

FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

STINGRAY BEHAVIOUR AND HABITAT USE IN RESPONSE TO SHARKS IN
CARIBBEAN CORAL REEF ECOSYSTEMS

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

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2023

To: Dean Michael R. Heithaus
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Chapter 1 entitled Buried in the Sand: Uncovering the Ecological Roles and Importance of Rays was published in the journal Fish and Fisheries (2021, vol. 22, iss. 1). Permission for reuse in this dissertation granted on September 23, 2022, License Number 5394891202688, © 2020 John Wiley & Sons Ltd.

DEDICATION

To my parents for fostering my passion for the ocean and providing endless support of my ambitions.

To Jenica, Eva, and Jack, my nieces and nephew. May you always remain curious and never lose your sense of adventure.

To Charlie, who tried to be here for me till the very end. Rest in peace.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my partner, Demian Chapman, for the love, support, and guidance he has provided. Thank you for being by my side throughout this process and for trying to keep a smile on my face, even in the cruelest moments. You bring so much joy into my life, and for that I am forever grateful.

Importantly, I would like to thank my entire committee for their dedication to and support of my success. In particular, I would like to thank Beth Babcock for her unwavering patience and incredible mentorship. With almost no formal mathematical or statistical training, I began my degree facing knowledge gaps I feared were insurmountable. But Beth was always there to answer my questions, guide me to important readings, and she ultimately turned my fear into curiosity. I still have so much to learn but will always be grateful for her support. I appreciate that she always saw my passion for conservation and looked for ways to contribute to my career goals. I am also grateful for Joel Trexler for teaching one of the most rewarding courses I've ever been in, who always worked hard to make me a better scientist, and who always made me feel like I belong in the scientific community. Thank you to Mike Heithaus who trusted me with the Global FinPrint dataset and no matter how busy he was took the time to give me detailed feedback. Finally, thank you to Yannis Papastamatiou for taking me on as a graduate student, believing in me from our first phone call, and being on this journey with me.

This dissertation would not have been possible without my extended Belize family. Especially Bert Miranda, Norlan Lamb, Buck Nuñez, and Ken Gale. Thank you for sharing your expertise and making every day in the field successful, exciting, and fun. Having you all by my side was an incredible experience I will remember for a lifetime. I am grateful for Linda McCaul for believing in our Belize team and sharing her joy, kindness, perseverance, and passion for the ocean with us. I would like to thank the Belize Fisheries Department for granting us our research permits and Beverly Wade for her incredible commitment to preserving rays, sharks, and fisherfolk livelihoods.

Thank you to everyone who has participated in fieldwork that isn't already acknowledged elsewhere including Sergio Hoare, Monique Lamb, Brian Lamb, Shamika Martinez, Gina Clementi, Jessica Quinlan, Devanshi Kasana, Maurits van Zinnicq Bergmann, Hector Daniel Martinez, Neri Monzon, Mark Bond, Jasmine Valentin, Diego Cardeñosa, Lindsay Segawa, Raphael Martinez, and Edgar Gonzalez. A special shout out to the outstanding Earthwatch volunteers who helped with these projects and shared so many wonderful memories with our team in Belize.

A huge thank you to the entire Global FinPrint team including the principal investigators, postdoctoral researchers, graduate students, collaborators, undergraduate students, and volunteer BRUVS analysts. I graciously acknowledge María del Pilar Blanco Parra, Nadia Sandoval Laurrabaquio, Cassiopea Carrier Doneys, and Jhonatan Alberth Canul Ku for sharing their data to be included in Chapter II. Thank you and congratulations to Sara Casareto,

Candace Fields, Sara Schoen, William Sample, and Valerie Hagan for being part of the QAQC team for Chapter II. This work was a massive undertaking, and your efforts will benefit all future Global FinPrint publications.

A heartfelt thank you to the entire Canadian Statistical Sciences Institute hidden Markov model team led by Vianey Leos Barajas and Marie Auger-Méthé for helping me learn how to run hidden Markov models in Chapter IV.

I extend my gratitude to past professors and mentors including Moira McLaughlin, Craig Proulx, Bob Cerrato, and Anthony Dvarskas. I am especially grateful for Aaron Henderson, who welcomed me into the field of ray and shark science and continues to be an inspiration. I thank Alain Duran for providing me with an opportunity when I thought I had no other choice but to leave the Ph.D. program and Wensong Wu for making statistics approachable. Without these exceptional people, I would not be where I am today.

Finally, I would like to thank all my family and friends. I started as an ichthyologist when Mike and Edith Cogswell allowed me to sit and stare at their fishes for hours on end as a child. From the beginning, my closest family including my nan, parents, and sister were always there for me, helping me become the woman I am today. Thank you to Megan Kelley for your friendship, our time in the field together, and for teaching me to be a better human and mentor. Your ability to remain kind, patient, and professional in a world that can so often be against us is strength that I will always look up to. Thank you to all my lab mates in the Predator Ecology and Conservation Lab and the Network for the Conservation and Research of Chondrichthyans of the Mesoamerican Reef

for showing me what supportive collaborations look like. I am grateful for Aileen Maldonado, Angela Nicoletti, and Erin Spencer for being my cheerleaders and reminding me I deserve to be here.

This dissertation was funded primarily by the Mays Family Foundation, Paul G. Allen Philanthropies (Global FinPrint), Earthwatch Institute, and the Roe Foundation. Additional financial support was provided by FIU CASE, FIU Tropical Conservation Institute, FIU Coastlines and Oceans Division, the Judith Evans Parker scholarship, the Canadian Statistical Sciences Institute, and the Hector, Beyer, & Graham scholarship.

ABSTRACT OF THE DISSERTATION
STINGRAY BEHAVIOUR AND HABITAT USE IN RESPONSE TO SHARKS IN
CARIBBEAN CORAL REEF ECOSYSTEMS

by

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Florida International University, 2023

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Shark declines may cause trophic cascades, which is partially dependent on how sharks influence prey abundance and behaviour. Rays are mesopredators that play a unique role in ecosystems as bioturbators. My dissertation investigates whether sharks induce changes in ray sightings, behaviour, and habitat use across multiple spatial and temporal scales. First, I reviewed the ray ecology literature and found limited evidence for risk-induced ray trait responses (Chapter 1). Next, using a baited remote underwater video station (BRUVS) survey, I found that southern stingray (*Hypanus americanus*) sightings were negatively associated with shark abundance throughout the tropical Western Atlantic Ocean (Chapter 2). Other important predictors of southern stingray sightings in the region included habitat complexity, geomorphology, and bottom fishing gear. At a smaller spatial scale inside the Glover's Reef Marine Reserve in Belize, a BRUVS survey revealed southern stingray sightings and behaviour remained stable between 2009 – 2019 despite a concurrent decline in the relative abundance of Caribbean reef sharks (*Carcharhinus perezii*) (Chapter 3). Habitat

complexity explained southern stingray sightings and behaviour on BRUVS, which may be due to their preference for soft bottom habitats and/or because we are less likely to detect stingrays on BRUVS in areas with high reef relief. Passive acoustic telemetry showed Caribbean reef and lemon (*Negaprion brevirostris*) sharks use shallow lagoon habitat, which was also the preferred habitat of southern stingrays, suggesting it is unlikely a refuge from predators. Finally, using accelerometry and hidden Markov models, I found that southern stingray activity is crepuscular and nocturnal, with high individual variation (Chapter 4). Southern stingrays were highly active in shallow water (<5 m), which is likely associated with prey activity and availability. My findings emphasize the context dependent nature of predation risk effects and the need to take a multimethod approach to understand ray behaviour and habitat use.

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CHAPTER I

BURIED IN THE SAND: UNCOVERING THE ECOLOGICAL ROLES AND IMPORTANCE OF RAYS

ABSTRACT

Rays (superorder Batoidea) are the most diverse group of elasmobranchs and many are threatened with extinction. However, there remain areas where research on the ecology of this group is lacking, from trophic interactions to their importance to ecosystem structure and function. Such ecological insights are critical for predicting the potential consequences of changes in their population sizes. Our aim was to synthesize the existing ray ecology literature and identify key knowledge gaps in order to provide a framework for future research.

Numerous studies describe ray diets and the number of studies using biochemical methods to address ray trophic interactions is increasing. The implications of ray predator-prey interactions on population dynamics of prey and how ray foraging might influence ecosystem dynamics through bioturbation remain relatively unexplored, despite claims that rays are ecologically important because they are bioturbators and because of their potential to deplete stocks of commercially important bivalves. Therefore, to better integrate rays in our understanding of marine community dynamics there is a need to: (1) combine behavioural data with dietary information to describe predator-prey interactions (2) understand how ray bioturbation affects biogeochemical cycles and infaunal

communities, (3) elucidate conditions under which rays might initiate or transmit trophic cascades through consumptive and non-consumptive pathways, and (4) consider anthropogenic influences on the ecological roles and importance of rays.

INTRODUCTION

Rays (superorder Batoidea: skates, stingrays, electric rays, and shovelnose rays) are widely distributed in freshwater, brackish, shallow coastal, and deep-sea environments (Aschliman *et al.*, 2012; Last *et al.*, 2016). Despite being widespread and, in some cases, commercially important, this group of fishes has received less scientific attention than most vertebrate groups (Aschliman *et al.*, 2012; Bräutigam *et al.*, 2015). Rays evolved in the Lower Jurassic period (Aschliman *et al.*, 2012) and among vertebrates, their proportional risk of extinction is high and exceeded only by that of amphibians (Last *et al.*, 2016). Rays are threatened primarily by overfishing, with benthic species being particularly susceptible to trawl and gillnet fisheries and semi-pelagic species being vulnerable to longline and drift net fisheries (Dulvy *et al.*, 2014). Rays are also valuable to tourism industries around the world, with ray watching tourism generating millions of dollars in multiple countries (Haas, Fedler, & Brooks, 2017; O'Malley, Lee-Brooks, & Medd, 2013; Vaudo *et al.*, 2018). Knowledge of the ecological role and importance of rays is needed in order to understand how species declines, or in some cases predatory or

competitive release, may affect ecosystem function and structure. Such an understanding can be important for making appropriate management decisions for species and ecosystems. It is likely that we will underestimate the importance of some rays like large sawfishes (Pristidae) and skates (Rajidae) given widespread declines that preceded modern ecological reporting (Stevens, Bonfil, Dulvy, & Walker, 2000). Local ecological knowledge about trophic interactions involving rays offers valuable insight into more pristine ecosystems (e.g. Bonfil *et al.*, 2018). It is plausible that under pre-disturbed conditions large sawfishes and skates acted as top predators.

A key distinction when evaluating the ecology of any species is the difference between ecological roles and importance. The ecological role of an organism mainly considers its trophic position, but can include any type of interaction, regardless of its significance to the functioning of whole ecosystems, while the ecological importance of a species considers the consequences of a change in species abundance to community structure and function (Heithaus, Frid, Vaudo, Worm, & Wirsing, 2010). The ecological roles and importance of rays was reviewed briefly by Heithaus *et al.* (2010), and a recent review by Martins, Heupel, Chin, and Simpfendorfer (2018) highlighted several ecological roles of rays in relation to nursery areas. Here, we expand on these previous reviews to consider ray ecological roles and importance across taxa and all life stages and identify gaps in our current understanding to develop a prospectus for future research. We assessed peer-reviewed primary literature published as of 04 October 2018 using a variety of search term combinations (S1 Table) in

Google Scholar (<https://scholar.google.ca>). Several key papers published after our original search have been included in this review due to their importance to the field of study. Relevant citations found in original research articles were also included, leading to an examination of > 500 studies. It was not possible to describe every study in this review; therefore, we have focused on central examples from the literature that was assembled. Only two of the 26 described ray families were not represented in the literature from our search (i.e. Hexatrygonidae and Pleisiobatidae). Taxonomic classifications reported are based on Last *et al.* (2016), with the exception of devil rays (Mobulidae) that are based on Hosegood *et al.* (2018). Figure 1 outlines ray interactions with other species and the environment that will be explored in this paper.

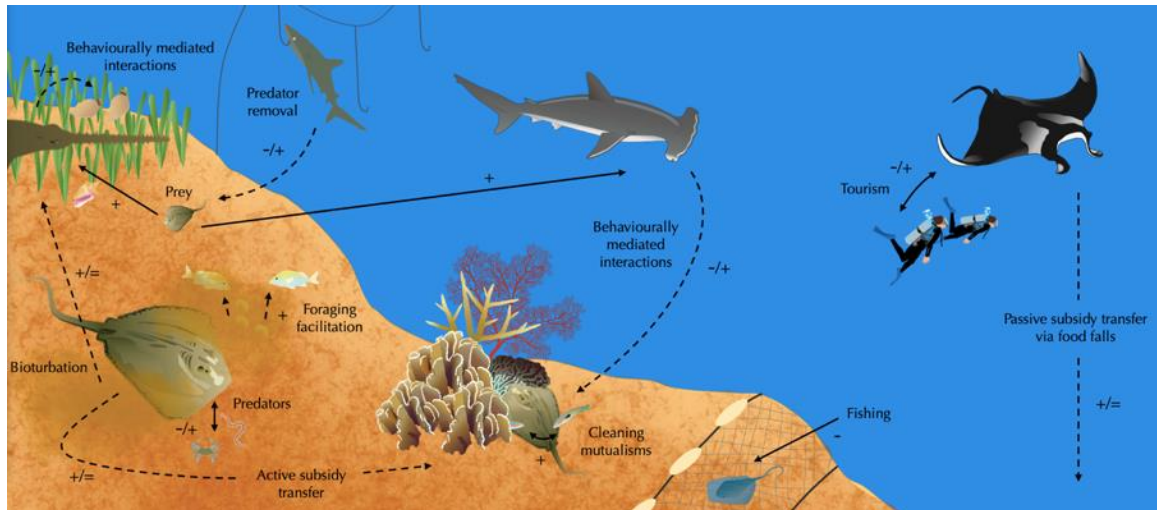


Figure 1: Conceptual diagram of the interactions between rays, other species, and their environment in a coral reef system. Solid black arrows represent direct effects, while dashed arrows represent indirect effects. “+” represents a positive effect, “-” a negative effect, and “=” no effect or an insignificant effect relative to other processes. Rays directly provide energy to other species as a prey source and indirectly via foraging facilitation. Cleaning mutualisms are assumed to provide positive benefits for the ray and cleaner fishes. In some cases, rays negatively affect prey densities via direct predation. However, in other cases ray foraging can benefit prey through refugia created after pit formation or by promoting diversity and smoothing out distribution patterns. While rays turn over high volumes of sediment, the effect of bioturbation may be negligible compared to other biogeochemical processes like tidal flux and ocean currents. Nutrients released during this process may be transferred across habitats, which could affect ecosystem productivity. Nutrients may also cross habitat boundaries by ray behaviour (e.g. feeding in seagrass habitat and defecating on reefs) and as food falls post-mortem. Vigilance by filter-feeding bivalves in response to the presence of ray predators may reduce their propensity to feed; however, in some cases it is possible that behaviourally mediated effects could promote co-existence. Similarly, top-down effects on rays by predators like sharks may negatively affect ray densities or push them into unprofitable habitats. However, behaviourally mediated effects may also stabilize ray populations. The loss of top predators may lead to positive benefits for the ray population (ray release) or negative consequences resulting from density-mediated effects following increases in population size. Fishing generally has a negative effect on ray populations, unless sustainably managed. Tourism can provide conservation benefits for rays but may also lead to a decrease in overall body condition if not properly managed. Images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/), with the exclusion of the Caribbean reef shark, which was created using Pixelmator v. 3.8.5.

PREDATOR-PREY INTERACTIONS

Who is eating whom?

Approximately 60% of the ray ecology literature (320 of 520 publications) examines basic trophic relationships and multiple species have had their diets extensively studied. For example, stomach contents of the thornback skate (*Raja clavata*, Rajidae) have been described in 18 studies throughout its range in the Eastern Atlantic Ocean and Mediterranean Sea (e.g. Ajayi, 1982). The diets of 198 ray species were documented in the literature (S2 Table), with only four of the 26 ray families not represented (i.e. Hexatrygonidae, Narkidae, Pleisiobatidae, Zanobatidae). Although rays primarily consume crustaceans, molluscs, teleosts, and worms (S2 Table), diets varied within and among species, across life stages, spatially, and temporally. Sex differences in diets occur in some species (e.g. Delpiani, Spath, & Figueroa, 2013; Lipej, Mavric, Paliska, & Capapé, 2013; Orlov, 1998), which may be due to sexual dimorphism, spatiotemporal segregation, and increased energetic requirements during gestation (Delpiani *et al.*, 2013). Many rays showed seasonal and/or regional variation in diet, which has been hypothesized to be related to changes in prey availability, abundance, and distribution (Barbini & Lucifora, 2011; Bornatowski, Robert, & Costa, 2010; Braccini & Perez, 2005; Kadri, Saidi, Marouani, Bradai, & Bouain, 2013; Molina & Cazorla, 2015; Saglam, Ak, Kutlu, & Aydin, 2010; Saglam & Bascinar, 2008; San Martin, Braccini, Tamini, Chiaramonte, & Perez,

2007; Szczepanski & Bengtson, 2014), but could also be related to ray seasonal migrations influenced by environmental variables (Schlaff, Heupel, & Simpfendorfer, 2014). Ontogenetic shifts in ray diets are widespread, where larger prey items were consumed with increasing body size (e.g. Brown, Bizzarro, Cailliet, & Ebert, 2012). While some rays are consuming prey items based on availability (e.g. Ajemian, Powers, & Murdoch, 2012), others may be specializing on particular prey taxa. For example, in an Argentinian scallop fishery where yellownose skates (*Zearaja chilensis*, Rajidae) were collected for a diet study, bycatch is primarily made up of invertebrates, yet the most common prey items in yellownose skate stomach contents were teleosts (Lucifora, Valero, Bremec, & Lasta, 2000). Understanding changes in diet and prey selection is useful for determining the ability of rays to impact prey populations across space and time.

Ray trophic levels (TL) reported in the literature ranged from 3.1 – 4.5, suggesting that most rays are secondary to tertiary level consumers (Table 1). These TLs are comparable to the standardized values calculated for skates (3.48 – 4.22; Ebert & Bizzarro, 2007) as well as for stingrays and electric rays (3.10 – 4.24; Jacobsen & Bennett, 2013). TLs varied by species, location, and in some cases by individual, while the comparison of different methodologies (i.e. stable isotope analysis vs stomach content analysis) showed slight variation in the TL value (Burgess *et al.*, 2016; Yemişken, Forero, Megalofonou, Eryilmaz, & Navarro, 2018). Trophic level increased with body size for some species like the longtail stingray (*Hypanus longus*, Dasyatidae; Navia, Mejía-Falla, López-García,

Giraldo, & Cruz-Escalona, 2016), the polkadot skate (*Dipturus chinensis*, Rajidae; Hara, Furumitsu, & Yamaguchi, 2018), the rasptail skate (*Rostroraja velezi*, Rajidae; Navia *et al.*, 2016), the southern banded guitarfish (*Zapteryx xyster*, Trygonnorhinidae; Navia *et al.*, 2016), and the yellowspotted fanray (*Platyrrhina tangi*, Platyrrhinidae; Yamaguchi, Furumitsu, Tanaka, & Kume, 2012); however, body size is not always indicative of trophic position (Barría, Coll, & Navarro, 2015). Small rays such as the Persian Gulf torpedo ray (*Torpedo sinuspersici*, Torpedinidae; mean weight 1.4 kg [Rastgoo, Navarro, & Valinassab, 2018]) and the longtail butterfly ray (*Gymnura poecilura*, Gymnuridae; mean weight 3.8 kg [Rastgoo *et al.*, 2018]) had high TLs (4.5; Rastgoo & Navarro, 2016; Rastgoo *et al.*, 2018), while larger species such as the shark ray (*Rhina ancylostoma*, Rhinidae; mean weight 77.4 kg [D'Alberto, White, Chin, Dharmadi, & Simpfendorfer, 2019]) and the spotted eagle ray (*Aetobatus ocellatus*, Aetobatidae; mean weight 41.4 kg [D'Alberto *et al.*, 2019]) had relatively low TLs (3.2; Borell, Cardona, Kumarran, & Aguilar, 2011; Vaudo & Heithaus, 2011). Due to the differences in diet with maturity and size, future work should report juvenile and adult diets and TLs separately (Navia *et al.*, 2016). Where possible, we have reported TLs by life stage (S3 Table).

Species	Trophic level (TL)	Method	References
Speckle skate (<i>Raja polystigma</i> , Rajidae)	3.1	SCA	Barría <i>et al.</i> , 2015
Spotted eagle ray (<i>Aetobatus ocellatus</i> , Aetobatidae)	3.2	SIA	Vaudo & Heithaus, 2011
Bullnose eagle ray (<i>Myliobatis freminvillei</i> , Myliobatidae)	3.2 3.5	SCA SCA	Szczepanski & Bengtson, 2014 Woodland, Secor, & Wedge, 2011
Southern eagle ray (<i>Myliobatis goodei</i> , Myliobatidae)	3.2	SCA	Molina & Cazorla, 2015
Cowtail ray (<i>Pastinachus sephen</i> , Dasyatidae)	3.2 3.3	SCA SCA	Rastgoo <i>et al.</i> , 2018 Rastgoo & Navarro, 2016
Shark ray (<i>Rhina ancylostoma</i> , Rhinidae)	3.2	SIA	Borrell <i>et al.</i> , 2011
Giant manta ray (<i>Mobula birostris</i> , Mobulidae)	3.4	SIA	Burgess <i>et al.</i> , 2016
Giant devil ray (<i>Mobula mobular</i> , Mobulidae)	3.4	SIA	Sampson, Galván-Magaña, De Silva-Dávila, Aguiniga-Garcia, & O'Sullivan, 2010
American cownose ray (<i>Rhinoptera bonasus</i> , Rhinopteridae)	3.4	SCA	Bornatowski <i>et al.</i> , 2014b
Freshwater whiplay (<i>Urogymnus dalyensis</i> , Dasyatidae)	3.4	SIA	Every <i>et al.</i> , 2017
Boreal skate (<i>Amblyraja hyperborea</i> , Rajidae)	3.5	SIA	McKinney <i>et al.</i> , 2012
Brown stingray (<i>Bathytoshia lata</i> ,	3.5	SCA	Dale, Wallsgrove, Popp, &

Dasyatidae)			Holland, 2011
Scaly whiplay (<i>Brevitrygon walga</i> , Dasyatidae)	3.5 3.6	SCA SCA	Rastgoo <i>et al.</i> , 2018 Rastgoo & Navarro, 2016
Sharpnose skate (<i>Dipturus oxyrinchus</i> , Rajidae)	3.5 3.6	SCA SCA	Barría <i>et al.</i> , 2015 Mulas <i>et al.</i> , 2015
Giant guitarfish (<i>Glaucostegus typus</i> , Glaucostegidae)	3.5	SIA	Vaudo & Heithaus, 2011
<i>Himantura</i> sp. (Dasyatidae)	3.5	SIA	Vaudo & Heithaus, 2011
Southern stingray (<i>Hypanus americanus</i> , Dasyatidae)	3.5	SCA	Tilley, López-Angarita, & Turner, 2013a
Blackspotted whiplay (<i>Maculabatis astra</i> , Dasyatidae)	3.5	SIA	Vaudo & Heithaus, 2011
Bentfin devil ray (<i>Mobula thurstoni</i> , Mobulidae)	3.5	SIA	Sampson <i>et al.</i> , 2010
Broad cowtail ray (<i>Pastinachus ater</i> , Dasyatidae)	3.5	SIA	Vaudo & Heithaus, 2011
Pink whiplay (<i>Pateobatis fai</i> , Dasyatidae)	3.5	SIA	Vaudo & Heithaus, 2011
Zipper sand skate (<i>Psammobatis extenta</i> , Arhynchobatidae)	3.5	SCA	Braccini & Perez, 2005
Whitesnout guitarfish (<i>Pseudobatos leucorhynchus</i> , Rhinobatidae)	3.5	SCA	Navia <i>et al.</i> , 2016
Spotted skate (<i>Raja montagui</i> , Rajidae)	3.5	SCA	Barría <i>et al.</i> , 2015
Chilean round ray (<i>Urotrygon chilensis</i> , Urotrygonidae)	3.5	SCA	Oñate-González, Amezcua, Buszkiewicz, Castellanos-Cendales, & Amezcua-

	3.6	SCA	Linares, 2017 Silva-Garay <i>et al.</i> , 2018
Roger's round ray (<i>Urotrygon rogersi</i> , Urotrygonidae)	3.5	SCA	Navia <i>et al.</i> , 2016
Shortnose guitarfish (<i>Zapteryx brevirostris</i> , Trygonorrhinidae)	3.5	SCA	Bornatowski <i>et al.</i> , 2014b
Bering skate (<i>Bathyraja interrupta</i> , Arhynchobatidae)	3.6	SCA	Kemper, Bizzarro, & Ebert, 2017
Longnose skate (<i>Beringraja rhina</i> , Rajidae)	3.6	SCA	Kemper <i>et al.</i> , 2017
Sharpnose guitarfish (<i>Glaucostegus granulatus</i> , Glaucostegidae)	3.6	SIA	Borrell <i>et al.</i> , 2011
Large-eye stingray (<i>Hypanus marianae</i> , Dasyatidae)	3.6	SCA	Costa, Thayer, & Mendes, 2015
<i>Mobula</i> sp. (Mobulidae)	3.6	SIA	Borrell <i>et al.</i> , 2011
Speckled guitarfish (<i>Pseudobatos glaucostigmus</i> , Rhinobatidae)	3.6	SCA	de la Rosa-Meza, Sosa-Nishizaki, & de la Dueva-Salcedo, 2013
Chola guitarfish (<i>Pseudobatos percellens</i> , Rhinobatidae)	3.6	SCA	Bornatowski <i>et al.</i> , 2014b
Shovelnose guitarfish (<i>Pseudobatos productus</i> , Rhinobatidae)	3.6	SCA	Valenzuela- Quiñonez, Galván-Magaña, Ebert, & Aragón-Noriega, 2018
Spotted guitarfish (<i>Rhinobatos punctifer</i> , Rhinobatidae)	3.6	SCA	Rastgoo & Navarro, 2016; Rastgoo <i>et al.</i> , 2018
Whitespotted wedgefish (<i>Rhynchobatus djiddensis</i> , Rhinidae)	3.6 4	SCA SCA	Razzaghi, Mashjoor, & Kamrani, 2017 Abdurahiman, Nayak, Zacharia, & Mohamed, 2010

Smallnose fanskate (<i>Sympterygia bonapartii</i> , Arhynchobatidae)	3.6	SCA	Estalles, Perier, & Di Giacomio, 2016
<i>Aetomylaeus</i> sp. (Myliobatidae)	3.7	SIA	Borrell <i>et al.</i> , 2011
Whitespotted skate (<i>Dentiraja cerva</i> , Rajidae)	3.7	SCA	Treloar <i>et al.</i> , 2007
Whitespotted whiplay (<i>Maculabatis gerrardi</i> , Dasyatidae)	3.7	SCA	Rastgoo & Navarro, 2016; Rastgoo <i>et al.</i> , 2018a
Arabian banded whiplay (<i>Maculabatis randalli</i> , Dasyatidae)	3.7	SCA	Rastgoo <i>et al.</i> , 2018
Leopard numbfish (<i>Narcine leoparda</i> , Narcinidae)	3.7	SCA	Navia <i>et al.</i> , 2016
Yellowspotted fanray (<i>Platyrrhina tangi</i> , Platyrrhinidae)	3.7	SCA	Yamaguchi <i>et al.</i> , 2012
Shortfin sand skate (<i>Psammobatis normani</i> , Arhynchobatidae)	3.7	SCA	Mabragaña & Giberto, 2007
Pacific guitarfish (<i>Pseudobatos planiceps</i> , Rhinobatidae)	3.7	SCA	Silva-Garay <i>et al.</i> , 2018
Thornback skate (<i>Raja clavata</i> , Rajidae)	3.7 3.9 4.1	SCA SCA SCA	Morato, Sola, Gros, & Menezes, 2003 Yemişken <i>et al.</i> , 2018 Barría <i>et al.</i> , 2015
Rio skate (<i>Rioraja agassizi</i> , Arhynchobatidae)	3.7	SCA	Bornatowski <i>et al.</i> , 2014b
<i>Rhynchobatus</i> sp. (Rhinidae)	3.7 3.8	SIA SIA	Borrell <i>et al.</i> , 2011 Vaudo & Heithaus, 2011

Spinytail round ray (<i>Urotrygon aspidura</i> , Urotrygonidae)	3.7	SCA	Navia <i>et al.</i> , 2016
Australian thornback skate (<i>Dentiraja lemprieri</i> , Rajidae)	3.8	SCA	Treloar <i>et al.</i> , 2007
Polkadot skate (<i>Dipturus chinensis</i> , Rajidae)	3.8	SCA	Hara <i>et al.</i> , 2018
Diamond stingray (<i>Hypanus dipterus</i> , Dasyatidae)	3.8	SCA	Silva-Garay <i>et al.</i> , 2018
Longtail stingray (<i>Hypanus longus</i> , Dasyatidae)	3.8 3.9	SCA SCA	Navia <i>et al.</i> , 2016 López-García, Navia, Mejía-Falla, & Rubio, 2012
Chilean eagle ray (<i>Myliobatis chilensis</i> , Myliobatidae)	3.8	SCA	Silva-Garay <i>et al.</i> , 2018
Bleeker's whiplay (<i>Pateobatis bleekeri</i> , Dasyatidae)	3.8	SIA	Borrell <i>et al.</i> , 2011
Atlantic starry skate (<i>Raja asterias</i> , Rajidae)	3.8 3.9	SCA SCA	Barría <i>et al.</i> , 2015 Coll, Navarro, & Palomera, 2013; Navarro, Coll, Preminger, & Palomera, 2013; Yemişken <i>et al.</i> , 2018
Brown skate (<i>Raja miraletus</i> , Rajidae)	3.9	SCA	Kadri, Marouani, Bradai, & Bouaïn, 2014
Rough skate (<i>Raja radula</i> , Rajidae)	3.9	SCA	Kadri <i>et al.</i> , 2013
Rasptail skate (<i>Rostroraja velezi</i> , Rajidae)	3.9	SCA	Navia <i>et al.</i> , 2016
Bignose fanskate (<i>Sympterygia acuta</i> , Arhynchobatidae)	3.9	SCA	Barbini & Lucifora, 2016
Southern banded guitarfish (<i>Zapteryx xyster</i> ,	3.9	SCA	Navia <i>et al.</i> , 2016

Trygonorrhinidae)			
Cuckoo skate (<i>Leucoraja naevus</i> , Rajidae)	4	SCA	Barría <i>et al.</i> , 2015
Peruvian eagle ray (<i>Myliobatis peruvianus</i> , Myliobatidae)	4	SCA	Silva-Garay <i>et al.</i> , 2018
Green sawfish (<i>Pristis zijsron</i> , Pristidae)	4	SCA	Razzaghi <i>et al.</i> , 2017
Smallthorn sand skate (<i>Psammobatis rudis</i> , Arhynchobatidae)	4	SCA	Mabragana & Giberto, 2007
Bight skate (<i>Dipturus gudgeri</i> , Rajidae)	4.1	SCA	Treloar <i>et al.</i> , 2007
Spiny butterfly ray (<i>Gymnura altavela</i> , Gymnuridae)	4.1 4.2	SCA SCA	Barría <i>et al.</i> , 2015 Yemişken <i>et al.</i> , 2018
Pelagic stingray (<i>Pteroplatytrygon violacea</i> , Dasyatidae)	4.1	SCA	Varghese, Somvanshi, & Dalvi, 2014
Clearence skate (<i>Rostroraja eglanteria</i> , Rajidae)	4.1	SCA	Woodland <i>et al.</i> , 2011
Banded guitarfish (<i>Zapteryx exasperata</i> , Trygonorrhinidae)	4.1	SCA	Blanco-Parra, Galván-Magaña, Márquez-Farías, & Niño-Torres, 2012
Broadnose skate (<i>Bathyraja brachyurops</i> , Arhynchobatidae)	4.2	SCA	Belleggia <i>et al.</i> , 2008
Largetooth sawfish (<i>Pristis pristis</i> , Pristidae)	4.2 4.5	SCA SIA	Thorburn, Gill, & Morgan, 2014 Every <i>et al.</i> , 2017
Melbourne skate (<i>Spiniraja whitleyi</i> , Rajidae)	4.2	SCA	Treloar <i>et al.</i> , 2007
Great torpedo (<i>Tetronarce</i>	4.2	SCA	Barría <i>et al.</i> , 2015

<i>nobiliana</i> , Torpedinidae)			
Marbled torpedo (<i>Torpedo marmorata</i> , Torpedinidae)	4.2	SCA	Barría <i>et al.</i> , 2015
Ocellate torpedo (<i>Torpedo torpedo</i> , Torpedinidae)	4.2	SCA	Barría <i>et al.</i> , 2015
<i>Pristis</i> sp. (Pristidae)	4.3	SIA	Borrell <i>et al.</i> , 2011
Longtail butterfly ray (<i>Gymnura poecilura</i> , Gymnuridae)	4.5	SCA	Rastgoo & Navarro, 2016; Rastgoo <i>et al.</i> , 2018
Persian Gulf torpedo (<i>Torpedo sinuspersici</i> , Torpedinidae)	4.5	SCA	Rastgoo & Navarro, 2016; Rastgoo <i>et al.</i> , 2018
Yellownose skae (<i>Zearaja chilensis</i> , Rajidae)	4.5	SCA	Belleggia <i>et al.</i> , 2016

Table 1: Ray trophic levels (TLs) reported in the literature, rounded to the nearest decimal. Mean TL was calculated when studies only reported TLs across (1) seasons, (2) size classes, or (3) cardinal directions (north, east, south, west). Stomach content analysis (SCA) was the most common methodology used to assess TLs, therefore TLs calculated from stable isotope analysis (SIA) were only reported when TLs from SCA were not available.

A diverse array of organisms feed on rays including other elasmobranchs, teleosts, mammals, birds, invertebrates, and reptiles (S4 Table). Rays were found most commonly in the diet of elasmobranchs and mammals (Figure 2). Rays (*Dasyatidae* and *Rhinobatidae*) are important prey items for great hammerhead sharks (*Sphyrna mokarran*, *Sphyrinidae*; Cliff, 1995) and thorny skates (*Amblyraja radiata*; *Rajidae*) are important prey for Greenland sharks (*Somniosus microcephalus*, *Somniosidae*) in western Greenland (index of

relative importance = 84.38; Yano, Stevens, & Compagno, 2007). In New Zealand, killer whales (*Orcinus orca*, Delphinidae) use unique benthic hunting strategies to capture rays (Visser, 1999). A killer whale was observed catching 15 rays (Dasyatidae and Myliobatidae) in one day, which may suggest these whales are ray specialists (Visser, 1999). Coyotes (*Canis latrans*, Canidae), have been found with ray spines and vertebrae (Dasyatidae and Rhinobatidae) in their scat, likely a result of scavenging on carcasses that wash ashore (Rose & Polis, 1997). Rays consume other rays (within and across families) and this is most common among skates (S4 Table). Certain skate species like the yellownose skate consume conspecifics (Koen Alonso *et al.*, 2001) and members within the same family (e.g. Barbini & Lucifora, 2011). Similarly, adult female southern stingrays (*Hypanus americanus*, Dasyatidae) have been found with large-eye stingrays (*Hypanus marianae*, Dasyatidae) in their stomachs (Branco-Nunes, Albuquerque, Nunes, Oliveira, & Hazin, 2016). Stingray spines have been found in wedgefish, guitarfish, and sawfish jaws (Dean, Bizzarro, Clark, Underwood, & Johanson, 2017), while stingray (Dasyatidae) DNA was identified in fecal samples of the smalltooth sawfish (*Pristis pectinata*, Pristidae) along with a stingray tail in the mouth of a captured individual (Poulakis *et al.*, 2017). Rays feeding on other rays is likely opportunistic.

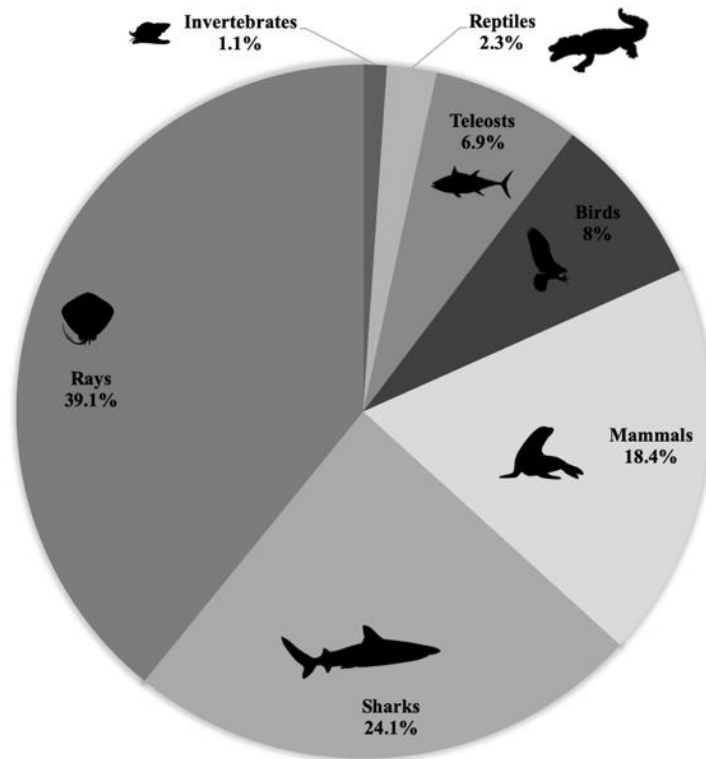


Figure 2: Proportional representation of ray predator taxa based on the total number of predator species described in the literature (N=88). Graphics downloaded from www.phylopic.org made available by CC0 1.0 Public Domain Dedication and Public Domain Mark 1.0 licenses (whelk excluded). Whelk drawn using Pixelmator v. 3.8.5.

Diet information can provide valuable insight into predator-prey dynamics. Since many ray species have had their diets comprehensively studied and the majority of rays feed on the same major taxa, research should focus on placing this information in broader context with behavioural data. For example, predicting the consequences of shifts in community dynamics will require combining short term diet descriptions (i.e. from stomach content analyses) with longer term diet descriptions (i.e. from stable isotope analyses) and working to understand these descriptions in relation to predator and prey behaviour (Heupel, Knip,

Simpfendorfer, & Dulvy, 2014). Specifically, we need to know: (1) predator-prey interaction strength (Heupel *et al.*, 2014; Roff *et al.*, 2016), (2) prey profitability (i.e. the energetic value of a prey item once prey digestive quality and time to chase, capture, and handle prey have been considered; Fall & Fiksen, 2020; MacArthur & Pianka 1966; Sih & Christensen, 2001), which is influenced by a variety of predator-prey tactics (Heithaus, 2004), and (3) the dispersal capabilities of both predator and prey.

Using diet information to understand sympatric species coexistence

Research on resource partitioning can broaden our understanding of species coexistence within the same geographic locations (Schoener, 1974) and there is evidence that ray species partition their resources (Barría *et al.*, 2015; Belleggia, Scenna, Barbini, Figueroa, & Díaz De Astarloa, 2014; Bornatowski, Wosnick, Do Carmo, Corrêa, & Abilhoa, 2014b; Espinoza, Munroe, Clarke, Fisk, & Wehrtmann, 2015; Every, Pethybridge, Fulton, Kyne, & Crook, 2017; Navarro-González, Bohórquez-Herrera, Navia, & Cruz-Escalona, 2012; Pardo, Burgess, Teixeira, & Bennett, 2015; Platell, Potter, & Clarke, 1998; Rastgoo *et al.*, 2018; Shibuya, Araújo, & Zuanon, 2009; Silva-Garay, Pacheco, & Vélez-Zuazo, 2018; Stewart *et al.*, 2017; Treloar, Laurie, Laurenson, & Stevens, 2007; Yemişken *et al.*, 2018; Yick, Tracey, & White, 2011). For example, in Peru, the pygmy devil ray (*Mobula munkiana*, Mobulidae) had minimal isotopic niche overlap with three other devil ray species (*M. birostris*, *M. mobular*, *M. thurstoni*), which suggests

that the pygmy devil ray may be feeding in a different area or on a different prey source than the other species (Stewart *et al.*, 2017). In some cases, high dietary overlap was found among sympatric species, but differences in their preferred prey item were found (e.g. Brickle, Laptikhovsky, Pompert, & Bishop, 2003). At Ningaloo reef, dietary overlap between ray species was high and coexistence of these species may instead be driven by abundant resources or space partitioning (O'Shea *et al.*, 2013). Mechanisms of resource partitioning among rays also include differences in mouth morphology (Barbini & Lucifora, 2012; Rastgoo *et al.*, 2018; Smale & Cowley, 1992), habitat use (Barbini & Lucifora 2012; Platell *et al.*, 1998), behaviour (e.g. foraging tactics; Barbini & Lucifora, 2012; Rastgoo *et al.*, 2018), and body size (Smale & Cowley, 1992). While competition is often the mechanism used to explain resource partitioning, the link between the two has not been measured in ray field studies (Papastamatiou, Wetherbee, Lowe, & Crow, 2006; Schoener, 1974; Yick *et al.*, 2011).

Anti-predator behaviour by rays

Ray predators might influence ray behaviour, populations, and ecological interactions through non-lethal mechanisms (Heithaus, 2004). Indeed, most animals invest in anti-predator behaviour (Lima & Dill, 1990). The probability of prey death via predation depends in part on avoidance tactics like hiding, aggregating, vigilance, escaping, defense, and modifying activity levels and/or habitat use (Heithaus, 2004; Lima & Dill, 1990). While not thoroughly

investigated, rays appear to be influenced by the risk of predation. Gastropods prey on skate egg cases (Cox & Koob, 1993; Cox, Walker, & Koob, 1999; Hoff, 2009; Lucifora & Garcia, 2004; Smith & Griffiths, 1997) and the use of egg-case nurseries by skates (i.e. high densities of egg cases in a relatively small area) reduces predation rates (Hoff, 2009). In Shark Bay, Western Australia, whiprays (*Himantura* sp., Dasyatidae) respond faster to boat approaches (proxy for a predator) than cowtail rays (*Pastinachus sephen*, Dasyatidae), which suggests that the cowtail rays may benefit from grouping with whiprays that may detect predators sooner (Semeniuk & Dill, 2006). Whiprays and giant guitarfish (*Glaucostegus typus*, Glaucostegidae) rest in warm shallow water during the day in the warm season in Shark Bay, Western Australia, which corresponds with an increased abundance of tiger sharks and may be a refuging tactic (Vaudo & Heithaus, 2013). Resting in warm water suggests these rays likely incur metabolic costs, demonstrating that this behaviour is not consistent with behavioural thermoregulation (Vaudo & Heithaus, 2013). Other work has hypothesized that stingray activity, habitat use, and/or movements may be driven at least in part by predation risk (e.g. Cartamil, Vaudo, Lowe, Wetherbee, & Holland, 2003; Cerutti-Pereyra *et al.*, 2014; Davy, Simpfendorfer, & Heupel, 2015; Kanno, Schlaff, Heupel, & Simpfendorfer, 2019; Tilley, Lopez-Angarita, & Turner, 2013b); however, none of these studies set out to test the effect of sharks on rays and alternative hypotheses could also explain the observed patterns (e.g. behavioural thermoregulation, interspecific competition, or prey density and distribution). Between 1970 and 2012 in the Gulf of St. Lawrence,

Canada, thorny skates responded to an increase in grey seal (*Halichoerus grypus*, Phocidae) abundance by moving into lower risk areas in deeper waters (Swain, Benoît, & Hammill, 2015). It was hypothesized that since skate body condition is poor in deeper waters where they were refuging that skates exhibit a trade-off between foraging opportunities and safety (Swain *et al.*, 2015). The foraging-safety trade-off is common among many taxa (Brown & Kotler, 2004; Lima & Dill, 1990). Caribbean reef sharks (*Carcharhinus perezii*, Carcharhinidae) in Belize may induce similar habitat shifts in southern stingrays because southern stingrays were seen more frequently on fished forereefs with low reef shark abundance than on protected forereefs with higher reef shark abundance (Bond *et al.*, 2019). Additionally, southern stingrays on the shallow sandflats spent more time at baited remote underwater video station (BRUVS) bait cages and had fewer injuries than southern stingrays in deeper forereef habitat where shark relative abundance was higher (Bond *et al.*, 2019). Similar results were found using BRUVS across six countries in the western Pacific Ocean, where fewer small rays (*Neotrygon* spp. and *Taeniura* spp., Dasyatidae) were sighted in places where predatory shark and wedgefish abundance was high (Sherman, Heupel, Moore, Chin, & Simpfendorfer, 2020). Rays also spent more time in the video frame and were more likely to make feeding attempts on the bait bag where there were fewer predators (Sherman *et al.*, 2020). This work highlights the need to consider mesopredator behaviour when looking for evidence of mesopredator release (Sherman *et al.*, 2020). While existing evidence suggests that rays may modify habitat use patterns and behaviour in response to predation

risk, more studies that test *a priori* predictions and explicitly address alternative hypotheses are needed to understand the conditions under which predators shape ray anti-predator behaviour.

