocerdo cuvier*), dominant (Caribbean reef *C. perezi*, adult lemon *Negaprion brevirostris*, and nurse *Ginglymostoma cirratum* sharks) and subordinate mesopredators (blacktip *C. limbatus*, subadult lemon sharks, and southern stingrays *Hypanus americanus*) in Bimini, The Bahamas. Observed elasmobranch space use patterns were then compared to predicted distributions resulting from custom-built individual-based models, based on behavioral mechanisms of competition, predation, and intraguild predation. Results from this investigation showed that predator/prey (e.g., southern stingrays versus great hammerhead sharks) and intraguild predation among apex and subordinate elasmobranchs (e.g., blacktip versus great hammerhead sharks) exhibited the strongest spatial separation, and weaker spatial separation by intraguild predation among apex and dominant elasmobranchs (e.g., Caribbean reef versus tiger sharks). Additionally, I found that potentially competing species (e.g., bull versus tiger sharks) overlapped more strongly although microhabitat use patterns differed. Taken together, this study suggests that when interference among elasmobranch species is strong, so is the degree of spatial separation, whereas for competitors, habitat-specific competitive advantages may be necessary for spatial separation to exist.

I then investigated whether fecal residues could be collected from shark cloacas, followed by metabarcoding of fecal DNA, to assess shark diets. Specifically, I first conducted a controlled feeding experiment with captive juvenile lemon sharks to test whether a known prey species that does not naturally occur in the diet of this species can be accurately identified without incurring environmental DNA contamination. I then tested the method under field conditions by sampling juvenile bull sharks from the Florida Coastal Everglades ecosystem. The controlled feeding experiment validated cloacal swab fecal DNA metabarcoding. The fed teleost prey species was the only species detected on the swabs (teleost reef species that were detected in water filters from the same tank in which sharks were housed were not detected on the swabs). This indicates no environmental DNA contamination occurred and that the fed teleost prey species detected on swabs did not originate from the surrounding water in which the bait was immersed, and only after the juvenile lemon sharks commenced feeding. Results from wild bull shark swabs were generally consistent with what we know about the diet of this species and life stage in this ecosystem from published studies. Combined, these results emphasize the utility of fecal DNA metabarcoding as a potential tool to elucidate diets.

Finally, I used biotelemetry, with applied movement models for investigated species, integrated with systematic conservation planning to evaluate the design and effectiveness of new and proposed MPAs in Bimini to assess whether the 30% conservation targets (i.e., elasmobranch core and general use areas, habitat classes and known lemon shark nursery areas) would be met. The systematic conservation planning approach allowed for the identification of spatially explicit MPAs that maximize the protection of conservation targets at minimum MPA size. I found that while the proposed

MPA in North Bimini would indeed contribute to elasmobranch conservation, it fell short and an additional dense cluster of high conservation value would need to be included in any future MPA design for the island if Bimini is to meet internationally agreed upon conservation targets. This area appeared important in analysis of both permanent MPAs and seasonal time-area closures, suggesting that seasonal time-area closures are unlikely to work when considering multiple species that vary in movement strategies (e.g., year-round resident versus migrant). In Bimini, there were always species present in important conservation areas, highlighting the importance of using a holistic, multi-species approach to conservation management. My integrative approach demonstrates how animal movement models, constructed from biotelemetry data, can be used in a quantitative framework to guide MPA design and location to meet explicit biodiversity targets. This is particularly important for conservation considering that most MPAs designed for elasmobranchs are not spatially explicit, are not optimized, and consequently may be suboptimal in terms of conservation benefits and implementation cost.

Taken together, this dissertation advances the field of predator ecology and conservation by providing 1) a deeper understanding of spatial coexistence within elasmobranch communities, and predator communities more generally, 2) a minimally invasive and efficient method to elucidate shark diets, which has the potential to bridge the large gap in our knowledge on shark diets, and 3) an improved MPA design that protects important elasmobranch habitats in Bimini that meets international calls to protect 30% of marine and near-shore marine resources by 2030, and 4) an integrative method using biotelemetry, with applied movement models and systematic conservation planning, to optimize MPA design within a spatially explicit framework to meet explicit conservation objectives. However, much remains to be done. For example, diet occupies a central position in feeding and community ecology, as well as in conservation management, but diet information is largely lacking for most investigated elasmobranch species in Bimini, and across their range. Including elasmobranch diet concurrently with prey surveys will greatly advance our understanding how ecological interactions vary among species, across space and time, but also which areas are important for foraging, and therefore for conservation. The minimally invasive and efficient molecular method to assess shark diets that is developed here, will enable the elucidation and quantification of elasmobranch diets in this study system, and is expected to contribute valuably to these causes. However, while this method has successfully been applied to juvenile sharks, many questions remain that warrant further investigation before the method can be more broadly applied. For example, we currently do not know the temporal window of the diet that is reflected in collected elasmobranch feces. Studies that investigate the relationship between food retention time and signal decay will improve the interpretation of cloacal swab fecal DNA metabarcoding results. Furthermore, investigating the relationship between ingested prey biomass and sequence read abundance through mixed-diet feeding experiments might provide insight into the importance of prey items to the diet of sampled individuals. While the method has been developed using juvenile sharks, further research on larger sharks, and other large vertebrate species (e.g., teleosts, birds, reptiles, amphibians) for which the diet is difficult or impossible to observe directly is needed to broaden the applicability of the method. Furthermore, while the optimization of MPA designs to protect important elasmobranch habitats in Bimini is a step in the right direction, ultimately, inclusion of socio-economic factors and a willing government will prove important if moving from MPA design to implementation.

VITA

MAURITS P. M. VAN ZINNICQ BERGMANN

2006-2011	B.Sc., Marine Biology University of Groningen Groningen, The Netherlands
2011-2013	M.Sc., Marine Biology University of Groningen, Groningen, The Netherlands
2015-2019	Principal Investigator Bimini Biological Field Station Foundation Bimini, The Bahamas

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