CURRENT UNDERSTANDING OF RAY EFFECTS ON ECOSYSTEMS

Potential impacts on prey densities

An overarching question in ray ecology is the degree to which their predator-prey interactions and disturbance of the benthos might affect prey population dynamics, community structure, and ecosystem function. There are, however, limited empirical data to address these questions. For example, there are few studies that investigate if, and when, rays influence prey densities. Yet, this is an important area of study since rays have been blamed for declines in commercially important bivalves which has led to ray population control programs (Gray, Mulligan, & Hannah, 1997; Grubbs *et al.*, 2016; Myers, Baum, Shepherd, Powers, & Peterson, 2007; Yamaguchi, Kawahara, & Ito, 2005). However, in many cases, rays were not actually important predators of bivalves (e.g. Bade, Balakrishnan, Pilgrim, McRae, & Luczkovich, 2014; Gray *et al.*, 1997) and moratoria on ray hunting were instated, with managers pressing for further research (Lloyd, 2017; van Hees, Pien, Ebert, Cailliet, & Smith, 2015). While prey-density thresholds can trigger ray feeding (Ajemian *et al.*, 2012; Ajemian & Powers, 2013; Armstrong *et al.*, 2016; Hines *et al.*, 1997; Peterson, Fodrie,

Summerson, & Powers, 2001; Takeuchi & Tamaki, 2014), our understanding of ray effects on prey populations remains limited to in-situ experiments with varying results (Ajemian *et al.*, 2012; Ajemian & Powers, 2013; Peterson *et al.*, 2001; Peterson, Summerson, Prescott, & Fegley, 1989; Thrush, Pridmore, Hewitt, & Cummings, 1994). In North Carolina, initial work showed a decline in bay scallops (*Argopecten irradians*, Pectinidae) between October and December 1983, which coincided primarily with the arrival of herring gulls (*Larus argentatus*, Laridae) and ring-billed gulls (*Larus delawarensis*, Laridae; Peterson *et al.*, 1989). The seagulls had a negative effect on bay scallop densities over a short time period at low tide on the shallow sandflat (Peterson *et al.*, 1989). The migration of American cownose rays (*Rhinoptera bonasus*, Rhinopteridae) occurs in August and early September, which did not overlap with the scallop decline (Peterson *et al.*, 1989). In a field enclosure, small American cownose rays did not consume any tethered scallops over the course of six days, and scallop mortality was attributed to large whelks due to the lack of shell damage (Peterson *et al.*, 1989). The seasonal decline of bay scallops was later attributed to adult American cownose rays because stockades prevented large rays from consuming mullet (Mugilidae) in a mesocosm, and the average number of recovered scallops from a ray exclosure field experiment was more than ten times the number of scallops collected from the control treatment that did not exclude rays (Peterson *et al.*, 2001). However, the stockades may have also excluded other potential scallop predators (Grubbs *et al.*, 2016), so it remains unclear if the impact of American cownose rays was overestimated. Predator

exclusion experiments in Manukau Harbour, New Zealand revealed that bivalve (*Macromona liliana*, Tellinidae), crustacean (*Colurostylis lemurum*, Diastylidae), sea cucumber (*Taeniogyrus dendyi*, Chiridotidae), and ribbon worm (Nemertea) densities were negatively affected by New Zealand eagle ray and shorebird predation (Thrush *et al.*, 1994). In contrast to this, polychaete (*Scoeleleopsis* sp., Spionidae and *Heteromastus filiformis*, Capitellidae) densities were positively influenced by eagle ray and shorebird predation (Thrush *et al.*, 1994). While it was clear there was a combined negative effect of shorebirds and eagle ray predation on the majority of infaunal prey densities, the effect of eagle rays alone was not estimated (Thrush *et al.*, 1994). In Harrington Sound, Bermuda, calico clams (*Macrocallista maculate*, Veneridae) are the most abundant infauna and are the most important prey species in whitespotted eagle ray (*Aetobatus narinari*, Aetobatidae) diets (Ajemian *et al.*, 2012). In an enclosure experiment with seeded calico clams in low, medium, and high density patches, the proportional mortality rate of clams was similar across treatments, despite whitespotted eagle rays preferentially selecting high density patches (Ajemian *et al.*, 2012). In Alabama, United States, an enclosure experiment demonstrated that American cownose rays did not impact amphipod densities (Ajemian & Powers, 2013). However, amphipods may have been replenished outside of the enclosures due to movement or sediment disturbance, hindering the team's ability to detect ray effects (Ajemian & Powers, 2013). A manipulative experiment demonstrated that blue crabs (*Callinectes sapidus*, Portunidae) were the primary source of hard clam (*Mercenaria* sp., Veneridae) mortality, not American

cownose rays (Ajemian & Powers, 2013). In California, bat eagle rays (*Myliobatis californicus*, Myliobatidae) were the presumed cause of oyster declines; however, there was limited evidence of oysters in their diet and bat eagle rays are important predators of the red rock crab (*Cancer productus*, Cancridae), a species known to eat oysters (Gray *et al.*, 1997). Predator and prey behaviour and life histories should also be considered when testing ray effects on prey density. Bivalves are able to emigrate in response to varying water flow regimes (Powers & Peterson, 2000) and predators (Peterson, Ambrose, & Hunt, 1982), while amphipods may reduce intraspecific competition through nocturnal activity (Hill, 1992). If prey growth is density independent, predators may smooth out prey distribution patterns and keep prey population levels near equilibrium. Small-scale disturbances from ray feeding promote bivalve diversity, likely by prohibiting one species from becoming competitively dominant (Glaspie & Seitz, 2017). Impacts of rays on prey populations will also vary depending on whether the rays are resident or migratory. For example, the seasonal movements of American cownose rays may have a larger impact on bay scallop populations because the timing of predation precedes the autumn bay scallop spawning event (Peterson *et al.*, 2001). The experimental results from various studies highlight that ray effects may be site-specific and influenced by experimental design. Therefore, caution should be taken prior to assuming that experimental results can be extended across large spatial scales (Grubbs *et al.*, 2016). A deeper understanding of prey life history and spatiotemporal patterns in ray

predation are needed to evaluate the potential impacts rays have on prey densities.

Effects of direct predation and risk on wider community

Marine predators can have large impacts on their prey and ecosystems by inducing predator avoidance behaviour (e.g. Heithaus, Frid, Wirsing, & Worm, 2008; Madin, Dill, Ridlon, Heithaus, & Warner, 2016). Experimental work has demonstrated that rays might be able to affect benthic communities by altering the behaviour of their prey. For example, European green crabs (*Carcinus maenas*, Portunidae) limited their movements in the presence of smalleye skates (*Raja microocellata*, Rajidae), which led to a decrease in juvenile bivalve mortality when no mature blue mussel (*Mytilus edulis*, Mytilidae) beds were present (Barrios-O'Neill, Bertolini, & Collins, 2017). When mature mussel beds were present, bivalve mortality did not differ in the presence or absence of skates, demonstrating that benthic complexity can limit predator effects (Barrios-O'Neill *et al.*, 2017). Another laboratory experiment showed that the invasive mussel (*Arcuatula senhousia*, Mytilidae) fed less in the presence of chemical cues of the native Haller's round ray (*Urobatis halleri*, Urotrygonidae; Castorani & Hovel, 2016). Both experiments reveal the potential for rays to influence the benthic environment as well as open water environments. A decrease in mussel filter feeding through vigilance or direct mortality could lead to changes in plankton abundance. In the wild, prey densities likely differ from experimental

settings, and predation risk varies spatially and temporally (Lima & Bednekoff, 1999). Caution should be taken when considering experimental results, since effects from prey behavioural responses to predators are expected to be greater under acute risk (Lima & Bednekoff, 1999). However, these examples highlight that in some circumstances rays may act as initiators of behaviourally mediated ecosystem interactions with outcomes that have the potential to extend beyond benthic environments.

A decline in apex predators can lead to an increase in the abundance of their prey, a phenomenon known as “mesopredator release” (Ritchie & Johnson, 2009). The depletion of apex species can then cause cascading effects through the ecosystem, where their loss indirectly affects lower trophic levels via the increase and/or behavioural changes of mesopredators (Heithaus *et al.*, 2008; Ritchie & Johnson, 2009). In order to demonstrate this empirically, ray abundance, distribution, or behaviour would have to be driven by top-down processes and rays would have to be able to significantly impact benthic communities directly or indirectly. Evidence of ray release from apex predators has been documented in studies that rely primarily on species abundance and relative contribution to fisheries trends (Myers *et al.*, 2007; Pradervand, Mann, & Bellis, 2007; Ward & Myers, 2005). For example, pelagic stingray (*Pteroplatytrygon violacea*, Dasyatidae) abundance increased in the tropical Pacific Ocean following a decline in top pelagic predators like sharks and tunas (Ward & Myers 2005), and the relative contribution of ray catch in a South African recreational fishery increased following a decrease in the relative contribution of

dusky (*Carcharhinus obscurus*, Carcharhinidae) and milk (*Rhizoprionodon acutus*, Carcharhinidae) shark catch (Pradervand *et al.*, 2007). Another example presented evidence of a trophic cascade: a decline of predatory sharks due to fishing resulted in an increased abundance of several ray species including the American cownose ray, and a subsequent decline in bay scallops (Myers *et al.*, 2007). Recent work casts doubt on the described shark mediated trophic cascade via direct predation exclusively (Grubbs *et al.*, 2016). There remains a debate as to whether or not behaviour could be an explanatory mechanism for the patterns discovered by Myers *et al.*, (2007). The negative effect of predation risk on prey populations can be as strong as direct predation alone (Peacor & Werner, 2000; Schmitz, Beckerman, & O'Brien, 1997), while risk effects and their interaction with direct predation can have larger effects on populations than direct predation alone (Creel & Christianson, 2008; Preisser, Bolnick, & Bernard, 2005). Furthermore, predators need not affect the densities of prey populations to influence lower trophic levels through behavioural mechanisms (e.g. Creel & Christianson, 2008; Heithaus *et al.*, 2008, 2010; Preisser *et al.*, 2005). To date, the evidence that declining top predator abundance can lead to ray release is equivocal and warrants further investigation.

Trophic redundancy may increase food web complexity and could protect some systems from the negative effects of the loss of top predators as a type of biological insurance (Navia *et al.*, 2016). A topological analysis has suggested that in tropical networks the loss of one or more mesopredator ray species would not likely have an impact on overall system dynamics (Navia, Cortés, & Mejía-

Falla, 2010). In contrast to this, a similar analysis in a subtropical food web proposed that the shortnose guitarfish (*Zapteryx brevirostris*, Trygonorrhinidae) is likely a central species in the network (Bornatowski, Navia, Braga, Abilhoa, & Corrêa, 2014a). The difference in the relative importance of rays across the tropical and subtropical systems can be explained by latitude and species richness (Bornatowski *et al.*, 2014a). Although topological models can be informative predictive tools, they assume that network parameters are random and that all species are interacting with one another, which does not accurately represent real world scenarios (Proulx, Promislow, & Phillips, 2005). Discovering ways to incorporate environmental stochasticity and varying interaction strengths into network models has been identified as a priority in ecological function analysis (Brodie, Redford, & Doak, 2018). Many trophic models combine all rays and/or mesopredators into one category assuming high redundancy; however, moving forward it is important to understand how these groupings affect model ability to detect the consequences of changes in ray abundance (Navia *et al.*, 2010; Ruocco & Lucifora, 2017). Similarly, lumping species without taking into account individual specializations may obscure important interactions (e.g. Bolnick *et al.*, 2011).

Bioturbation and nutrient dynamics

Rays are 'bioturbators', a functional group that excavate and disturb sediments (e.g. Howard, Mayou, & Heard, 1977), which can lead to abiotic and

biotic changes in the surrounding environment (Berke, 2010; Clifton & Hunter, 1973; Kogure & Wada, 2005; Laverock, Gilbert, Tait, Osborn, & Widdicombe, 2011; Meysman, Middelburg, & Heip, 2006). However, there is a paucity of information on the importance of small-scale ray disturbances to ecosystems. Bioturbation by rays can lead to high rates of sediment displacement (Takeuchi & Tamaki 2014) and benthic disturbance that affects infaunal community structure (VanBlaricom, 1982). While spatial and temporal change in sediment resuspension has been correlated with the abundance and activity of benthic fishes on several coral reefs in the Red Sea (Yahel, Yahel, & Genin, 2002), its implication for carbon sequestration and benthic oxygen cycling remains unclear (Yahel *et al.*, 2008). Research that has explored the potential for nutrient accumulation inside feeding pits and community composition changes following ray bioturbation have come up with contrasting results (Table 2). Varying results across studies are likely due to differences in methodologies, locations, and study species (Sherman, Reidenauer, Thistle, & Meeter, 1983; Thrush, Pridmore, Hewitt, & Cummings, 1991). The focus of recent research has been on the quantity of sediment turned over by rays, which does not clearly identify its importance to ecosystems, especially compared to other biogenic and physical processes. For example, as much as 42% of an intertidal area measuring < 1 km² may be reworked annually due to bioturbation by broad cowtail rays (*Pastinachus ater*; Dasyatidae), whiprays (*Himantura* spp., Dasyatidae), porcupine whiprays (*Urogymnus asperrimus*; Dasyatidae), and bluespotted fantail rays (*Taeniura lymma*, Dasyatidae; O'Shea, Thums, van Kuelen, &

Meeken, 2012), while average daily sediment turnover rates by rays vary from <1% (Grant, 1983) to 91% (Sherman *et al.*, 1983). In Tomioka Bay, Japan, as many as 18,103 new pits were formed per day in an area less than 1 km² (Takeuchi & Tamaki, 2014), an estimate much greater than that in Manukau Harbour, New Zealand where approximately 21 new pits per day in an area similar in size to the study in Japan (Hines *et al.*, 1997). Varying results may be due to ray density, body condition, behaviour (e.g. perceived risk in the area), and differences in methodologies across studies (e.g. pit measurements vs. infilling pits with known sediment volumes). Relative to other biological and physical processes, especially tidal sediment reworking, ray (*Dasyatidae*) bioturbation was not important on the Debidue Flat in South Carolina, USA (Grant, 1983). The pioneering work of VanBlaricom (1982) has, to our knowledge, not been replicated or built upon. This study focused on describing an infaunal community based on the effects of a multi-predator assemblage. This included testing the effects of ray disturbance on community structure, accumulation of organic matter and nutrient concentrations in pits, the subsequent recolonization of infauna into the pits, and the potential importance of foraging opportunities for teleosts created by ray disturbance (Table 2).

Species	Location	Measured response variable(s)	Ray effect significant?	Reference
Atlantic stingray (<i>Hypanus sabinus</i> , Dasyatidae)	Saint George Sound, Florida, USA	Harpacticoid copepod community structure	No	Reidenauer & Thistle, 1981
Haller's round ray (<i>Urobatis halleri</i> , Urotrygonidae)	La Jolla, California, USA	Infauna community structure	Yes (varied response across taxa)	VanBlaricom, 1982
Bat eagle ray (<i>Myliobatis californicus</i> , Myliobatidae)		Organic N and C concentrations	Yes (+)	
		Organic matter accumulation	Yes (+)	
Stingrays (Dasyatidae)	Debidue Flat, South Carolina, USA	Sediment turnover relative to other biological and physical processes	No	Grant, 1983
Atlantic stingray	Saint George Sound, Florida, USA	Nematode community structure	No	Sherman <i>et al.</i> , 1983
New Zealand eagle ray (<i>Myliobatis tenuicaudatus</i> , Myliobatidae)	Manukau Harbour, North Island, New Zealand	Infauna community structure	No	Thrush <i>et al.</i> , 1991
		Organic C concentration (bivalve dominated community)	No	
		Organic C concentration (polychaete dominated community)	Yes (+)	
Stingrays (Dasyatidae)	Debidue Flat, South Carolina, USA	Dissolved oxygen concentration	Yes (-)	D'Andrea, Aller, & Lopez, 2002
		Dissolved organic	Yes (+)	

		carbon Organic matter accumulation Advective porewater flux	Yes (+) Yes (-)	
American cownose rays (<i>Rhinoptera bonasus</i> , Rhinopteridae)	Chesapeake Bay, Virginia, USA	Thin-shelled deposit feeding bivalve density Bivalve diversity	Yes (-) Yes (+)	Glaspie & Seitz, 2017

Table 2: Responses to small-scale ray feeding disturbances. Significant effects on response variables labelled as “-” (negative) or “+” (positive). Studies measuring only sedimentation rates by rays are not included, as the significance of turnover by rays compared to other processes was not tested.

Although the importance of ray bioturbation to nutrient dynamics remains understudied, it is likely important in many systems (Heithaus *et al.*, 2010). Organic carbon (C) and organic nitrogen (N) accumulate at greater rates inside manufactured ray pits for at least 15 days compared to areas outside the pits (VanBlaricom, 1982). For example, the mean %C in ray pits after six days was 0.89 compared to 0.16 in control sites and the mean %N in ray pits after six days was 0.11 compared to 0.02 in control sites (VanBlaricom, 1982). The nutrient content in manufactured pits decreased over time and no significant differences between pit and control site values were detected at 37 days after pit creation (VanBlaricom, 1982). C:N ratios were only significantly different between control sites and pits after six days (6.67 and 7.95 respectively; VanBlaricom, 1982). Ray movements across habitats may generate nutrient subsidies (Earl & Zollner, 2017) since foraging can take place in one habitat and excretion/egestion can

occur in another. This may be the case for reef manta rays (*Mobula alfredi*, Mobulidae) that feed in the mesopelagic zone and move into shallow surface waters (Burgess *et al.*, 2016), reef manta rays that travel between coral reef and pelagic ecosystems (Peel *et al.*, 2019), and smalltooth sawfish that move from deep coastal to shallow mangrove habitats (Papastamatiou *et al.*, 2015a). Additionally, large aggregations of rays, such as reef manta rays, may generate nutrient hotspots within specific areas given their propensity to exhibit philopatric behaviours (Peel *et al.*, 2019). Fundamental to our understanding of these nutrient dynamics will be calculating the duration of ray feeding, egestion, and excretion, which has only been done for Atlantic stingrays (*Hypanus sabinus*, Dasyatidae; Di Santo & Bennett, 2011). Rays themselves can be vectors of allochthonous resources. For example, ray carcasses provide a feeding opportunity in deep sea environments (Higgs, Gates, & Jones, 2014). Scavengers feeding on three devil ray (Mobulidae) carcasses found greater than 1000 m included eelpouts, hagfish, grenadiers, a skate, and an eel; however, the community abundance around the carcasses did not compare to the high abundance of fauna around whale carcasses (Higgs *et al.*, 2014). Despite this, the carbon input to an area of 1.23 km² by the devil ray carcasses and one whale shark (*Rhincodon typus*, Rhincodontidae) carcass accounted for approximately 4% of the daily particulate organic carbon flux (Higgs *et al.*, 2004). In a shallow coastal system in Australia, a stingray carcass facilitated a unique infaunal community, primarily nematode species indicative of anoxic environments (Fonseca, Hutchings, Vieira, & Gallucci, 2011).

Facilitation and other symbiotic relationships

Foraging facilitation is a commensal relationship whereby ray activity enhances another species' ability to access food items (Boaden & Kingsford, 2012). Rays have been documented facilitating foraging for birds (Kajiura, Macesic, Meredith, Cocks, & Dirk, 2009) and numerous teleost taxa (breams [Nemipteridae; Boaden & Kingsford, 2012], characids [Characidae & Hemiodontidae; Neto & Carvalho, 2011], cobia [Rachycentridae; Smith & Merriner, 1982], flounders [Paralichthyidae; VanBlaricom, 1982], grunts [Hamulidae; Strand, 1988], jacks [Carangidae; Kiszka, Heithaus, & Quod, 2014], porcupinefish [Diodontidae; Strand, 1988], porgies [Sparidae; Strand, 1988], and wrasses [Labridae; Strand, 1988]). These interactions typically occur when rays search for prey, disturbing organisms that get released into the surrounding environment to become available for other predators. However, foraging facilitation may also manifest from other ray behaviours. For example, in Brazil Guiana dolphins (*Sotalia guianensis*; Delphinidae) feed on teleosts displaced from breaching giant manta rays (*Mobula birostris*, Mobulidae; Domit, Broadhurst, & Bornatowski, 2017). In La Jolla, California, speckled sanddabs (*Citharichthys stigmaeus*, Paralichthyidae) near pits dug by researchers along transects had a higher frequency of occurrence of several prey species in their stomach contents when compared with sanddab stomach contents in areas lacking disturbance (VanBlaricom, 1982). In order to understand the importance of foraging facilitation by rays for other taxa, net energy gain of associated

species relative to other foraging options and other potential benefits need to be quantified.

Another symbiotic relationship involving rays includes “piggybacking” or “hitchhiking”, whereby organisms including octopus and pink whiprays (*Pateobatis fai*, Dasyatidae) have been observed using the back of stingrays to facilitate travel or reduce predation risk (Meekan, Trevitt, Simpfendorfer, & White, 2016; Souza, Ilarri, & Valentim, 2007). Remoras are often associated with megafauna including rays and despite the potential benefits gained by both ray (e.g. removal of parasites [Ritter & Brunnschwiler 2003]) and remora (e.g. food acquisition, risk aversion, and transportation [Norman, 1939; Ritter & Brunnschwiler 2003]) that would suggest a mutualistic relationship, there are hydrodynamic and body condition issues created by an attached remora (Beckert, Flammang, Anderson, & Nadler, 2016; Schwartz, 1977) that justify further investigation into the costs and benefits of attached remoras. Cleaning mutualisms also exist (Vaughan, Grutter, Costello, & Hutson, 2017), where southern stingrays and giant manta rays have been observed displaying behavioural changes at cleaning stations to signal the cleaner fish (O’Shea, Kingsford, & Seymour, 2010; Snelson, Gruber, Murru, & Schmid, 1990). The relative importance of symbiotic interactions involving rays to populations of symbiotic species and community dynamics is unknown.

ANTHROPOGENIC DRIVERS OF RAY ECOLOGY

Predicting ray responses to climate change

The effects of anthropogenic climate change on ray ecology are still largely unknown and are likely to increase in the future. Vulnerability to climate change varies by species and will likely be exacerbated by multiple other stressors like development and fishing (Chin, Kyne, Walker, & McAuley, 2010), while in certain cases, climate change may have beneficial outcomes for rays. For example, little skate (*Leucoraja erinacea*, Rajidae) embryos exposed to higher CO₂ levels increased mineralization of crura and jaw cartilage, which may boost feeding performance (Di Santo, 2019). Direct effects of climate change on rays are those that are expected to alter physiological processes or life history parameters. For example, little skate embryos from two different locations off the east coast of the United States (Georges Bank and the Gulf of Maine) had longer development times, higher metabolic costs, poor body condition, and decreased survival when exposed experimentally to increased temperatures and acidification (Di Santo, 2015). However, the hatchlings from the two locations responded differently: the Georges Bank skates were smaller than the Gulf of Maine skates, suggesting that intraspecific responses to climate change will also vary depending on location (Di Santo, 2015). Smaller skates were healthier and less sensitive to acidification (Di Santo, 2015). Individual variation will affect how rays respond to climate change (e.g. Sih, Cote, Evans, Fogarty, & Pruitt, 2012).

For example, individual Atlantic cod (*Gadus morhua*, Gadidae) with reactive personalities reduced their home range as temperature increased, while proactive (bold) individuals maintained their home range size or expanded it as waters warmed (Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2018). Bold personalities may be selected for under current predictions of global climate change (Villegas-Ríos *et al.*, 2018). Ultimately, effect sizes will depend on the ability of species to adapt over longer periods of time than cannot be captured in laboratory experiments. Indirect effects of climate change on rays are those that are brought on by behavioural responses to altered habitats and species interactions. The most at-risk ray species in Australia live in freshwater and estuaries and will be impacted by saltwater intrusion due to sea level rise, warming water temperatures, and increased storm intensity (e.g. porcupine whiprays and freshwater whiprays [*Urogymnus dalyensis*, Dasyatidae]; Chin *et al.*, 2010). Elasmobranchs use temperature to aid physiological processes (Di Santo & Bennett, 2011; Matern, Cech, & Hopkins, 2000; Papastamatiou *et al.*, 2015b; Sims *et al.*, 2006), and long-term changes in temperatures may alter ray behaviour. In the North Sea, the cuckoo skate (*Leucoraja naevus*, Rajidae) moved into deeper water in response to increased temperatures, but its distribution did not change latitudinally (Perry, Low, Ellis, & Reynolds, 2005). Shifting habitats may mean rays incur fitness costs through the inability to find food, increased predation risk (e.g. Swain *et al.*, 2015), and/or increased competition with other mesopredators. The cost of locomotion can be high at temperatures above species' thermal optima and philopatric species may be

disproportionately affected by warming water if their cost of transport is high (Lauder & Di Santo, 2015). For example, little skates have some of the highest costs of transport of any elasmobranch, measured by oxygen consumption rates, suggesting their ability to migrate in response to changing abiotic conditions may be limited (Di Santo & Kenaley, 2016). Further evidence supporting this is the decreased mineralization in the pectoral fin cartilage of little skate embryos exposed to increased temperatures, a direct effect of climate change, which may further increase the metabolic costs of locomotion and decrease their chances of moving into cooler refuges (Di Santo, 2019). The frequency and intensity of predator-prey interactions may be reshaped by climate change. For example, higher stress levels and poor body condition may limit rays' ability to seek refuge from predators, whose distributions may also be changing due to warming seas (e.g. Hazen *et al.*, 2013). These examples highlight the need to combine behavioural and physiological research in order to predict ray species vulnerability to climate change.

Fisheries impacts

Rays are subject to both target and incidental fisheries around the world (Dulvy *et al.*, 2014). At least 37% of all ray species (235 of 633 described) experience fishing pressure in some form (S5 Table) and this estimate is highly conservative due to the lack of species-specific reporting (Bonfil, 1994; Curtis & Sosebee, 2015; De-Franco, Mendonça, Oliveira, & Foresti, 2012; Dell'Apa,

Kimmel, & Clò, 2012; Dulvy, Metcalfe, Glanville, Pawson, & Reynolds, 2000; Figueiredo *et al.*, 2007; Machado, Gordo, & Figueiredo, 2004), the grouping of rays in fishery data (Moore, McCarthy, Carvalho, & Peirce, 2012; Silva, Ellis, & Catchpole, 2012), and the use of only primary literature in this review. Large sawfishes (Pristidae) have been completely eradicated in many places and undergone severe range restrictions due to fishing (e.g. Dulvy *et al.*, 2016). Similar local extinctions of skates have occurred, for example, commercial fishing in the northwest Black Sea led to the disappearance of the common stingray (*Dasyatis pastinaca*, Dasyatidae) and the thornback skate in the early 2000s, which consequently led to food webs with fewer trophic links and connectivity (Bănaru, Harmelin-Vivien, & Boudouresque, 2010). Declines in large skate species due to commercial fishing are well documented (e.g. Bănaru *et al.*, 2010; Brander, 1981) and in some cases induced community shifts because of competitive release (Agnew, Nolan, Beddington, & Baranowski, 2000; Dulvy *et al.*, 2000; Ruocco, Lucifora, Astarloa, & Menni, 2012; Walker & Heesen, 1996). When large species decline, smaller species may be released from interspecies competition and take over the niche of larger species (Dulvy *et al.*, 2000; Ruocco *et al.*, 2012). Declining predator abundance affects rays directly and indirectly (e.g. Bond *et al.*, 2019; Ward & Myers, 2005) and until we gain a clearer understanding of ray impacts on prey populations and nutrient dynamics it is difficult to predict ecosystem level consequences of ray declines. Trawling threatens rays directly because they are bycatch, but also indirectly through the depletion of prey sources like shrimp or changes in demersal prey species

assemblages (e.g. Espinoza *et al.*, 2015). Since many rays are generalists, measuring the effect of prey declines on ray populations will likely be challenging as rays may simply switch to other prey taxa. This could lead to increased intra- and interspecific competition. With tremendous impacts to populations of rays, their predators, and their prey and wider impacts on ecosystems, the contribution of fisheries to ray ecology cannot be overlooked.

Interactions with tourism

Elasmobranch tourism benefits national economies (Brunnschweiler, 2010; Haas *et al.*, 2017; O'Malley *et al.*, 2013; Topelko & Dearden, 2005; Vaudo *et al.*, 2018) and the economic importance of rays to tourism industries has contributed to several successful conservation initiatives (e.g. "Belize Fisheries Resources Act", 2020; Cayman Islands, 2013; Ward-Paige, 2017). Although tourism is often promoted as an alternative to fishing (Gallagher *et al.*, 2015), left unmanaged it can have deleterious cascading effects on ecosystems (e.g. Ripple & Beschta, 2006). Tourism is also linked to recreational fisheries, but these fisheries have remained relatively understudied from a tourism perspective (Borch, Aas, & Polincansky, 2008). Of primary concern for most ray tourism operations is the potential for overcrowding (O'Malley *et al.*, 2013). Provisioning is a common practice that entices rays to come close to boats and tourists (Lewis & Newsome 2003, Newsome, Lewis, & Moncrieff, 2004, Gaspar, Chateau, & Galzin, 2008, Corcoran *et al.*, 2013) and also occurs when fishers clean their

catch (Pini-Fitzsimmons, Knott, & Brown, 2018). Provisioning can lead to increased density at the feeding site (Corcoran *et al.*, 2013), reverse normal diel stingray activity (Shackley, 1998, Corcoran *et al.*, 2013), cause some individuals to exhibit anticipatory behaviour (Gaspar *et al.*, 2008, Pini-Fitzsimmons *et al.*, 2018), lead to aggression between individuals (Newsome *et al.*, 2004), increase parasite loads (Semeniuk & Rothley, 2008), and negatively influence body condition (Semeniuk, Bourgeon, Smith, & Rothley, 2009; Semeniuk & Rothley, 2008; Semeniuk, Speers-Roesch, & Rothley, 2007). Higher boat traffic to tourism hotspots may also increase the chance of vessel strikes on rays (McGregor, Richardson, A. J. Armstrong, A. O. Armstrong, & Dudgeon, 2019). Concentration of individuals into small areas may lead to higher competition for food and attract predators. The latter would be particularly concerning for smaller individuals who may be in poor body condition resulting from competitive conflict and not have the energy to invest in anti-predator behaviour. Provisioning likely also reduces pressure on nearby prey populations, while on the other hand may reduce sediment turnover rates. Hypothesis-driven research is needed to understand how and when tourism could have ecosystem level effects. Management strategies are the ideal way to ensure sustainable and responsible tourism practices, such as working with and respecting Indigenous communities, limiting the number of tourists per site visit, controlling the type and amount of food offered daily, and enforcing a minimum human or boat to ray distance (Lawrence *et al.*, 2016).

CONCLUSION AND PATH FORWARD

There is a wealth of literature on broad topics in ray ecology, yet there remains ample opportunity to assess the importance of rays to community dynamics and ecosystem function. While we have a basic understanding of ray trophic roles and interactions with their environment, our knowledge on the relative strength and importance of species and habitat interactions is limited, and in many cases based on speculative hypotheses derived from manipulative experiments or studies with goals that were not focused on addressing the ecological importance of rays. The need to resolve species complexes and address the lack of basic biological information for many ray species hinders our ability to grapple with more elaborate ecological questions. We urge researchers to focus on hypothesis driven research in order to gain a better understanding of ray ecological roles and importance. Attention should be focused on three key areas, while attempting to measure ultimate, rather than proximate response variables (Table 3; Brodie *et al.*, 2018):

(1) Ray effects on prey:

There are many studies describing ray diets, yet we are still lacking a broad understanding of which species are true prey specialists. Given the occurrence of conspecific and congeneric predation by rays, research should clarify if this type of predation is occurring in order to reduce competition amongst sympatric species, or if it results simply from being a generalist feeder. The role rays play in structuring prey populations and

potentially whole ecosystems remains open to interpretation based on conflicting results across studies. This underpins the value of considering both consumptive and non-consumptive effects when studying prey responses to changes in ray abundance. It has been largely assumed that rays have a negative effect on prey densities and research has yet to reach a consensus regarding this hypothesis. The impact of ray foraging on prey densities is expected to be influenced by a variety of factors including the presence of potential ray predators and competitors as well as ray movements (migratory or philopatric). Prey responses will likely be species specific and based on life history parameters (e.g. growth rates) as well as escape tactics. Preliminary experiments suggest that crabs and bivalves are able to respond behaviourally to perceived risk (e.g. Barrios-O'Neill *et al.*, 2017; Castorani & Hovel, 2016), which may have the potential to affect ecosystem dynamics.

(2) Predator effects on rays:

Future research examining trophic relationships should attempt to understand the relative importance of rays to predator diets. Apex predator size classes are the most likely to exhibit concentrated predation and thus exert top down effects on mesopredators (Heupel *et al.*, 2014). The extent to which mesopredator (ray) release occurs following the decline of top predators is unresolved and warrants further investigation. There is no doubt that rays respond to perceived predation risk (e.g. Bond *et al.*, 2019, Swain *et al.*, 2015), but it will be important to measure the

effects of predation risk on ecosystem dynamics and prey population growth rates rather than prey behavioural responses alone (e.g. habitat shifts) in order to gain a thorough understanding of how risk effects may cascade through ecosystems (Table 3). Mathematical predictions suggest that risk effects can stabilize prey populations, promote predator-prey coexistence, and reduce the spread of disease in prey populations (Sarkar & Khajanchi, 2020; Sha, Samanta, Martcheva, & Chattopadhyay, 2019). Prey with high growth rates may also be less sensitive to risk effects (Sarkar & Khajanchi, 2020). Empirical testing of these predictions should be prioritized in order to identify the conditions under which top-down effects will be beneficial or detrimental to ray populations.

(3) Nutrient dynamics:

While rays are bioturbators, our understanding of this process' importance is limited as many studies focus on measuring proximate response variables alone (i.e. amount of sediment disturbed by rays across small areas, measured through pit volume and density). Ultimately, we want to gain an understanding of how bioturbation by rays may affect community structure and ecosystem productivity (Table 3). In other words, our focus should be on measuring the importance of nutrient release from ray bioturbation to surrounding communities (e.g. seagrass, coral reef), rather than simply how much sediment is turned over in a particular area over time. The presumed benefits of bioturbation via foraging facilitation also requires further investigation, which could include comparing the diet of

ray attendant species in areas where rays are present and areas where rays are absent. Movement ecology and physiology will provide insight on active subsidy transfer (movement of nutrients across ecosystems) by rays and the extent to which these processes affect ecosystem function (Earl & Zollner, 2017).

Function	Independent variable(s)	Proximate response variable(s)	Ultimate response variable(s)
Bioturbation	Ray density	Pit density Pit volume Nutrient release Sediment turnover rates	Infauna community density Infauna community structure Ecosystem change Ecosystem productivity
Nutrient transport	Ray movements between habitats Ray carcass density	Nutrient transport rates	Ecosystem productivity
Predation on rays	Predator density	Ray density	Primary consumer density Primary consumer diversity
Predation by rays	Ray density	Prey density	Detritus accumulation Infauna community structure Plankton concentrations
Predator avoidance by rays and their prey	Perceived risk	Predator density Predator-prey spatiotemporal overlap Predator avoidance tactics	Prey fitness Prey population growth rates Ecosystem change Ecosystem productivity
Foraging facilitation	Ray density	Follow rates by attendant species Consumption rates by attendant species	Importance of prey items excavated by rays to attendant species

Table 3: Ecological functions involving rays and the identification of proximate and ultimate response variables. While measuring proximate response variables can be informative, in order to determine the importance of rays to ecosystems, research questions should be developed that seek to measure ultimate response variables. Constructed based off Brodie *et al.*, 2018.

While our recommendations to measure ultimate response variables should serve as a guide to test ecological theory (Table 3), we recognize that this list is not exhaustive. A thorough comprehension of predator-prey interactions will require combining trophic information with behavioural data. We emphasize the need to move past basic diet descriptions and measurements of ray sediment turnover towards behavioural experiments and quantifying the importance of rays to the maintenance of ecosystem function and structure. Otherwise, our knowledge of the ecological roles and importance of rays may remain buried in the sand.

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10.1111/j.1439-0426.2011.01819.x

SUPPLEMENTARY TABLES FOR CHAPTER I

Category 1	Category 2
Batoid	Bioturbation
Batoidea	Community structure
Ray	Competition
Stingray	Diet
Wedgefish	Ecological role
Guitarfish	Ecology
Sawfish	Ecosystem engineer
Skate	Facilitation
	Fear effects
	Feeding
	Fishing
	Foraging
	Indirect effects
	Interaction
	Niche partitioning
	Nutrients
	Predation
	Prey
	Resource partitioning
	Risk effects
	Trophic

Supplementary Table 1: Literature search term combinations. All terms in Category 1 were paired with each term in Category 2 using Google Scholar.

	A G N	A V E	B R Y	C H E	C H I	C N I	C R U	E C H	I N S	L A N	M O L	P L K	P L T	R A Y	S H A	S P O	T E L	T U N	W O R	References
Aetobatidae																				
<i>Aetobatus flagellum</i>	-	-	-	-	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	Yamaguchi <i>et al.</i> , 2005
<i>Aetobatus narinari</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	-	-	-	Randall, 1964; Iversen <i>et al.</i> , 1986; Ajemian <i>et al.</i> , 2012; Serrano-Flores <i>et al.</i> , 2018
<i>Aetobatus ocellatus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	-	-	✓	Schluessel <i>et al.</i> , 2010
Arhynchobatidae																				
<i>Atlantoraja castelnaui</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	✓	-	-	✓	-	-	Barbini & Lucifora, 2012a
<i>Atlantoraja cyclophora</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	✓	-	-	✓	-	✓	Viana & Vianna, 2014; Barbini & Lucifora, 2016b
<i>Bathyraja albomaculata</i>	✓	-	-	-	-	✓	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Brickle <i>et al.</i> , 2003; Ruocco <i>et al.</i> , 2009; Ruocco <i>et al.</i> , 2012
<i>Bathyraja aleutica</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	✓	✓	Orlov, 1998; Brown <i>et al.</i> , 2012
<i>Bathyraja brachyurops</i>	✓	-	-	-	-	-	✓	✓	-	-	✓	-	✓	✓	-	-	✓	-	✓	Brickle <i>et al.</i> , 2003; Mabragaña <i>et al.</i> , 2005; Belleggia <i>et al.</i> , 2008
<i>Bathyraja cousseauae</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Belleggia <i>et al.</i> , 2014
<i>Bathyraja griseocauda</i>	✓	-	-	-	-	✓	✓	-	-	-	✓	-	✓	✓	-	-	✓	-	✓	Brickle <i>et al.</i> , 2003; Mabragaña <i>et al.</i> , 2005; Belleggia <i>et al.</i> , 2014
<i>Bathyraja interrupta</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Orlov, 1998; Paquin <i>et al.</i> , 2014; Kemper <i>et al.</i> , 2017
<i>Bathyraja kincaidii</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Bizzarro <i>et al.</i> , 2007; Rinewalt <i>et al.</i> , 2007
<i>Bathyraja macloviana</i>	-	-	-	-	-	✓	✓	✓	-	-	✓	-	-	-	-	-	-	-	✓	Mabragaña <i>et al.</i> , 2005; Scenna <i>et al.</i> , 2006; Ruocco <i>et al.</i> , 2012; Barbini <i>et al.</i> , 2013
<i>Bathyraja maculata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Orlov, 1998
<i>Bathyraja magellanica</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	✓	Mabragaña <i>et al.</i> , 2005; Barbini <i>et al.</i> , 2010
<i>Bathyraja matsubarae</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Orlov, 1998
<i>Bathyraja minispinosa</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Orlov, 1998
<i>Bathyraja multispinis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	-	✓	Mabragaña <i>et al.</i> , 2005; Belleggia <i>et al.</i> , 2014
<i>Bathyraja parmifera</i>	-	-	-	-	-	✓	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Orlov, 1998; Paquin <i>et al.</i> , 2014; Grigorov <i>et al.</i> , 2015
<i>Bathyraja scaphiops</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Mabragaña <i>et al.</i> , 2005; Belleggia <i>et al.</i> , 2014
<i>Bathyraja smithii</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Ebert <i>et al.</i> , 1991

<i>Bathyrāja spinicauda</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	✓	-	-	✓	-	✓	Dolgov, 2005
<i>Bathyrāja violacea</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Orlov, 1998
<i>Psammobatis bergi</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	✓	-	-	✓	-	✓	San Martín <i>et al.</i> , 2007; Barbini & Lucifora, 2012b
<i>Psammobatis extenta</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Muto <i>et al.</i> , 2001; Braccini & Perez, 2005; Barbini & Lucifora, 2012b; Viana <i>et al.</i> , 2017
<i>Psammobatis normani</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	✓	✓	Mabragaña <i>et al.</i> , 2005; Mabragaña & Gilberto, 2007
<i>Psammobatis rudis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Mabragaña <i>et al.</i> , 2005; Mabragaña & Gilberto, 2007
<i>Psammobatis rutrum</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Viana <i>et al.</i> , 2017
<i>Rioraja agassizii</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	✓	-	✓	✓	-	✓	Soares <i>et al.</i> , 1999; Muto <i>et al.</i> , 2001; Barbini & Lucifora, 2011; Pasquino <i>et al.</i> , 2011; Bornatowski <i>et al.</i> , 2014; Motta <i>et al.</i> , 2016; Viana <i>et al.</i> , 2017
<i>Sympterygia acuta</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	✓	-	-	✓	-	✓	Barbini & Lucifora, 2016a
<i>Sympterygia bonapartii</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Estalles <i>et al.</i> , 2016
Dasyatidae																				
<i>Bathytoshia centroura</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Hess, 1961
<i>Bathytoshia lata</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Dale <i>et al.</i> , 2011
<i>Brevitrygon heterura</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Lim <i>et al.</i> , 2018
<i>Brevitrygon imbricata</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	-	-	-	✓	-	✓	Kizhakudan <i>et al.</i> , 2010
<i>Brevitrygon walga</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	-	✓	Rastgoo <i>et al.</i> , 2018b
<i>Dasyatis chrysonata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Ebert & Cowley, 2003
<i>Dasyatis hypostigma</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	-	-	-	✓	-	✓	Ruocco & Lucifora, 2017
<i>Dasyatis pastinaca</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Ismen, 2003; Surugiu, 2006; Yeldan <i>et al.</i> , 2009; Saglam <i>et al.</i> , 2010; Ponte <i>et al.</i> , 2016
<i>Fontitrygon colarensis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Charvet-Almeida <i>et al.</i> , 2008
<i>Hemitrygon akajei</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Taniuchi & Shimizu, 1993
<i>Hemitrygon bennetti</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Lim <i>et al.</i> , 2018
<i>Hemitrygon fluviorum</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Pardo <i>et al.</i> , 2015
<i>Himantura uarnak</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Devadoss, 1978; Vaudo & Heithaus, 2011; O'Shea <i>et al.</i> , 2013

<i>Hypanus americanus</i>	-	-	-	-	-	-	✓	✓	-	✓	✓	-	✓	✓	-	-	✓	-	✓	Randall, 1964; Howard <i>et al.</i> , 1977; Snelson & Williams, 1981; Stokes & Holland, 1992; Gilliam & Sullivan, 1993; Ajemian & Powers, 2013; Branco-Nunes <i>et al.</i> , 2016; Grun, 2016
<i>Hypanus dipterurus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Navarro-González <i>et al.</i> , 2012; Silva-Garay <i>et al.</i> , 2018
<i>Hypanus longus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Navia <i>et al.</i> , 2007; López-García <i>et al.</i> , 2012
<i>Hypanus marianae</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Shibuya & de Souza Rosa, 2011; Costa <i>et al.</i> , 2015
<i>Hypanus sabinus</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	✓	Howard <i>et al.</i> , 1977; Snelson & Williams, 1981; Ajemian & Powers, 2013
<i>Hypanus say</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Hess, 1961; Howard <i>et al.</i> , 1977; Snelson & Williams, 1981
<i>Maculabatis astra</i>	-	-	-	-	-	-	✓	✓	-	✓	✓	-	-	-	-	-	✓	-	✓	Jacobsen & Bennett, 2011; Vaudo & Heithaus, 2011
<i>Maculabatis gerrardi</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Rastgoo <i>et al.</i> , 2018a
<i>Maculabatis randalli</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Rastgoo <i>et al.</i> , 2018b
<i>Maculabatis toshi</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Pardo <i>et al.</i> , 2015
<i>Megatrygon microps</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	✓	-	-	Purushottama <i>et al.</i> , 2018
<i>Neotrygon annotata</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Jacobsen & Bennett, 2012
<i>Neotrygon kuhlii</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Jacobsen & Bennett, 2012; O'Shea <i>et al.</i> , 2013; Pardo <i>et al.</i> , 2015
<i>Neotrygon picta</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Jacobsen & Bennett, 2012
<i>Pastinachus ater</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	-	-	✓	Vaudo & Heithaus, 2011; O'Shea <i>et al.</i> , 2013
<i>Pastinachus sephen</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Devadoss, 1978; Rastgoo <i>et al.</i> , 2018b
<i>Pateobatis bleekeri</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	✓	✓	Devadoss, 1978
<i>Pateobatis fai</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Vaudo & Heithaus, 2011
<i>Pteroplatytrygon violacea</i>	-	-	-	-	-	✓	✓	-	-	-	✓	-	✓	-	-	-	✓	✓	✓	Wilson & Beckett, 1970; Somvanshi <i>et al.</i> , 2009; Vêras <i>et al.</i> , 2009; Lipej <i>et al.</i> , 2013; Varghese <i>et al.</i> , 2014; Weidner <i>et al.</i> , 2017; Purushottama <i>et al.</i> , 2018
<i>Taeniura lymma</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	O'Shea <i>et al.</i> , 2013
<i>Telatrygon biasa</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Lim <i>et al.</i> , 2018
<i>Urogymnus asperrimus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	-	✓	O'Shea <i>et al.</i> , 2013; Elston <i>et al.</i> , 2017

Glaucostegidae																				
<i>Glaucostegus granulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	✓	-	-	-	-	Dean <i>et al.</i> , 2017	
<i>Glaucostegus typus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	-	-	✓	-	✓	White <i>et al.</i> , 2004; Vaudo & Heithaus, 2011
Gurgesiellidae																				
<i>Cruriraja parcomaculata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Ebert <i>et al.</i> , 1991; Smale & Cowley, 1992
<i>Gurgesiella dorsalifera</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Rincon <i>et al.</i> , 2008
Gymnuridae																				
<i>Gymnura altavela</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	✓	-	✓	-	-	Daiber & Booth, 1960; Psomadakis <i>et al.</i> , 2005; Barria <i>et al.</i> , 2015; Yemişken <i>et al.</i> , 2018
<i>Gymnura australis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Jacobsen <i>et al.</i> , 2009
<i>Gymnura micrura</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Daiber & Booth, 1960; Yokota <i>et al.</i> , 2013
<i>Gymnura natalensis</i>	-	-	-	-	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	Smale <i>et al.</i> , 2001
<i>Gymnura poecilura</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	✓	-	-	Rastgoo <i>et al.</i> , 2018b
Hypnidae																				
<i>Hypnos monopterygius</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Frost <i>et al.</i> , 2017
Mobulidae																				
<i>Mobula alfredi</i>	-	-	-	-	-	-	✓	-	-	-	✓	✓	-	-	-	-	-	-	✓	Jaine <i>et al.</i> , 2012; Armstrong <i>et al.</i> , 2016
<i>Mobula birostris</i>	-	-	-	-	-	-	✓	-	-	-	✓	✓	✓	-	-	-	✓	-	-	Dewar <i>et al.</i> , 2008; Burgess <i>et al.</i> , 2016; Stewart <i>et al.</i> , 2016; Rohner <i>et al.</i> , 2017
<i>Mobula mobular</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	-	-	✓	-	✓	Notarbartolo di Sciara, 1988; Rohner <i>et al.</i> , 2017; Masangcay <i>et al.</i> , 2018
<i>Mobula munkiana</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	-	Notarbartolo di Sciara, 1988
<i>Mobula tarapacana</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Notarbartolo di Sciara, 1988; Rohner <i>et al.</i> , 2017
<i>Mobula thurstoni</i>	-	-	-	-	-	-	✓	-	✓	-	-	-	✓	-	-	-	-	-	✓	Notarbartolo di Sciara, 1988; Gadig <i>et al.</i> , 2003; Rohner <i>et al.</i> , 2017
Myliobatidae																				
<i>Aetomylaeus nichofii</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Devadoss, 1978
<i>Myliobatis aquila</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Jardas <i>et al.</i> , 2004; Valls <i>et al.</i> , 2011; Ponte <i>et al.</i> , 2016
<i>Myliobatis californicus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Gray <i>et al.</i> , 1997

<i>Myliobatis chilensis</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Silva-Garay <i>et al.</i> , 2018
<i>Myliobatis freminvillei</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	-	-	✓	-	✓	Woodland <i>et al.</i> , 2011; Szczepanski & Bengtson, 2014
<i>Myliobatis goodei</i>	-	-	-	-	-	✓	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Molina & Cazorla, 2015; Ruocco & Lucifora, 2017
<i>Myliobatis peruvianus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	✓	-	✓	Silva-Garay <i>et al.</i> , 2018
<i>Myliobatis ridens</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	-	-	Ruocco & Lucifora, 2017
<i>Myliobatis tenuicaudatus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	✓	-	-	-	✓	-	✓	Sommerville <i>et al.</i> , 2011
Narcinidae																				
<i>Discopyge tschudii</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	-	✓	Arrighetti <i>et al.</i> , 2005; Spath <i>et al.</i> , 2013; Spath <i>et al.</i> , 2015
<i>Narcine brasiliensis</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Goitein <i>et al.</i> , 1998; Ferreira & Vooren, 2012
<i>Narcinops tasmaniensis</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	✓	Yick <i>et al.</i> , 2011
Platyrrhinidae																				
<i>Platyrrhina tangi</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	-	-	-	✓	-	✓	Yamaguchi <i>et al.</i> , 2012
Potamotrygonidae																				
<i>Paratrygon aiereba</i>	-	-	-	-	-	-	✓	-	✓	-	-	-	-	-	-	-	✓	-	-	Shibuya <i>et al.</i> , 2009; Shibuya & Zuanon, 2013
<i>Plesiotrygon iwamae</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Shibuya & Zuanon, 2013
<i>Potamotrygon falkneri</i>	-	-	-	-	-	-	✓	-	✓	-	✓	-	-	-	-	-	✓	-	-	Silva & Uieda 2007; Neto & Uieda, 2009
<i>Potamotrygon motoro</i>	-	-	-	-	-	-	✓	-	✓	-	✓	-	✓	-	-	-	✓	-	✓	Silva & Uieda 2007; Shibuya <i>et al.</i> , 2009; Almeida <i>et al.</i> , 2010
<i>Potamotrygon orbignyi</i>	-	-	-	-	-	-	✓	-	✓	-	-	-	-	-	-	-	✓	-	-	Shibuya <i>et al.</i> , 2009
<i>Potamotrygon signata</i>	-	-	-	✓	-	-	✓	-	✓	-	✓	-	-	-	-	-	✓	-	-	Moro <i>et al.</i> , 2012
<i>Potamotrygon wallacei</i>	-	-	-	-	-	-	✓	-	✓	-	-	-	-	-	-	-	✓	-	-	Shibuya <i>et al.</i> , 2009
Pristidae																				
<i>Pristis pectinata</i>	-	-	-	-	-	✓	✓	-	-	-	✓	-	-	✓	-	-	✓	-	✓	Poulakis <i>et al.</i> , 2017
<i>Pristis pristis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	✓	-	✓	-	✓	Devadoss, 1978; Thorburn <i>et al.</i> , 2014
Rajidae																				
<i>Amblyraja doellojuradoi</i>	-	-	-	✓	-	✓	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Mabragaña <i>et al.</i> , 2005; Delpiani <i>et al.</i> , 2013

<i>Amblyraja georgiana</i>	-	-	-	-	-	✓	✓	✓	-	-	✓	-	-	-	-	-	✓	✓	✓	Main & Collins, 2011
<i>Amblyraja hyperborea</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Dolgov, 2005
<i>Amblyraja radiata</i>	✓	-	-	-	-	✓	✓	✓	-	-	✓	-	-	✓	-	-	✓	-	✓	McEachran <i>et al.</i> , 1976; Templeman, 1982; Pedersen, 1995; Skjæraasen & Bergstad, 2000; Link <i>et al.</i> , 2002; Link & Garrison, 2002; Dolgov, 2005; Link, 2007; Link & Sosebee, 2008; Hanson, 2009; Boudreau & Worm, 2010
<i>Beringraja binoculata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Bizzarro <i>et al.</i> , 2007; Paquin <i>et al.</i> , 2014
<i>Beringraja inornata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Bizzarro <i>et al.</i> , 2007
<i>Beringraja rhina</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	✓	✓	Bizzarro <i>et al.</i> , 2007; Robinson <i>et al.</i> , 2007; Paquin <i>et al.</i> , 2014; Kemper <i>et al.</i> , 2017
<i>Dentiraja cerva</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	✓	-	✓	-	-	Treloar <i>et al.</i> , 2007
<i>Dentiraja confusa</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	✓	Macpherson & Roel, 1987
<i>Dentiraja lemprieri</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	-	Treloar <i>et al.</i> , 2007
<i>Dentiraja polyommata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Kyne <i>et al.</i> , 2008
<i>Dipturus batis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	✓	Dolgov, 2005
<i>Dipturus chinensis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	✓	-	✓	-	-	Hara <i>et al.</i> , 2018
<i>Dipturus doutrei</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Macpherson & Roel, 1987
<i>Dipturus gudgeri</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Treloar <i>et al.</i> , 2007
<i>Dipturus innominatus</i>	-	-	-	-	✓	-	✓	-	-	-	✓	-	-	✓	✓	-	✓	✓	-	Forman & Dunn, 2012
<i>Dipturus laevis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	✓	Link, 2007; Schmitt <i>et al.</i> , 2015
<i>Dipturus nidarosiensis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Follesa <i>et al.</i> , 2012
<i>Dipturus oxyrinchus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	✓	-	-	✓	-	✓	Yigin & Ismen, 2010; Barría <i>et al.</i> , 2015; Mulas <i>et al.</i> , 2015; Valls <i>et al.</i> , 2017
<i>Dipturus pullopunctatus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Ebert <i>et al.</i> , 1991; Smale & Cowley, 1992
<i>Dipturus springeri</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Ebert <i>et al.</i> , 1991
<i>Leucoraja erinacea</i>	-	✓	-	-	-	✓	✓	✓	-	-	✓	-	✓	✓	-	✓	✓	-	✓	McEachran <i>et al.</i> , 1976; Link <i>et al.</i> , 2002; Link, 2007; Link & Sosebee, 2008; Boudreau & Worm, 2010; Perry <i>et al.</i> , 2013; Smith <i>et al.</i> , 2014; Malek <i>et al.</i> , 2016
<i>Leucoraja garmani</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	-	✓	Link & Sosebee, 2008

<i>Leucoraja naevus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Holden & Tucker, 1974; Ellis <i>et al.</i> , 1996; Farias <i>et al.</i> , 2006; Valls <i>et al.</i> , 2011; Barria <i>et al.</i> , 2015
<i>Leucoraja ocellata</i>	-	-	-	-	-	✓	✓	✓	-	-	✓	-	✓	✓	-	-	✓	-	✓	McEachran <i>et al.</i> , 1976; Link <i>et al.</i> , 2002; Link & Garrison, 2002; Link, 2007; Boudreau & Worm, 2010; Kelly & Hanson, 2013; Smith <i>et al.</i> , 2014; Malek <i>et al.</i> , 2016
<i>Leucoraja wallacei</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	✓	-	✓	-	✓	Ebert <i>et al.</i> , 1991; Smale & Cowley, 1992; Walmsley-Hart <i>et al.</i> , 1999
<i>Malacoraja senta</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	McEachran <i>et al.</i> , 1976; Link, 2007; Boudreau & Worm, 2010
<i>Malacoraja spinacidervis</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Ebert <i>et al.</i> , 1991
<i>Neoraja stehmanni</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	-	Ebert <i>et al.</i> , 1991
<i>Okamejei kenojei</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Baeck <i>et al.</i> , 2011
<i>Raja asterias</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Romanelli <i>et al.</i> , 2007; Coll <i>et al.</i> , 2013; Navarro <i>et al.</i> , 2013; Barria <i>et al.</i> , 2015; Yemişken <i>et al.</i> , 2018
<i>Raja brachyura</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Holden & Tucker, 1974; Ellis <i>et al.</i> , 1996; Farias <i>et al.</i> , 2006; Catalano <i>et al.</i> , 2007; Follesa <i>et al.</i> , 2010
<i>Raja clavata</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	✓	✓	✓	-	✓	-	✓	Holden & Tucker, 1974; Ajayi, 1982; Gibson & Ezzi, 1987; Macpherson & Roel, 1987; Ebert <i>et al.</i> , 1991; Ellis <i>et al.</i> , 1996; Kabasakal, 2002; Morato <i>et al.</i> , 2003; Demirhan <i>et al.</i> , 2005; Farias <i>et al.</i> , 2006; Demirhan <i>et al.</i> , 2007; Saglam & Bascinar, 2008; Valls <i>et al.</i> , 2011; Šantić <i>et al.</i> , 2012; Barria <i>et al.</i> , 2015; Eronat & Ozaydin, 2015; Valls <i>et al.</i> , 2017; Yemişken <i>et al.</i> , 2018
<i>Raja microocellata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	✓	Ajayi, 1982
<i>Raja miraletus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Smale & Cowley, 1992; Follesa <i>et al.</i> , 2010; Valls <i>et al.</i> , 2011; Šantić <i>et al.</i> , 2013; Kadri <i>et al.</i> , 2014
<i>Raja montagui</i>	-	-	-	-	-	✓	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Holden & Tucker, 1974; Ajayi, 1982; Ellis <i>et al.</i> , 1996; Farias <i>et al.</i> , 2006; Barria <i>et al.</i> , 2015
<i>Raja polystigma</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Valls <i>et al.</i> , 2011; Barria <i>et al.</i> , 2015
<i>Raja radula</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	✓	-	-	-	✓	-	✓	Consalvo <i>et al.</i> , 2010; Kadri <i>et al.</i> , 2013
<i>Raja straeleni</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	✓	Macpherson & Roel, 1987
<i>Rajella barnardi</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Ebert <i>et al.</i> , 1991
<i>Rajella caudaspinosa</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Ebert <i>et al.</i> , 1991
<i>Rajella dissimilis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Ebert <i>et al.</i> , 1991
<i>Rajella fyllae</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Dolgov, 2005

<i>Rajella leoparda</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	-	-	✓	-	✓	Ebert <i>et al.</i> , 1991
<i>Rajella lintea</i>	-	-	-	-	-	-	✓	✓	-	-	-	-	-	-	-	-	✓	-	-	Dolgov, 2005
<i>Rajella ravidula</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Ebert <i>et al.</i> , 1991
<i>Rostroraja alba</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	✓	-	✓	-	-	Ebert <i>et al.</i> , 1991; Smale & Cowley, 1992
<i>Rostroraja eglanteria</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	✓	-	-	-	✓	-	✓	Sagarese <i>et al.</i> , 2011; Woodland <i>et al.</i> , 2011; Buchheister & Latour, 2015
<i>Rostroraja velezi</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Navia <i>et al.</i> , 2007; Espinoza <i>et al.</i> , 2012; Espinoza <i>et al.</i> , 2015
<i>Spiniraja whiteyi</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	-	Treloar <i>et al.</i> , 2007
<i>Zearaja chilensis</i>	✓	-	-	-	-	✓	✓	✓	-	-	✓	-	-	✓	-	-	✓	✓	✓	Lucifora <i>et al.</i> , 2000; Koen Alonso <i>et al.</i> , 2001; Mabragaña <i>et al.</i> , 2005; Aburto <i>et al.</i> , 2008; Belleggia <i>et al.</i> , 2016
<i>Zearaja maugeana</i>	-	-	-	-	-	-	✓	-	-	-	-	-	✓	-	-	-	✓	-	✓	Treloar <i>et al.</i> , 2017
Rhinidae																				
<i>Rhina ancylostoma</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Raje, 2006
<i>Rhynchobatus djiddensis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Devadoss, 1978; Raje, 2006; Abdurahiman <i>et al.</i> , 2010
Rhinobatidae																				
<i>Acroteriobatus annulatus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Harris <i>et al.</i> , 1988
<i>Pseudobatos glaucostigmus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Navarro-González <i>et al.</i> , 2012; de la Rosa-Meza <i>et al.</i> , 2013; Lara-Mendoza <i>et al.</i> , 2015
<i>Pseudobatos horkelii</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Goitein <i>et al.</i> , 1998
<i>Pseudobatos leucorhynchus</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Navia <i>et al.</i> , 2007
<i>Pseudobatos percellens</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Bornatowski <i>et al.</i> , 2010; Bornatowski <i>et al.</i> , 2014; Do Carmo <i>et al.</i> , 2015
<i>Pseudobatos planiceps</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Silva-Garay <i>et al.</i> , 2018
<i>Pseudobatos productus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	-	-	✓	-	-	Valenzuela-Quinonez <i>et al.</i> , 2017
<i>Rhinobatos annandalei</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	-	Raje, 2006
<i>Rhinobatos punctifer</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	✓	-	✓	Rastgoo <i>et al.</i> , 2018b
<i>Rhinobatos rhinobatos</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Abdel-Aziz <i>et al.</i> , 1993; Ismen <i>et al.</i> , 2007
Rhinopteridae																				

<i>Rhinoptera bonasus</i>	-	-	-	-	-	-	✓	✓	-	✓	✓	-	✓	-	-	-	✓	✓	✓	Orth, 1975; Smith & Merriner, 1985; Collins <i>et al.</i> , 2007; Ajemian & Powers, 2012; Ajemian & Powers, 2013; Bade <i>et al.</i> , 2014; Bornatowski <i>et al.</i> , 2014; Mann <i>et al.</i> , 2016
<i>Rhinoptera javanica</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Devadoss, 1978
<i>Rhinoptera steindachneri</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	✓	-	-	-	✓	-	✓	Navarro-González <i>et al.</i> , 2012; Violante-González <i>et al.</i> , 2018
Torpedinidae																				
<i>Tetronarce californica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	✓	-	-	Bray & Hixon, 1978
<i>Tetronarce nobiliana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	✓	-	-	Barría <i>et al.</i> , 2015
<i>Tetronarce tremens</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Espinoza <i>et al.</i> , 2015
<i>Torpedo marmorata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	✓	Abdel-Aziz, 1994; Barría <i>et al.</i> , 2015
<i>Torpedo sinuspersici</i>	-	-	-	-	-	-	-	-	-	-	✓	-	-	-	-	-	✓	-	-	Rastgoo <i>et al.</i> , 2018b
<i>Torpedo torpedo</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	✓	-	-	✓	-	✓	Abdel-Aziz, 1994; Barría <i>et al.</i> , 2015
Trygonorrhinidae																				
<i>Aptychotrema rostrata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Kyne & Bennett, 2002
<i>Aptychotrema vincentiana</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	-	-	✓	-	✓	Sommerville <i>et al.</i> , 2011
<i>Trygonorrhina fasciata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	✓	-	-	✓	-	✓	Marshall <i>et al.</i> , 2007
<i>Zapteryx brevirostris</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	-	-	-	✓	-	✓	Barbini <i>et al.</i> , 2011; Marion <i>et al.</i> , 2011; Bornatowski <i>et al.</i> , 2014
<i>Zapteryx exasperata</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	-	Blanco-Parra <i>et al.</i> , 2012
<i>Zapteryx xyster</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Navia <i>et al.</i> , 2007; Espinoza <i>et al.</i> , 2013; Espinoza <i>et al.</i> , 2015
Urolophidae																				
<i>Trygonoptera mucosa</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	✓	-	-	-	✓	-	✓	Platell <i>et al.</i> , 1998
<i>Trygonoptera personata</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	✓	-	-	-	-	-	✓	Platell <i>et al.</i> , 1998
<i>Trygonoptera testacea</i>	-	-	-	-	-	-	✓	-	-	✓	✓	-	-	-	-	-	✓	-	✓	Marshall <i>et al.</i> , 2008
<i>Urolophus cruciatus</i>	-	-	-	-	-	✓	✓	-	✓	-	✓	-	-	-	-	✓	-	-	✓	Treloar & Laurenson, 2006; Yick <i>et al.</i> , 2011
<i>Urolophus expansus</i>	-	-	-	-	-	✓	✓	-	-	-	-	-	-	-	-	✓	-	-	✓	Treloar & Laurenson, 2006
<i>Urolophus kapalensis</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Marshall <i>et al.</i> , 2008

<i>Urolophus lobatus</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	✓	-	-	-	✓	-	✓	Platell <i>et al.</i> , 1998
<i>Urolophus paucimaculatus</i>	-	-	-	-	-	-	✓	✓	-	-	✓	-	✓	-	-	-	✓	-	✓	Edwards, 1980; Platell <i>et al.</i> , 1998
Urotrygonidae																				
<i>Urobatis halleri</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Valadez-González <i>et al.</i> , 2001; Flores-Ortega <i>et al.</i> , 2011
<i>Urobatis jamaicensis</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	✓	O'Shea <i>et al.</i> , 2018
<i>Urotrygon aspidura</i>	-	-	-	-	-	-	✓	-	-	-	-	-	-	-	-	-	-	-	-	Navarro-González <i>et al.</i> , 2012
<i>Urotrygon chilensis</i>	-	-	✓	-	-	-	✓	✓	-	-	✓	-	-	-	-	-	✓	-	✓	Oñate-González <i>et al.</i> , 2017; Silva-Garay <i>et al.</i> , 2018
<i>Urotrygon munda</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Flores-Ortega <i>et al.</i> , 2011
<i>Urotrygon nana</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	-	-	✓	Navarro-González <i>et al.</i> , 2012
<i>Urotrygon rogersi</i>	-	-	-	-	-	-	✓	-	-	-	✓	-	-	-	-	-	✓	-	✓	Flores-Ortega <i>et al.</i> , 2011; Navia <i>et al.</i> , 2011; Navarro-González <i>et al.</i> , 2012

Supplementary Table 2: Presence of prey items in ray diets organized by ray families, represented by “✓”. AGN = agnathans, AVE = aves, BRY = bryozoans, CHE = chelicerates, CHI = chimaera, CNI = cnidarians, CRU = crustaceans, ECH = echinoderms, INS = insects, LAN = lancelets, MOL = molluscs, PLK = plankton, PLT = plants, RAY = rays, SHA = sharks, SPO = sponges, TEL = teleosts, TUN = tunicates, WOR = worms. Algae are included in the “plant” column, and the following phyla were categorized under “worms”: Annelida, Chaetognatha, Sipuncula, Hemichordata, Nermertea, Platyhelminthes, Priapulida.

Species	TL pooled	TL YOY	TL juvenile	TL adult	Method	References
<i>Myliobatis freminvillei</i>	3.2 3.3	3.3 3.5	3.1 3.2	3.1 NA	SCA SIA	Szczepanski & Bengtson, 2014 Woodland <i>et al.</i> , 2011
<i>Pseudobatos leucorhynchus</i>	3.5	NA	3.5	3.5	SCA	Navia <i>et al.</i> , 2016
<i>Rostroraja eglanteria</i>	3.5	NA	3.5	3.7	SIA	Woodland <i>et al.</i> , 2011
<i>Urotrygon rogersi</i>	3.5	NA	3.5	3.5	SCA	Navia <i>et al.</i> , 2016
<i>Platyrrhina tangi</i>	3.7	NA	3.6	3.7	SCA	Yamaguchi <i>et al.</i> , 2012
<i>Hypanus longus</i>	3.8	NA	3.7	4	SCA	Navia <i>et al.</i> , 2016
<i>Raja asterias</i>	3.9	NA	3.9	3.9	SCA	Navarro <i>et al.</i> , 2013
<i>Rostroraja velezi</i>	3.9	NA	3.5	4.3	SCA	Navia <i>et al.</i> , 2016
<i>Sympterygia acuta</i>	3.9	NA	3.6	4.2	SCA	Barbini & Lucifora, 2016
<i>Zapteryx xyster</i>	3.9	NA	3.8	3.9	SCA	Navia <i>et al.</i> , 2016
<i>Zapteryx exasperata</i>	4.2	NA	4.1	4.2	SIA	Blanco-Parra <i>et al.</i> , 2012

Supplementary Table 3: Ray trophic levels (TLs) reported by life stage, rounded to the nearest decimal. Mean TL was calculated for the “pooled” column when not provided. Stomach content analysis (SCA) was the most common methodology used to assess TLs, therefore TLs calculated from stable isotope analysis (SIA) were only reported when TLs from SCA were not available. “YOY” = young of year.

Ray predators	References
<i>Elasmobranchs</i>	
Rays	
<i>Amblyraja radiata</i>	McEachran <i>et al.</i> 1976, Dolgov 2005
<i>Atlantoraja castelnaui</i>	Barbini & Lucifora 2012
<i>Atlantoraja cyclophora</i>	Viana & Vianna 2014, Barbini & Lucifora 2016b
<i>Bathyraja aleutica</i>	Orlov 1998
<i>Bathyraja magellanica</i>	Barbini <i>et al.</i> 2010
<i>Bathyraja brachyurops</i>	Brickle <i>et al.</i> 2003, Belleggia <i>et al.</i> 2008
<i>Bathyraja griseocauda</i>	Brickle <i>et al.</i> 2003
<i>Bathyraja spinicauda</i>	Dolgov 2005
<i>Dentiraja cerva</i>	Treloar <i>et al.</i> 2007
<i>Dentiraja lemprieri</i>	Treloar <i>et al.</i> 2007
<i>Dipturus batis</i>	Dolgov 2005
<i>Dipturus chinensis</i>	Hara <i>et al.</i> 2018
<i>Dipturus innominatus</i>	Forman & Dunn 2012
<i>Dipturus laevis</i>	Link 2007
<i>Dipturus oxyrinchus</i>	Mulas <i>et al.</i> 2015
<i>Glaucostegus granulatus</i>	Dean <i>et al.</i> 2017
<i>Hypanus americanus</i>	Branco-Nunes <i>et al.</i> 2016
<i>Leucoraja erinacea</i>	McEachran <i>et al.</i> 1976
<i>Leucoraja ocellata</i>	McEachran <i>et al.</i> 1976
<i>Leucoraja wallacei</i>	Walmsley-Hart <i>et al.</i> 1999
<i>Pristis pectinata</i>	Poulakis <i>et al.</i> 2017
<i>Pristis</i> sp.	Dean <i>et al.</i> 2017
<i>Psammobatis bergi</i>	San Martin <i>et al.</i> 2007
<i>Raja clavata</i>	Ellis <i>et al.</i> 1996
<i>Raja microocellata</i>	Ajayi 1982
<i>Rhynchobatus</i> sp.	Dean <i>et al.</i> 2017
<i>Rioraja agassizii</i>	Muto <i>et al.</i> 2001, Barbini & Lucifora 2011
<i>Rostroraja alba</i>	Smale & Cowley 1992
<i>Spiniraja whitleyi</i>	Treloar <i>et al.</i> 2007
<i>Sympterygia acuta</i>	Barbini & Lucifora 2016a
<i>Torpedo marmorata</i>	Abdel-Aziz 1994
<i>Torpedo torpedo</i>	Abdel-Aziz 1994
<i>Trygonorrhina fasciata</i>	Marshall <i>et al.</i> 2007
<i>Zearaja chilensis</i>	Koen Alonso <i>et al.</i> 2001, Belleggia <i>et al.</i> 2016
Sharks	

<i>Carcharhinus amboinensis</i>	Tillett <i>et al.</i> 2014
<i>Carcharhinus brachyurus</i>	Lucifora <i>et al.</i> 2009b
<i>Carcharhinus galapagensis</i>	Papastamatiou <i>et al.</i> 2006
<i>Carcharhinus leucas</i>	Snelson & Williams 1981, Snelson <i>et al.</i> 1984, Cliff & Dudley 1991, Tillett <i>et al.</i> 2014, Trystram <i>et al.</i> 2016, Estupiñán-Montano <i>et al.</i> 2017
<i>Carcharhinus limbatus</i>	Dudley & Cliff 1993, Castro 1996, Hoffmayer & Parsons 2003, Bornatowski <i>et al.</i> 2014, Estupiñán-Montano <i>et al.</i> 2018
<i>Carcharhinus obscurus</i>	Gelsleichter <i>et al.</i> 1999, Bornatowski <i>et al.</i> 2014
<i>Carcharhinus plumbeus</i>	McElroy <i>et al.</i> 2006, Ellis & Musick 2007, Papastamatiou <i>et al.</i> 2006, Saidi <i>et al.</i> 2007
<i>Carcharias taurus</i>	Gelsleichter <i>et al.</i> 1999, Smale 2005, Lucifora <i>et al.</i> 2009a
<i>Carcharodon carcharias</i>	Cliff <i>et al.</i> 1989
<i>Galeocerdo cuvier</i>	Simpfendorfer 1992, Simpfendorfer <i>et al.</i> 2001, Heithaus 2001, Shibuya <i>et al.</i> 2005, Lowe <i>et al.</i> 1996, Papastamatiou <i>et al.</i> 2006, Bornatowski <i>et al.</i> 2014, Trystram <i>et al.</i> 2016, Dicken <i>et al.</i> 2017
<i>Galeorhinus galeus</i>	Lucifora <i>et al.</i> 2006
<i>Hexanchus griseus</i>	Ebert 1994
<i>Isurus oxyrinchus</i>	Stillwell & Kohler 1982
<i>Negaprion acutidens</i>	White <i>et al.</i> 2004
<i>Negaprion brevirostris</i>	Snelson & Williams 1981, Cortés & Gruber 1990, Newman <i>et al.</i> 2010
<i>Notorynchus cepedianus</i>	Ebert 1991, Lucifora <i>et al.</i> 2005, Barnett <i>et al.</i> 2010, Abrantes & Barnett 2011, Barnett <i>et al.</i> 2017
<i>Rhizoprionodon terraenovae</i>	Gelsleichter <i>et al.</i> 1999, Hoffmayer & Parsons 2003
<i>Scyliorhinus stellaris</i>	Ellis <i>et al.</i> 1996
<i>Somniosus microcephalus</i>	Yano <i>et al.</i> 2007, McMeans <i>et al.</i> 2012
<i>Sphyrna lewini</i>	Stevens & Lyle 1989, Bornatowski <i>et al.</i> 2014
<i>Sphyrna mokarran</i>	Stevens & Lyle 1989, Strong 1990, Cliff 1995, Chapman & Gruber 2002
Teleosts	
Anglerfish	
<i>Lophius americanus</i>	Armstrong <i>et al.</i> 1996
Billfish	
<i>Kajikia audax</i>	Baker 1966
Cod	
<i>Gadus macrocephalus</i>	Yang 2004
Cod icefish	
<i>Dissostichus mawsoni</i>	Fenaughty <i>et al.</i> 2003, Park <i>et al.</i> 2015
Scorpionfish	
<i>Neosebastes pandus</i>	Greenwell <i>et al.</i> 2018

Tuna	
<i>Thunnus thynnus</i>	Chase 2002, Logan <i>et al.</i> 2015
Mammals	
Apes	
<i>Homo sapiens</i>	See S5 Table
Canids	
<i>Canis latrans</i>	Rose & Polis 1998
Cetaceans	
<i>Monodon monoceros</i>	Finley & Gibb 1982, Laidre & Heide-Jørgensen 2005
<i>Orcinus orca</i>	Visser 1999, Alava & Merlen 2009
<i>Physeter macrocephalus</i>	Cox & Koob 1993, Santos <i>et al.</i> 1999, Flinn <i>et al.</i> 2002
<i>Tursiops truncatus</i>	Conway & McFee 2017
Otters	
<i>Enhydra lutris</i>	Wolt <i>et al.</i> 2012
Pinnipeds	
<i>Arctocephalus gazella</i>	Green <i>et al.</i> 1989, Green <i>et al.</i> 1991, Reid 1995
<i>Arctocephalus pusillus</i>	Deagle <i>et al.</i> 2009, Volpov <i>et al.</i> 2015, Kernaléguen <i>et al.</i> 2016
<i>Eumetopias jubatus</i>	Womble & Sigler 2006, Sigler <i>et al.</i> 2009, Tollit <i>et al.</i> 2015, Tollit <i>et al.</i> 2017
<i>Halichoerus grypus</i>	Murie & Lavigne 1992, Bowen & Harrison 1994
<i>Mirounga angustirostris</i>	Huey 1930, Condit & Le Boeuf 1984, Sinclair 1994
<i>Monachus monachus</i>	Pierce <i>et al.</i> 2011
<i>Pagophilus groenlandicus</i>	Sergeant 1973
<i>Phoca vitulina</i>	Payne & Selzer 1989, Tollit & Thompson 1996, Browne <i>et al.</i> 2002, Lance <i>et al.</i> 2012
<i>Phocartos hookeri</i>	Childerhouse <i>et al.</i> 2001, Augé <i>et al.</i> 2012, Lalas & Webster 2014, Roberts & Lalas 2015
<i>Zalophus californianus</i>	Orr <i>et al.</i> 2011
Birds	
Raptors	
<i>Haliaeetus leucocephalus</i>	Cash <i>et al.</i> 1985
<i>Pandion haliaetus</i>	Cartron & Molles 2002, Fernández-Ordóñez <i>et al.</i> 2016
Waterbirds	
<i>Ardea cinerea</i>	Tojo 1996
<i>Ardea herodias</i>	Ajemian <i>et al.</i> 2011
<i>Leucocarbo nivalis</i>	Green <i>et al.</i> 1990
<i>Pelecanus occidentalis</i>	Bostic & Banks 1966
<i>Thalassarche</i> sp.	McInnes <i>et al.</i> 2017
Invertebrates	

Gastropods	
Unknown species	Cox & Koob 1993, Smith & Griffiths 1997, Cox <i>et al.</i> 1999, Lucifora & Garcia 2004, Hoff 2009
<i>Reptiles</i>	
Alligators	
<i>Alligator mississippiensis</i>	Nifong & Lowers 2017
Crocodiles	
<i>Crocodylus johnstoni</i>	Morgan <i>et al.</i> 2017

Supplementary Table 4: Ray predators.

	Type	Category	Region	IUCN status	Notes	References
Aetobatidae						
<i>Aetobatus flagellum</i>	ART, REC	BYC, TAR	EIO, NIO, WCP	EN		Devadoss 1978, Moore <i>et al.</i> 2012, Shiffman <i>et al.</i> 2014, White & Dharmadi 2007
<i>Aetobatus laticeps</i>	COMM	BYC	ECP	NA		Clarke <i>et al.</i> 2018, Dapp <i>et al.</i> 2013, Navia & Mejia-Falla 2016
<i>Aetobatus narinari</i>	ART, COMM	BYC, TAR	WCA, WNA	NT		Cuevas-Zimbron <i>et al.</i> 2011, Morgan <i>et al.</i> 2010, Perez-Jimenez & Mendez-Loeza 2015, Rodriguez-Ibarra <i>et al.</i> 2018, Serrano-Flores <i>et al.</i> 2018, Tagliagico <i>et al.</i> 2012
<i>Aetobatus ocellatus</i>	ART, COMM, REC, SCP	BYC, TAR	EIO, ESA, NIO, WIO, WCP, WNP, WSP	VU		Barrowclift <i>et al.</i> 2017, Dudley & Cliff 1993, Fennessy 1994, Guastella 1994, Harry <i>et al.</i> 2011, Henderson <i>et al.</i> 2007, Kizhakudan <i>et al.</i> 2010, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Prandervand <i>et al.</i> 2007, Robinson & Sauer 2013, Schluessel <i>et al.</i> 2010, da Silva <i>et al.</i> 2015, Spaet & Berumen 2015, van der Elst 1979, White & Dharmadi 2007
Arhynchobatidae						
<i>Atlantoraja castelnaui</i>	COMM	BYC	WSA	EN		Estalles <i>et al.</i> 2011, Núñez <i>et al.</i> 2018, Orlando <i>et al.</i> 2011, Tamini <i>et al.</i> 2006
<i>Atlantoraja cyclophora</i>	COMM	BYC	WSA	VU		Estalles <i>et al.</i> 2011, Núñez <i>et al.</i> 2018, Orlando <i>et al.</i> 2011, Tamini <i>et al.</i> 2006

<i>Atlantoraja platana</i>	COMM	BYC	WSA	VU		Estalles <i>et al.</i> 2011, Moya <i>et al.</i> 2017
<i>Bathyrāja albomaculata</i>	COMM	BYC, TAR	WSA	VU	Managed fishery through licenses; usually thrown back alive; post-release mortality unknown	Agnew <i>et al.</i> 2000, Brickle <i>et al.</i> 2003, Cedrola <i>et al.</i> 2005, Winter <i>et al.</i> 2015
<i>Bathyrāja aleutica</i>	COMM	BYC	ENP, WNP	NA		Stevenson & Lewis 2001
<i>Bathyrāja brachyurops</i>	COMM	BYC, TAR	WSA	LC	Managed fishery through licenses	Agnew <i>et al.</i> 2000, Brickle <i>et al.</i> 2003, Estalles <i>et al.</i> 2011, Núñez <i>et al.</i> 2018, Winter <i>et al.</i> 2015
<i>Bathyrāja griseocauda</i>	COMM	BYC, TAR	WSA	EN	Managed fishery through licenses; disappeared from catches in southern fishing zone in 1995; fishery in that zone subsequently closed in 1996	Agnew <i>et al.</i> 2000, Brickle <i>et al.</i> 2003, Winter <i>et al.</i> 2015
<i>Bathyrāja interrupta</i>	COMM	BYC	ENP, WNP	LC		Stevenson & Lewis 2001
<i>Bathyrāja lindbergi</i>	COMM	BYC	ENP, WNP	LC		Stevenson & Lewis 2001
<i>Bathyrāja macloviana</i>	COMM	BYC, TAR	WSA	NT	Managed fishery through licenses	Agnew <i>et al.</i> 2000, Estalles <i>et al.</i> 2011, Núñez <i>et al.</i> 2018
<i>Bathyrāja maculata</i>	COMM	BYC	ENP, WNP	LC		Stevenson & Lewis 2001
<i>Bathyrāja magellanica</i>	COMM	TAR	WSA	DD	Managed fishery through licenses	Agnew <i>et al.</i> 2000
<i>Bathyrāja minispinosa</i>	COMM	BYC	ENP, WNP	LC		Stevenson & Lewis 2001
<i>Bathyrāja multispinis</i>	COMM	TAR	WSA	NT	Managed fishery through licenses	Agnew <i>et al.</i> 2000, Winter <i>et al.</i> 2015
<i>Bathyrāja parmifera</i>	COMM	BYC, TAR	ENP, WNP	LC		Grigorov <i>et al.</i> 2015, Stevenson & Lewis 2001
<i>Bathyrāja scaphiops</i>	COMM	TAR	WSA	NT	Managed fishery through licenses	Agnew <i>et al.</i> 2000, Winter <i>et al.</i> 2015

<i>Bathyrāja spinosissima</i>	ART	BYC	ECP	LC		Ramirez-Amaro <i>et al.</i> 2013
<i>Bathyrāja taranetzi</i>	COMM	BYC	ENP, WNP	LC		Stevenson & Lewis 2001
<i>Bathyrāja trachura</i>	COMM	BYC	ENP, WNP	LC		Stevenson & Lewis 2001
<i>Psammobatis bergi</i>	COMM	BYC	WSA	LC		Núñez <i>et al.</i> 2018, San Martin <i>et al.</i> 2007, Tamini <i>et al.</i> 2006
<i>Psammobatis extenta</i>	COMM	BYC	WSA	LC		Braccini & Perez 2005, Núñez <i>et al.</i> 2018, Tamini <i>et al.</i> 2006
<i>Psammobatis lentiginosa</i>	COMM	BYC	WSA	DD		Núñez <i>et al.</i> 2018
<i>Psammobatis normani</i>	COMM	BYC	WSA	DD	Usually thrown back alive; post-release mortality unknown	Cedrola <i>et al.</i> 2005, Núñez <i>et al.</i> 2018
<i>Psammobatis rudis</i>	COMM	BYC	WSA	DD	Usually thrown back alive; post-release mortality unknown	Cedrola <i>et al.</i> 2005, Núñez <i>et al.</i> 2018
<i>Psammobatis scobina</i>	COMM	TAR	WSA	DD	Managed fishery through licenses	Agnew <i>et al.</i> 2000
<i>Rioraja agassizii</i>	ART, COMM	BYC	WSA	VU	Released	Bornatowski <i>et al.</i> 2014a, Bornatowski <i>et al.</i> 2014b, Pasquino <i>et al.</i> 2011, Rodrigues <i>et al.</i> 2018, Tamini <i>et al.</i> 2006
<i>Sympterygia acuta</i>	COMM	BYC	WSA	VU		Núñez <i>et al.</i> 2018
<i>Sympterygia bonapartii</i>	COMM	BYC	WSA	DD	Usually thrown back alive; post-release mortality unknown	Cedrola <i>et al.</i> 2005, Estalles <i>et al.</i> 2011, Estalles <i>et al.</i> 2016, Núñez <i>et al.</i> 2018, Tamini <i>et al.</i> 2006
Dasyatidae						
<i>Bathytoshia brevicaudata</i>	ART, COMM, REC	BYC, TAR	EIO, ESA, WIO	LC		Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Jones <i>et al.</i> 2010, Lamberth 2006
<i>Bathytoshia centroura</i>	COMM	BYC	WCA, WNA, WSA	LC		Morgan <i>et al.</i> 2010, Schmidt <i>et al.</i> 2015

<i>Bathytoshia lata</i>	ART, COMM, REC	BYC, TAR	ESA, WIO	LC		Best <i>et al.</i> 2015, Barrowclift <i>et al.</i> 2017, Fennessy 1994
<i>Brevitrygon imbricata</i>	ART	BYC, TAR	NIO, WCP	DD		Fazrul <i>et al.</i> 2015, Kizhakudan <i>et al.</i> 2010, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012
<i>Brevitrygon walga</i>	ART, COMM	BYC, TAR	EIO, NIO, WCP	NT		Md-Zain <i>et al.</i> 2018, White & Dharmadi 2007
<i>Dasyatis chrysonata</i>	ART, COMM, REC	BYC, TAR	ESA, WIO	NA		Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Fennessy 1994, Lamberth 2006, Prandervand <i>et al.</i> 2007
<i>Dasyatis hypostigma</i>	ART	BYC	WSA	DD		Rodrigues <i>et al.</i> 2018, Schmidt <i>et al.</i> 2015
<i>Dasyatis marmorata</i>	SCP	BYC	WIO	DD		Dudley & Cliff 1993
<i>Dasyatis pastinaca</i>	ART, COMM, REC	BYC, TAR	ECA, MED, WIO, WSA	DD	Disappeared from the Romanian Black Sea fishery in 1971	Bănară <i>et al.</i> 2010; Cross 2015, Tamini <i>et al.</i> 2006, Tiralongo <i>et al.</i> 2018, van der Elst 1979, Yeldan <i>et al.</i> 2009
<i>Dasyatis</i> spp.	ART, COMM, REC, SCP	BAI, BYC, TAR	ECP, ESA, ESP, WCA, WNA, WIO		Bait for recreational shark fishing in WCA	Ajemian <i>et al.</i> 2016, Alfaro-Shigueto <i>et al.</i> 2010, Best <i>et al.</i> 2015, Bizzarro <i>et al.</i> 2009, Dudley & Cliff 1993, Morgan <i>et al.</i> 2010, Smith <i>et al.</i> 2009
<i>Fontitrygon margarita</i>	COMM, REC	BYC, TAR	ECA	EN		Cross 2015, Shiffman <i>et al.</i> 2014
<i>Hemitrygon akajei</i>	NA	BYC, TAR	EIO, WCP, WNP	NT		Taniuchi & Shimizu 1993, White & Dharmadi 2007
<i>Hemitrygon fluviorum</i>	ART, COMM	BYC	WSP	VU		Harry <i>et al.</i> 2011, Pardo <i>et al.</i> 2015

<i>Himantura uarnak</i>	ART, COMM, REC, SCP	BYC, TAR	EIO, ESA, NIO, WCP, WIO	VU		Barrowclift <i>et al.</i> 2017, da Silva <i>et al.</i> 2015, Devadoss 1978, Dudley & Cliff 1993, Everett & Fennessy 2007, Fazrul <i>et al.</i> 2015, Fennessy 1994, Guastella 1994, Henderson <i>et al.</i> 2007, Jaiteh <i>et al.</i> 2014, Kizhakudan <i>et al.</i> 2010, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Moore & Peirce 2013, Prandervand <i>et al.</i> 2007, Spaet & Berumen 2015, van der Elst 1979, White & Dharmadi 2007
<i>Himantura undulata</i>	NA	BYC, TAR	EIO, WCP	VU		White & Dharmadi 2007
<i>Hypanus americanus</i>	ART, COMM	BYC, TAR	WCA, WNA, WSA	DD		Cuevas-Zimbron <i>et al.</i> 2011, Morgan <i>et al.</i> 2010, Perez-Jimenez & Mendez-Loeza 2015, Serrano-Flores <i>et al.</i> 2018, Schmidt <i>et al.</i> 2015
<i>Hypanus dipterurus</i>	ART, COMM	BYC, TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, Cartamil <i>et al.</i> 2011, Dapp <i>et al.</i> 2013, Ehemann <i>et al.</i> 2017, Gonzalez <i>et al.</i> 2012, Moreno-Báez <i>et al.</i> 2012, Navarro- Ramirez- Amaro <i>et al.</i> 2013, Smith <i>et al.</i> 2007, Smith <i>et al.</i> 2009
<i>Hypanus guttatus</i>	ART, COMM	BYC	WSA	DD		Bornatowski <i>et al.</i> 2014a, Rodrigues <i>et al.</i> 2018, Schmidt <i>et al.</i> 2015

<i>Hypanus longus</i>	ART, COMM	BYC, TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, Clarke <i>et al.</i> 2018, Dapp <i>et al.</i> 2013, Ehemann <i>et al.</i> 2017, Navia <i>et al.</i> 2007, Smith <i>et al.</i> 2009
<i>Hypanus marianae</i>	ART	BYC, TAR	WSA	DD		Costa <i>et al.</i> 2015, Shibuya & de Souza Rosa 2011
<i>Maculabatis ambigua</i>	ART	TAR	WIO	NA		Barrowclift <i>et al.</i> 2017
<i>Maculabatis astra</i>	ART	BYC	WSP	LC		Harry <i>et al.</i> 2011
<i>Maculabatis gerrardi</i>	ART, COMM, REC, SCP	BYC, TAR	EIO, ESA, NIO, WCP, WIO	VU		da Silva <i>et al.</i> 2015, Dudley & Cliff 1993, Everett & Fennessy 2007, Fazrul <i>et al.</i> 2015, Fennessy 1994, Guastella 1994, Henderson <i>et al.</i> 2007, Kizhakudan <i>et al.</i> 2010, Md-Zain <i>et al.</i> 2018, Mohanraj <i>et al.</i> 2009, Prandervand <i>et al.</i> 2007, Spaet & Berumen 2015, White & Dharmadi 2007
<i>Maculabatis randalli</i>	NA	NA	NIO	LC		Moore & Peirce 2013
<i>Maculabatis toshi</i>	COMM	BYC, TAR	EIO, WCP, WSP	LC		Pardo <i>et al.</i> 2015, White & Dharmadi 2007
<i>Megatrygon microps</i>	NA	BYC, TAR	EIO, NIO, WCP	DD		Purushottama <i>et al.</i> 2018, White & Dharmadi 2007
<i>Neotrygon annotata</i>	NA	BYC, TAR	EIO, WCP	NT		White & Dharmadi 2007
<i>Neotrygon caeruleopunctata</i>	ART	TAR	WIO	NA		Barrowclift <i>et al.</i> 2017
<i>Neotrygon kuhlii</i>	ART, COMM	BYC, TAR	EIO, ESA, NIO, WCP, WIO, WSP	DD		da Silva <i>et al.</i> 2015, Jaiteh <i>et al.</i> 2014, Kizhakudan <i>et al.</i> 2010, Md-Zain <i>et al.</i> 2018, Mohanraj <i>et al.</i> 2009, Pardo <i>et al.</i> 2015
<i>Pastinachus ater</i>	ART	TAR	WIO	LC		Barrowclift <i>et al.</i> 2017

<i>Pastinachus sephen</i>	ART, COMM	BYC, TAR	EIO, NIO, WCP	NT		Devadoss 1978, Henderson <i>et al.</i> 2007, Jaiteh <i>et al.</i> 2014, Kizhakudan <i>et al.</i> 2010, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Moore & Peirce 2013, Spaet & Berumen 2015, White & Dharmadi 2007
<i>Pastinachus solocistrostris</i>	NA	BYC, TAR	EIO, WCP	EN		White & Dharmadi 2007
<i>Pateobatis bleekeri</i>	ART, COMM	TAR	NIO	NA		Borrell <i>et al.</i> 2011, Devadoss 1978, Kizhakudan <i>et al.</i> 2010, Mohanraj <i>et al.</i> 2009
<i>Pateobatis fai</i>	ART	BYC, TAR	EIO, NIO, WCP	VU		Moore 2012, Moore <i>et al.</i> 2012, White & Dharmadi 2007
<i>Pateobatis hortlei</i>	NA	BYC, TAR	EIO, WCP	VU		White & Dharmadi 2007
<i>Pateobatis jenkinsii</i>	ART, COMM	BYC, TAR	EIO, NIO, WCP	VU		Henderson <i>et al.</i> 2007, Kizhakudan <i>et al.</i> 2010, Md-Zain <i>et al.</i> 2018, Mohanraj <i>et al.</i> 2009, White & Dharmadi 2007
<i>Pateobatis uarnacoides</i>	NA	BYC, TAR	EIO, WCP	VU		White & Dharmadi 2007

<i>Pteroplatytrygon violacea</i>	ART, COMM	BYC, TAR	ECA, ECP, EIO, ESA, MED, NIO, WCA, WCP, WIO, WNA, WSA, WSP	LC		Baez <i>et al.</i> 2017, Cartamil <i>et al.</i> 2011, Dapp <i>et al.</i> 2013, da Silva <i>et al.</i> 2015, Domingo <i>et al.</i> 2005, Echwikhi <i>et al.</i> 2014, Espinola de Siqueira <i>et al.</i> 2007, Piovano & Gilman 2017, Purushottama <i>et al.</i> 2018, Ramirez-Amaro <i>et al.</i> 2013, Shester & Micheli 2011, Vêras <i>et al.</i> 2009, Ward & Myers 2005, Weidner <i>et al.</i> 2017, White & Dharmadi 2007, Wilson & Beckett 1970
<i>Taeniura lymma</i>	ART, COMM	BYC, TAR	EIO, ESA, NIO, WCP, WIO	NT		Barrowclift <i>et al.</i> 2017, da Silva <i>et al.</i> 2015, Spaet & Berumen 2015, White & Dharmadi 2007
<i>Taeniurops meyeri</i>	ART, COMM	BYC, TAR	EIO, WCP, WIO	VU		Barrowclift <i>et al.</i> 2017, Fazrul <i>et al.</i> 2015, Jaiteh <i>et al.</i> 2014, White & Dharmadi 2007
<i>Telatrygon zugei</i>	ART, COMM	BYC, TAR	EIO, NIO, WCP	NT		Fazrul <i>et al.</i> 2015, Md-Zain <i>et al.</i> 2018, Mohanraj <i>et al.</i> 2009, White & Dharmadi 2007
<i>Urogymnus asperrimus</i>	NA	BYC, TAR	EIO, WCP	VU		White & Dharmadi 2007
<i>Urogymnus dalyensis</i>	ART	NA	WCP, WSP	LC	Indigenous cultural and subsistence fishing	Jackson <i>et al.</i> 2012
<i>Urogymnus granulatus</i>	ART	BYC, TAR	EIO, NIO, WCP, WIO	VU		Barrowclift <i>et al.</i> 2017, Moore 2012, White & Dharmadi 2007
Glaucostegidae						

<i>Glaucostegus cemiculus</i>	ART, COMM, REC	BYC, TAR	ECA, MED	CR		Cross 2015, Echwikhi <i>et al.</i> 2014, Rafrafi-Nouira <i>et al.</i> 2015, Shiffman <i>et al.</i> 2014,
<i>Glaucostegus granulatus</i>	ART, COMM	BYC, TAR	NIO	CR		Borrell <i>et al.</i> 2011, Devadoss 1978, Jabado 2018, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Raje 2006
<i>Glaucostegus halavi</i>	ART, COMM	BYC, TAR	NIO	CR		Henderson <i>et al.</i> 2007, Jabado 2018, Moore 2012, Moore <i>et al.</i> 2012, Moore & Peirce 2013, Spaet & Berumen 2015
<i>Glaucostegus obtusus</i>	COMM	BYC, TAR	NIO	CR		Mohanraj <i>et al.</i> 2009, Raje 2006
<i>Glaucostegus thouin</i>	NA	BYC, TAR	EIO, WIO	CR		White & Dharmadi 2007
<i>Glaucostegus typus</i>	ART, COMM	BYC, TAR	EIO, WIO, WSP	CR		Appleyard <i>et al.</i> 2018, Jaiteh <i>et al.</i> 2014, White & Dharmadi 2007, White <i>et al.</i> 2013
Gurgesiellidae						
<i>Cruriraja</i> spp.	ART, COMM	BYC, TAR	ESA, WIO			da Silva <i>et al.</i> 2015
<i>Gurgesiella furvescens</i>	NA	BYC	ESP	LC		Ñacari <i>et al.</i> 2018
Gymnuridae						
<i>Gymnura altavela</i>	ART, COMM, REC	BYC, TAR	ECA, MED, WSA	VU		Cross 2015, Rodrigues <i>et al.</i> 2018, Shiffman <i>et al.</i> 2014, Yemiskien <i>et al.</i> 2018
<i>Gymnura japonica</i>	NA	BYC, TAR	EIO, WSP	DD		White & Dharmadi 2007

<i>Gymnura marmorata</i>	ART, COMM	BYC, TAR	ECP	LC		Cartamil <i>et al.</i> 2011, Clarke <i>et al.</i> 2018, Ehemann <i>et al.</i> 2017, Moreno-Báez <i>et al.</i> 2012, Navia & Mejia-Falla 2016, Shester & Micheli 2011
<i>Gymnura micrura</i>	COMM	BYC	WSA	DD		Shepherd & Myers 2005, Yokota <i>et al.</i> 2013
<i>Gymnura natalensis</i>	ART, COMM, REC, SCP	BYC, TAR	ESA, WIO	LC		Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Dudley & Cliff 1993, Fennessy 1994, Guastella 1994, Lamberth 2006, Prandervand <i>et al.</i> 2007, van der Elst 1979
<i>Gymnura poecilura</i>	ART	BYC, TAR	EIO, NIO, WSP	NT		Henderson <i>et al.</i> 2007, Kizhakudan <i>et al.</i> 2010, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Moore & Peirce 2013, White & Dharmadi 2007
<i>Gymnura zonura</i>	NA	BYC, TAR	EIO, WSP	VU		White & Dharmadi 2007
<i>Gymnura spp.</i>	ART	BYC, TAR	ECP			Bizzarro <i>et al.</i> 2009, Smith <i>et al.</i> 2009
Hypnidae						
<i>Hypnos monopterygius</i>	COMM	BYC	EIO, WSP	LC		Frost <i>et al.</i> 2017, Jones <i>et al.</i> 2010
Mobulidae						
<i>Mobula alfredi</i>	ART	BYC, TAR	WCP	VU		Acebes <i>et al.</i> 2016, Acebes & Tull 2016,

<i>Mobula birostris</i>	ART, COMM, SCP	BYC, TAR	ECP, EIO, ESP, NIO, WCP, WIO, WSP	VU	Philippines implemented a ban on fishing and trade of this species in 1998, but no evidence of enforcement; only devil ray protected in Peru but still observed one landing	Acebes & Tull 2016, Alfaro-Cordova <i>et al.</i> 2017, Dudley & Cliff 1993, Mohanraj <i>et al.</i> 2009, Piovano & Gilman 2017, Stewart <i>et al.</i> 2017, White <i>et al.</i> 2006, White & Dharmadi 2007
<i>Mobula eregoodootenkee</i>	ART	BYC	NIO	NT		Moore 2012, Moore <i>et al.</i> 2012
<i>Mobula hypostoma</i>	COMM	BYC	WCA, WNA	EN		Morgan <i>et al.</i> 2010
<i>Mobula kuhlii</i>	ART, COMM	BYC, TAR	EIO, NIO, WCP, WSP	DD		Spaet & Berumen 2015, White & Dharmadi 2007, White <i>et al.</i> 2006
<i>Mobula mobular</i>	ART, COMM	BAI, BYC, TAR	ECP, EIO, ESP, NIO, WCP, WSA, WSP	EN	Species protected in Mexico in 2007; high proportion released alive in WSA based on Uruguayan observer data	Acebes & Tull 2016, Alfaro-Cordova <i>et al.</i> 2017, Alfaro-Cordova <i>et al.</i> 2018, Bizzarro <i>et al.</i> 2009, Borrell <i>et al.</i> 2011, Cartamil <i>et al.</i> 2011, Kizhakudan <i>et al.</i> 2010, Mas <i>et al.</i> 2015, Masangcay <i>et al.</i> 2018, Mohanraj <i>et al.</i> 2009, Notarbartolo di Sciara 1988, Sampson <i>et al.</i> 2010, Smith <i>et al.</i> 2009, Stewart <i>et al.</i> 2017, White & Dharmadi 2007, White <i>et al.</i> 2006
<i>Mobula munkiana</i>	ART	BYC, TAR	ECP, ESP, NIO	VU	Species protected in Mexico in 2007	Alfaro-Cordova <i>et al.</i> 2017, Bizzarro <i>et al.</i> 2009, Ehemann <i>et al.</i> 2017, Kizhakudan <i>et al.</i> 2010, Notarbartolo di Sciara 1988, Smith <i>et al.</i> 2009, Stewart <i>et al.</i> 2017

<i>Mobula tarapacana</i>	ART	BAI, BYC, TAR	ECP, EIO, ESP, NIO, WCP, WSP	EN		Acebes & Tull 2016, Dapp <i>et al.</i> 2013, Notarbartolo di Sciara 1988, Stewart <i>et al.</i> 2017, White & Dharmadi 2007, White <i>et al.</i> 2006
<i>Mobula thurstoni</i>	ART, COMM	BYC, TAR	ECP, EIO, ESP, NIO, WCP, WSA, WSP	EN	Species protected in Mexico in 2007; high proportion released alive in WSA based on Uruguayan observer data	Acebes & Tull 2016, Alfaro-Cordova <i>et al.</i> 2017, Bizzarro <i>et al.</i> 2009, Dapp <i>et al.</i> 2013, Henderson <i>et al.</i> 2007, Mas <i>et al.</i> 2015, Notarbartolo di Sciara 1988, Sampson <i>et al.</i> 2010, Smith <i>et al.</i> 2009, Spaet & Berumen 2015, Stewart <i>et al.</i> 2017, White & Dharmadi 2007, White <i>et al.</i> 2006
<i>Mobula spp.</i>	ART, COMM, SCP	BYC, TAR	ECP, EIO, ESA, ESP, WIO, WSA, WSP		Species protected in Mexico in 2007; high proportion released alive in WSA based on Uruguayan observer data	Alfaro-Shigueto <i>et al.</i> 2010, Bizzarro <i>et al.</i> 2009, Dapp <i>et al.</i> 2013, da Silva <i>et al.</i> 2015, Dudley & Cliff 1993, Harry <i>et al.</i> 2011, Jaiteh <i>et al.</i> 2014, Mas <i>et al.</i> 2015, Robinson & Sauer 2013, Smith <i>et al.</i> 2009
Myliobatidae						
<i>Aetomylaeus bovinus</i>	ART, COMM, REC, SCP	BYC, TAR	ESA, WIO	DD		Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Dudley & Cliff 1993, Fennessy 1994, Lamberth 2006, Prandervand <i>et al.</i> 2007
<i>Aetomylaeus maculatus</i>	COMM	BYC, TAR	EIO, NIO, WCP	EN		Borrell <i>et al.</i> 2011, White & Dharmadi 2007
<i>Aetomylaeus milvus</i>	ART	BYC	NIO	EN		Moore <i>et al.</i> 2012, Moore & Peirce 2013

<i>Aetomylaeus nichofii</i>	ART, COMM	BYC, TAR	EIO, NIO, WCP, WSP	VU		Devadoss 1978, Harry <i>et al.</i> 2011, Henderson <i>et al.</i> 2007, Moore <i>et al.</i> 2012, Moore & Peirce 2013, Spaet & Berumen 2015, White & Dharmadi 2007
<i>Aetomylaeus vespertilio</i>	ART	BYC, TAR	EIO, NIO, WCP, WSP	EN		Benjamin <i>et al.</i> 2012, Harry <i>et al.</i> 2011, White & Dharmadi 2007
<i>Myliobatis aquila</i>	ART, COMM, REC, SCP	BYC, TAR	ENA, ESA, WIO	DD		Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Dudley & Cliff 1993, Fennessy 1994, Lamberth 2006, Prandervand <i>et al.</i> 2007, Silva <i>et al.</i> 2014, van der Elst 1979
<i>Myliobatis californicus</i>	ART, REC	BYC, TAR	ECP, ENP	LC		Carlisle <i>et al.</i> 2007, Cartamil <i>et al.</i> 2011, Bizzarro <i>et al.</i> 2009, Ehemann <i>et al.</i> 2017, Shester & Micheli 2011, Smith <i>et al.</i> 2009
<i>Myliobatis freminvillei</i>	ART	BYC	WSA	DD		Araújo <i>et al.</i> 2018
<i>Myliobatis goodei</i>	ART, COMM	BYC	WSA	DD		Araújo <i>et al.</i> 2018, Bornatowski <i>et al.</i> 2014a, Milessi <i>et al.</i> 2005, Núñez <i>et al.</i> 2018, Tamini <i>et al.</i> 2006, Velasco <i>et al.</i> 2011
<i>Myliobatis longirostris</i>	ART	BYC, TAR	ECP	NT		Bizzarro <i>et al.</i> 2009, Ehemann <i>et al.</i> 2017, Smith <i>et al.</i> 2009
<i>Myliobatis ridens</i>	ART	BYC	WSA	NA		Araújo <i>et al.</i> 2018
<i>Myliobatis tenuicaudatus</i>	COMM	BYC	EIO	LC		Jones <i>et al.</i> 2010, Sommerville <i>et al.</i> 2011
<i>Myliobatis tobijei</i>	NA	BYC, TAR	EIO, WCP	DD		White & Dharmadi 2007

<i>Myliobatis</i> spp.	ART	BYC, TAR	ECP, ESP, WSA			Alfaro-Shigueto <i>et al.</i> 2010, Araújo <i>et al.</i> 2018, Bizzarro <i>et al.</i> 2009, Moreno-Báez <i>et al.</i> 2012, Ramirez-Amaro <i>et al.</i> 2013, Smith <i>et al.</i> 2009
Narcinidae						
<i>Diplobatis ommata</i>	COMM	BYC	ECP	VU		Clarke <i>et al.</i> 2018
<i>Discopyge tschudii</i>	COMM	BYC	WSA	NT		Núñez <i>et al.</i> 2018, Tamini <i>et al.</i> 2006
<i>Narcine brasiliensis</i>	ART	BYC	WSA	DD		Bornatowski <i>et al.</i> 2014a, Rodrigues <i>et al.</i> 2018
<i>Narcine entemedor</i>	ART, COMM	BYC, TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, Cartamil <i>et al.</i> 2011, Clarke <i>et al.</i> 2018, Ehemann <i>et al.</i> 2017, Navia & Mejia-Falla 2016, Smith <i>et al.</i> 2009
<i>Narcine leoparda</i>	COMM	BYC	ECP	NT		Navia & Mejia-Falla 2016
<i>Narcine vermiculata</i>	COMM	BYC	ECP	NT		Clarke <i>et al.</i> 2018
<i>Narcine</i> spp.	ART	BYC, TAR	ECP, EIO, WSP			Bizzarro <i>et al.</i> 2009, Smith <i>et al.</i> 2009, White & Dharmadi 2007
Narkidae						
<i>Heteronarce garmani</i>	ART, COMM	BYC, TAR	ESA, WIO	VU		da Silva <i>et al.</i> 2015
<i>Narke capensis</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015, Lamberth 2006
Platyrrhinidae						
<i>Platyrrhina sinensis</i>	REC	TAR	NA	VU		Shiffman <i>et al.</i> 2014
<i>Platyrrhinoidis triseriata</i>	ART, REC	BYC, TAR	ECP, ENP	LC		Carlisle <i>et al.</i> 2007, Cartamil <i>et al.</i> 2011, Ramirez-Amaro <i>et al.</i> 2013, Shester & Micheli 2011

Plesiobatidae						
<i>Plesiobatis daviesi</i>	NA	BYC, TAR	EIO, WSP	LC		White & Dharmadi 2007
Potamotrygonidae						
<i>Potamotrygon brachyura</i>	ART, REC	TAR	FRW	DD		Lucifora <i>et al.</i> 2016
<i>Potamotrygon falkneri</i>	COMM	BYC	FRW	DD	Released alive when possible; sometimes consumed locally	Silva & Uieda 2007
<i>Potamotrygon motoro</i>	COMM	BYC	FRW	DD	Released alive when possible; sometimes consumed locally	Silva & Uieda 2007
<i>Styracura schmardae</i>	ART	BYC	WCA	DD		Cuevas-Zimbron <i>et al.</i> 2011
Pristidae						
<i>Anoxypristis cuspidata</i>	ART, COMM, SCP	BYC, TAR	NIO, WCP, WSP	EN	No-take post-2008 in Australia; protected by Wildlife Act 2012 in Bangladesh but not enforced and no fisher education	Appleyard <i>et al.</i> 2018, Harry <i>et al.</i> 2011, Hossain <i>et al.</i> 2015, Jabado <i>et al.</i> 2017, Leeney <i>et al.</i> 2018, White <i>et al.</i> 2013, Wueringer 2017
<i>Pristis clavata</i>	SCP	BYC	WSP	EN		Wueringer 2017

<i>Pristis pectinata</i>	ART, COMM, REC	BYC, TAR	NIO, WCA, WIO	CR	This species not currently distributed in NIO, suspect species misidentification; likely locally extirpated in Mexico, but juvenile caught alive in Barra de Cazones in 2016 put in Veracruz Aquarium; protected in Mexico by environmental legislation in 2002 and then by fisheries in 2007 but no communication or enforcement	Bonfil <i>et al.</i> 2017, Borrell <i>et al.</i> 2011, van der Elst 1979

<i>Pristis pristis</i>	ART, COMM, REC	BYC, TAR	ECA, ECP, EIO, ESP, NIO, WCA, WCP, WSA, WSP	CR	Protected by Wildlife Act 2012 in Bangladesh but not enforced and no fisher education; likely locally extirpated in many places; protected in Mexico by environmental legislation in 2002 and then by fisheries in 2007 but no communication or enforcement; fishing & trade in Brazil illegal since 2004 but meat found in markets labelled as shark	Bonfil <i>et al.</i> 2017, Devadoss 1978, Giglio <i>et al.</i> 2015, Hossain <i>et al.</i> 2015, Jackson <i>et al.</i> 2012, Leeney & Downing 2016, Leeney <i>et al.</i> 2018, Mendoza <i>et al.</i> 2017, Palmeira <i>et al.</i> 2013, Reis-Filho <i>et al.</i> 2016, Shiffman <i>et al.</i> 2014, Thorburn <i>et al.</i> 2014, Thorburn 1982, White & Dharmadi 2007
<i>Pristis zijsron</i>	ART, COMM, SCP	BYC	EIO, NIO, WSP	CR	Protected by the Australian Environmental 541 Protection and Biodiversity Conservation Act 1999	Harry <i>et al.</i> 2011, Jabado <i>et al.</i> 2017, Jabado 2018, Jaiteh <i>et al.</i> 2014, Razzaghi <i>et al.</i> 2017, Wueringer 2017,
<i>Pristis spp.</i>	COMM, GN, SCP	BYC	NIO, WCP, WSP			Grey <i>et al.</i> 2005, Gunn <i>et al.</i> 2010, Raje 2006, Wueringer 2017
Rajidae						
<i>Amblyraja hyperborea</i>	COMM	BYC	ENA	LC		Silva <i>et al.</i> 2012

<i>Amblyraja radiata</i>	COMM, REC	BYC, TAR	ENA, WNA	VU	Species landing prohibition in the United States (2003) but still mean of 22 tonnes landed between 2007-2012	Benoit 2013, Curtis & Sosebee 2015, Link 2007, Shiffman <i>et al.</i> 2014, Silva <i>et al.</i> 2012, Walker & Heessen 1996,
<i>Beringraja binoculara</i>	COMM	BYC	ENP, WNP	LC		Farrugia <i>et al.</i> 2015, Stevenson & Lewis 2001
<i>Beringraja cortezensis</i>	COMM	BYC	ECP	DD		Clarke <i>et al.</i> 2018
<i>Beringraja inornata</i>	ART	BYC, TAR	ECP	LC		Bizzarro <i>et al.</i> 2009, Cartamil <i>et al.</i> 2011, Ramirez-Amaro <i>et al.</i> 2013
<i>Beringraja rhina</i>	ART, COMM	BYC	ECP, ENP, WNP	LC		Farrugia <i>et al.</i> 2015, Shester & Micheli 2011, Stevenson & Lewis 2001
<i>Dentiraja cerva</i>	COMM	BYC	EIO, WSP	NA		Treloar <i>et al.</i> 2007
<i>Dentiraja lemprieri</i>	COMM	BYC	EIO, WSP	LC		Treloar <i>et al.</i> 2007
<i>Dipturus batis</i>	COMM	BYC, TAR	ENA	CR	EU vessels prohibited from retaining since 2011	Brander 1981, Dulvy <i>et al.</i> 2000
<i>Dipturus innominatus</i>	COMM	BYC	WSP	LC	Typically discarded	Forman & Dunn 2012
<i>Dipturus laevis</i>	COMM	BYC, TAR	WNA	EN	Near extinction; species landing prohibition in the United States (2003)	Casey & Myers 1998, Curtis & Sosebee 2015, Link 2007, Schmitt <i>et al.</i> 2015
<i>Dipturus nidarosiensis</i>	COMM	BYC	ENA	NT		Silva <i>et al.</i> 2012
<i>Dipturus oxyrinchus</i>	COMM	BYC	ENA, MED	NT		Figueiredo <i>et al.</i> 2007, Silva <i>et al.</i> 2012, Yigin & Ismen 2010
<i>Dipturus pullopunctatus</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015, Walmsley-Hart <i>et al.</i> 1999

<i>Dipturus springeri</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015
<i>Dipturus trachydermus</i>	COMM	BYC	WSA	VU	Usually thrown back alive; post-release mortality unknown	Cedrola <i>et al.</i> 2005, Estalles <i>et al.</i> 2011, Núñez <i>et al.</i> 2018
<i>Dipturus</i> spp.	NA	BYC, TAR	EIO, WSP			White & Dharmadi 2007
<i>Leucoraja circularis</i>	COMM	BYC	ENA	EN		Figueiredo <i>et al.</i> 2007, Silva <i>et al.</i> 2012
<i>Leucoraja erinacea</i>	COMM	BAI, BYC, TAR	WNA	NT	Used for lobster bait; Magnuson-Stevens Fishery Conservation & Management Act Annual Catch Limit of all skates combined (2006)	Link 2007, Curtis & Sosebee 2015
<i>Leucoraja fullonica</i>	COMM	BYC, TAR	ENA	VU		Dulvy <i>et al.</i> 2000, Griffiths <i>et al.</i> 2013, Silva <i>et al.</i> 2012
<i>Leucoraja garmani</i>	COMM	BYC	WNA	LC	Magnuson-Stevens Fishery Conservation & Management Act Annual Catch Limit of all skates combined (2006)	Curtis & Sosebee 2015
<i>Leucoraja naevus</i>	ART, COMM	BYC, TAR	ENA	LC		Dulvy <i>et al.</i> 2000, Figueiredo <i>et al.</i> 2007, Gallagher <i>et al.</i> 2005, Griffiths <i>et al.</i> 2013, Machado <i>et al.</i> 2004, Silva <i>et al.</i> 2012

<i>Leucoraja ocellata</i>	COMM	BYC, TAR	WNA	EN	Magnuson-Stevens Fishery Conservation & Management Act Annual Catch Limit of all skates combined (2006)	Benoit 2013, Curtis & Sosebee 2015, Link 2007, Sulikowski <i>et al.</i> 2018
<i>Leucoraja wallacei</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015, Walmsley-Hart <i>et al.</i> 1999
<i>Malacoraja senta</i>	COMM	BYC	WNA	EN	Species landing prohibition in the United States (2003)	Benoit 2013, Curtis & Sosebee 2015, Link 2007
<i>Malacoraja spinacidervis</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015
<i>Raja asterias</i>	COMM	BYC, TAR	MED	NT		Coll <i>et al.</i> 2013, Romanelli <i>et al.</i> 2007, Yemiskén <i>et al.</i> 2018
<i>Raja brachyura</i>	ART, COMM	BYC, TAR	ENA, MED	NT		Catalano <i>et al.</i> 2007, Dulvy <i>et al.</i> 2000, Figueiredo <i>et al.</i> 2007, Gallagher <i>et al.</i> 2005, Griffiths <i>et al.</i> 2013, Machado <i>et al.</i> 2004, Silva <i>et al.</i> 2012
<i>Raja clavata</i>	ART, COMM	BYC, TAR	ENA, MED	NT	Disappeared from the Romanian Black Sea fishery in 1971; typically discarded with 81% survival rate after 48h in Mediterranean	Bănară <i>et al.</i> 2010, Dulvy <i>et al.</i> 2000, Eronat & Ozaydin 2015, Figueiredo <i>et al.</i> 2007, Gallagher <i>et al.</i> 2005, Griffiths <i>et al.</i> 2013, Machado <i>et al.</i> 2004, Šantić <i>et al.</i> 2012, Saygu & Deval 2014, Silva <i>et al.</i> 2012, Walker & Heessen 1996, Yemiskén <i>et al.</i> 2018
<i>Raja doellojuradoi</i>	COMM	TAR	WSA	LC	Managed fishery through licenses	Agnew <i>et al.</i> 2000

<i>Raja microocellata</i>	ART, COMM	BYC, TAR	ENA	NT		Dulvy <i>et al.</i> 2000, Figueiredo <i>et al.</i> 2007, Griffiths <i>et al.</i> 2013, Machado <i>et al.</i> 2004, Silva <i>et al.</i> 2012
<i>Raja miraletus</i>	ART, COMM	BYC, TAR	ENA, ESA, MED, WIO	LC	Typically discarded with 21% survival rate after 48h in Mediterranean	da Silva <i>et al.</i> 2015, Fennessy 1994, Figueiredo <i>et al.</i> 2007, Lamberth 2006, Machado <i>et al.</i> 2004, Saygu & Deval 2014
<i>Raja montagui</i>	ART, COMM	BYC, TAR	ENA	LC		Dulvy <i>et al.</i> 2000, Figueiredo <i>et al.</i> 2007, Gallagher <i>et al.</i> 2005, Griffiths <i>et al.</i> 2013, Machado <i>et al.</i> 2004, Silva <i>et al.</i> 2012
<i>Raja radula</i>	ART	BYC, TAR	MED	EN		Consalvo <i>et al.</i> 2010, Echwikhi <i>et al.</i> 2014, Tiralongo <i>et al.</i> 2018
<i>Raja straeleni</i>	ART, COMM, REC	BYC, TAR	ESA, WIO	DD		Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Lamberth 2006
<i>Raja undulata</i>	ART, COMM, REC	BYC, TAR	ENA	EN	EU vessels prohibited from retaining since 2011	Figueiredo <i>et al.</i> 2007, Machado <i>et al.</i> 2004, Shiffman <i>et al.</i> 2014, Silva <i>et al.</i> 2012
<i>Raja spp.</i>	ART, COMM, REC	BYC, TAR	ECP, ENP, ESA, MED, WIO, WNP		Landings increased in Italy following 1983 law that managed all fish except elasmobranchs & between 1945-2012 skate landings declined to near zero tonnes	Barausse <i>et al.</i> 2014, Best <i>et al.</i> 2015, Bizzarro <i>et al.</i> 2009, da Silva <i>et al.</i> 2015, Dell'Apa <i>et al.</i> 2012, Ramirez-Amaro <i>et al.</i> 2013, Stevenson & Lewis 2001
<i>Rajella barnardi</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015
<i>Rajella leoparda</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015

<i>Rajella ravidula</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015
<i>Rostroraja alba</i>	ART, COMM, REC	BYC, TAR	ENA, ESA, WIO	EN	EU vessels prohibited from retaining since 2011	Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Figueiredo <i>et al.</i> 2007, Lamberth 2006, Machado <i>et al.</i> 2004, Silva <i>et al.</i> 2012,
<i>Rostroraja eglanteria</i>	COMM	BYC	WCA, WNA	LC	Magnuson-Stevens Fishery Conservation & Management Act Annual Catch Limit of all skates combined (2006)	Curtis & Sosebee 2015, Morgan <i>et al.</i> 2010
<i>Rostroraja equatorialis</i>	COMM	BYC	ECP	DD		Clarke <i>et al.</i> 2018
<i>Rostroraja velezi</i>	ART, COMM	TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, Clarke <i>et al.</i> 2018, Espinoza <i>et al.</i> 2012, Espinoza <i>et al.</i> 2015, Navia <i>et al.</i> 2007, Navia & Mejia-Falla 2016
<i>Spiniraja whiteleyi</i>	COMM	BYC	EIO, WSP	VU		Jones <i>et al.</i> 2010, Treloar <i>et al.</i> 2007
<i>Zearaja chilensis</i>	COMM	BYC, TAR	WSA	VU	Managed fishery through licenses; usually thrown back alive; post-release mortality unknown	Agnew <i>et al.</i> 2000, Cedrola <i>et al.</i> 2005, Estalles <i>et al.</i> 2011, Koen Alonso <i>et al.</i> 2001, Milessi <i>et al.</i> 2005, Núñez <i>et al.</i> 2001, Tamini <i>et al.</i> 2006, Winter <i>et al.</i> 2015
Rhinidae						
<i>Rhina ancylostoma</i>	ART, COMM	BYC, TAR	EIO, NIO, WIO	CR		Borrell <i>et al.</i> 2011, Fennessy 1994, Henderson <i>et al.</i> 2007, Jabado 2018, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Raje 2006, Robinson & Sauer 2013, Spaet & Berumen 2015, White & Dharmadi 2007

<i>Rhynchobatus australiae</i>	ART, COMM	BYC, TAR	EIO, NIO, WCP, WIO,WSP	CR		Appleyard <i>et al.</i> 2018, Jaiteh <i>et al.</i> 2014, Jones <i>et al.</i> 2010, Md-Zain <i>et al.</i> 2018, White & Dharmadi 2007
<i>Rhynchobatus djiddensis</i>	ART, COMM, REC	BYC, TAR	ESA, NIO, WIO	CR	Fins highly valued in export market	Abdurahiman <i>et al.</i> 2010, Borrell <i>et al.</i> 2011, da Silva <i>et al.</i> 2015, Devadoss 1978, Fennessy 1994, Fields <i>et al.</i> 2018, Grey <i>et al.</i> 2005, Guastella 1994, Henderson <i>et al.</i> 2007, Humber <i>et al.</i> 2017, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Prandervand <i>et al.</i> 2007, Purushottama <i>et al.</i> 2018, Raje 2006, Razzaghi <i>et al.</i> 2017, Shiffman <i>et al.</i> 2014, van der Elst 1979
<i>Rhynchobatus laevis</i>	ART	TAR	NIO	CR		Humber <i>et al.</i> 2017
<i>Rhynchobatus luebberti</i>	REC	TAR	NA	CR		Shiffman <i>et al.</i> 2014
<i>Rhynchobatus</i> spp.	ART, COMM	BYC, TAR	NIO, ESP, WIO		Bag limits post 2008 in Australia	Fields <i>et al.</i> 2018, Harry <i>et al.</i> 2011, Jabado 2018 Moore 2012, Moore & Peirce 2013, Robinson & Sauer 2013, Spaet & Berumen 2015, White <i>et al.</i> 2013
Rhinobatidae						
<i>Acroteriobatus annulatus</i>	ART, COMM, REC	BYC, TAR	ESA, WIO	LC	Not retained in recreational fishery	Best <i>et al.</i> 2015, da Silva <i>et al.</i> 2015, Everett & Fennessy 2007, Fennessy 1994, Lamberth 2006, Prandervand <i>et al.</i> 2007,

						van der Elst 1979
<i>Acroteriobatus blochii</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015
<i>Acroteriobatus leucospilus</i>	ART, COMM, REC	BYC, TAR	ESA, WIO	EN		da Silva <i>et al.</i> 2015, Fennessy 1994, Guastella 1994, Prandervand <i>et al.</i> 2007
<i>Acroteriobatus ocellatus</i>	ART, COMM	BYC, TAR	ESA, WIO	DD		da Silva <i>et al.</i> 2015
<i>Acroteriobatus omanensis</i>	ART	BYC, TAR	NIO	DD		Jabado 2018
<i>Acroteriobatus salalah</i>	ART	BYC, TAR	NIO	NT		Jabado 2018
<i>Acroteriobatus zanzibarensis</i>	ART	TAR	WIO	NT		Barrowclift <i>et al.</i> 2017
<i>Pseudobatos glaucostigmus</i>	ART, COMM	BYC, TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, de la Rosa-Meza <i>et al.</i> 2013, Navarro-Gonzalez <i>et al.</i> 2012
<i>Pseudobatos horkelii</i>	ART, COMM	BYC	WCA, WSA	CR	Prohibited species in Brazil since 2004, but still prevalent in fisheries due to confusion with other guitarfish	De-Franco <i>et al.</i> 2012, Rodrigues <i>et al.</i> 2018
<i>Pseudobatos leucorhynchus</i>	ART, COMM	BYC, TAR	ECP	NT		Bizzarro <i>et al.</i> 2009, Clarke <i>et al.</i> 2018, Navia <i>et al.</i> 2007, Navia & Mejia-Falla 2016
<i>Pseudobatos percellens</i>	ART, COMM	BYC	WCA, WSA	NT		Bornatowski <i>et al.</i> 2010, Bornatowski <i>et al.</i> 2014a, Bornatowski <i>et al.</i> 2014b, De-Franco <i>et al.</i> 2012, Rodrigues <i>et al.</i> 2018
<i>Pseudobatos planiceps</i>	ART	TAR	ECP, ESP	DD		Alfaro-Shigueto <i>et al.</i> 2010, Ortiz <i>et al.</i> 2016

<i>Pseudobatos productus</i>	ART, COMM, REC	BYC, TAR	ECP, ENP	NT		Bizzarro <i>et al.</i> 2009, Carlisle <i>et al.</i> 2007, Cartamil <i>et al.</i> 2011, Márquez-Farias 2005, Márquez-Farias 2011, Meltzer <i>et al.</i> 2012, Moreno-Báez <i>et al.</i> 2012, Shester & Micheli 2011, Smith <i>et al.</i> 2009, Valenzuela-Quíñonez <i>et al.</i> 2017
<i>Rhinobatos annandalei</i>	COMM	BYC	NIO	DD		Jabado 2018, Raje 2006,
<i>Rhinobatos holcorhynchus</i>	ART, COMM	BYC, TAR	ESA, WIO	DD		da Silva <i>et al.</i> 2015
<i>Rhinobatos jimbaranensis</i>	NA	BYC, TAR	EIO, WIO	VU		White & Dharmadi 2007
<i>Rhinobatos penggali</i>	NA	BYC, TAR	EIO, WIO	VU		White & Dharmadi 2007
<i>Rhinobatos punctifer</i>	ART	BYC, TAR	NIO	NT		Henderson <i>et al.</i> 2007, Jabado 2018, Moore <i>et al.</i> 2012, Moore & Peirce 2013
<i>Rhinobatos rhinobatos</i>	ART, COMM	BYC, TAR	ECA, MED	EN		Cross 2015, Echwikhi <i>et al.</i> 2014, Meissa & Gascuel 2015
<i>Rhinobatos sainsburyi</i>	COMM	BYC	EIO	LC		Jaiteh <i>et al.</i> 2014
<i>Rhinobatos spp.</i>	ART	BYC, TAR	ECP, NIO, WSA			Bizzarro <i>et al.</i> 2009, Humber <i>et al.</i> 2017, Jabado 2018, Milessi <i>et al.</i> 2005, Ramirez-Amaro <i>et al.</i> 2013, Smith <i>et al.</i> 2009
Rhinopteridae						
<i>Rhinoptera bonasus</i>	ART, COMM, REC	BYC, TAR	WCA, WNA, WSA	NT		Bade <i>et al.</i> 2014, Bornatowski <i>et al.</i> 2014b, Cuevas-Zimbron <i>et al.</i> 2011, Rodrigues <i>et al.</i> 2018

<i>Rhinoptera javanica</i>	ART, COMM, SCP	BYC, TAR	EIO, NIO, WCP, WIO	VU		Barrowclift <i>et al.</i> 2017, Devadoss 1978, Dudley & Cliff 1993, Kizhakudan <i>et al.</i> 2010, Mohanraj <i>et al.</i> 2009, Moore <i>et al.</i> 2012, Spaet & Berumen 2015, White & Dharmadi 2007
<i>Rhinoptera jayakari</i>	ART, COMM	BYC, TAR	NIO	NA		Henderson <i>et al.</i> 2007, Moore <i>et al.</i> 2012, Spaet & Berumen 2015
<i>Rhinoptera steindachneri</i>	ART, COMM	BYC, TAR	ECP	NT		Bizzarro <i>et al.</i> 2007, Bizzarro <i>et al.</i> 2009, Clarke <i>et al.</i> 2018, Ehemann <i>et al.</i> 2017, Meltzer <i>et al.</i> 2012, Navarro-Gonzalez <i>et al.</i> 2012, Smith <i>et al.</i> 2009, Violante-González <i>et al.</i> 2018
<i>Rhinoptera spp.</i>	ART, REC	BAI, BYC, TAR	EIO, NIO, WCP, WCA, WSA, WSP		Bait for recreational shark fishing in WCA	Ajemian <i>et al.</i> 2016, Bornatowski <i>et al.</i> 2014a, Harry <i>et al.</i> 2011, Moore & Peirce 2013, White & Dharmadi 2007
Torpedinidae						
<i>Tetronarce californica</i>	ART	BYC	ECP	LC		Ramirez-Amaro <i>et al.</i> 2013, Shester & Micheli 2011
<i>Tetronarce cowleyi</i>	ART, COMM	BYC, TAR	ESA, WIO	LC		da Silva <i>et al.</i> 2015
<i>Tetronarce tremens</i>	COMM	BYC	ECP	DD		Clarke <i>et al.</i> 2018, Espinoza <i>et al.</i> 2015,
<i>Torpedo fuscomaculata</i>	ART, COMM	BYC, TAR	ESA, WIO	DD		da Silva <i>et al.</i> 2015, Lamberth 2006
<i>Torpedo marmorata</i>	ART, REC	BYC	ESA, MED	DD	Discarded alive in MED	Best <i>et al.</i> 2015, Tiralongo <i>et al.</i> 2018

<i>Torpedo sinuspersici</i>	ART, COMM, REC, SCP	BYC, TAR	ESA, WIO	DD		da Silva <i>et al.</i> 2015, Dudley & Cliff 1993, Fennessy 1994, Guastella 1994, Prandervand <i>et al.</i> 2007
<i>Torpedo torpedo</i>	ART	BYC	MED	DD	Discarded alive	Tiralongo <i>et al.</i> 2018
<i>Torpedo</i> spp.	REC, SCP	BYC	WIO ESA			Best <i>et al.</i> 2015, Dudley & Cliff 1993
Trygonorrhinidae						
<i>Aptychotrema rostrata</i>	COMM	BYC	WSP	LC		Kyne <i>et al.</i> 2016
<i>Aptychotrema vincentiana</i>	COMM	BYC	EIO	LC		Jones <i>et al.</i> 2010, Sommerville <i>et al.</i> 2011
<i>Trygonorrhina dumerilii</i>	COMM	BYC	EIO	LC		Jones <i>et al.</i> 2010
<i>Zapteryx brevirostris</i>	ART, COMM	BYC	WCA, WSA	VU		Bornatowski <i>et al.</i> 2014a, Bornatowski <i>et al.</i> 2014b, De-Franco <i>et al.</i> 2012, Rodrigues <i>et al.</i> 2018, Tamini <i>et al.</i> 2006
<i>Zapteryx exasperata</i>	ART	BYC, TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, Blanco-Parra <i>et al.</i> 2009, Blanco-Parra <i>et al.</i> 2012, Cartamil <i>et al.</i> 2011, Shester & Micheli 2011, Smith <i>et al.</i> 2009
<i>Zapteryx xystris</i>	COMM	BYC	ECP	DD		Clarke <i>et al.</i> 2018, Espinoza <i>et al.</i> 2013, Espinoza <i>et al.</i> 2015, Navia & Mejia-Falla 2016
Urolophidae						
<i>Urolophus cruciatus</i>	COMM	BYC	EIO	LC		Treloar & Laurenson 2006
<i>Urolophus expansus</i>	COMM	BYC	EIO	LC		Treloar & Laurenson 2006
<i>Urolophus kapalensis</i>	COMM	BYC	WSP	NT		Kyne <i>et al.</i> 2016, Marshall <i>et al.</i> 2008
<i>Urolophus lobatus</i>	COMM	BYC	EIO	LC		Jones <i>et al.</i> 2010

<i>Urolophus paucimaculatus</i>	COMM	BYC	EIO	LC		Jones <i>et al.</i> 2010
<i>Urolophus sufflavus</i>	COMM	BYC	WSP	VU		Kyne <i>et al.</i> 2016
<i>Trygonoptera mucosa</i>	COMM	BYC	EIO	LC		Jones <i>et al.</i> 2010
<i>Trygonoptera personata</i>	COMM	BYC	EIO	LC		Jones <i>et al.</i> 2010
<i>Trygonoptera testacea</i>	COMM	BYC	WSP	NT		Kyne <i>et al.</i> 2016, Marshall <i>et al.</i> 2008
Urotrygonidae						
<i>Urobatis concentricus</i>	ART	BYC	ECP	DD		Ramirez-Amaro <i>et al.</i> 2013
<i>Urobatis halleri</i>	ART, REC	BYC, TAR	ECP, ENP	LC		Bizzarro <i>et al.</i> 2009, Carlisle <i>et al.</i> 2007, Cartamil <i>et al.</i> 2011, Ehemann <i>et al.</i> 2017, Ramirez-Amaro <i>et al.</i> 2013, Shester & Micheli 2011, Smith <i>et al.</i> 2009
<i>Urobatis maculatus</i>	ART	TAR	ECP	DD		Bizzarro <i>et al.</i> 2009
<i>Urobatis</i> spp.	ART	BYC, TAR	ECP			Bizzarro <i>et al.</i> 2009, Smith <i>et al.</i> 2009
<i>Urotrygon aspidura</i>	COMM	BYC	ECP	DD		Clarke <i>et al.</i> 2018, Navarro-Gonzalez <i>et al.</i> 2012, Navia & Mejia-Falla 2016
<i>Urotrygon chilensis</i>	ART, COMM	TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, Clarke <i>et al.</i> 2018, Ramirez-Amaro <i>et al.</i> 2013
<i>Urotrygon cimar</i>	COMM	BYC	ECP	NA		Clarke <i>et al.</i> 2018
<i>Urotrygon munda</i>	COMM	BYC	ECP	DD		Clarke <i>et al.</i> 2018
<i>Urotrygon nana</i>	ART, COMM	BYC	ECP	DD		Clarke <i>et al.</i> 2018, Navarro-Gonzalez <i>et al.</i> 2012, Ramirez-Amaro <i>et al.</i> 2013

<i>Urotrygon rogersi</i>	ART, COMM	BYC, TAR	ECP	DD		Bizzarro <i>et al.</i> 2009, Clarke <i>et al.</i> 2018, Navarro-Gonzalez <i>et al.</i> 2012, Navia <i>et al.</i> 2011, Navia & Mejia-Falla 2016, Ramirez-Amaro <i>et al.</i> 2013
<i>Urotrygon</i> sp.	ART, COMM	BYC, TAR	ECP			Bizzarro <i>et al.</i> 2009, Navia & Mejia-Falla 2016

Supplementary Table 5: Ray species landed in fisheries. Type codes: ART = artisanal, COMM = commercial, REC = recreational, SCP = shark control program, GN = ghost net, NA = not described. Fishing types were chosen based on author classification and their definitions were not consistent across studies. Therefore, they should only be used as a baseline for understanding ray fisheries. Category codes: BAI = bait, BYC = bycatch, TAR = target, NA = not described. Region codes were designated from the “Checklist of World Rays Map” in Last *et al.*, 2016 (ENP = Eastern North Pacific, ECP = Eastern Central Pacific, ESP = Eastern South Pacific, WNA = Western North Atlantic, WCA = Western Central Atlantic, WSA = Western South Atlantic, ENA = Eastern North Atlantic, ECA = Eastern Central Atlantic, ESA = Eastern South Atlantic, MED = Mediterranean, NIO = Northern Indian Ocean, WIO = Western Indian Ocean, EIO = Eastern Indian Ocean, WNP = Western North Pacific, WCP = Western Central Pacific, WSP = Western South Pacific), “NA” for not assessed, and “FRW” for neotropical freshwater stingrays. International Union for the Conservation of Nature (IUCN) Red List status as of February 2020.

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CHAPTER II

SPATIAL VARIATION IN CORAL REEF ASSOCIATED RAY SIGHTINGS IN THE TROPICAL WESTERN ATLANTIC OCEAN

ABSTRACT

Globally, rays (superorder Batoidea) are threatened primarily by overfishing. In the tropical Western Atlantic Ocean, rays are part of artisanal, commercial, and recreational fisheries, yet management is sparse and hindered by a lack of species-specific population data and resources for monitoring and enforcement. Drivers of ray abundance on coral reefs in the region are not well-understood. To address this knowledge gap, I took advantage of a regional baited remote underwater video station (BRUVS) dataset, composed of 2835 BRUVS set across 71 coral reefs, to understand what predicts ray sightings on coral reefs in the tropical Western Atlantic Ocean. I compared ray sightings per unit effort (MaxN) across gradients of human pressure (market gravity), fishing regulations, fishing gear, shark MaxN, and environmental variables using generalized linear mixed models and model averaging. At least nine ray species were detected, of which 78% are threatened with extinction. There was a negative association between ray sightings and habitat structural complexity. Southern stingrays (*Hypanus americanus*), the only species abundant enough to be analyzed at the species level, were less likely to be observed in places with high habitat complexity, high shark abundance, and in areas that used bottom fishing gear.

Southern stingrays were more likely to be sighted around islands than continental shelves, which may be due to habitat availability. However, variance in the most parsimonious model was primarily explained by the random effect of country and territory. Sampling key ray habitats (i.e., soft bottom) using multiple survey techniques, elucidating species-specific patterns, and including more informative local scale fishing information are imperative to improve management recommendations for threatened ray species.

INTRODUCTION

Coral reef associated sharks ('reef sharks') are mainly threatened by overfishing and are considered functionally extinct on 20% of reefs sampled in a global survey (MacNeil *et al.* 2020, Sherman *et al.* 2023). Reef sharks often benefit from areas that are remote, where shark fishing is closed (e.g., shark sanctuaries, marine reserves), with management in place (e.g., seasonal closures, size and gear restrictions, marine protected areas), and with good governance (e.g., Ward-Paige *et al.* 2010, Speed *et al.* 2018, MacNeil *et al.* 2020, Clementi *et al.* 2021a). Rays typically face the same threats as sharks but are more vulnerable to extinction, yet less data are available to assess their status and the conservation potential of different management approaches (e.g., Dulvy *et al.* 2021, Talwar *et al.* 2022, Sherman *et al.* 2023). Although there are reef sharks that can complete their life cycle strictly on coral reefs, few rays complete their entire life cycle in this habitat (Chapman *et al.* 2022). Rather,

many species are partial reef residents, spending much of their time in soft bottom coral reef associated habitats like seagrass beds, mangroves, sandflats, and lagoons (Last *et al.* 2016, Chapman *et al.* 2022) or moving to coral reefs as they mature (Aguilar *et al.* 2009). However, significant knowledge gaps remain in our understanding of ray habitat use, biology, ecology, and behaviour (Frisk 2010, Simpfendorfer & Heupel 2012, Flowers *et al.* 2016, Last *et al.* 2016, Flowers *et al.* 2021).

Contrary to global findings, in the Western Atlantic Ocean sharks are more threatened with extinction than rays (Talwar *et al.* 2022). Rays are part of bycatch and targeted fisheries in the Western Atlantic (Flowers *et al.* 2021, Chapter 1 S5 Table). However, there is limited information on small-scale artisanal fisheries in the region and even though rays are not always targeted, they are often still sold or kept for food (e.g., Cáceres 2019, da Silva Rodrigues Filho 2020, Talwar *et al.* 2022). Long-term sightings data from a marine protected area in Belize and catch rates from a longline fishery in Tabasco, Mexico suggest southern stingray (*Hypanus americanus*) abundance may be stable (Lara-Mendoza *et al.* 2016, Chapter 3). For other species though, fisherfolk and divers have reported catch and sightings declines (e.g., Ward-Paige *et al.* 2011, Cuevas-Zimbrón *et al.* 2011, Blanco-Parra *et al.* 2022, Cáceres *et al.* 2022). Few studies have explored what factors could influence tropical ray abundance. In Brazil, Lutz's stingray (*Hypanus berthallutzae*) abundance was predicted by month and the lunar cycle (Branco-Nunes *et al.* 2021). Based on surveys in other ocean basins, it is likely that habitat complexity, habitat type (e.g., consolidated

vs unconsolidated), and other environmental variables influence ray sightings and abundance alongside anthropogenic factors (Hoisington & Lowe 2005, Le Port *et al.* 2012, White *et al.* 2013, Kanno *et al.* 2019, Sherman *et al.* 2020, Keeping *et al.* 2021, Cortelezzi *et al.* 2022).

Regional abundance and sightings surveys have been conducted for reef sharks in the tropical Western Atlantic Ocean (Ward-Paige *et al.* 2010, MacNeil *et al.* 2020), but similar large-scale studies are lacking for rays. Only a single-species survey has been carried out for the yellow round ray (*Urobatis jamaicensis*) in the greater Caribbean (Ward-Paige *et al.* 2011) and it remains unclear if anthropogenic factors are key predictors of ray sightings in the tropical Western Atlantic Ocean. Yellow round ray declines were found throughout the greater Caribbean region, despite this species not being part of major fisheries (Ward-Paige *et al.* 2011). Jamaica was an exception, where there was an increase in yellow round ray sightings (Ward-Paige *et al.* 2011). This increase was hypothesized to have occurred due to release from predation when large predators like teleosts and sharks declined due to exploitation (Ward-Paige *et al.* 2011). This idea was also proposed when Clementi (2017) showed that ray sightings were lower inside marine protected areas in Belize compared to areas open to shark fishing, and higher in Belize than in The Bahamas where sharks are fully protected from fishing. Predation risk imposed by Caribbean reef sharks (*Carcharhinus perezii*) was later hypothesized to induce a habitat shift by southern stingrays from forereefs to shallow lagoon habitats (Bond *et al.* 2019). Research emphasis has been on what may happen to rays and their behaviour

when sharks decline, but few studies focus on understanding other possible predictors of ray abundance and additional work is required to clarify the mechanisms behind the relationship between ray and shark sightings (Flowers *et al.* 2021, Chapter 1).

My aim was to understand what predicts ray sightings in the tropical Western Atlantic using a regional baited remote underwater video station (BRUVS) dataset provided by Global FinPrint (previously published data in Kessel *et al.* 2018, Bruns & Henderson 2020, Dwyer *et al.* 2020, MacNeil *et al.* 2020, Schmid *et al.* 2020, Clementi *et al.* 2021a & b, Cáceres *et al.* 2022, and Flowers *et al.* 2022). Although the global survey was primarily designed to monitor shark abundance and species richness on coral reefs, many ray species use coral reef habitats for part of their life so the dataset can still be insightful (e.g., Pikitch *et al.* 2005, Aguiar *et al.* 2009, Tilley & Strindberg 2013, Chapman *et al.* 2022). This dataset afforded the opportunity to test whether ray sightings are higher in areas with fewer sharks on a large spatial scale while also investigating other possible anthropogenic and environmental predictors of ray sightings.

METHODOLOGY

Baited remote underwater video station (BRUVS) surveys

BRUVS surveys were conducted between 2015 and 2021 using GoPro cameras attached to a stainless steel, rebar, or polyvinyl chloride frame at depths between 2 – 40 m. An arm extended ~1.5 m forward with an attached bait box containing one kilogram of oily bait fish. Bait was primarily from the families Clupeidae and Scrombridae except for sites where obtaining fishes from these families was not logistically feasible: in Montserrat where gar was used (Lepisosteidae), the Turks and Caicos Islands where barracuda was used (Sphyraenidae, Bruns & Henderson 2020), and Brazil where a mix of reef fishes was occasionally used. Attached to each BRUVS was floating rope and at least one float to facilitate deployment and retrieval. Several research teams used red or magenta filters on some of their cameras, and it is unknown how this could affect detection probability. Detection probability is the probability of observing any species of interest on a BRUVS conditional on their presence at the BRUVS deployment location. Data from 71 coral reefs (N = 2835 BRUVS) were included in analyses (Table 1). A coral reef is defined as an area of at least 4 km² that includes a continuous coral reef or a set of patch reefs within it. Although some data were collected in backreef or lagoon habitats, they were excluded from this study due to their rarity within the dataset (N = 4 coral reefs). Inside each coral reef area, at least 50 sets of coordinates were randomly generated for BRUVS

deployment locations using Esri's ArcGIS (Bond *et al.* 2012) or Google Earth and the University of New Hampshire Cooperative Extension KML Tools Project (<https://extension.unh.edu/kmlTools>). At each coral reef, 24 - 60 BRUVS drops occurred (median = 39; Table 1), where each camera filmed at least 65 minutes of footage (Currey-Randall *et al.* 2020). I did not include sites that had fewer than 20 BRUVS deployments or any BRUVS that were set deeper than 40 m (outside the standard Global FinPrint protocol). Several coral reefs were sampled multiple times across years, therefore I only included the sampling event (i.e., year) with the highest number of BRUVS set. When BRUVS deployments occurred in the same 60-minute filming period, they were spaced at least 500 m apart to ensure independent sampling (Harvey *et al.* 2019). Wherever possible, protected and non-protected reefs were sampled in the same country or territory for comparative purposes. Water temperature (collected at surface < 1 m) and water depth were recorded in the field. Five coral reefs were missing associated water temperature data; therefore, I extracted sea surface temperatures generated using European Space Agency Climate Change Initiative/Copernicus Climate Change Service Information datasets (2016 – 2018, level 4 combined product, v 2.1, Good *et al.* 2019, Merchant *et al.* 2019) using BRUVS deployment coordinates for each relevant date of BRUVS sampling using Esri's ArcGIS Pro software (v 10.8.2).

Country or Territory	Location	Coral Reef	Year	N BRUVS
Antigua & Barbuda	Barbuda	Palaster	2016	51
Bahamas	Abaco	Bight	2016	52
Bahamas	Abaco	Elbow Cay	2015	35
Bahamas	Abaco	Green Turtle	2015	38
Bahamas	Abaco	Guana Cay	2016	42
Bahamas	Andros	North	2016	47
Bahamas	Andros	South	2016	46
Bahamas	Conception	Conception	2016	38
Bahamas	The Exumas	North	2015	32
Bahamas	The Exumas	Middle	2015	29
Bahamas	The Exumas	South	2015	32
Bahamas	New Providence	North	2016	32
Bahamas	New Providence	South	2016	34
Bahamas	San Salvador	San Salvador	2016	45
Barbados	Barbados	Northeast	2017	32
Barbados	Barbados	Northwest	2017	33
Barbados	Barbados	Southeast	2017	33
Barbados	Barbados	Southwest	2017	35
Belize	Belize City	Belize City	2015	39
Belize	Glover's Reef	East	2017	43
Belize	Glover's Reef	West	2017	41
Belize	Lighthouse Reef	Halfmoon	2015	36
Belize	Lighthouse Reef	Sandbore	2015	27
Belize	South Water Caye	South Water Caye	2017	43
Bermuda	Bermuda	North	2018	26
Brazil	Abrolhos	Abrolhos Archipelago	2018	37
Brazil	Abrolhos	Parcel dos Abrolhos	2018	25
Brazil	Abrolhos	Parcel das Paredes	2018	28
Brazil	Fernando de Noronha	APA Area	2017	28
Brazil	Fernando de Noronha	National Park	2017	29
Brazil	Recife	North	2017	44
Brazil	Recife	South	2017	37
Colombia	Cayo Serranilla	Cayo Serranilla	2017	41

Colombia	Cayos de Albuquerque	Albuquerque	2018	36
Colombia	Islas de San Bernardo	Isla Mangle	2016	50
Colombia	Islas de San Bernardo	Isla Tintipan	2016	50
Colombia	Islas Del Rosario	Isla Grande	2016	49
Colombia	Islas Del Rosario	Isla Tesoro	2016	50
Colombia	Isla de Providencia	Old Providence	2018	36
Cuba	Guanahacabibes	Guanahacabibes	2017	50
Cuba	Guanahacabibes	María la Gorda	2017	56
Cuba	Isla de la Juventud	Punta Frances North	2016	52
Cuba	Isla de la Juventud	Punta Frances South	2016	56
Cuba	Jardines de la Reina	Jardines de la Reina	2018	60
Dominican Republic	Bayahibe	Bayahibe	2017	39
Dominican Republic	Boca Chica	Boca Chica	2017	43
Dominican Republic	Santo Domingo	La Caleta	2017	43
Dutch Caribbean	Bonaire	North Coast	2016	29
French West Indies	Martinique	Reef 1	2016	42
French West Indies	Martinique	Reef 2	2016	46
Jamaica	Jamaica	Dragon Point	2016	25
Jamaica	Jamaica	East Portland	2016	36
Jamaica	Jamaica	Negril	2016	35
Jamaica	Jamaica	Ocho Rios	2017	42
Jamaica	Pedro Bank	Pedro Bank	2017	50
Mexico	Quintana Roo	Mahahual	2021	49
Montserrat	Montserrat	Montserrat West	2016	45
Puerto Rico	Bajo de Sico	Bajo de Sico	2017	47
Puerto Rico	La Parguera	La Parguera	2017	38
Trinidad & Tobago	Tobago	Atlantic	2016	50
Trinidad & Tobago	Tobago	Buccoo	2016	29
Trinidad & Tobago	Tobago	Canoe Bay	2016	38
Trinidad & Tobago	Tobago	Caribbean	2018	41
Trinidad & Tobago	Tobago	Charlottetown	2016	24
Trinidad & Tobago	Tobago	Sisters	2016	49
Turks and Caicos	South Caicos	Reserve	2016	44
United States	Florida	Keys Tip	2017	27

United States	Florida	Lower Keys	2016	44
United States	Florida	Miami-Dade	2019	38
United States	Florida	Middle Keys	2016	52
United States	Florida	Upper Keys	2016	35
			TOTAL	2835

Table 1: Summary of baited remote underwater video station (BRUVS) survey data included in this chapter from the tropical Western Atlantic. All data were part of the Global FinPrint project except the data from Mexico, which were kindly shared by Dr. María del Pilar Blanco-Parra (Universidad de Quintana Roo, Fundación Internacional para la Naturaleza y la Sustentabilidad A.C.).

Video and habitat annotation

All video data were uploaded into the Global FinPrint Annotator (Vulcan, Inc., Paul G. Allen Family Foundation). For each reef, 60 minutes of footage from each BRUVS was watched in real time by at least one analyst beginning at the time the BRUVS settled on the seafloor (“mark zero” time). Species were verified by an experienced analyst. In some instances, footage was watched by one experienced team member between real time and 10x speed. For each BRUVS set, the maximum number of individuals for each elasmobranch species in the video field of view at once was recorded (MaxN; Cappo *et al.* 2001). MaxN was used as a measure of sightings per unit effort. I use “sightings” rather than “abundance” when referring to ray MaxN because it may be a biased metric of abundance (Bond *et al.* 2019, Sherman *et al.* 2020). Using Benthobox software (www.benthobox.com), visibility and habitat complexity (reef relief) were estimated for each deployment using a still image from the video footage after

the BRUVS settled on the bottom. A 5 x 4 gridded rectangle was laid on top of the still image and each of the smaller rectangles was given a score between 0 (flat) to 5 (highly complex) unless the rectangle only contained open water (Polunin & Roberts 1993, Wilson *et al.* 2007). Mean habitat complexity was then calculated from each grid for every BRUVS set.

Quality assurance, quality control (QAQC) procedure

A QAQC procedure can ensure data quality is known and reduce error rates (Stribling *et al.* 2008), which is important when working with a large dataset and numerous investigators that vary in experience. Additionally, some ray species are difficult to detect on BRUVS because they can be buried in the sand, camouflaged in seagrasses, or hidden inside coral reef structure (e.g., Spieler *et al.* 2013). Therefore, I watched 10% of the data collected in each country and territory in the Western Atlantic BRUVS dataset (n = 435 BRUVS) at 6x speed to identify potential errors. Using the performance metrics provided by Stribling *et al.* (2008) as a guide, I created BRUVS data quality criteria for each taxon (sharks, rays, sharks and rays combined) that in some cases were less stringent, given that it is not always possible to identify discrete morphological characteristics in video data:

- (1) Percentage taxonomic disagreement (PTD) should be < 15. This metric helps us understand species identification disagreements that could lead

to false positives and negatives in the data (species listed as present when it was absent; or species listed as absent when it was present):

$$PTD = \left(1 - \left[\frac{a}{N}\right]\right) * 100 \quad (\text{equation 1})$$

where a = total number of species agreements between the master dataset and my observations; and N = total number of taxon observations in largest count.

(2) Percent difference in enumeration (PDE) should be < 10 and is a relative difference between counts. This metric gives us an idea of how often sharks and/or rays were missed in the video footage, which could lead to false negatives in the data (species listed as absent when it was present):

$$PDE = \left(\frac{|n1-n2|}{n1+n2}\right) * 100 \quad (\text{equation 2})$$

where $n1$ = number of taxon observations in master dataset, and $n2$ = number of taxon observations made by me. PDE does not take underestimation of MaxN into account, which I also found within the master dataset.

Few species disagreements occurred ($PTD < 4$ for sharks and rays); however, sharks and rays were frequently missed in the master dataset (country and territory level PDE for sharks and rays combined ranged from 0 to 50). Ten countries and territories had a PDE > 10 for sharks and rays combined. To improve data quality (i.e., reduce the PDE) in these places, I trained experienced analysts to rewatch all data in countries and territories that did not meet the quality standards outlined above. We also rewatched BRUVS that were identified as previously only having been watched by one analyst. In total, we rewatched > 1400 BRUVS sets at 5-6x speed. I excluded reefs from this chapter that were from countries or territories with a PDE > 10 but were not rewatched. During this process we also identified BRUVS sets that did not meet the Global FinPrint standards (e.g., did not have 60 minutes of video footage after taking mark zero into account; bait did not remain in the cage for the full 60 minutes; BRUVS flipped throughout deployment changing the field of view, etc.) and removed them from the dataset. All incorrect MaxN, species misidentifications, and missed observations were corrected in the Global FinPrint Annotator. Higher level classifications were made whenever we were unable to identify an observation to the species level (e.g., to genus, family, order, or superorder). During the QAQC procedure, I also identified a consistent error within the Global FinPrint Annotator creating false depths of 7.77 m. I filtered for these depths and updated each BRUVS set to the correct depth from original data sheets and/or data books. A significant number of BRUVS were missing covariate data. I was able to fill in data gaps for water temperature (see above) and market gravity (Cinner & Maire

2018, Cinner *et al.* 2018). However, annotating missing habitat data was not feasible, therefore I used mean coral reef level data rather than set level data for analyses, ignoring the missing covariate data. For reefs where BRUVS sets occurred both inside and outside protected areas (5/71 reefs), I considered the entire reef a reserve, a marine protected area, or not protected based on where most BRUVS were set. For example, 7/42 BRUVS were set inside a reserve in Ocho Rios, Jamaica and 35/42 BRUVS were set outside of the reserve, so I categorized the whole reef as not protected.

Statistical analyses

MaxN was pooled for all rays and for all sharks on each BRUVS set prior to calculating the mean shark and ray MaxNs per coral reef. Blacknose sharks (*Carcharhinus acronotus*), sharpnose sharks (*Rhizoprionodon* spp.), bonnethead sharks (*Sphyrna tiburo*), and dogfishes (*Mustelus* spp.) were removed from the pooled shark MaxN because they are unlikely ray predators. The number of ray species observed was tallied per country or territory. Seaflower Biosphere Reserve, Colombia and Pedro Bank, Jamaica were separated from the main country and territory data for nominal species richness and mean ray MaxN plots, following MacNeil *et al.* 2020. Puerto Rico was separated from mainland United States of America for all analyses. I used generalized linear mixed models (GLMMs) to test what factors predict ray MaxN (all species pooled) and southern stingray MaxN at the coral reef level (e.g., Osgood *et al.* 2019, Sherman *et al.*

2020). All coral reefs in Brazil were removed for the southern stingray GLMM because the species there was recently redescribed as Lutz's stingray (Petean *et al.* 2020). Multiple environmental and anthropogenic predictor variables were included in each model as fixed effects, and country was included as a random effect (Table 2). To evaluate the distribution of the scaled residuals, I used the R package “*DHARMA*” (Hartig 2022) and found that the Tweedie distribution best described the data. The Tweedie distribution is useful in situations where there are many zeros mixed with some positive values and uses a scale (ϕ) and power parameter (μ^p) to model the variance (Tweedie 1984). Tweedie models were run using the R package “*glmmTMB*” (Brooks *et al.* 2017). When checking for multicollinearity using the R package “*performance*” (Lüdecke *et al.* 2021), I found that ray fishing covaried with protection status with variance inflation factors > 1 (Stine 1995, Lüdecke *et al.* 2021). Therefore, I removed the variable “ray fishing” from all analyses. I used model averaging and an information theoretic approach (Akaike's Information Criterion, “AIC”, Akaike 1998) for parameter selection using the R package “*MuMIn*” (Bartoń 2020). All parameters in supported models (i.e., $\Delta\text{AIC} \leq 2$) were retained for model averaging to obtain estimates (Bartoń 2020). The most parsimonious models were selected based on the lowest AIC value and largest model weight. To interpret the possible significance of predictor variables from the most parsimonious models, I used Wald χ^2 statistics (Brooks *et al.* 2022). To calculate the proportion of variance explained (coefficient of determination, R^2), I used the R package “*performance*” (Nakagawa *et al.* 2017, Lüdecke *et al.* 2021). This library uses Nakagawa's

method to calculate both the marginal R^2 (variance explained by the fixed effects) and the conditional R^2 (variance explained by the fixed and random effects together).

Predictor variable	Levels	Explanations
Reef protection status ^{C, F}	reserve MPA none	strict no-take area general use zone with some restrictions not a MPA or reserve
Ray fishing ^{C, F}	open restricted closed	ray fishing allowed restriction(s) in place (species, area, gear, time, etc.) shark & ray sanctuary or ban on ray fishing
Rays landed ^{C, F}	yes no	evidence of rays landed in fisheries (target or incidental) no evidence of rays landed
Bottom gear ^{C, F}	yes no	drumlines, longlines, seines, gillnets, and/or trawls used none of the above gear used
Market gravity ^{N, F}	NA	measure of human pressure: function of travel time to nearest market & human population size (Cinner <i>et al.</i> 2018)
Shark abundance ^{N, F}	NA	pooled shark MaxN excluding small sharks
Water temperature ^{N, F}	NA	temperature measured at surface (°C)
Water depth ^{N, F}	NA	depth of BRUVS set in meters

Visibility ^{N, F}	NA	estimated using Benthobox in meters
Geomorphology ^{C, F}	Continental	reef connected to continental land via slope or shallow water
	Low island	reef connected to island formed by sedimentation or coral build-up
	High island	reef connected to island formed by volcanic activity
Habitat complexity ^{N, F}	NA	mean reef relief per baited remote underwater video station (Polunin & Roberts 1993, Wilson <i>et al.</i> 2007), estimated in Benthobox
Country or territory ^{C, R}	NA	Sampling locations

^C categorical; ^N numerical

^F fixed effect; ^R random effect

Table 2: Summary of predictor variables considered for each generalized linear mixed effects model. Few country or coral reef level landings data were available, so “Rays landed” became a categorical variable at the country or territory level. All other variables were at the coral reef level. Ray fishing was ultimately removed from all models because it covaried with reef protection status. “MPA” = marine protected area. Benthobox was managed at the Australian Institute of Marine Science (<https://benthobox.com/>).

RESULTS

Country and territory level ray nominal species richness ranged from 0 (Bermuda) to 5 (Jamaica) (Figure 1). Southern stingrays were detected in every country except Bermuda and Brazil, which are outside their normal distribution (Figure 1). Whitespotted eagle rays (*Aetobatus narinari*) were also detected in most countries and territories (Figure1). There was one manta ray sighting at Pedro Bank, Jamaica that was either *Mobula birostris* or *Mobula cf. birostris* (Figure 1). Atlantic chupares (*Styracura schmardae*) and yellow round rays were

detected in multiple countries, but their distributions may be patchy and are poorly known (e.g., Spieler *et al.* 2013, O'Shea *et al.* 2017, Bruns & Henderson 2020, Sales *et al.* 2020). Other species detected in our surveys may be rare visitors to coral reefs, may not be interested in the bait, may have population levels too low for detection within our sampling parameters, or they have restricted ranges (Figure 1, Table 3). Mean ray MaxN for the entire Western Atlantic dataset was 0.21 (± 0.47 SD), and mean shark MaxN was 0.49 (± 0.92 SD). Southern stingrays had the highest mean MaxN (0.13 ± 0.37 SD), while the manta ray had the lowest mean MaxN (0.0004 ± 0.0188 SD) (Table 3). Country and territory level mean ray MaxN was low and similar across locations (Figure 2).

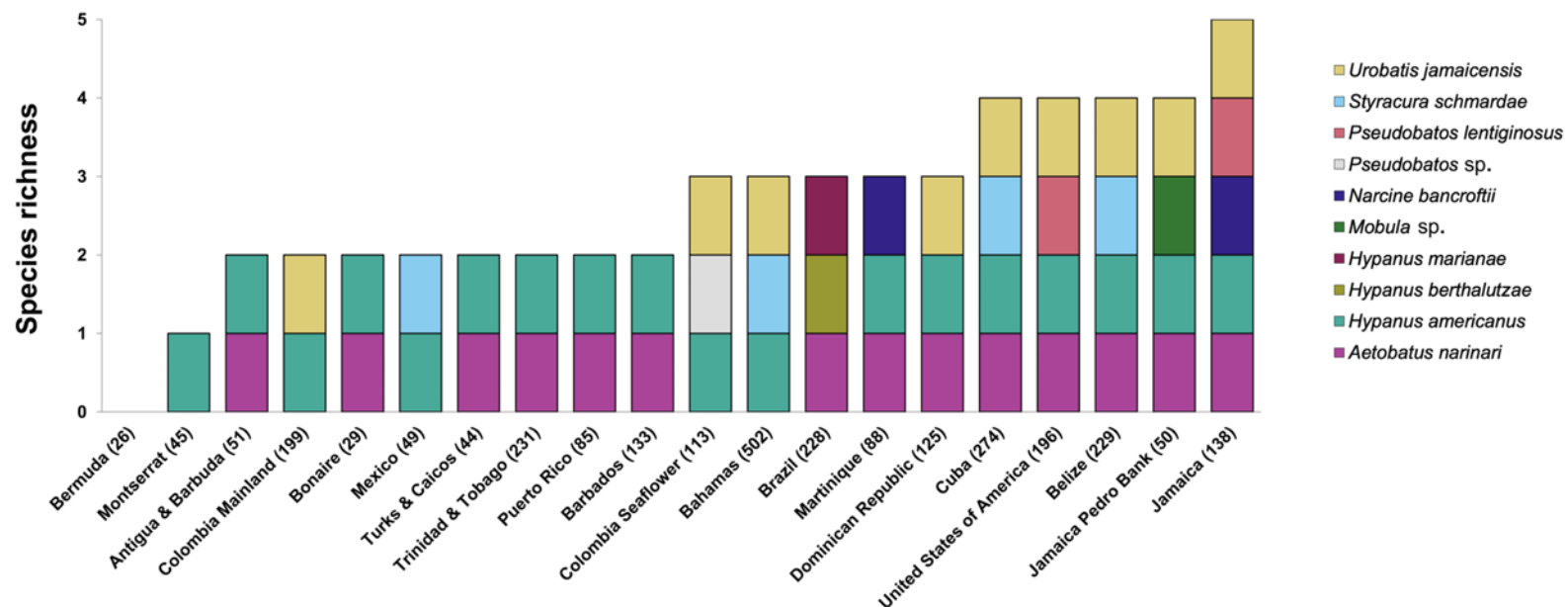


Figure 1: Ranked (lowest to highest from left to right) country and territory level ray nominal species richness. The number of baited remote underwater video stations set in each location is in parentheses.

Ray common name	Ray species	Mean MaxN $\pm$ SD
Whitespotted eagle ray	<i>Aetobatus narinari</i>	0.02 $\pm$ 0.15
Southern stingray	<i>Hypanus americanus</i>	0.13 $\pm$ 0.37
Lutz's stingray	<i>Hypanus berthalutzae</i>	0.13 $\pm$ 0.36 *
Large-eye stingray	<i>Hypanus marianae</i>	0.004 $\pm$ 0.066 *
Oceanic or Caribbean manta	<i>Mobula</i> sp.	0.0004 $\pm$ 0.0188
Caribbean numbfish	<i>Narcine bancroftii</i>	0.0007 $\pm$ 0.0266
Freckled guitarfish	<i>Pseudobatos lentiginosus</i>	0.0007 $\pm$ 0.0266
Freckled or chola guitarfish	<i>Pseudobatos</i> sp.	0.0007 $\pm$ 0.0266
Atlantic chupare	<i>Styracura schmardae</i>	0.004 $\pm$ 0.059
Yellow round ray	<i>Urobatis jamaicensis</i>	0.04 $\pm$ 0.20

Table 3: Ray species level mean MaxN $\pm$ standard deviation (SD) calculated from the entire dataset (N = 2835 BRUVS). * The large-eye stingray and Lutz's stingray are endemic to Brazil, therefore their mean MaxN $\pm$ SD was calculated from Brazil BRUVS (N = 228).

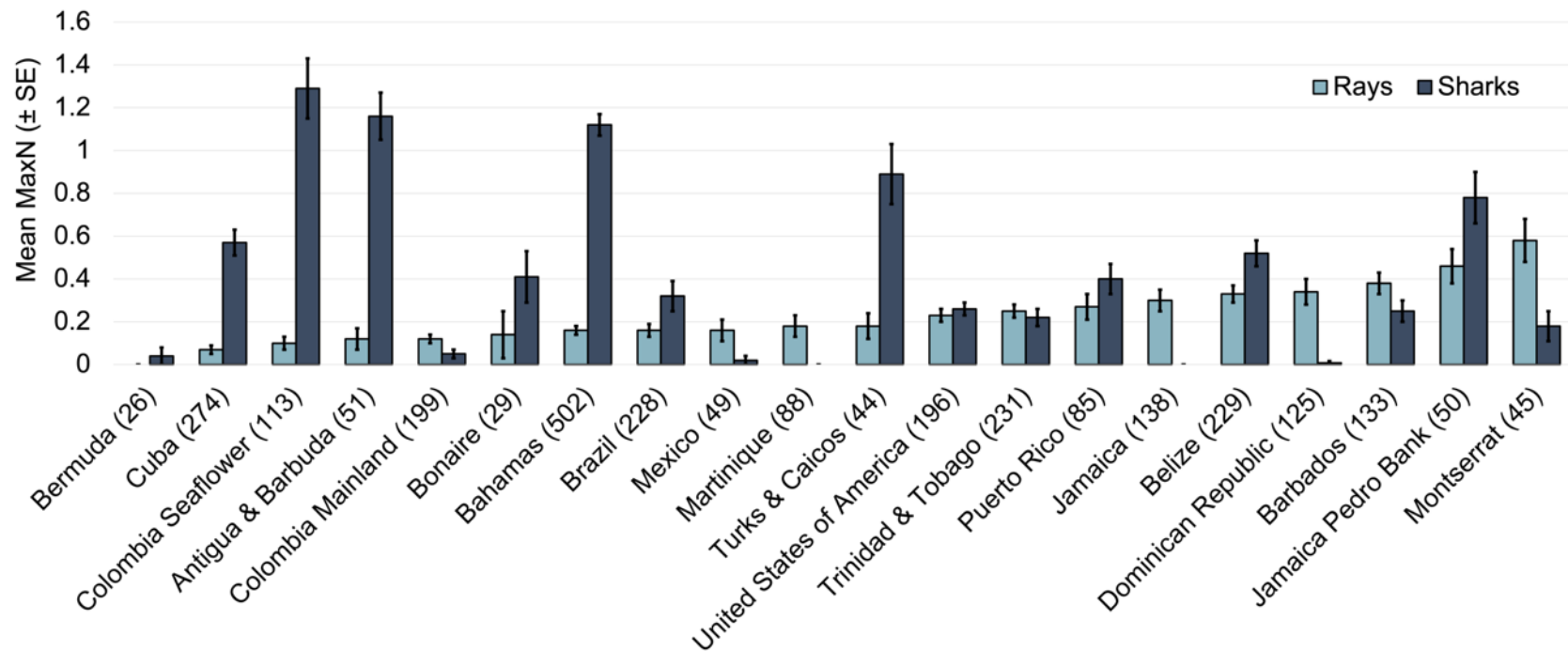


Figure 2: Ranked (lowest to highest from left to right) country and territory level mean ray MaxN ($\pm$ SE) and unranked mean shark MaxN ($\pm$ SE). The number of baited remote underwater video stations set in each location is in parentheses. Mean shark MaxN does not include blacknose sharks (*Carcharhinus acronotus*), sharpnose sharks (*Rhizoprionodon* spp.), bonnethead sharks (*Sphyrna tiburo*), and dogfishes (*Mustelus* spp.) because they are unlikely ray predators.

Model averaging revealed little evidence that any variable predicted overall ray MaxN ($p > 0.1$, Table 4, S1 Table). However, the most parsimonious model showed a negative association between ray MaxN and reef relief ($p = 0.06$, Table 5, Figure 3). The estimated slope coefficient implied a 48% decrease in ray MaxN from low (0.2) to high mean reef relief (3.4); however, this was highly uncertain (Figure 3). Alone, reef relief explained 7% of the variance, while reef relief and the random country and territory effect explained 34% of the variance.

For the most parsimonious model of southern stingray MaxN (Figure 4), total variance explained with fixed and random effects was 73%. Of the fixed effects, reef relief explained the highest variance (10%), followed by geomorphology (6%), shark MaxN (5%), and water temperature (2%). There was a small negative change in R^2 for bottom gear (-0.04); however, R^2 for bottom gear when modelled alone with the random country and territory effect was 3%. This implies that R^2 was so small it was close to zero and that bottom gear explained only a small amount of the variance. The coefficients of the most parsimonious southern stingray model implied a 75% decrease in southern stingray MaxN from low (0) to high shark MaxN (2.2); 70% decrease in southern stingray MaxN between low (0.2) and high mean relief (3.4); 35% decrease in southern stingray MaxN in places that used bottom gear compared to places that did not; and a predicted 85% increase in southern stingray MaxN from low (25°C) to high water temperatures (32°C) (Figure 5). There was a predicted 162% increase in southern stingray MaxN from continental sites to high islands; 184% increase in southern stingray MaxN from continental sites to low islands; and an

8% predicted increase in southern stingray MaxN from high islands to low islands (Figure 5). Using Muff *et al.* (2022)'s language to frame p-values in terms of strength of evidence against the Null hypothesis of no effect, in the most parsimonious model there was very strong evidence that shark MaxN predicted southern stingray MaxN, strong evidence that reef relief predicted southern stingray MaxN, moderate evidence that geomorphology and use of bottom gear predicted southern stingray MaxN, and little or no evidence that water temperature predicted southern stingray MaxN (Table 5). For the model averaged coefficients, there was strong evidence for shark MaxN and low islands compared to continents, moderate evidence for reef relief and high islands compared to continents, and less evidence for the other coefficients (Table 4, S1 Table).

Generalized linear mixed model	Estimate	Standard error	z value	Pr (> z)
Response = mean log coral reef level ray MaxN				
intercept	- 2.18	1.69	1.28	0.20
reef relief	-0.18	0.13	1.43	0.15
temperature	0.04	0.06	0.60	0.55
depth	-8.19 x 10 ⁻³	0.02	0.50	0.62
market gravity	5.93 x 10 ⁻⁶	1.55 x 10 ⁻⁵	0.38	0.71
high island	0.04	0.15	0.29	0.78
low island	-0.01	0.11	0.10	0.92
shark MaxN	-0.02	0.08	0.25	0.81
bottom gear - yes	-6.29 x 10 ⁻³	0.06	0.11	0.91
rays landed - yes	2.90 x 10 ⁻³	0.07	0.04	0.97
visibility	1.22 x 10 ⁻⁴	9.02 x 10 ⁻³	0.01	0.99
Response = mean log coral reef level southern stingray MaxN				
intercept	-3.18	1.63	1.92	0.05
bottom gear - yes	-0.31	0.25	1.24	0.21
high island	1.08	0.46	2.30	0.02
low island	1.13	0.39	2.84	4.47 x 10⁻³
reef relief	-0.32	0.13	2.51	0.01
shark MaxN	-0.58	0.18	3.08	2.05 x 10⁻³
temperature	0.04	0.06	0.71	0.48
market gravity	1.13 x 10 ⁻⁵	1.71 x 10 ⁻⁵	0.65	0.51
depth	-0.01	0.02	0.70	0.48
visibility	5.43 x 10 ⁻⁴	0.01	0.04	0.97
rays landed – yes	-8.18 x 10 ⁻⁴	0.09	9.00 x 10 ⁻³	0.99

Table 4: Full model averaged fixed coefficient estimates from the supported models ($\Delta AIC \leq 2$) describing mean coral reef level ray MaxN (all species pooled) and southern stingray (*Hypanus americanus*) MaxN. Bolded text represents a predictor variable with a p-value < 0.05.

Model	χ^2	df	Pr ($>\chi^2$)
Response = mean coral reef level ray MaxN			
reef relief	3.58	1	0.06
Response = mean coral reef level southern stingray MaxN			
geomorphology	7.54	2	0.02
shark MaxN	13.27	1	2.70×10^{-4}
temperature	2.63	1	0.11
reef relief	10.00	1	1.57×10^{-3}
bottom gear	4.89	1	0.03

Table 5: Analysis of deviance table (Wald χ^2) for the most parsimonious generalized linear mixed model ($\Delta\text{AIC} = 0$) for mean coral reef level ray MaxN (all species pooled) and southern stingray MaxN (*Hypanus americanus*).

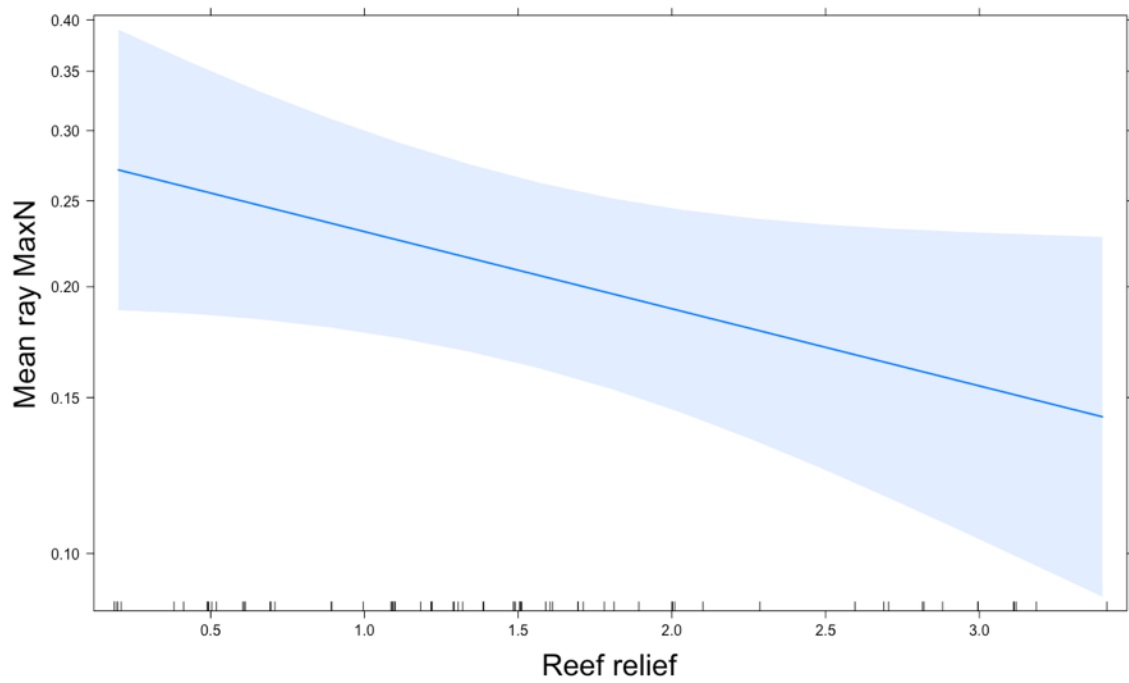


Figure 3: Predicted relationship between reef relief and coral reef level mean ray MaxN (all species pooled) with shaded 95% confidence intervals from the most parsimonious generalized linear mixed model (Δ AIC = 0).

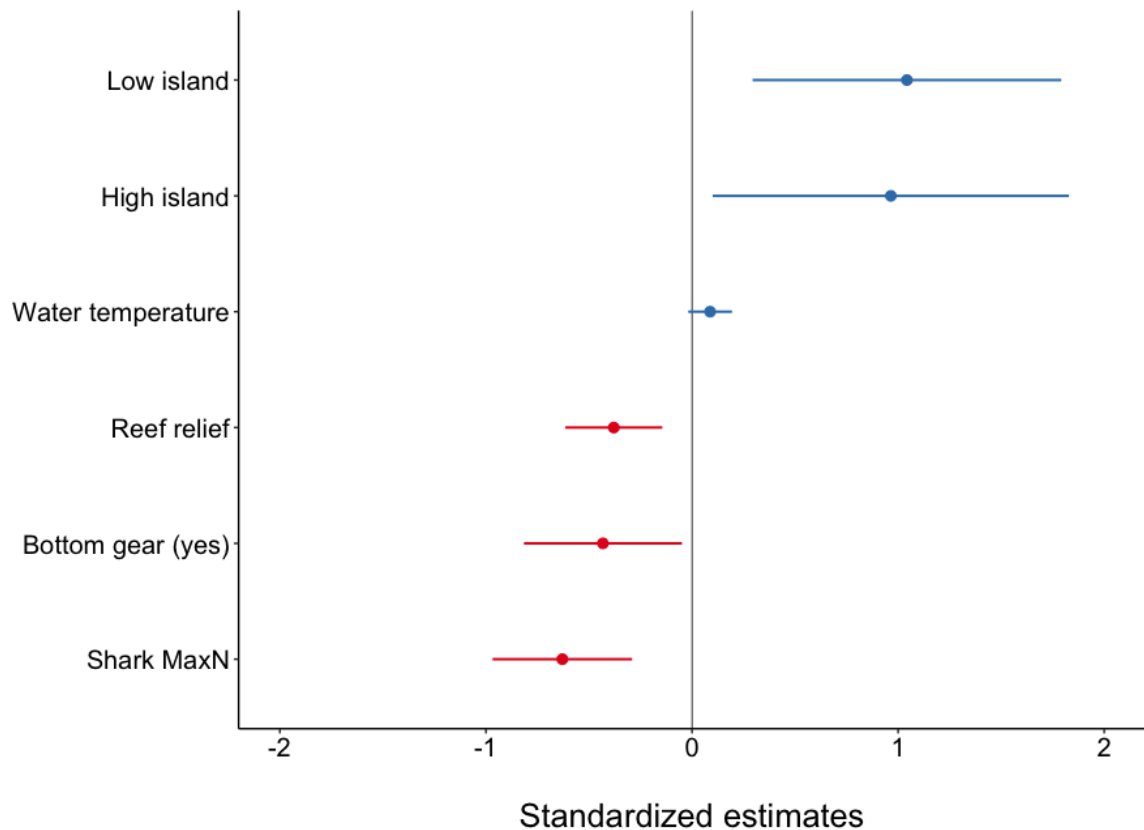


Figure 4: Standardized estimates of the coefficients (fixed effects) with 95% confidence intervals from the most parsimonious model of southern stingray MaxN ($\Delta\text{AIC} = 0$). Plotted on a log-odds scale because Tweedie uses a log link function. Standardized estimates ~ 0 have no effect, > 0 have a positive effect, and < 0 have a negative effect. The effects of low island and high island are relative to the continental reference level.

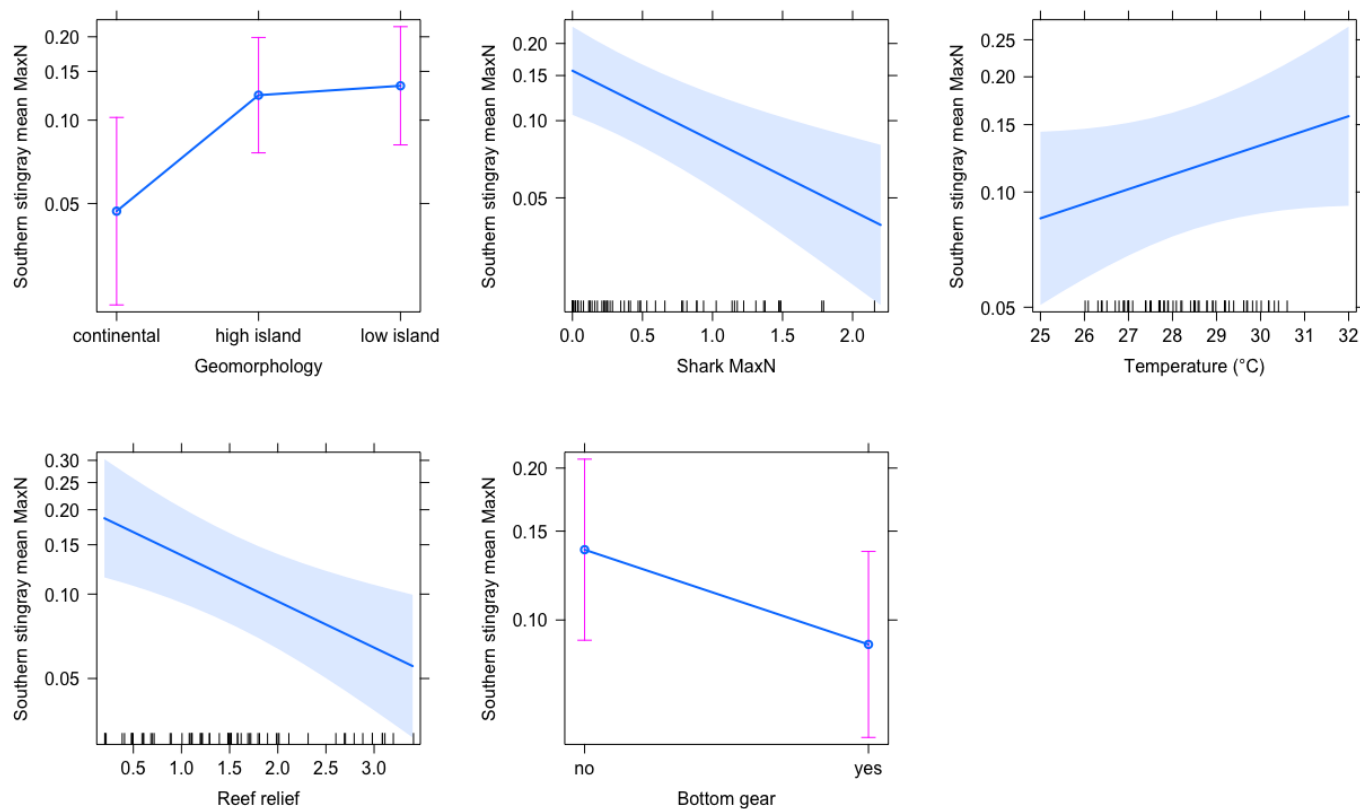


Figure 5: Predicted relationship between covariates and coral reef level mean southern stingray MaxN (*Hypanus americanus*) from the most parsimonious generalized linear mixed model ($\Delta AIC = 0$). Numerical variables show shaded 95% confidence intervals (shark MaxN, temperature, reef relief) and categorical variables show 95% confidence interval bars (geomorphology and bottom gear).

DISCUSSION

At least one ray was sighted on 97% of coral reefs sampled in the tropical Western Atlantic Ocean (69/71). However, MaxN values were relatively low and pooling species decreases our ability to understand local and species-specific responses to various factors like fishing. Low MaxN may be due to limited use of coral reefs by rays, a lack of interest in the bait (e.g., Bruns & Henderson 2020), structural complexity decreasing detection probability, low abundance due to overexploitation or some other cause, cryptic behaviour, restricted ranges, or most likely a combination of multiple factors. Several species are probably less likely to be observed on coral reef BRUVS because they are semi-pelagic (e.g., whitespotted eagle rays) or pelagic (e.g., devil and manta rays). Other species may prefer muddy and other soft bottom habitats. However, yellow round rays use hard bottom frequently and hide in the sand (Fahy 2004) or within coral reef structure (personal observation). Because southern stingrays were common on BRUVS, they may use coral reef habitats more than other ray species and be more detectable due to their size and behaviour. Lutz's stingrays were also common in Brazil where they are endemic. Although overall variance explained in the southern stingray model was high, it was mainly due to the random country and territory effect, suggesting that there are differences between countries that were unaccounted for.

Consistent with recent findings of a BRUVS study comparing southern stingray sightings in fished and protected areas (Bond *et al.* 2019), I found that

shark abundance predicted southern stingray sightings and explained 5% of model variance. Evidence that sharks influence the abundance and behaviour of mesopredators is widespread but is highly context dependent, especially on coral reefs (Heithaus *et al.* 2008, Heithaus *et al.* 2022). For example, in some places mesopredator competition and habitat heterogeneity are more important than predator abundance (Desbiens *et al.* 2021, Lester *et al.* 2021). Prey size and body condition can also influence responses to predation risk (e.g., Heithaus *et al.* 2007, Heithaus *et al.* 2022). Stingray abundance and behaviour are likely influenced by both direct predation by sharks and predation risk, although predation risk is often hypothesized as an important factor influencing stingray sightings on BRUVS in reef-associated habitats (Bond *et al.* 2019, Sherman *et al.* 2020). Resolving the mechanisms behind these findings requires a multimethod approach and hypothesis driven research (Sherman *et al.* 2020, Flowers *et al.* 2021). One site that did not follow the pattern of fewer ray sightings in places with high shark abundance was Pedro Bank in Jamaica, where both shark and ray MaxN were relatively high (0.78 ± 0.12 SE and 0.46 ± 0.08 SE respectively). High ray MaxN at this coral reef was driven primarily by yellow round rays (mean MaxN = 0.32 ± 0.07 SE). Additionally, mean reef relief was the highest in the region (3.1 ± 0.12 SE), which suggests yellow round rays may benefit from structurally complex habitat, likely via refuge from predators (Fahy 2004). This example highlights how species-specific responses and habitat heterogeneity contribute to the context dependent nature of predation risk effects. Research

should focus on studying species-specific ray abundance and behaviour at sites like Pedro Bank to compare across shark depleted sites.

Reef relief was the most important fixed effect in the southern stingray model (10% variance explained), while a weak effect of reef relief was the only fixed effect included in the AIC best model for all rays combined. Reef sharks are typically associated with high reef complexity (Rizzari *et al.* 2014, Desbiens *et al.* 2021), so it is possible that the negative relationship is due to divergent habitat preferences rather than species interactions. However, reef relief and shark MaxN were not collinear, suggesting this is not solely the case. Rays may prefer soft bottom habitats for refuging and higher prey abundances (e.g., Semeniuk & Dill 2006, Tilley 2011, Vaudo & Heithaus 2013, Costa *et al.* 2015, Meese & Lowe 2019, Martins *et al.* 2020, Elston *et al.* 2021, Flowers *et al.* 2021). The negative relationship between both ray and southern stingray sightings with reef relief could also be influenced by the survey technique. For example, we do not know if we are less likely to detect rays in highly complex habitats (e.g., via obscured field of view [see Chapter 3] or cryptic behaviour) or if rays simply prefer soft bottom habitat, although it may be a combination of both. In an Indo-Pacific BRUVS study, there were species-specific ray responses to reef relief suggesting that it is possible to detect certain species in highly complex areas (Sherman *et al.* 2020), like my findings for yellow round rays at Pedro Bank, Jamaica. Further research is required to investigate the possibility that certain species are less detectable in complex habitats.

The hypothesis that fish abundance, biomass, and diversity are higher around high islands than around low islands has typically been associated with the idea that these regions are highly productive with a wide range of available habitats (Dalzell *et al.* 1996, Donaldson 2002). However, the predictions of this hypothesis have rarely been tested for sharks and rays, and reef sharks tend to be associated more with low islands, atolls, and banks (McKibben & Nelson 1986, Dalzell *et al.* 1996, Wetherbee *et al.* 1997, Friedlander & DeMartini 2002). My results suggest that southern stingrays were more likely to be sighted at an island regardless of whether it is high or low. This is likely an artefact of the relative amount of available habitat at these locations and the limited number of continental sites in my study (10/71) (Wetherbee *et al.* 1997, Donaldson 2002). Indeed, geomorphology only accounted for 6% of model variance. My results could also suggest that rays are more abundant further away from coastal continental shelves where anthropogenic impacts may be higher. However, there was no support for market gravity in the AIC best southern stingray sightings model, which I would have expected if human pressures were important predictors of southern stingray sightings. Many reef fish predators, including sharks, are negatively impacted by market gravity (Valdivia *et al.* 2017, Cinner *et al.* 2018, MacNeil *et al.* 2020), but moray eels benefit from being close to high human population centers (Clementi *et al.* 2021b). Market gravity was, however, included in multiple supported models for all rays combined and southern stingrays (S1 Table). Since the coefficient estimates were positive, rays may respond to market gravity in the same way as moray eels in the region. This

hypothesis needs further testing; however, one reason for this could be due to predator depletion near human population centers (Clementi *et al.* 2021b).

Despite the potential positive association with market gravity, rays are exploited in the greater Caribbean (e.g., Morgan *et al.* 2010, Cuevas-Zimbrón *et al.* 2011, Pérez-Jiménez & Mendez-Loeza 2015, da Silva Rodrigues Filho 2020, Flowers *et al.* 2021, Puentes *et al.* 2022, Talwar *et al.* 2022). Benthic rays are particularly susceptible to capture by bottom fishing gear (e.g., longlines, drumlines, seines, gillnets, and trawls; Stevens *et al.* 2000, Last *et al.* 2016) and there was a negative relationship in the AIC best model between southern stingray sightings and places that used at least one type of bottom fishing gear, which explained 3% of model variance. Reef protection status was not a good predictor of southern stingray sightings, which could be due to the varying levels of compliance and enforcement within marine protected areas (MPAs) and reserves, especially in nations where resources for management are sparse (e.g., Mascia 1999, Appeldoorn & Lindeman 2003, Camargo *et al.* 2008, Dalton *et al.* 2015, Cáceres *et al.* 2022, Talwar *et al.* 2022). However, it is unlikely that rays were considered in the design and implementation of any of the protected areas considered in this study. Patterns of ray sightings inside and outside protected areas are context dependent (White *et al.* 2013, Clementi 2017, Bond *et al.* 2019, Osgood *et al.* 2019, Cortelezzi *et al.* 2022), although many ray species are philopatric and would therefore benefit from carefully designed protected areas (Flowers *et al.* 2016). Regardless, my findings stress the value of bottom gear restrictions for managing southern stingray populations because

sightings were higher in places that did not use any type of bottom gear (drumlines, gillnets, longlines, seines, or trawls).

This study has several important limitations. First, this was not a study designed specifically for rays. It was designed to assess shark abundance and species richness on forereefs, which may not be key ray habitat (Chapman *et al.* 2022). Studies across soft bottom habitats like seagrass beds, sandflats, lagoons, mangroves, and deep muddy banks are needed to more thoroughly sample rays in the tropical Western Atlantic Ocean. Second, the territory with the highest ray MaxN was Montserrat in the British West Indies. One possible reason for this is the use of a different bait type (gar). Interest in bait can depend on type of bait used and species-specific preferences (e.g., Wraith *et al.* 2013, Walsh *et al.* 2016). Another site that used a different bait (barracuda) was South Caicos in the Turks and Caicos Islands. Due to the low sightings of rays on BRUVS compared to their encounter rate on snorkels and dives, Bruns & Henderson (2020) hypothesized that rays may not be attracted to barracuda. However, ray MaxN in South Caicos was comparable to ray MaxN in The Bahamas, which is also part of the Lucayan archipelago. All other sites in the Global FinPrint project consistently used similar oily bait fishes or a mix with reef fishes. Finally, the full geographic distributions of some rays in this study remain poorly known and may not span the entire tropical Western Atlantic Ocean (e.g., Spieler *et al.* 2013, Bruns & Henderson 2020, Sales *et al.* 2020, Jorgensen *et al.* 2022). This makes interpreting a species' absence from a site challenging: was it not detected because it is rare, is locally extinct, or because it was never there to begin with?

In my study, this was likely only an issue for the pooled data because southern stingrays were detected everywhere they were expected, and I was able to remove data from Brazil since the species previously thought to be *Hypanus americanus* there was recently described as *H. berthalutzae* (Petean *et al.* 2020).

My study supports the hypothesis that sharks affect southern stingray sightings at large spatial scales; however, other predictor variables explained a higher percent of model variance. Rays may simply be selecting for soft bottom habitats, and/or they may be less detectable on BRUVS in places with complex structure. Multiple survey techniques are needed to resolve this possibility. Like reef sharks, southern stingrays were commonly sighted around low islands, but also around high islands. Finally, my results support improved management via bottom gear restrictions. Local scale fisheries landings data could help us understand the possible impacts of ray fishing at the coral reef level. I was unable to model species-specific sightings except for southern stingrays, which are considered Near Threatened by the International Union for the Conservation of Nature (IUCN) red list of threatened species (Carlson *et al.* 2020). Almost every other species detected on BRUVS are threatened with extinction (apart from the yellow round ray); however, they were too rare to model their sightings individually. Future studies should prioritize studying what factors affect ray abundance in their primary habitats using additional survey techniques.

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SUPPLEMENTARY TABLE FOR CHAPTER II

Generalized linear mixed model	df	Δ AIC	ω
Response = mean coral reef level ray MaxN			
relief + random (country)	5	0.00	0.08
relief + temperature + random (country)	6	0.01	0.08
depth + relief + random (country)	6	0.58	0.06
gravity + relief + temperature + random (country)	7	1.10	0.05
geomorphology + relief + temperature + random (country)	8	1.12	0.05
relief + shark MaxN + random (country)	6	1.12	0.05
depth + random (country)	5	1.17	0.05
relief + shark MaxN + temperature + random (country)	7	1.17	0.05
depth + relief + temperature + random (country)	7	1.22	0.04
depth + gravity + random (country)	6	1.31	0.04
gravity + relief + random (country)	6	1.33	0.04
depth + gravity + relief + random (country)	7	1.47	0.04
NULL	4	1.49	0.04
geomorphology + relief + random (country)	7	1.55	0.04
geomorphology + gravity + relief + temperature + random	9	1.74	0.03

(country)

bottom gear + relief + random (country)	6	1.75	0.03
depth + relief + shark MaxN + random (country)	7	1.76	0.03
depth + geomorphology + relief + random (country)	8	1.78	0.03
bottom gear + relief + temperature + random (country)	7	1.81	0.03
rays landed + relief + random (country)	6	1.94	0.03
depth + gravity + relief + temperature + random (country)	8	1.96	0.03
relief + visibility + random (country)	6	1.99	0.03
rays landed + relief + temperature + random (country)	7	2.00	0.03

Response = mean coral reef level southern stingray MaxN

bottom gear + geomorphology + relief + shark MaxN + temperature + random (country)	10	0.00	0.13
bottom gear + geomorphology + gravity + relief + shark MaxN + temperature + random (country)	11	0.58	0.10
bottom gear + geomorphology + relief + shark MaxN + random (country)	9	0.58	0.10
depth + geomorphology + gravity + relief + shark MaxN + random (country)	10	0.72	0.09
bottom gear + depth + geomorphology + gravity + relief + shark MaxN + random (country)	11	0.87	0.09

bottom gear + depth + geomorphology + relief + shark MaxN + random (country)	10	0.94	0.08
bottom gear + geomorphology + gravity + relief + shark MaxN + random (country)	10	1.36	0.07
depth + geomorphology + relief + shark MaxN + random (country)	9	1.40	0.07
bottom gear + depth + geomorphology + relief + shark MaxN + temperature + random (country)	11	1.46	0.06
bottom gear + depth + geomorphology + gravity + relief + shark MaxN + temperature + random (country)	12	1.52	0.06
depth + geomorphology + gravity + relief + shark MaxN + temperature + random (country)	11	1.78	0.05
bottom gear + geomorphology + relief + shark MaxN + temperature + visibility + random (country)	11	1.97	0.05
bottom gear + geomorphology + rays landed + relief + shark MaxN + temperature + random (country)	11	2.00	0.05

Supplementary Table 1: Models used to describe mean coral reef level ray MaxN (pooled) and southern stingray MaxN (*Hypanus americanus*) where model selection was based on delta Akaike's Information Criterion (ΔAIC) values and Akaike's weights (ω). Only supported models ($\Delta AIC \leq 2$) are shown here.

CHAPTER III

A SPATIOTEMPORAL EVALUATION OF SOUTHERN STINGRAY SIGHTINGS, BEHAVIOUR, AND HABITAT USE ACROSS A CARIBBEAN REEF SHARK DECLINE

ABSTRACT

As shark declines occur around the world, studying the potential for cascading effects remains a priority. Spatial comparisons of stingray sightings across gradients of reef shark abundance suggest that predation risk alters stingray sightings, foraging behaviour, and habitat use. In Belize, the risk of predation from Caribbean reef sharks (*Carcharhinus perezii*) is the hypothesized driver of southern stingray (*Hypanus americanus*) habitat selection. To investigate the role reef-associated sharks (*C. perezii* and *Ginglymostoma cirratum*), whitespotted eagle rays (*Aetobatus narinari*), environmental factors, and habitat complexity play in predicting southern stingray sightings and long-term behaviour, we took advantage of a ten year standardized baited remote underwater video station (BRUVS) survey at Glover's Reef Marine Reserve (GRMR) in Belize that has documented declining Caribbean reef shark abundance. To understand elasmobranch habitat use at GRMR, we estimated core and general use areas for southern stingrays, Caribbean reef sharks, and lemon sharks (*Negaprion brevirostris*) with passive acoustic telemetry and dynamic Brownian bridge movement models. There was little support for sharks or a potential competitor

(whitespotted eagle rays) as predictors of southern stingray sightings or behaviour on BRUVS (time spent in field of view of the camera), which were stable between 2009 – 2019 in forereef habitat. Intra- and interspecific interactions on BRUVS were rare and southern stingray interest in the bait was not correlated to Caribbean reef shark abundance. Instead, we found that reef structural complexity predicted southern stingray sightings and behaviour on BRUVS. Southern stingrays are likely selecting for soft bottom habitat, but we cannot rule out that highly complex habitats may diminish our ability to detect this species when present, especially on BRUVS alone. All elasmobranchs commonly use the shallow lagoon at GRMR, with mean core use areas of 0.14 – 0.57 km². Caribbean reef sharks also use forereef habitat around the coral reef atoll. The use of shallow sandflats by lemon sharks suggests this habitat was not a refuge from potential predators for southern stingrays from 2017 to 2022 and that southern stingrays may be selecting this habitat for other reasons. Our results add to a growing body of literature that suggests declining shark abundance may not always lead to mesopredator release and that risk-induced prey trait responses are highly context dependent. We highlight the need to investigate other potential drivers of southern stingray habitat use, including but not limited to prey availability, interspecific competition, and dynamic predation risk across the seascape.

INTRODUCTION

Mounting evidence of shark declines demands our consideration of the potential ecosystem ramifications. A possible consequence of top predator declines is ‘mesopredator release’, where mid-level predators increase (in abundance, biomass, or density), change their behaviour, and/or change their distribution following apex predator declines (Soulé *et al.* 1988, Prugh *et al.* 2009, Ritchie & Johnson 2009, Brashares *et al.* 2010). Shark declines have been hypothesized to lead to mesopredator release (e.g., Ward & Myers 2005, Myers *et al.* 2007, DeMartini *et al.* 2008, Heithaus *et al.* 2008, Ferretti *et al.* 2010, Ruppert *et al.* 2013, Barley *et al.* 2017, Bond *et al.* 2019, Sherman *et al.* 2020), although the mechanisms by which it occurs remain largely unknown and, in some cases, contested (Grubbs *et al.* 2016, Roff *et al.* 2016, Flowers *et al.* 2021). Disentangling predation risk effects from direct consumption effects in the wild can be challenging because they are occurring at the same time (Abrams 1992, Werner & Peacor 2003, Peers *et al.* 2018, Mitchell & Harborne 2020). Detecting changes in population size could take years across multiple generations, whereas it may be possible to rapidly identify changes in behaviour because prey can respond quickly to temporal changes in predation risk (Lima & Bednekoff 1999, Werner & Peacor 2003). Indeed, examples of anti-predator behaviour (hereafter ‘risk-induced trait responses’ *sec.* Peacor *et al.* 2020) are well established (Lima & Dill 1990, Brown & Kotler 2004), yet evidence for how, if, and when mesopredator responses lead to fitness and population level

changes is limited (Peers *et al.* 2018, Mitchell & Harborne 2020, Sheriff *et al.* 2020, Peacor *et al.* 2022). Regardless, predation risk can impact prey mortality and trophic dynamics in ways that may be at least equal to direct consumptive effects (Schmitz *et al.* 1997, Schmitz 1998, Brown *et al.* 1999, Preisser *et al.* 2005, Creel & Christianson 2008).

Our understanding of the effects of predation risk in coral reef systems relies primarily on studies using predator models (e.g., Rizzari *et al.* 2014, Catano *et al.* 2016, Lester *et al.* 2020) and studies comparing prey trait responses across spatial and/or temporal gradients of predator abundance (e.g., Madin *et al.* 2010, McCauley *et al.* 2012, Ory *et al.* 2014, Davis *et al.* 2017, Bond *et al.* 2019, Sherman *et al.* 2020). Predation risk effects are context dependent, often being influenced by habitat complexity, environmental conditions, and an organism's body size, physiological condition, and escape ability (e.g., Lima & Dill 1990, Heithaus *et al.* 2007, Heithaus *et al.* 2009, Leahy *et al.* 2011, Matassa & Trussell 2014, Catano *et al.* 2016, Phenix *et al.* 2019, Mitchell & Harborne 2020, Wirsing *et al.* 2021). In some cases, mesopredator abundance and behaviour is related to the presence of other similarly sized competitors or reef complexity rather than to sharks (Desbiens *et al.* 2021, Lester *et al.* 2021). The threat sensitivity hypothesis predicts that prey will trade-off certain activities for predator avoidance depending on a given threat level (Helfman 1989, Lima & Dill 1990). Risk induced trait responses are expected to be strongest when predation risk is acute and rare (Lima & Bednekoff 1999, Creel 2018). For example, mesopredators in Shark Bay, Western Australia respond both spatially and

temporally to risk induced by tiger sharks (*Galeocerdo cuvier*; Heithaus & Dill 2002, Heithaus 2005, Heithaus *et al.* 2007, Wirsing *et al.* 2007, Vaudo & Heithaus 2013). However, spatially concentrated and chronic predation risk can also lead to relatively strong prey trait responses (e.g., Bond *et al.* 2019). Unlike tiger sharks, reef-associated sharks (hereafter ‘reef sharks’) are mesopredators (Heupel *et al.* 2014, Frisch *et al.* 2016, Roff *et al.* 2016, Bond *et al.* 2018) and often exhibit residency (Chapman *et al.* 2015). In Belize, southern stingrays (*Hypanus americanus*) may respond spatially to the threat of Caribbean reef sharks (*Carcharhinus perezii*) by selecting shallow lagoon habitat instead of protected forereefs where Caribbean reef shark abundance is higher (Bond *et al.* 2019). Similarly, there are fewer small rays (*Neotrygon* and *Taeniura* spp.) observed in Southeast Asia and the Western Pacific Ocean where reef shark abundance is high (Sherman *et al.* 2020). Stingrays also spend less time interacting with bait on baited remote underwater video stations (BRUVS) in places with higher reef shark abundance (Bond *et al.* 2019, Sherman *et al.* 2020).

Spatial comparisons of predator and prey abundance are informative, but only offer a view of complex ecological dynamics at one point in time. Temporal datasets and large-scale unreplicated natural experiments afford the unique opportunity to study predator-prey interactions across perturbations (e.g., Barley & Meeuwig 2017, Hammerschlag *et al.* 2019). A recent Caribbean reef shark decline inside the Glover’s Reef Marine Reserve (GRMR) in Belize (Flowers *et al.* 2022), created a natural experiment for us to investigate the relationship

between reef shark abundance and southern stingray sightings, behaviour, and habitat use. We combined a ten year BRUVS dataset to quantify temporal changes in stingray sightings and behaviour with passive acoustic telemetry tracking of southern stingrays and two potential predators, Caribbean reef sharks and lemon sharks (*Negaprion brevirostris*). We included environmental factors (depth and water temperature), fine scale habitat complexity (coral reef relief), and whitespotted eagle ray sightings as other potential predictors of southern stingray sightings and behaviour on BRUVS. If predation risk by Caribbean reef sharks was the primary driver of southern stingray habitat use (i.e., between lagoon and forereef habitats; Bond *et al.* 2019), we would expect southern stingrays to respond to decreasing shark abundance by moving to deeper forereef habitat from the lagoon, which we hypothesize would increase southern stingray sightings on forereef BRUVS over time. We also predicted that southern stingrays would spend more time in the video field of view (a proxy for interest in foraging; Brown & Kotler 2004) as relative Caribbean reef shark abundance decreased on the forereef. Prey still need to feed when living in risky areas (i.e., where risk is chronic and persistent), so interest in foraging is likely a measure of acute risk (i.e., whether there were predators within the vicinity, on or near the BRUVS, at the time of sampling). Finally, if the shallow lagoon is a refuge from predators (Bond *et al.* 2019), we would expect southern stingray core habitat use to be in the shallow lagoon, and core shark habitat use to be outside of the shallow lagoon.

METHODOLOGY

Study Site

Glover's Reef Marine Reserve (GRMR) is a multi-use 32,876 ha marine protected area (MPA) located approximately 45 km off mainland Belize (Figure1; Gibson *et al.* 2004, Wildtracks & Wildlife Conservation Society 2007). Its no-take zone (hereafter "replenishment zone") prohibits fishing, while its general use zone allows traditional fishing without the use of traps or nets (Gibson *et al.* 2004). Gillnets were banned in all of Belize in 2020 (Government of Belize 2020a), ray fishing was prohibited nationwide in 2020 (Government of Belize 2020b), and shark fishing was prohibited within the entire MPA and 3.2 km around the atoll's boundaries in 2021 (Government of Belize 2021). The replenishment zone of GRMR encompasses lagoon and reef habitats. The lagoon at Glover's Reef Atoll has over 700 patch reefs and reaches a depth of ~ 20 m (Stoddart 1962, Stoddart *et al.* 1982, McClanahan & Muthiga 1998). There are patches of seagrasses within the lagoon and the backreef is comprised of shallow sandflats. Southern stingray abundance and density is higher in the shallow lagoon than on the forereef, with females dominating in the lagoon (Pikitch *et al.* 2005, Tilley 2011). Within the replenishment zone is a channel less than 1 km wide between Long Caye and Northeast Caye that connects the lagoon and forereef (Stoddart 1962). There is a sand patch slope in front of Long Caye on the forereef known as "White Sands" that borders the channel where

southern stingrays occur in the highest densities and the sex ratio is equal (Tilley 2011). The forereef has a narrow shelf area (Stoddart *et al.* 1982, Shcherbina *et al.* 2008) and is primarily fringing reef interspersed with coral spurs and grooves (Mumby & Harborne 1999). Caribbean reef sharks are most common on the forereef and in the deep lagoon (Pikitch *et al.* 2005, Chapman *et al.* 2007).

Baited remote underwater video stations

Field procedures

Baited remote underwater video station (BRUVS) surveys occurred annually (May – July) between 2009 – 2019 on the forereef inside the replenishment zone, excluding 2014 and 2015 (Figure 1, Flowers *et al.* 2022). These surveys were designed to track reef shark abundance over time. Each year, between 22 and 45 BRUVS were set randomly within a standard polygon area of 3.5 km² (N = 316). Two BRUVS sets were removed from the Flowers *et al.* (2022) dataset during a quality assurance check (one from 2009 due to a missing original video that could not be watched for southern stingrays and one from 2010 due to the camera being flooded and fogged, which impaired the field of view), resulting in 314 forereef BRUVS included in this study. During the quality assurance check, we examined original datasheets and found that no BRUVS were deployed in August 2011 or April 2013 as previously suggested in the Global FinPrint Annotator (Vulcan, Inc., Paul G. Allen Philanthropies) and

reported in Flowers *et al.* (2022). BRUVS were also set in lagoon habitat in June 2012 (n = 40; Bond *et al.* 2019), June – July 2018 (n = 40), and June 2019 (n = 19; Figure 1). Deployments occurred in daylight hours and lasted at least 65 minutes (Currey-Randall *et al.* 2020). We recorded the time of day each BRUVS was deployed and hauled. The median number of forereef BRUVS set per day was 5 (2 – 16). When BRUVS were set within the same sampling period, they were spaced at least 500 m apart to ensure each set was independent (Harvey *et al.* 2018). A snorkeler guided each BRUVS to the seafloor to prevent contact with the coral reef. Depth and water temperature (< 1 m) were collected at each BRUVS deployment time (Bond *et al.* 2012, Flowers *et al.* 2022). Occasionally, water temperature was also collected at BRUVS haul time and in these cases, we used the mean water temperature of deployment and haul times for our analyses.

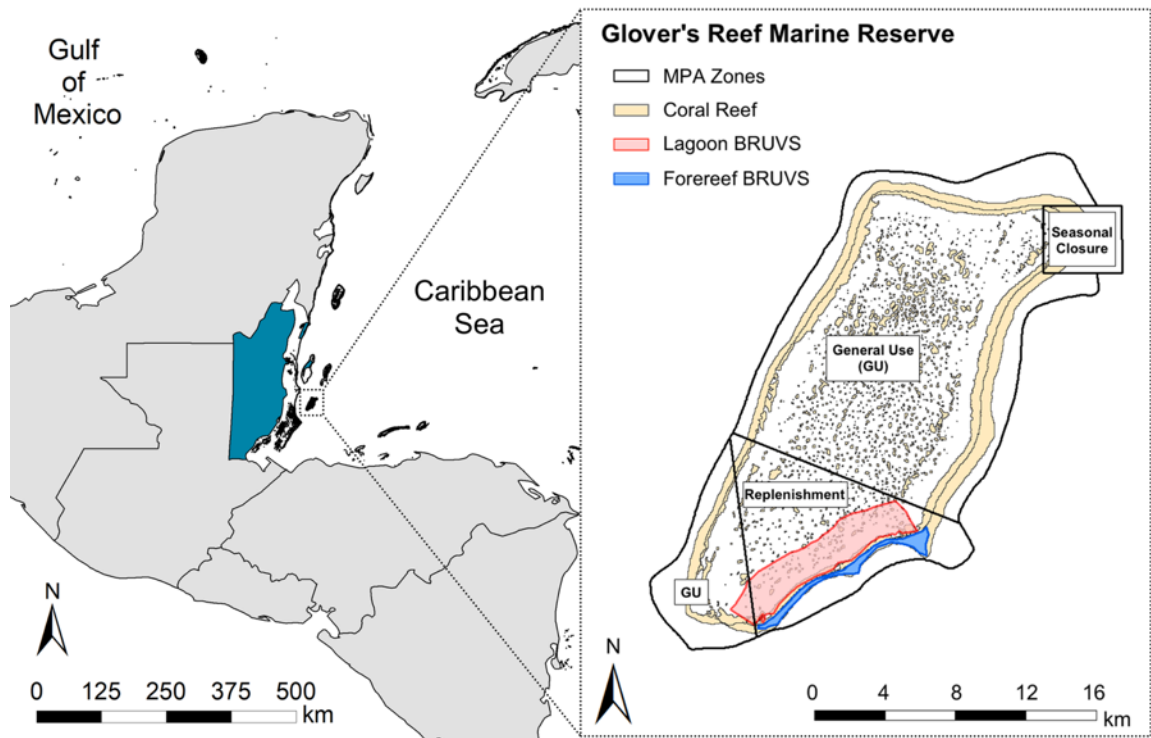


Figure 1: Map representing Belize (left panel, teal blue) and Glover's Reef Marine Reserve, a marine protected area (MPA) in Belize (right panel). Baited remote underwater video station (BRUVS) surveys occurred inside the blue polygon on the forereef from 2009 – 2013 and 2016 – 2019 (N = 314), entirely within the MPA's replenishment zone. Inside the lagoon, BRUVS surveys occurred within the red polygon in 2012, 2018, and 2019 (N = 99). The World Countries Generalized basemap (Esri, Garmin International, Inc., U.S. Central Intelligence Agency, National Geographic Society 2022) was used to create this figure and coral reefs were plotted in both maps using version 4.1 (March 2021) shapefiles from UNEP-WCMC, WorldFish Centre, WRI, TNC (2010) in ArcGIS software version 10.8.2 by Esri. The map text and legend in the right panel were updated in Pixelmator version 3.9.11 (2022).

Video analyses

I. MaxN

All videos were watched to 60 minutes for elasmobranchs by two trained volunteers in real time and/or by one experienced analyst at

normal to 5x playback speed, starting at the time the BRUVS settled on the seafloor (“mark zero”). Experienced analysts verified all species identifications. MaxN, the maximum number of individuals of any elasmobranch species in frame at once (Cappo *et al.* 2001), was used as a measure of sightings per unit effort. We use “sightings” rather than “abundance” when referring to southern stingray MaxN because stingray MaxN has been correlated to reef shark MaxN (Bond *et al.* 2019, Sherman *et al.* 2020) and therefore may not be an unbiased metric of abundance.

II. Total time in frame

BRUVS with a southern stingray MaxN of at least one on the forereef were watched in real time (N = 42). Time in frame for each stingray observation was calculated as the duration in seconds between the time a stingray entered the video field of view (FOV) to the time the stingray left the FOV (Sherman *et al.* 2020). Individual identification was not possible so each time a stingray entered and exited the FOV was considered one event. Total time in frame (TIF) was then calculated for each video as the sum of all time in frame events. On one BRUVS, a southern stingray buried itself in the sand and remained there throughout the 60 minute analysis phase. To avoid inflating TIF for this BRUVS, we considered burial in the sand as equivalent to the time the stingray left the FOV because it had no

interest in the bait. Southern stingrays only touched the bait cage on two forereef BRUVS (prior to 2016 when shark abundance was still comparatively high), or 6.3% of the time (8/126 events, excluding events where the bait box was not fully in FOV). Therefore “bait interaction time” (Bond *et al.* 2019) was not used. In the one case where two southern stingrays were in FOV at the same time, TIF was calculated for each individual separately. For each event, a stingray was recorded as “interested” or “not interested” in the bait. Stingrays logged as “not interested” travelled in a straight line in and out of FOV, while “interested” stingrays showed at least some movement towards and/or around the bait cage, often via tortuous movements. Inter- and intraspecific interactions were recorded when southern stingrays were in the FOV with another elasmobranch and logged as “flight” (a southern stingray swims away following detection of another individual or species), “follow” (a southern stingray follows another individual or species), or “no response” (a southern stingray shows no reaction to the presence of another individual or species). Sex was recorded as “male” based on presence of claspers or “unknown” based on no visible evidence of claspers. Sex specific analyses were not conducted because we were unable to verify any individuals were female with a ventral view of the cloacal region.

III. Habitat complexity

Reef relief was calculated for each forereef BRUVS set using Benthobox (www.benthobox.com, Australian Institute of Marine Science). A screenshot of each video was taken after the BRUVS settled to the seafloor. A 5 x 4 grid was then overlayed on the screenshot. Each rectangle within the grid was given a score from 0 (flat) to 5 (highly complex) unless the rectangle contained open water with no benthos (Polunin & Roberts 1993, Wilson *et al.* 2007). Finally, mean complexity was calculated per BRUVS deployment.

Statistical analyses

To investigate what factors predict southern stingray MaxN on the forereef (2009 – 2019), we used a generalized linear model (GLM). We initially considered using the negative binomial error distribution (Venables & Ripley 2002), which accounts for overdispersion and has been used in previous studies using MaxN as the response variable (e.g., Sherman *et al.* 2020, Clementi *et al.* 2021, Flowers *et al.* 2022). Residual diagnostics revealed the negative binomial and Poisson error distributions were both appropriate (Hartig 2020). However, Akaike's information criterion (AIC) preferred the Poisson distribution for our dataset because the negative binomial model estimated that the variance was equal to the mean. AIC was used for model selection (Akaike 1998). Variables

from supported models with a $\Delta AIC \leq 2$ were included for model averaging to obtain coefficients (Bartoń 2020).

A linear regression model (LM) was constructed to test what factors predict southern stingray TIF on the forereef (2009 – 2019). We log transformed the response variable, TIF, to normalize the data ($\log[TIF]$). Residual plots did not reveal any problematic trends in the LM. The analysis of TIF only included BRUVS deployments with a southern stingray MaxN of at least one ($N = 42$). AICc was used for model selection due to a low sample size (Burnham & Anderson 2004, Bartoń 2020); however, model averaging made little to no difference in the LM coefficient estimates (S1 Figure).

We considered a suite of covariates as numerical variables in all models (GLM and LM) including year (2009 - 2013, 2016 - 2019), depth (m), reef relief (0-5), hour of day, water temperature ($^{\circ}C$), an interaction between depth and water temperature, Caribbean reef shark MaxN, nurse shark (*Ginglymostoma cirratum*) MaxN, and whitespotted eagle ray (*Aetobatus narinari*) MaxN. The time a BRUVS was deployed was rounded to the hour of the day (e.g., 15:45 = 15). The predictor variables nurse shark MaxN and whitespotted eagle ray MaxN were included because nurse sharks are potential predators and competitors of southern stingrays (Compagno 2001, Tilley 2011), and whitespotted eagle rays are a potential competitor of southern stingrays. Multicollinearity was not an issue in any of our models because the variance inflation factor for each covariate was low and close to one (Stine 1995, Lüdecke *et al.* 2021). Due to the small sample size used for the LM, we conducted power analysis for the ability to detect the

year effect (Champely 2020), since it is likely a proxy for Caribbean reef shark abundance which has declined (Flowers *et al.* 2022).

The percentage of events where stingrays were interested in the bait was calculated as the number of events when a stingray was interested per BRUVS deployment divided by the total number of events per BRUVS deployment multiplied by 100. The mean percentage of interested events was calculated per year and regressed against the mean annual Caribbean reef shark MaxN to investigate the relationship between relative stingray interest in foraging and Caribbean reef shark MaxN.

To test whether southern stingray MaxN differed across forereef and lagoon habitats, we used a Poisson GLM with a habitat and year interaction. This GLM was run separately from the one described above because BRUVS were only set inside the lagoon in 2012, 2018, and 2019. We determined that the Poisson error distribution was appropriate (Hartig 2020).

All analyses were conducted in R version 4.2.1 (R Core Team 2022) using the packages “MASS” (GLMs; Venables & Ripley 2002), “DHARMA” (residual diagnostics for the GLMs; Hartig 2020), “*performance*” (multicollinearity check; Lüdecke *et al.* 2021), “*MuMIn*” (model averaging; Bartoń 2020), and “*pwr*” (power analysis; Champely 2020).

Passive acoustic telemetry

Field procedures

I. Passive acoustic receiver array

We tracked stingray and shark movements using 23 VR2W receivers (Vemco, AMIRIX Systems, Inc.) deployed at GRMR (Figure 2). Nine receivers were placed at various depths (7 – 17 m) on the outer forereef of Glover’s Reef Atoll, with a particular focus on entry and exit points into and out of the lagoon (“forereef”; Figure 2B). An additional 14 receivers were placed inside the southern portion of the lagoon (Figure 2C). Four receivers were set in the deeper part of the lagoon (“deep lagoon”, 6 – 8 m), six receivers in seagrass and patch reef habitat (“midline lagoon”, 2 – 4 m), and three receivers in very shallow sandflat and seagrass habitats (“shallow lagoon”, 1 – 2 m). One receiver was placed at the Wildlife Conservation Society’s field station dock (1 m). All lagoon receivers and the receiver at White Sands were attached to a PVC pole secured in cement and all forereef receivers were secured to floating rope attached to cinderblocks at the bottom and a float that remained near the surface of the water. All forereef sites had receivers in place by 24 January 2017, with the exception of White Sands, which had a receiver first placed on 14 June 2017. All lagoon sites had a receiver in place by 12 June 2017, with

the exception of the dock site, which had its first receiver added on 09 January 2019. Receiver downloads and battery replacements occurred annually.

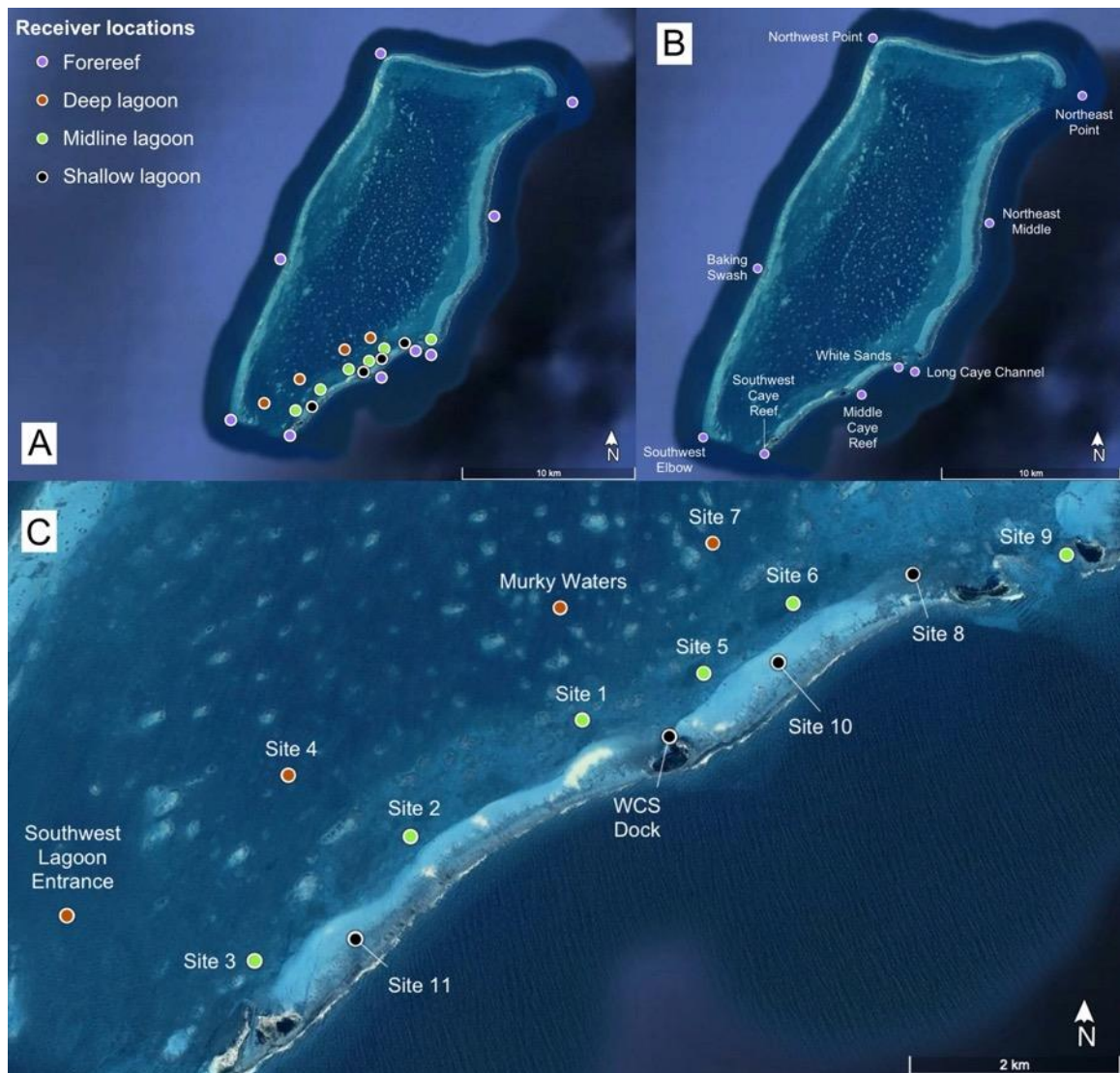


Figure 2: Passive acoustic receiver locations at Glover's Reef Marine Reserve: (a) coloured by habitat, (B) forereef sites, and (C) lagoon sites. "WCS" = Wildlife Conservation Society. Satellite imagery from Google Earth.

The approximate detection range of the receivers was estimated using one forereef site (Baking Swash), one very shallow sandflat site (Site 11), and one midline lagoon site (Site 1). Detection range was estimated in the lagoon by travelling in two directions: towards the reef crest (southeast shallow) and towards the deep lagoon (northwest). The distance from the receiver to the farthest point at which the transmitter could be heard in each direction was recorded. The average of the two directions was then used to classify detection ranges for each receiver in their respective depth bins: shallow lagoon sites had a detection range of 100 m and midline lagoon sites had a detection range of 350 m. Deep lagoon sites were not tested and detection range at those sites was conservatively estimated at 400 m (Chapman *et al.* 2005). The forereef sites were all estimated to have a detection range of at least 500 m in three directions based on the detection range of the receiver at Baking Swash. The average detection range was then calculated for each forereef site by measuring the distance from the receiver to the reef crest followed by a calculation of the average from the four directions (three open water, one towards reef crest), and rounded down to the nearest 50 m (e.g., if the average was 462 m, it was rounded to 450 m). For forereef sites that were at least 500 m away from a reef crest or shallow area, detection range was selected as 500 m based on our range test at

Baking Swash and previous acoustic telemetry studies at GRMR (Chapman *et al.* 2005, Bond *et al.* 2012).

II. Southern stingray tagging

Between 3 June 2017 and 8 January 2019, 30 female southern stingrays (56 – 87 cm disc width [DW]) were captured on research longlines (n hooks = 10 – 25) using 16/0 circle hooks (n = 16), traditional Belizean handlines (n = 5), a dip net (n = 1), and by cast nets (n = 8) inside the lagoon at Glover's Reef Atoll (Table 1). We were unable to capture males or any individuals in forereef habitat. All stingrays were brought on the boat using a dip net to remove their venomous barb for safety. Each stingray was scanned for an existing passive integrative transponder (PIT tag) and new individuals had a PIT tag (Biomark, Inc. Mini HPT8) implanted near the base of the tail where it connects to the pelvic fin. DW was measured for each individual and fin clips were collected for genetic analyses. While on the boat, stingray spiracles and gills were constantly flushed with seawater. All stingrays were brought into shallow water in a dip net and placed into tonic immobility for surgery. A coded V16 transmitter (69 kHz) with an approximate 10-year battery lifespan (Vemco, AMIRIX Systems, Inc.) was inserted ventrally into the body cavity. All stingrays were released in shallow water following surgery.

III. Shark tagging

Between 4 July 2016 and 1 May 2019, 30 Caribbean reef sharks (89 – 190 cm total length [stretched total length; STL]) and six lemon sharks (140 – 173 cm STL) were caught on research longlines with 16/0 circle hooks (n = 33), a Belizean handline (n = 1), and block rigs (n = 3) in lagoon and forereef habitats at GRMR (Table 1). Each individual (N = 37) was tied up along the side of the boat to be sexed, measured, and tagged with a PIT (Biomark, Inc. HPT9) to aid with identification in case of recapture. Fin clips were collected for genetic analyses. All sharks were placed into tonic immobility before conducting surgery. V16 coded transmitters (69 kHz; Vemco, AMIRIX Systems, Inc.) were implanted ventrally in the abdominal cavity of each shark. Following surgery, sharks were taken out of tonic immobility and released.

Individual ID	Capture date (dd-mon-yy)	Capture location	Species	Sex	DW (rays) or STL (sharks)	Maturity	Residency index	General use area
1	03-Jun-17	Lagoon	<i>H. americanus</i>	F	80 cm	Likely mature	N/A	N/A
2	03-Jun-17	Lagoon	<i>H. americanus</i>	F	75 cm	Likely mature	0.27	2.98 km ²
3	03-Jun-17	Lagoon	<i>H. americanus</i>	F	77 cm	Likely mature	N/A	N/A
4	04-Jun-17	Lagoon	<i>H. americanus</i>	F	73 cm	Immature	N/A	N/A
5	04-Jun-17	Lagoon	<i>H. americanus</i>	F	81 cm	Mature	0.65	2.72 km ²
6	14-Jun-17	Lagoon	<i>H. americanus</i>	F	80 cm	Likely mature	N/A	N/A
7	23-Jun-17	Lagoon	<i>H. americanus</i>	F	76 cm	Likely mature	0.005	N/A
8	24-Jun-17	Lagoon	<i>H. americanus</i>	F	76 cm	Likely mature	0.66	1.53 km ²
9	24-Jun-17	Lagoon	<i>H. americanus</i>	F	84 cm	Mature	N/A	N/A
10	24-Jun-17	Lagoon	<i>H. americanus</i>	F	79 cm	Likely mature	N/A	N/A
11	04-Apr-18	Lagoon	<i>H. americanus</i>	F	78 cm	Likely mature	0.26	1.57 km ²
12	05-Apr-18	Lagoon	<i>H. americanus</i>	F	87 cm	Mature	0.85	3.63 km ²
13	05-Apr-18	Lagoon	<i>H. americanus</i>	F	80 cm	Likely mature	0.52	2.92 km ²
14	06-Apr-18	Lagoon	<i>H. americanus</i>	F	86 cm	Mature	0.43	6.43 km ²
15	07-Apr-18	Lagoon	<i>H. americanus</i>	F	78 cm	Likely mature	N/A	N/A
16	05-Jun-18	Lagoon	<i>H. americanus</i>	F	77 cm	Likely mature	0.66	0.14 km ²
17	05-Jun-18	Lagoon	<i>H. americanus</i>	F	73 cm	Immature	N/A	N/A
18	11-Jun-18	Lagoon	<i>H. americanus</i>	F	61 cm	Immature	0.13	1.66 km ²
19	11-Jun-18	Lagoon	<i>H. americanus</i>	F	54 cm	Immature	0.009	N/A
20	11-Jun-18	Lagoon	<i>H. americanus</i>	F	77 cm	Likely mature	0.22	3.33 km ²
21	11-Jun-18	Lagoon	<i>H. americanus</i>	F	86 cm	Mature	0.06	1.52 km ²
22	18-Jun-18	Lagoon	<i>H. americanus</i>	F	62 cm	Immature	0.47	0.14 km ²
23	18-Jun-18	Lagoon	<i>H. americanus</i>	F	83 cm	Mature	N/A	N/A
24	07-Jan-19	Lagoon	<i>H. americanus</i>	F	63 cm	Immature	0.28	0.14 km ²
25	08-Jan-19	Lagoon	<i>H. americanus</i>	F	76 cm	Likely mature	0.31	0.13 km ²
26	08-Jan-19	Lagoon	<i>H. americanus</i>	F	56 cm	Immature	0.80	0.26 km ²
27	08-Jan-19	Lagoon	<i>H. americanus</i>	F	60 cm	Immature	0.30	0.14 km ²
28	08-Jan-19	Lagoon	<i>H. americanus</i>	F	60 cm	Immature	0.56	0.22 km ²
29	08-Jan-19	Lagoon	<i>H. americanus</i>	F	76 cm	Likely mature	0.03	0.11 km ²
30	08-Jan-19	Lagoon	<i>H. americanus</i>	F	65 cm	Immature	0.07	1.44 km
1	4-Jul-16	Lagoon	<i>C. perezii</i>	M	96 cm	Immature	N/A	N/A

2	21-Jan-17	Forereef	<i>C. perezii</i>	M	112 cm	Immature	N/A	N/A
3	21-Jan-17	Forereef	<i>C. perezii</i>	M	89 cm	Immature	N/A	N/A
4	21-Jan-17	Forereef	<i>C. perezii</i>	M	99 cm	Immature	N/A	N/A
5	21-Jan-17	Forereef	<i>C. perezii</i>	F	95 cm	Immature	0.06	11.05 km ²
6	21-Jan-17	Forereef	<i>C. perezii</i>	M	90 cm	Immature	N/A	N/A
7	21-Jan-17	Forereef	<i>C. perezii</i>	F	119 cm	Immature	0.07	2.86 km ²
8	22-Jan-17	Lagoon	<i>C. perezii</i>	M	94 cm	Immature	0.50	3.08 km ²
9	6-Jun-17	Lagoon	<i>C. perezii</i>	M	97 cm	Immature	N/A	N/A
10	6-Jun-17	Lagoon	<i>C. perezii</i>	M	149 cm	Immature	0.42	2.09 km ²
11	6-Jun-17	Lagoon	<i>C. perezii</i>	F	131 cm	Immature	N/A	N/A
12	6-Jun-17	Lagoon	<i>C. perezii</i>	F	182 cm	Immature	N/A	N/A
13	12-Jun-17	Lagoon	<i>C. perezii</i>	F	115 cm	Immature	0.39	2.47 km ²
14	12-Jun-17	Lagoon	<i>C. perezii</i>	F	120 cm	Immature	N/A	N/A
15 *	13-Jun-17	Lagoon	<i>C. perezii</i>	F	95 cm	Immature	0.01	2.16 km ²
16	14-Jun-17	Lagoon	<i>C. perezii</i>	F	123 cm	Immature	0.22	3.08 km ²
17	22-Jun-17	Lagoon	<i>C. perezii</i>	F	186 cm	Immature	0.93	2.55 km ²
18	4-Apr-18	Lagoon	<i>C. perezii</i>	M	118 cm	Immature	0.98	2.50 km ²
19	4-Jun-18	Lagoon	<i>C. perezii</i>	M	101 cm	Immature	0.14	6.79 km ²
20	6-Jun-18	Lagoon	<i>C. perezii</i>	M	116 cm	Immature	0.06	2.47 km ²
21	19-Jan-19	Lagoon	<i>C. perezii</i>	M	107 cm	Immature	0.04	3.94 km ²
22	29-Apr-19	Lagoon	<i>C. perezii</i>	F	115 cm	Immature	0.53	5.57 km ²
23	29-Apr-19	Lagoon	<i>C. perezii</i>	M	186 cm	Mature	0.20	3.34 km ²
24	29-Apr-19	Lagoon	<i>C. perezii</i>	M	120 cm	Immature	0.70	2.00 km ²
25	30-Apr-19	Lagoon	<i>C. perezii</i>	F	116 cm	Immature	0.04	3.93 km ²
26	1-May-19	Lagoon	<i>C. perezii</i>	M	178 cm	Mature	0.11	6.66 km ²
27	1-May-19	Lagoon	<i>C. perezii</i>	F	122 cm	Immature	0.03	3.72 km ²
28	1-May-19	Lagoon	<i>C. perezii</i>	F	176 cm	Immature	0.03	1.53 km ²
29	1-May-19	Lagoon	<i>C. perezii</i>	M	190 cm	Mature	0.08	4.57 km ²
30	1-May-19	Lagoon	<i>C. perezii</i>	M	154 cm	Immature	N/A	N/A
1	6-Jun-17	Lagoon	<i>N. brevirostris</i>	M	162 cm	Immature	0.48	1.80 km ²
2	5-Jun-18	Lagoon	<i>N. brevirostris</i>	F	140 cm	Immature	0.99	1.11 km ²
3	5-Jun-18	Lagoon	<i>N. brevirostris</i>	F	144 cm	Immature	0.98	2.08 km ²
4	9-Jan-19	Lagoon	<i>N. brevirostris</i>	M	153 cm	Immature	0.53	0.70 km ²
5	8-Jan-19	Lagoon	<i>N. brevirostris</i>	M	156 cm	Immature	0.04	1.95 km ²
6	30-Apr-19	Lagoon	<i>N. brevirostris</i>	M	173 cm	Immature	0.02	N/A

Table 1: Summary of elasmobranchs captured at Glover’s Reef Marine Reserve between July 2016 and June 2019 with their residency indices and scaled 95% general area use sizes between 22 June 2019 and 26 August 2020. Individuals with “N/A” listed under “Residency index” were not detected in the reduced dataset. Individuals with “N/A” listed under “General use area” did not have enough detections to calculate their utilization distributions. Males were classified as mature based on calcification of claspers and clasper ability to rotate forward. Southern stingray (*H. americanus*) maturity was classified based on McEachran & de Carvalho 2002, Henningsen & Leaf 2010, and Ramírez-Mosqueda *et al.* 2012. “Likely mature” represents individuals in the size range at which female southern stingrays mature (75 - 80 cm disc width [DW]). Female lemon shark (*N. brevirostris*) and Caribbean reef shark (*C. perezii*) maturity was based on Ebert *et al.* 2013. The asterisk (*) represents an individual that was confirmed to have died in November 2019 (Flowers *et al.* 2022). “F” = female, “M” = male, “STL” = stretched total length.

Data processing and detection summaries

Some receiver batteries did not last the full 12 months between download periods and receiver motherboards started to fail between our 2019 and 2020 downloads. As biofouling increased and receiver batteries died, detection probability likely decreased over time each year (e.g., Bond *et al.* 2012). To account for these issues and varying tagging periods throughout the course of the study, I selected a shortened time period between 22 June 2019 and 26 August 2020 for data analysis, unless otherwise noted. 22 June 2019 was a month after the last day a species of interest was tagged and 26 August 2020 was the day the last receiver download occurred when the receiver array size began decreasing due to failing motherboards (i.e., fewer receivers). This shortened time period maximized overlap between the species of interest; however, not all tagged individuals were detected within that time frame (see results section). One receiver at Site 4 had no detections in the August 2020 download session and was assumed to have failed given that tagged elasmobranchs previously used this site. Three receivers were found buried in the sand during the August 2020 download (sites Baking Swash, Middle Caye Reef, and Southwest Elbow), likely greatly reducing the detection ranges at these sites. However, we cannot identify with any degree of certainty when they detached from their floating ropes.

All data were downloaded using Vemco's VUE software (v. 2.5.0, AMIRIX Systems, Inc.). Type A false detections were removed from our dataset following

Simpfendorfer *et al.* 2015. Data were then organized by species and Abacus plots were built for the entire study period using the R package “VTrack” (Campbell *et al.* 2012). The reduced dataset (June 2019 – August 2020) was used to calculate the residency index (RI) for each individual southern stingray and shark (Espinoza *et al.* 2015):

$$RI = \frac{\text{number of days detected}}{\text{number of days monitored}} \quad (\text{equation 1}).$$

RI close to one represent high residency (Espinoza *et al.* 2015); however, RIs close to zero may be due to low residency, transmitter and/or receiver failure, mortality, or low receiver coverage at our study site. The reduced dataset was also used to summarize the total number of detections per species and individual in each habitat (forereef or lagoon) across eight hour diel periods. Dawn and dusk (crepuscular) detections were classified as occurring between the hours of 04:00 – 07:59 and 16:00 - 19:59; day detections occurred between the hours of 8:00 and 15:59; and night detections were logged as those occurring between the hours of 20:00 and 03:59 (Ito *et al.* 2022). Total number of detections can naturally vary across time of day and environmental factors, so these results should be interpreted with caution (Kessel *et al.* 2014, Selby *et al.* 2016, Heupel *et al.* 2019). Minimum linear dispersal (MLD), the straight-line distance travelled between the two farthest receivers at which an individual was detected, was calculated for each southern stingray (Bond *et al.* 2012).

Habitat use

Core (50%) and general (95%) utilization distributions (UDs) were created for each species using dynamic Brownian bridge movement models (dBBMM; Kranstauber *et al.* 2012) in the R package “*dBBMMhomeRange*” (Dedman & van Zinnicq Bergmann 2022). dBBMMs account for temporal autocorrelation and behavioural changes (Kranstauber *et al.* 2012). dBBMMs were constructed using receivers with detections. Individuals were removed when the number of relocations was less than the window size parameter value (23 for southern stingrays and Caribbean reef sharks, 27 for lemon sharks) (Dedman & van Zinnicq Bergmann 2022). VR2W receiver data and detection ranges for each receiver were input as arguments in the “*dBBMMhomeRange*” function and individual UD rasters were scaled from 0 to 1 using the “*scaleraster*” function (Dedman & van Zinnicq Bergmann 2022). UD s were plotted using the “*dBBMMplot*” function (Dedman & van Zinnicq Bergmann 2022) and a satellite basemap from Google maps in the R package “*ggmap*” (Kahle & Wickham 2013).

RESULTS

Baited remote underwater video stations

Southern stingray sightings comparisons across habitats (2012, 2018, 2019)

A Poisson GLM revealed a negative relationship between southern stingray MaxN and forereef habitat ($p < 0.001$, coefficient estimate = -73.96), suggesting that southern stingray sightings are higher in the lagoon than on the forereef (Figure 3). This pattern was consistent in 2012, 2018, and 2019 because there was little support for an interaction between year and habitat ($p = 0.71$). Southern stingray TIF was not compared across habitats because it depends on southern stingray abundance (e.g., TIF will be higher in places with more stingrays) and MaxN differed across habitats.

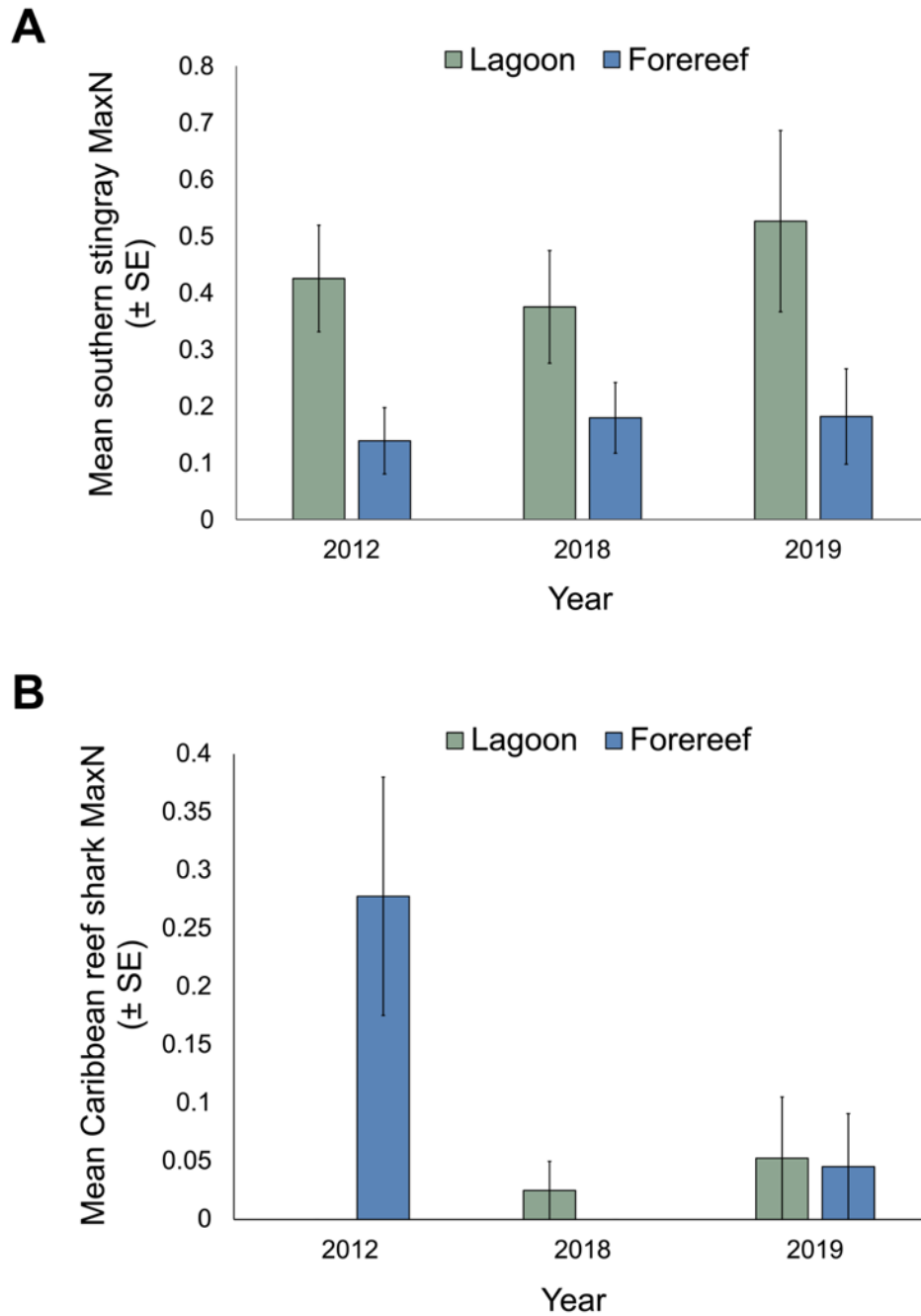


Figure 3: Mean MaxN ($\pm$ SE) across habitats for (A) southern stingrays and (B) Caribbean reef sharks at Glover's Reef Marine Reserve.

Southern stingray sightings on the forereef 2009 - 2019

For the forereef sets, the full model averaged coefficients from the nine supported models ($\Delta AIC \leq 2$, Table 2) demonstrated little to no evidence that year, Caribbean reef shark MaxN, nurse shark MaxN, whitespotted eagle ray MaxN, hour of day, depth, water temperature, or an interaction between depth and water temperature predicted southern stingray MaxN (Table 3). Southern stingray MaxN remained stable between 2009 – 2019 on the forereef inside the replenishment zone of GRMR (Figure 4A) as Caribbean reef shark MaxN declined (Figure 5; Flowers *et al.* 2022). Using Muff *et al.* (2022)'s language to frame p-values in terms of strength of evidence against the Null hypothesis of no effect, there was moderate evidence that reef relief predicted southern stingray MaxN, with an overall negative effect on southern stingray MaxN ($p = 0.02$, Table 2, Figs 4B & 6). The AIC best model (i.e., $\Delta AIC = 0$) included the predictor variables hour of day and reef relief (Table 4, Figure 6), with weak evidence that hour of day predicted southern stingray MaxN ($p = 0.08$; Table 4) and moderate evidence that reef relief predicted southern stingray MaxN ($p = 0.02$; Table 4).

Poisson generalized linear model	df	ΔAIC	Akaike weight
Response = southern stingray MaxN			
hour of day + relief	4	0.00	0.21
Caribbean reef shark MaxN + hour of day + relief	5	0.86	0.14
relief	3	1.07	0.12
depth + hour of day + relief + temperature + depth:temperature	7	1.30	0.11
whitespotted eagle ray MaxN + hour of day + relief	5	1.57	0.10
nurse shark MaxN + hour of day + relief	5	1.70	0.09
depth + hour of day + relief	5	1.98	0.08
hour of day + relief + year	5	1.99	0.08
hour of day + relief + temperature	5	2.00	0.08
Linear regression model	df	$\Delta AICc$	Akaike weight
Response = log southern stingray TIF			
relief + year	4	0.00	0.14
relief	3	0.07	0.13
depth	3	0.39	0.11
depth + relief	4	0.53	0.10
NULL	2	0.67	0.10
depth + relief + year	5	1.21	0.07
Caribbean reef shark MaxN + relief + year	5	1.60	0.06
year	3	1.67	0.06
nurse shark MaxN + relief + year	5	1.75	0.06
temperature	3	1.75	0.06
relief + temperature	4	1.87	0.05
depth + year	4	1.92	0.05

Table 2: Models used to describe southern stingray MaxN and total time in frame in seconds (TIF) on forereef BRUVS 2009 – 2019 where model selection was based on delta Akaike's Information Criterion (ΔAIC) values and $\Delta AICc$ corrected

for small sample size. Only supported models (ΔAIC and $\Delta AICc \leq 2$) are shown here. “.” refers to an interaction between variables.

Poisson generalized linear model	Estimate	Standard error	z value	Pr(> z)
Response = southern stingray MaxN				
intercept	1.22	28.80	0.04	0.97
year	3.39×10^{-4}	0.01	0.03	0.98
hour of day	0.09	0.06	1.40	0.16
relief	-0.50	0.22	2.29	0.02
whitespotted eagle ray MaxN	0.03	0.17	0.18	0.86
Caribbean reef shark MaxN	-0.05	0.18	0.27	0.79
nurse shark MaxN	-8.31×10^{-3}	0.06	0.14	0.89
depth	-0.32	1.00	0.32	0.75
temperature	-0.13	0.43	0.31	0.76
depth : temperature	0.01	0.03	0.32	0.75
Linear regression model	Estimate	Standard error	t value	Pr(> t)
Response = log southern stingray TIF				
intercept	-137.81	124.65	-1.11	0.28
year	0.08	0.05	1.46	0.16
hour of day	0.04	0.06	0.67	0.51
relief	-0.49	0.24	-2.01	0.05
whitespotted eagle ray MaxN	-0.69	0.60	-1.15	0.26
Caribbean reef shark MaxN	0.54	0.49	1.11	0.27
nurse shark MaxN	0.16	0.19	0.81	0.42
depth	-1.41	2.22	-0.63	0.53
temperature	-0.57	1.09	-0.52	0.61
depth : temperature	0.05	0.08	0.65	0.52

Table 3: Full model averaged coefficient estimates from the supported models ($\Delta AIC \leq 2$) describing southern stingray MaxN and coefficient estimates from the global total time in frame in seconds (TIF) model on BRUVS 2009 – 2019. “.”

refers to an interaction between variables. Bolded text represents a predictor variable with a p-value ≤ 0.05 .

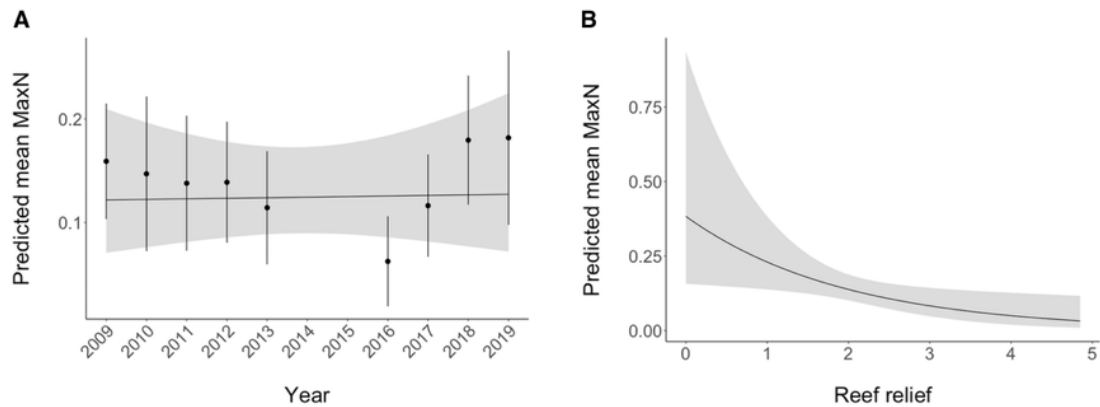


Figure 4: Predicted southern stingray mean MaxN (black trendline) over time (A) and across reef relief (B) with 95% confidence intervals (grey shaded area) on the forereef inside the replenishment zone of Glover’s Reef Marine Reserve. Points represent mean MaxN $\pm$ SE from observed data. Panel A predictions were made from the only supported model ($\Delta\text{AIC} \leq 2$) that included year (MaxN $\sim$ hour of day + reef relief + year) and panel B predictions were made from the best model ($\Delta\text{AIC} = 0$; MaxN $\sim$ hour of day + reef relief) using the R packages “*jtools*” (Long 2020) and “*ggplot2*” (Wickham 2016).

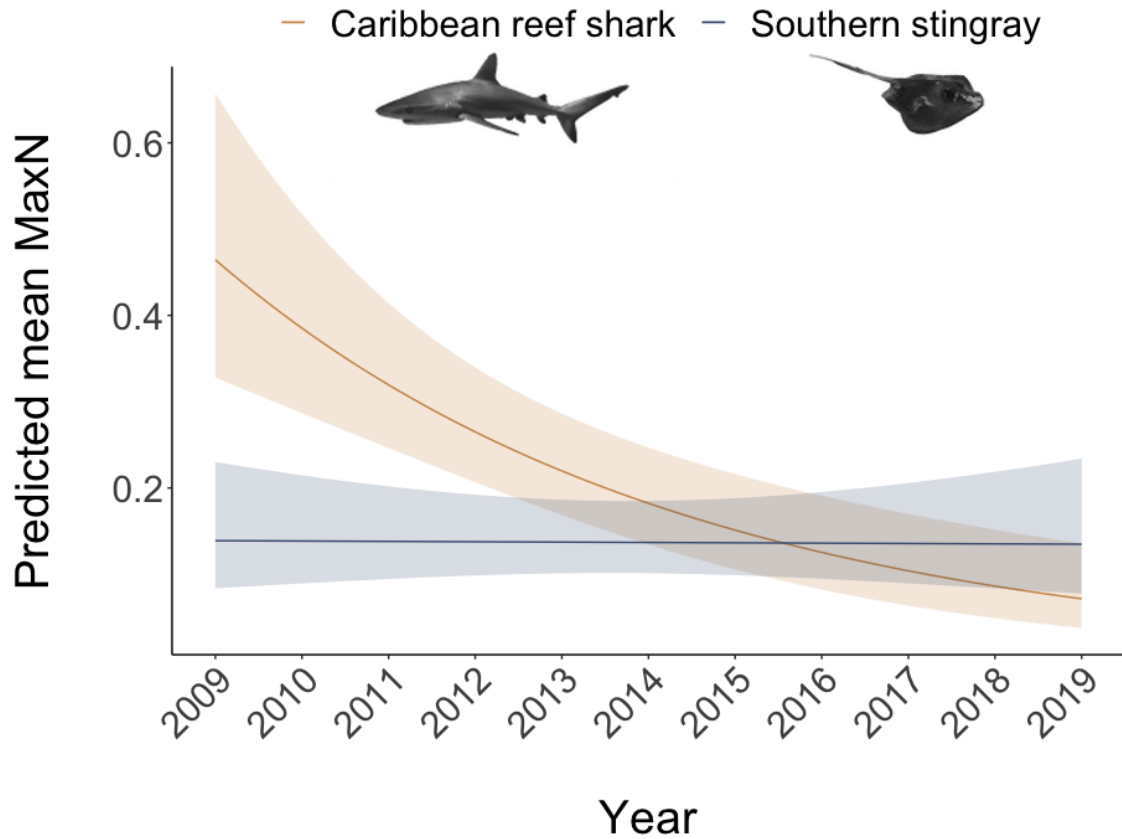


Figure 5: Predicted Caribbean reef shark and southern stingray mean MaxN over time with 95% confidence intervals on the forereef inside the replenishment zone of Glover’s Reef Marine Reserve. Predictions were made from models only including year as a covariate ($\text{MaxN} \sim \text{year}$) using the R packages “*jtools*” (Long 2020) and “*ggplot2*” (Wickham 2016). The Caribbean reef shark model and data are from Flowers *et al.* 2022.

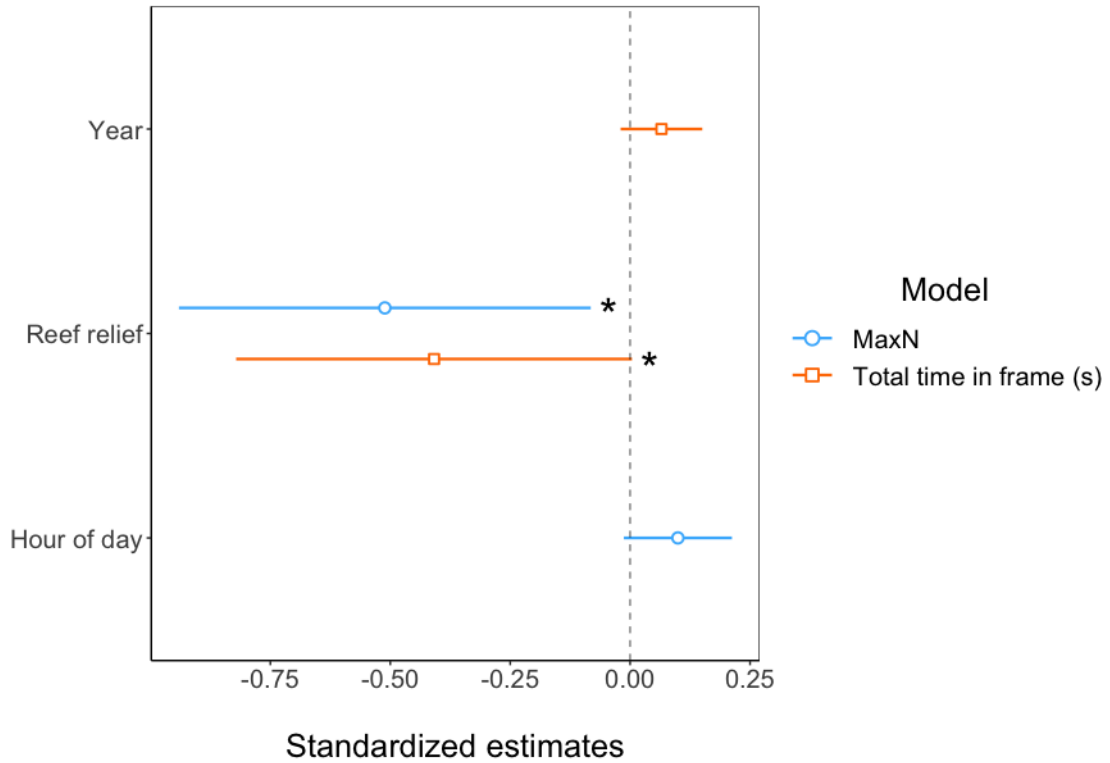


Figure 6: Standardized estimates of the coefficients for variables predicting southern stingray MaxN and total time in frame on the forereef from the best models (i.e., ΔAIC and $\Delta AIC_c = 0$). Bars represent 95% confidence intervals. Standardized estimates ~ 0 have no effect, > 0 have a positive effect, < 0 have a negative effect. One asterisk (*) represents $p < 0.05$. Figure created using R package “ggstance” (Henry *et al.* 2020).

	df	Deviance	Residual df	Residual deviance	Pr(>Chi)
Response = southern stingray MaxN					
NULL			313	173.74	
relief	1	5.15	312	168.59	0.02
hour of day	1	3.07	311	165.52	0.08

Table 4: Analysis of deviance table for the best generalized linear model ($\Delta AIC = 0$) for southern stingray MaxN on the forereef (2009 - 2019). Bolded text represents a predictor variable with a p-value < 0.05 .

Southern stingray behaviour on the forereef 2009 - 2019

Southern stingray TIF ranged from seven to 871 seconds per BRUVS deployment (median = 39.5). The total number of events per BRUVS deployment with a southern stingray MaxN of at least one ranged from one to 19 (median = 2). The total number of events was 131. Of the 12 supported models (Table 2), the AICc best model included the predictor variables year and reef relief (Table 5, Figure 6), with little to no evidence that year predicted southern stingray TIF ($p = 0.25$; Figure 7A) and weak to moderate evidence that reef relief predicted southern stingray TIF ($p = 0.05$; Figure 7B). However, our power to detect a year effect at $\alpha = 0.05$ was relatively low (21%). To detect our year effect size with reasonable power (80%), we would have needed to include approximately 245 BRUVS with southern stingrays present in our study. There was little to no evidence of a relationship between southern stingray interest in the bait and mean annual Caribbean reef shark MaxN ($df = 1$, $F = 0.63$, $R^2 = 0.08$, Figure 8). The percentage of events where stingrays were interested in the bait was highest in 2011 and 2019 (87.5%) and lowest in 2016 (0%) (Figure 9). Mean Caribbean reef shark MaxN was highest in 2011 (0.72 ± 0.19 SE) and lowest in 2018 (0; Flowers *et al.* 2022).

	df	Sum of squares	Mean squares	F value	Pr(>F)
Response = southern stingray TIF					
year	1	1.32	1.32	1.38	0.25
relief	1	3.83	3.83	4.01	0.05

Table 5: Analysis of variance table for the best linear regression model ($\Delta\text{AICc} = 0$) for total time in frame (TIF) in seconds on the forereef (2009 – 2019). Bolded text represents a predictor variable with a p-value = 0.05.

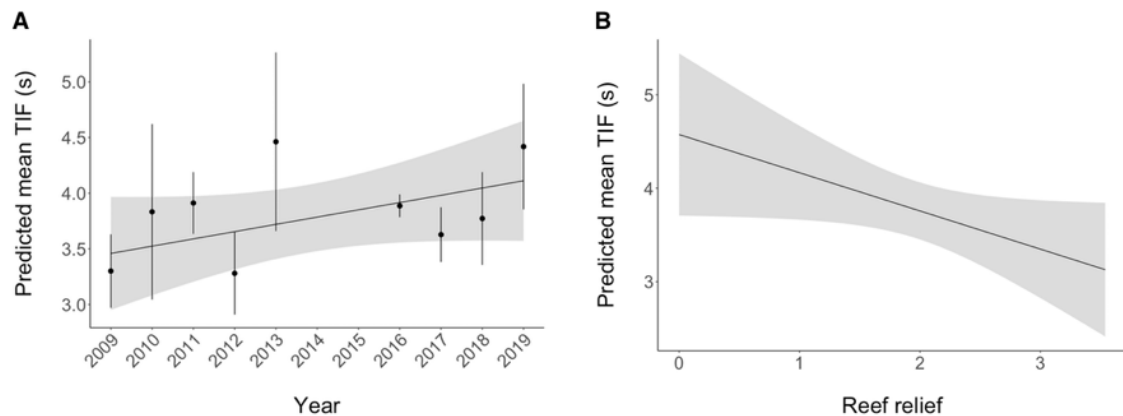


Figure 7: Predicted southern stingray mean total time in frame (TIF) in seconds (s) (black trendline) over time (A) and across reef relief (B) with 95% confidence intervals (grey shaded area) on the forereef inside the replenishment zone of Glover’s Reef Marine Reserve. Points represent mean $\text{MaxN} \pm \text{SE}$ from observed data. Predictions were made from the best model ($\Delta\text{AICc} = 0$; $\log[\text{TIF}] \sim \text{reef relief} + \text{year}$) using the R packages “*jtools*” (Long 2020) and “*ggplot2*” (Wickham 2016).

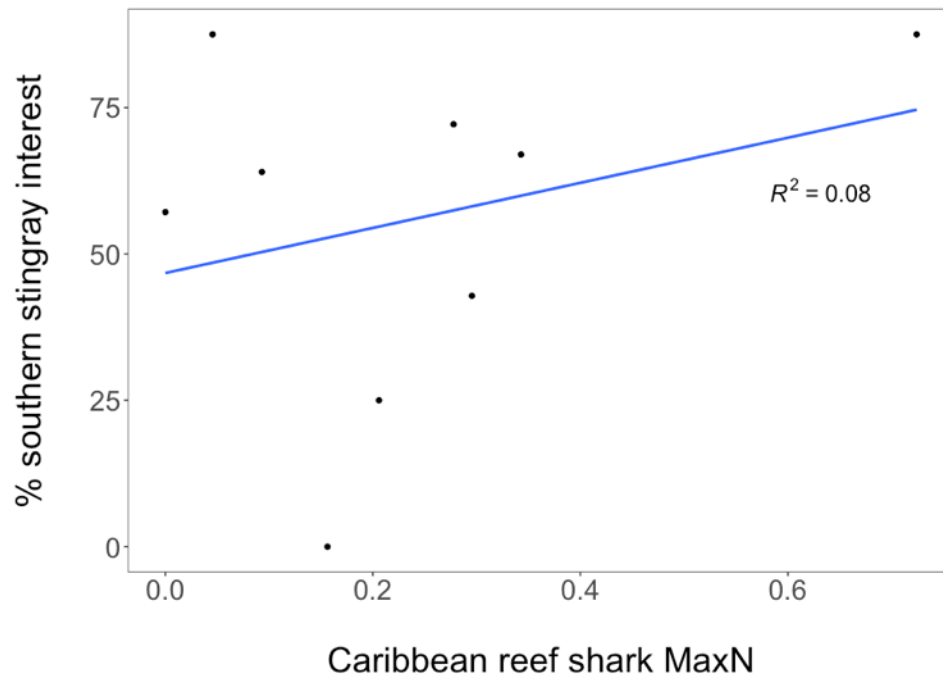


Figure 8: Linear regression model depicting little to no evidence of a relationship between Caribbean reef shark relative abundance (mean MaxN per year) and percentage of events where southern stingrays were interested in the bait (df = 1, $F = 0.63$, $p = 0.45$) on the forereef.

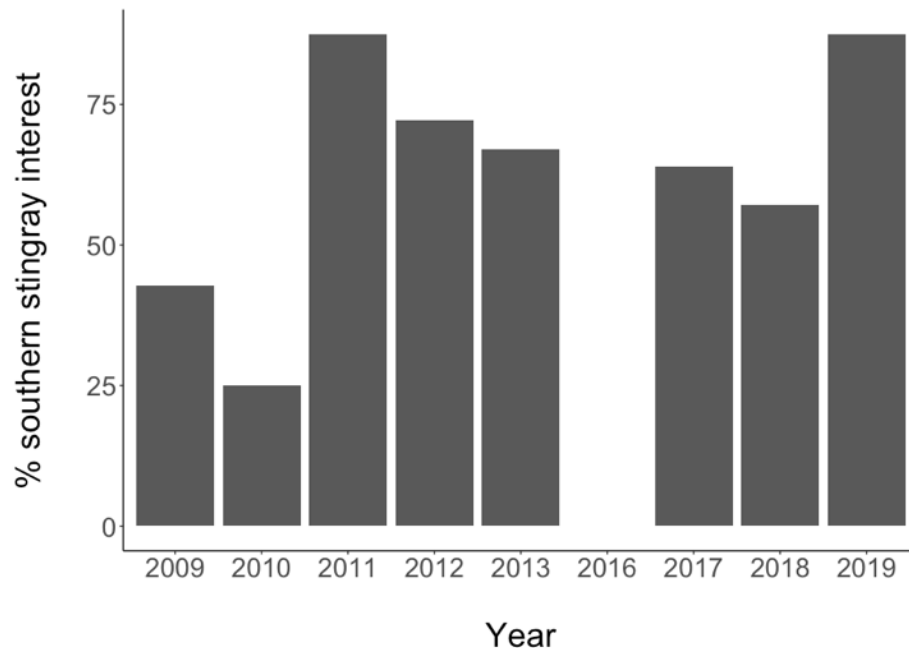


Figure 9: Percentage of events where southern stingrays were interested in the bait over time on the forereef. In 2016, southern stingrays were not interested in the bait in 3/3 events.

Inter- and intraspecies interactions were rare and only occurred on seven BRUVS. Southern stingrays co-occurred in the FOV with Caribbean reef sharks twice of 131 total events, 19 times with nurse sharks, never with whitespotted eagle rays, and twice with other southern stingrays. Both southern stingray interactions with a Caribbean reef shark involved “no response” and occurred on the same BRUVS set. In both events, a small Caribbean reef shark appeared to be startled by an approaching southern stingray. A southern stingray fled from a nurse shark in three of the 19 events but southern stingrays did not respond in the other 16 events with nurse sharks. In one case labelled “no response”, however, a southern stingray appeared to flee from the noise of nurse sharks interacting with the BRUVS frame.

Passive acoustic telemetry

Southern stingrays

Southern stingrays were frequently detected within our receiver array; however, by mid 2020 when receivers began to fail and needed to be removed from the array, fewer stingrays were detected (Figure 10). Southern stingrays were mainly resident to the GRMR lagoon for periods up to three years (Figure 10). Residency indices ranged from 0.002 – 0.85 (mean 0.34 ± 0.06 SE) (Table 1). Seven of thirty individuals were detected more than once on a forereef receiver and the two most frequently visited forereef sites were White Sands (33.1% of forereef detections) and Long Caye Channel (64.7% of forereef detections), indicating that southern stingrays rarely use complex reef habitats. Mean MLD for all southern stingrays was 5.9 km (± 0.9 SE) and Stingray 2 had the largest MLD (29.1 km). Stingray 2 was detected at multiple forereef receivers including Baking Swash, Northeast Point, Northwest Point, Middle Caye Reef, Southwest Elbow, and Southwest Caye Reef. However, she was consistently detected only at lagoon receivers for two years before making large scale forereef movements in the last week before detections ceased (see Appendix I). This may indicate a predation event occurred. Two individuals were only ever detected at the receiver closest to their original tagging location (MLD in both cases = 0.4 km).

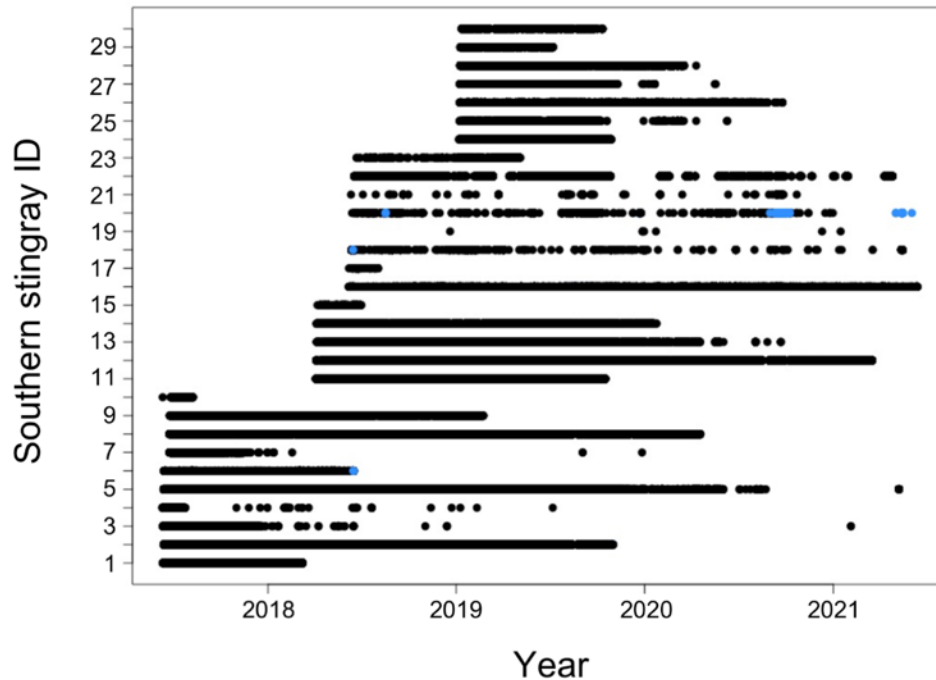


Figure 10: Abacus plot for southern stingrays summarizing detections on all receivers over time using full dataset. Black points represent lagoon detections and blue points represent reef detections.

Twenty two of 30 individuals were detected in the truncated dataset, but one individual was only detected once (Stingray 4). Comparison of mean number of detections across habitats and diel periods may indicate that a few individuals move into forereef habitat at night (Figure 11). However, these nightly detections on forereef receivers were dominated by Stingray 16 at White Sands. Southern stingrays were primarily detected inside the lagoon across all diel periods (Figure 11). The mean core use area across 19 individuals with a sufficient number of detections was 0.26 km^2 ($\pm 0.05 \text{ SE}$) and the mean general use area was 1.63 km^2 ($\pm 0.39 \text{ SE}$) as estimated by the dBBMMs. Southern stingrays primarily used shallow sandflat and seagrass habitats inside the lagoon (Figure 12).

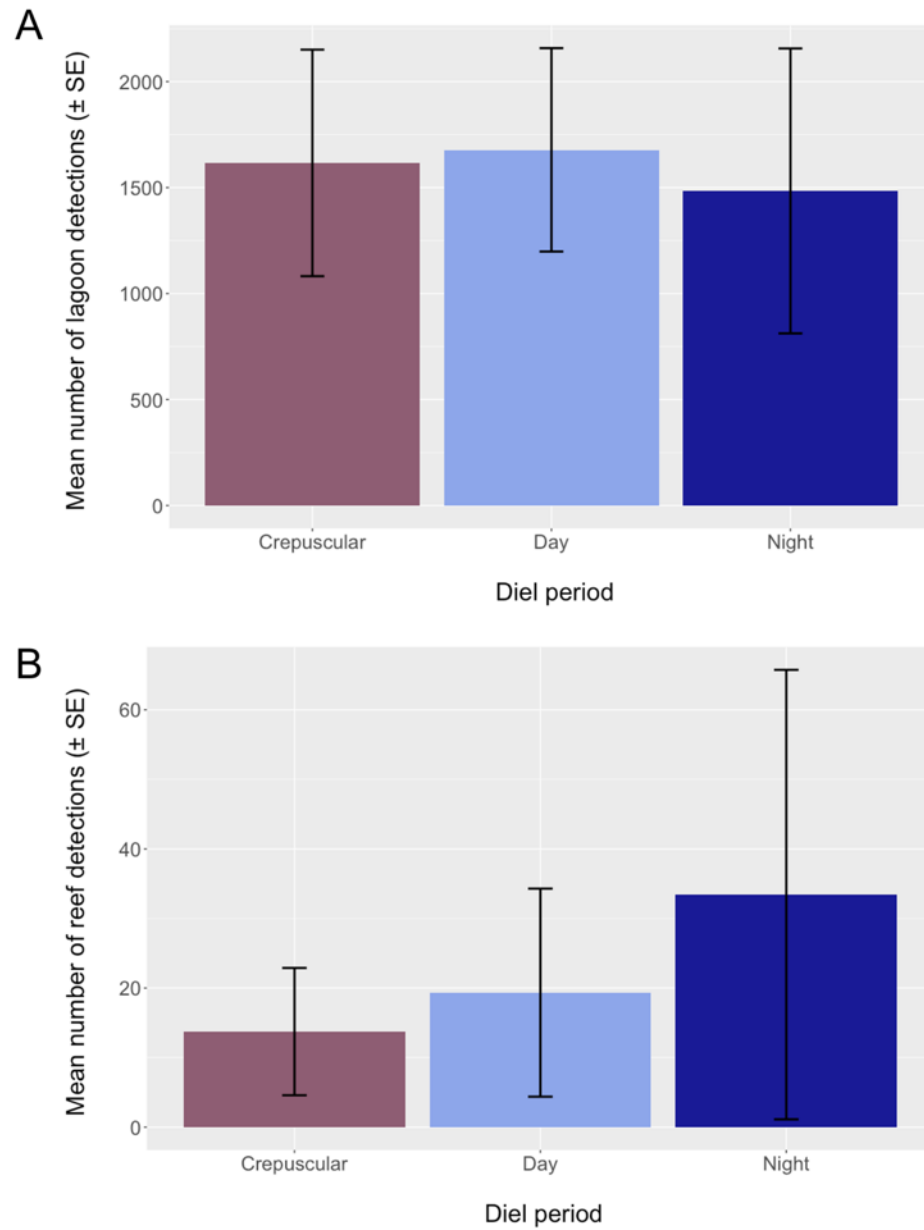


Figure 11: Mean total number of individual southern stingray detections with standard error (SE) bars across diel periods (A) in the lagoon and (B) on the forereef.

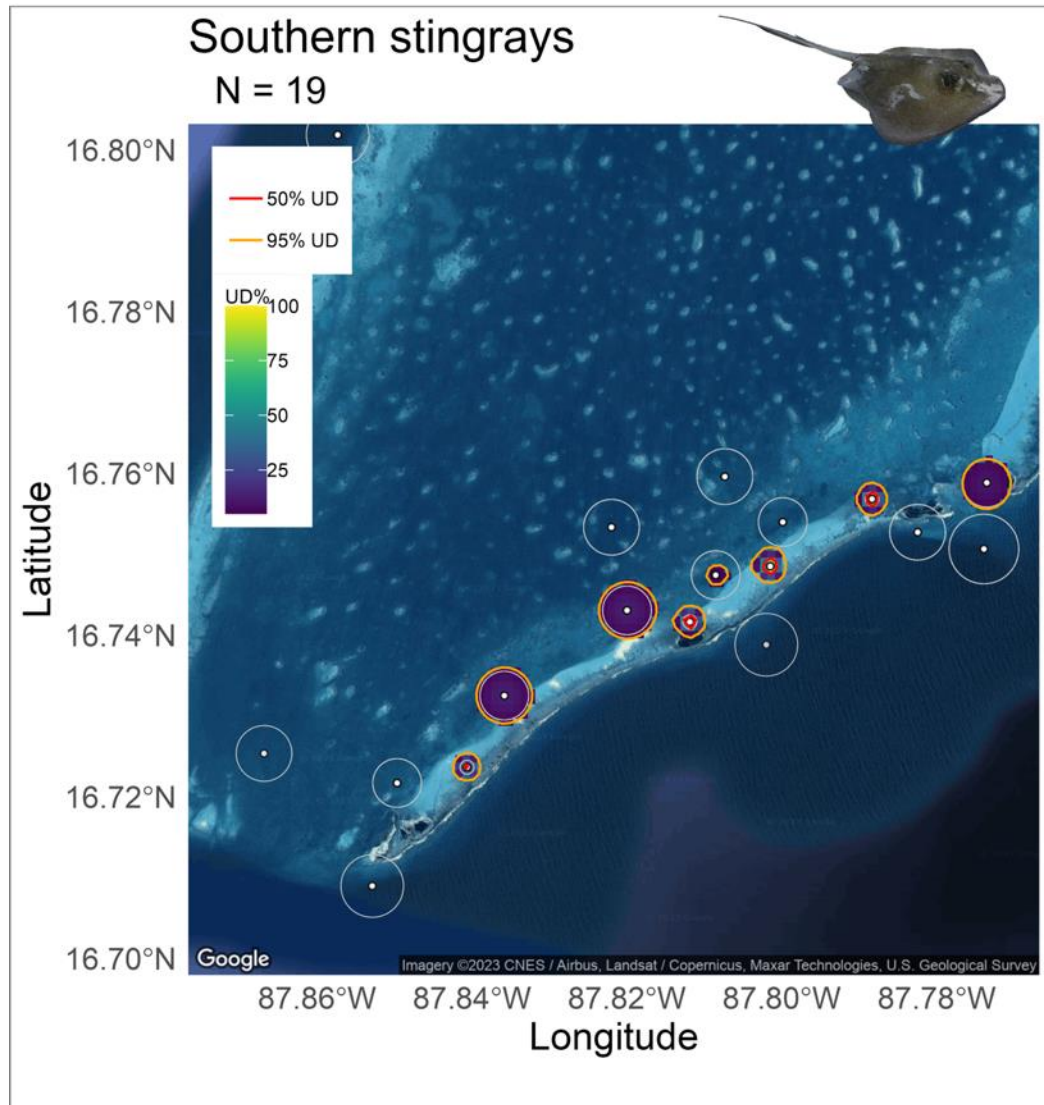


Figure 12: Southern stingray utilization distribution (UD) with 50% core use area outlined in red and 95% general use area outlined in orange, estimated using a dynamic Brownian bridge movement model. White points represent receiver locations with detection ranges depicted by open white circles. Only receivers where southern stingrays were detected are shown.

Caribbean reef sharks

Twenty seven out of 30 Caribbean reef sharks were detected in our array and many remained resident to GRMR throughout the duration of this study (Figure 13). Residency indices ranged from 0.01 – 0.98 (mean 0.28 ± 0.07 SE) (Table 1). Caribbean reef sharks used lagoon and forereef habitats (Figures 13 & 14). At least one of these sharks was lost due to illegal fishing (Caribbean reef shark 15; Flowers *et al.* 2022). Twenty individuals were detected in the truncated dataset. Mean number of detections across habitats and diel periods may indicate limited use of the lagoon during the day (Figure 14). Core use areas were primarily at Northwest Point on the forereef and Site 2 inside the lagoon (Figure 15). General use areas indicated that Caribbean reef sharks moved frequently in and around GRMR (Figure 15). Caribbean reef shark mean core use area was 0.57 km^2 (± 0.04 SE) and the mean general use area was 3.80 km^2 (± 0.50 SE) as estimated by the dBBMMs.

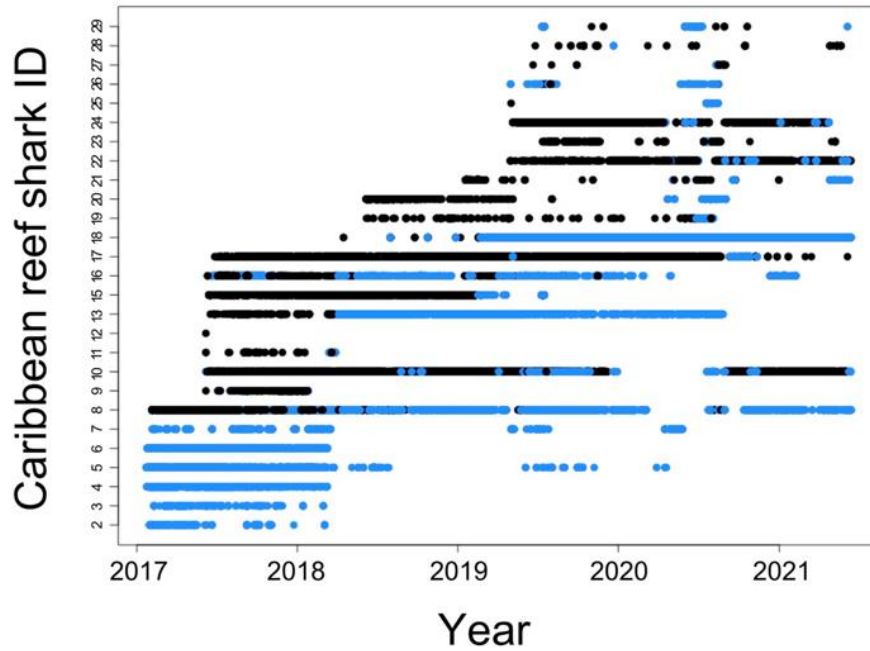


Figure 13: Abacus plot for Caribbean reef sharks summarizing detections on all receivers over time using full dataset. Black points represent lagoon detections and blue points represent reef detections. Shark 15 died in November 2019 when it was illegally fished (Flowers *et al.* 2022).

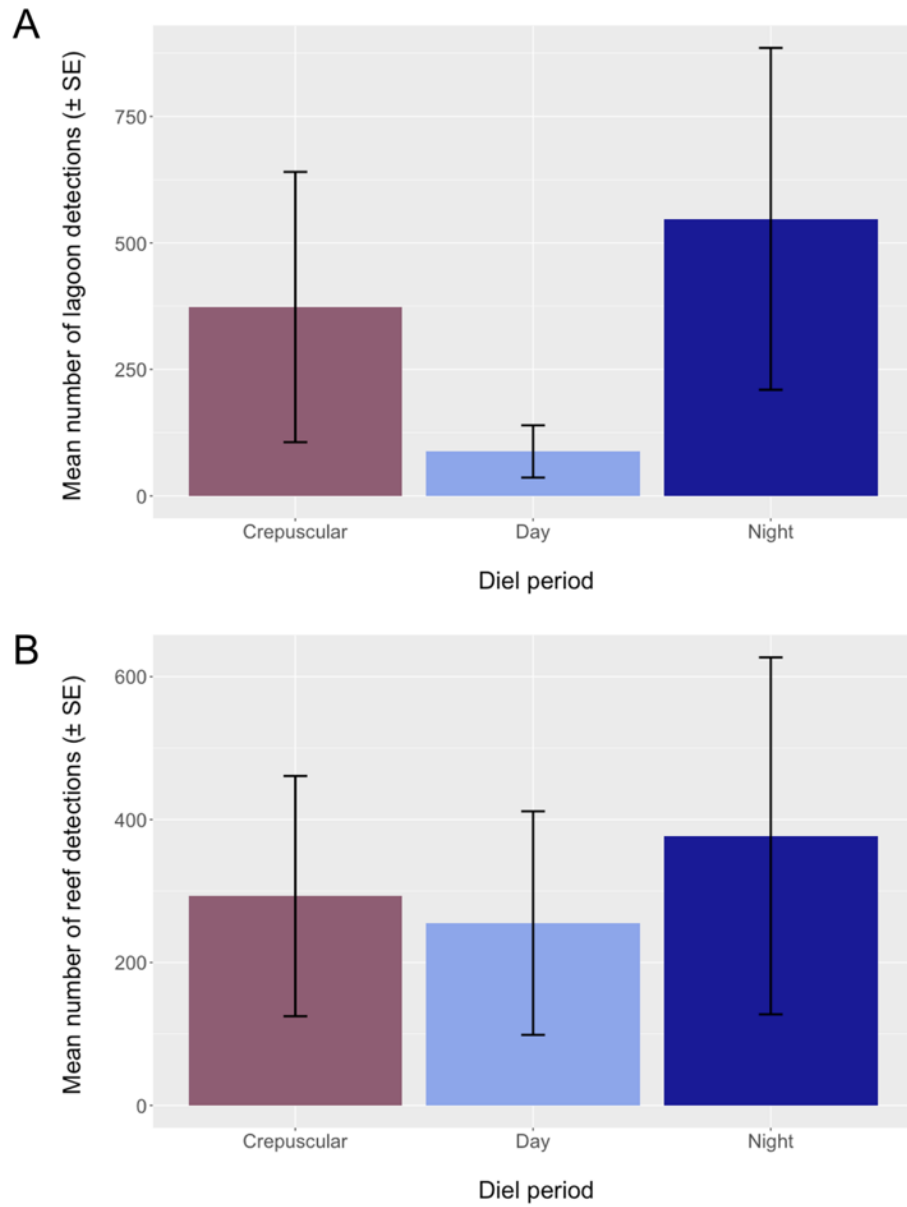


Figure 14: Mean total number of individual Caribbean reef shark detections across diel periods with standard error (SE) bars (A) in the lagoon and (B) on the forereef.

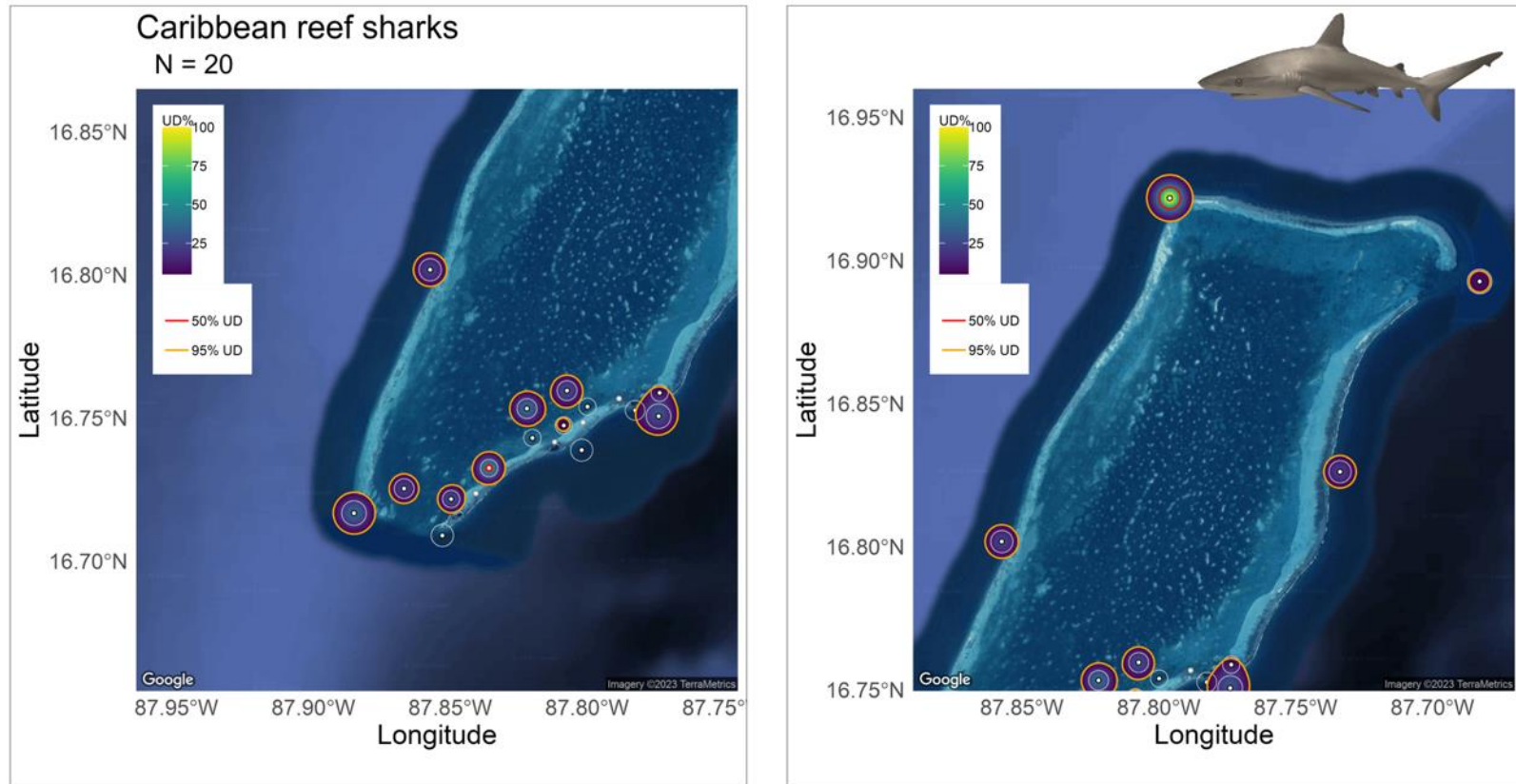


Figure 15: Caribbean reef shark utilization distribution (UD) with 50% core use area outlined in red and 95% general use area outlined in orange, estimated using a dynamic Brownian bridge movement model. White points represent receiver locations with detection ranges depicted by open white circles. Caribbean reef sharks were detected at each of our receiver sites, with the exception of Site 4. The receiver at Site 4 was pulled in August 2020 with no detections and suspected to have failed.

Lemon sharks

All tagged individuals were detected within our receiver array and the truncated dataset (Figure 16). Lemon sharks were resident to GRMR for periods of at least three years (Figure 16) and were mostly detected inside the lagoon, with no apparent diel pattern in mean number of detections (Figure 17). Residency indices ranged from 0.02 – 0.99 (mean 0.51 ± 0.17 SE) (Table 1). Core use and general use areas were estimated with five individuals that had enough detections and were located inside the lagoon along the shallow sandflats and on seagrass beds (Figure 18). Lemon shark mean core use area was $0.14 \text{ km}^2 (\pm 0.06 \text{ SE})$ and the mean general use area was $1.53 \text{ km}^2 (\pm 0.27 \text{ SE})$ as estimated by the dBBMMs.

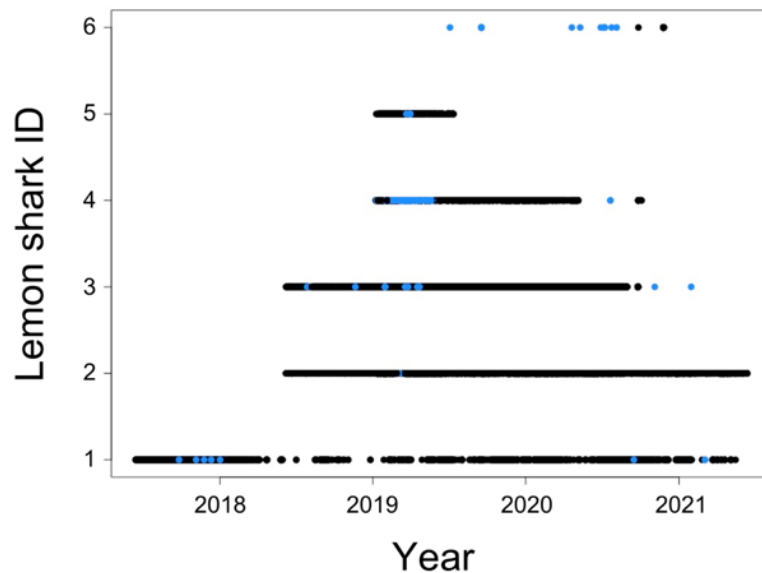


Figure 16: Abacus plot for lemon sharks summarizing detections on all receivers over time using full dataset. Black points represent lagoon detections and blue points represent reef detections.

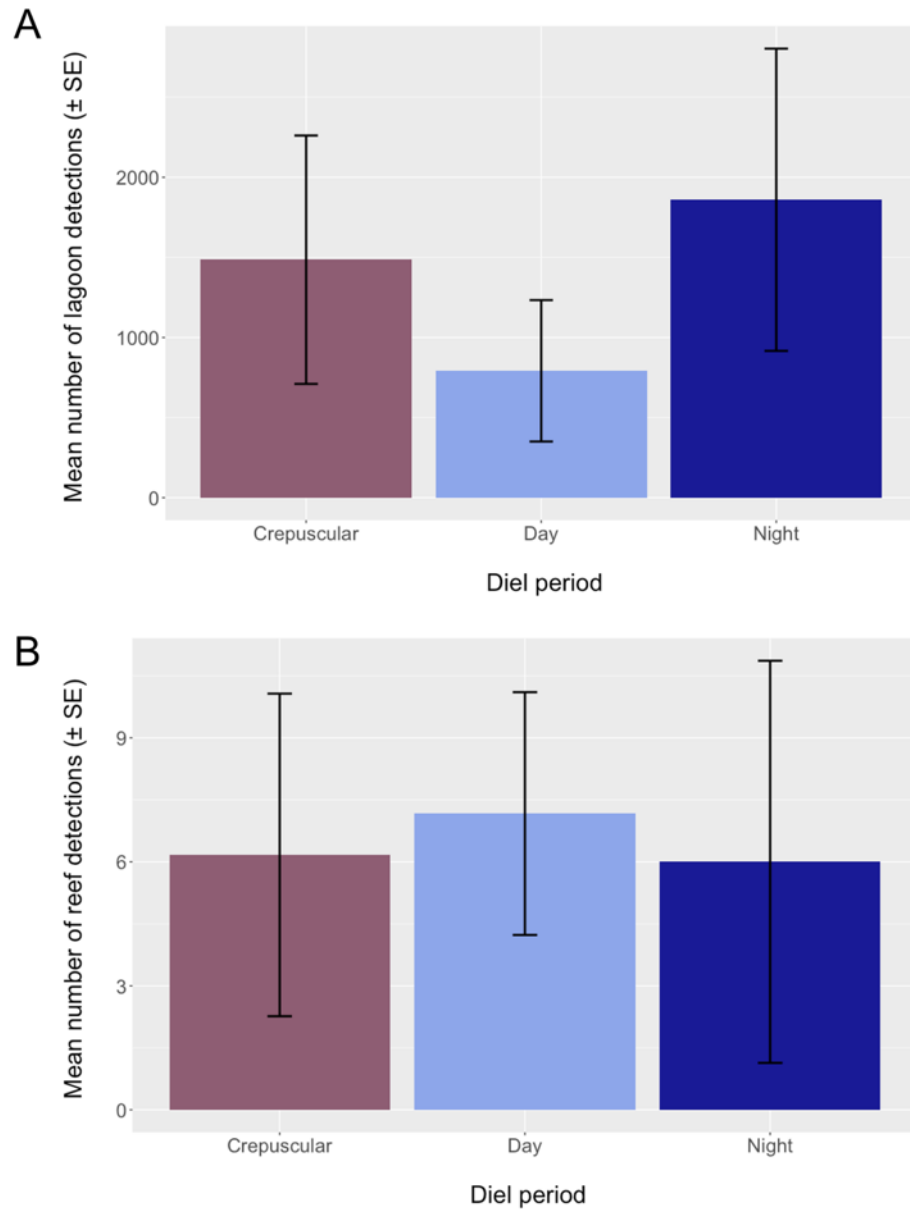


Figure 17: Mean total number of individual lemon shark detections with standard error (SE) bars across diel periods (A) in the lagoon and (B) on the forereef.

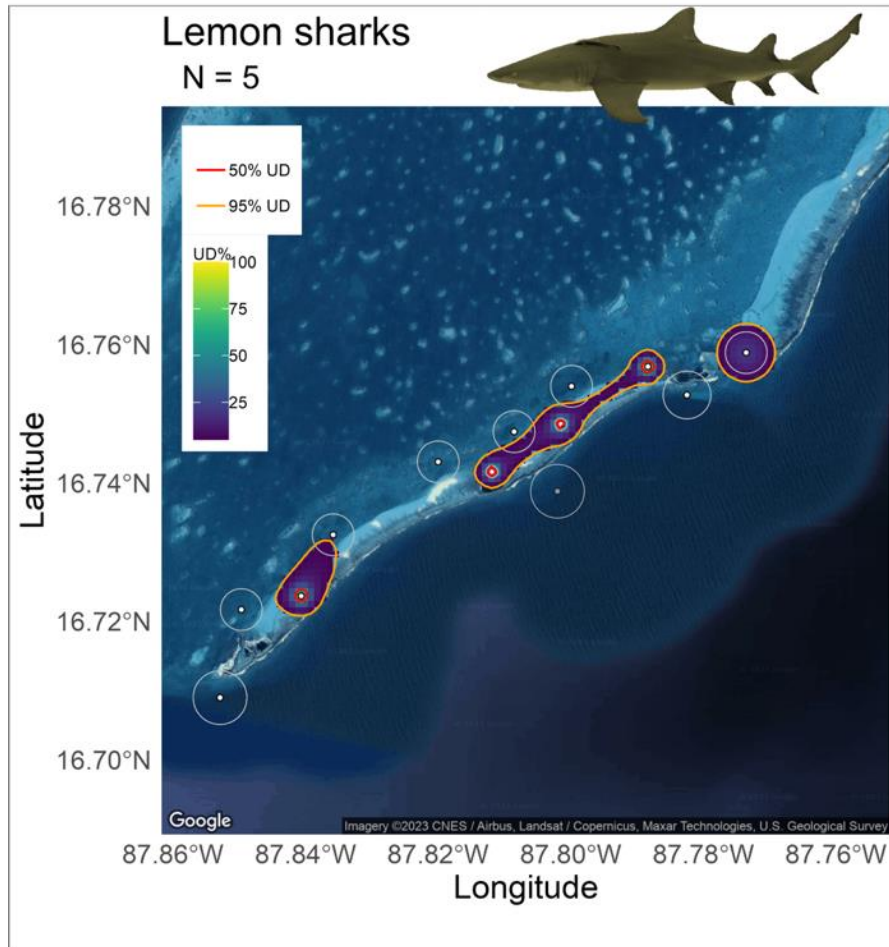


Figure 18: Lemon shark utilization distribution (UD) with 50% core use area outlined in red and 95% general use area outlined in orange, estimated using a dynamic Brownian bridge movement model. White points represent receiver locations with detection ranges depicted by open white circles. Only receivers where lemon sharks were detected are shown.

DISCUSSION

Our long-term BRUVS dataset did not reveal evidence of mesopredator release involving southern stingrays following a Caribbean reef shark decline at GRMR in Belize. Southern stingray sightings (MaxN) and behaviour (TIF) were stable between 2009 – 2019 on the forereef inside the replenishment zone.

Southern stingray sightings were consistently higher inside the lagoon at the beginning (2012) and end of our study (2018, 2019). These results aligned with our acoustic data that showed southern stingrays tagged inside the lagoon rarely venture into forereef habitat. Additionally, both Caribbean reef and lemon sharks at GRMR commonly use shallow sandflat and other lagoon habitat, therefore it is unlikely that the shallow lagoon is a spatial refuge from predation risk for southern stingrays.

If southern stingray behaviour was predominantly affected by predation risk induced by Caribbean reef sharks (Bond *et al.* 2019), we would have expected a habitat shift onto the forereef as Caribbean reef sharks declined. Yet, southern stingray sightings did not increase on the forereef BRUVS across years and southern stingrays tagged in the lagoon rarely moved out onto the forereef. Southern stingray core habitat use was inside the lagoon in soft bottom habitats, and there were more southern stingrays sighted in lagoon habitat compared to forereef habitat in 2012, 2018, and 2019. Combined, these results likely reflect a preference for lagoon habitat rather than a habitat shift induced by predation risk.

We did not find support for our prediction that southern stingray TIF would increase over time as Caribbean reef sharks declined. Instead, southern stingray TIF remained stable over time. Southern stingray TIF was positively correlated to year and year was included in the best TIF model, so we cannot rule out an effect of Caribbean reef sharks on southern stingray behaviour given that Caribbean reef sharks declined over time. However, southern stingray TIF also had a positive relationship with Caribbean reef shark MaxN, suggesting that they

may spend more time in frame when Caribbean reef shark abundance is higher. A positive correlation between southern stingray TIF and year may also be explained by declining reef relief over time that could have made it easier to detect rays when present in the later years of our study (S2 Figure). Southern stingray interest in bait was also not associated with Caribbean reef shark abundance.

Although Caribbean reef sharks were the only predator species considered in Bond *et al.* (2019), GRMR has a multi-predator assemblage including roving great hammerheads (*Sphyrna mokarran*) and tiger sharks (Pikitch *et al.* 2005, DKasana unpublished data). Small and medium-sized lemon sharks also frequent the shallow lagoon regularly at GRMR despite being absent on lagoon BRUVS in 2012 (Bond *et al.* 2019), 2018, and 2019. Random sampling may not always capture elasmobranch presence for species that are rare, exhibit philopatry, or have small core use areas. Lemon, tiger, and great hammerhead sharks are all apex species and likely pose an acute threat to southern stingrays of all size classes, potentially exerting stronger predation risk effects than resident mesopredator sharks (Lima & Bednekoff 1999). The southern stingray habitat shift hypothesis assumes that the shallow lagoon is a refuge where capture efficiency is reduced (Bond *et al.* 2019), but we show here that the lagoon is also risky habitat. This could explain why we found little to no evidence of a relationship between Caribbean reef shark and southern stingray MaxN, and does not mean southern stingray responses to other predators are not occurring (Sih 1984). When predators and prey have overlapping habitat

domains, which appears to be the case for southern stingrays and lemon sharks, time budget shifts are more likely than habitat shifts (Schmitz *et al.* 2017). Additionally, areas with high predator abundance are not always the riskiest places (Wirsing *et al.* 2010) and prey may not always avoid predators in space and time (e.g., Cusack *et al.* 2020).

Southern stingray sightings and behaviour on the forereef were predicted by fine scale habitat complexity. On BRUVS with high coral reef relief, there were fewer southern stingray sightings and they spent less time in the video FOV. We are unable to determine if this is due to southern stingrays selecting for less complex habitat and/or because detection probability on BRUVS decreases in places with high structural complexity (i.e., we are less likely to observe southern stingrays when present in areas with high reef relief – see S3 Figure for screenshots comparing BRUVS with low and high relief). Mean reef relief declined over time (S2 Figure) so it is possible that southern stingray detection probability was higher on BRUVS with less complex habitat in the FOV in the later years of our study. Lower reef relief in later years could be related to reef flattening and loss of hard coral cover (Alvarez-Filip *et al.* 2009, Alves *et al.* 2022); however, structural complexity of *Orbicella annularis* at colony scales at GRMR during our study period was stable (Roff *et al.* 2020). Thus, declining reef relief on BRUVS is likely a product of small differences in BRUVS placement on the seafloor over time (i.e., slightly further away from coral structures in later years, thus improving the FOV). Regardless, structural complexity often has a strong relationship with coral reef fish abundance, biomass, and diversity (e.g.,

Darling *et al.* 2017). Specifically, large teleost benthic forager biomass is negatively associated with hard coral cover (Russ *et al.* 2021) and the same could be true for southern stingrays because they are also large benthic feeders.

Southern stingray core and general use areas were inside the lagoon, and sightings were higher in low relief areas, which could simply reflect their feeding habits. Southern stingrays prey on benthic invertebrates, which are distributed in soft sediment and seagrass beds (Bigelow & Schroeder 1953, Snelson & Williams 1981, Gilliam & Sullivan 1993, Tilley 2011, Tilley *et al.* 2013).

Invertebrate biomass and richness may be higher in MPA lagoons than in non-protected lagoons, which could explain why southern stingray density was higher in a reserve lagoon (GRMR) than in a “fished” lagoon (South Water Caye) in Bond *et al.* (2019). Indeed, bivalve richness is higher at GRMR than at Turneffe Atoll, one of the non-protected sites in Bond *et al.* (2019) (Hauser *et al.* 2007). Thus, it is plausible that southern stingrays do not need to actively search for prey on MPA forereefs and are using MPA lagoons based on prey availability, rather than due to predator avoidance. Bivalve diversity, evenness, and richness at GRMR are higher in shallow habitats within the lagoon (Hauser *et al.* 2007). However, it remains unclear if southern stingrays are selecting for high density prey patches at GRMR, which could be resolved with prey sampling across habitats combined with acoustic tracking of southern stingrays (e.g., Heupel & Hueter 2002). Whitespotted eagle rays select for high density clam patches (Ajemian *et al.* 2012) and southern stingray diel movements have been altered by provisioning in the Cayman Islands (Corcoran *et al.* 2013), suggesting that

foraging is an important driver of ray behaviour. Combined, our results and these studies highlight the need to investigate the potential for prey to drive ray behaviour and habitat use either alone or in combination with other factors like predation risk and competition.

Low relief habitats may provide additional benefits to southern stingrays beyond foraging. For example, southern stingray maneuverability in complex habitats, especially at larger sizes, is limited compared to open habitats like sandflats and seagrass beds. Indeed, larger southern stingrays are found on the sandflats at GRMR, while smaller individuals are found on the forereef (Tilley 2011, Bond *et al.* 2019). Southern stingrays likely rely on crypsis (i.e., burying themselves in the sand) as their primary defense against predators, which requires soft bottom habitat. In soft bottom habitats, they can remain cryptic at a distance but once a predator detects them, they have a secondary defense (venomous tail barb) that is used as a warning signal and would increase handling time for a predator (Ruxton *et al.* 2004, Mukherjee & Heithaus 2013). The final southern stingray response would be to flee from predators, which is likely easier in open habitats with less complexity (Tilley 2011, Phenix *et al.* 2019).

Southern stingray sightings were also related to time of day. MaxN increased with hour of day, which could represent a change in activity. In Chapter 4, I show that southern stingrays are most likely active in crepuscular periods and at night. However, the probability of high activity starts to increase in the late afternoon, consistent with our BRUVS findings here. Our tracking data revealed

fewer detections of Caribbean reef sharks in the lagoon during the day compared to at night, consistent with longline capture data in Chapman *et al.* 2007.

Caribbean reef shark abundance and activity is highest at night (Chapman *et al.* 2007, Shipley *et al.* 2018), supporting a need to study diel patterns of risk across the seascape (Palmer *et al.* 2022).

Finally, we acknowledge that our study has limitations that may be contributing to our results. For example, our sample size used to predict the factors describing southern stingray TIF on the forereef was small. For this analysis, only BRUVS that had a southern stingray present (N BRUVS = 42) were included. Caribbean reef shark MaxN did not vary much within the truncated dataset (0 – 1) to determine if Caribbean reef shark MaxN predicted southern stingray TIF. Year was likely a better proxy for Caribbean reef shark abundance since abundance declined over time (Flowers *et al.* 2022), but reef relief also declined over time (S2 Figure). Our ability to detect a year effect was relatively low. Additionally, southern stingrays come in and out of the FOV often, so calculating time in frame should be done using 360° BRUVS (Kilfoil *et al.* 2017) and/or in cases where individual identification is possible (Sherman *et al.* 2020). This would make it easier to track individuals throughout each deployment and calculate mean time in video frame across all individuals rather than summed total time in video frame across events. The energetic state of the stingray may also affect interest in foraging (e.g., Brown & Kotler, 2004) and will be confounded within the TIF results. At our study site, elasmobranch behaviour may be influenced by human factors outside of our control. For example, in the

lagoon elasmobranchs are often sighted at fish cleaning sites and tourism operations sometimes attract elasmobranchs using bait. This could be contributing to increased elasmobranch use of shallow lagoon habitat compared to forereef habitat at GRMR. Southern stingray density is indeed high in the lagoon outside of the replenishment zone near where fishers clean their catch (Tilley & Strindberg 2013). Our receiver coverage is also quite low, particularly on the forereef and in the deep lagoon, limiting our ability to detect tagged individuals when they use these habitats. We were unable to catch and tag male southern stingrays or any southern stingrays on the forereef, so it remains unclear if there are individual or sex level differences in habitat use. The 95% general use area for one individual (Stingray 20) that was tagged close to forereef habitat did show some preference for habitats around White Sands and Long Caye Channel (Appendix 1). Our sample size of lemon sharks was small and we also did not catch any in forereef habitat. And although all lemon sharks were immature at time of capture, their relative size compared to southern stingrays was large enough to be presumed predators. Despite these limitations, we remain confident that southern stingray sightings were stable on the forereef in GRMR, in the relationship between habitat complexity and southern stingray sightings and behaviour on BRUVS, and that the lagoon is a key habitat for elasmobranchs at GRMR.

CONCLUSION

The context dependent nature of top-down processes in complex ecological systems demands our careful consideration of evidence for or against mesopredator release (Grubbs *et al.* 2016, Allen *et al.* 2017, Wirsing *et al.* 2021). There is a growing body of literature that suggests shark declines do not always lead to mesopredator release (e.g., Grubbs *et al.* 2016, Desbiens *et al.* 2021, Lester *et al.* 2021), which could be a possibility based on our findings here. Despite previous work on southern stingrays at GRMR suggesting that their behaviour is driven primarily by predation risk (Tilley 2011, Bond *et al.* 2019), our long-term and spatial work highlights the need for further investigation. Until alternative hypotheses for southern stingray habitat use and behaviour are explored and rigorously tested, we suggest that evidence for Caribbean reef sharks inducing a southern stingray habitat shift at GRMR remains weak. We show some evidence that reef complexity predicts southern stingray sightings and TIF, either because reef complexity affects stingray detectability on BRUVS, because of stingray habitat selection, or both. Resolving between the two requires further investigation using multiple and improved survey techniques; however, we show that southern stingray habitat use was primarily inside the lagoon between 2017 and 2022. Our results align with previous studies that stress the importance of incorporating fine scale habitat heterogeneity into studies aiming to answer complex biological and ecological questions (e.g., Ryer 1988, Forrester & Steele 2004, Kauffman *et al.* 2007, Catano *et al.* 2016, Darling

et al. 2017, Lester *et al.* 2021) and that stingrays likely prefer soft bottom habitats (e.g., Costa *et al.* 2015, Meese & Lowe 2019, Martins *et al.* 2020, Elston *et al.* 2021). Tracking data also highlighted the use of lagoon habitat by both Caribbean reef and lemon sharks, demonstrating that it is not likely a spatial refuge for southern stingrays. While the positive correlation between southern stingray TIF and year may hint at the possibility of a shark effect, both reef relief and Caribbean reef sharks declined over time making it difficult to interpret the mechanism driving that relationship. We emphasize the need to develop questions and experiments that will improve our understanding of the interaction strength between reef sharks and rays, consider diel patterns of risk, and test the potential for bottom-up processes, competition, and other unmeasured differences across study locations (e.g., mangrove cover, number of patch reefs inside lagoons, turbidity, sedimentation [Stoddart 1962, Gischler 1994, 2018]) to influence stingray abundance, density, habitat use, and behaviour (e.g., see Moll *et al.* 2017).

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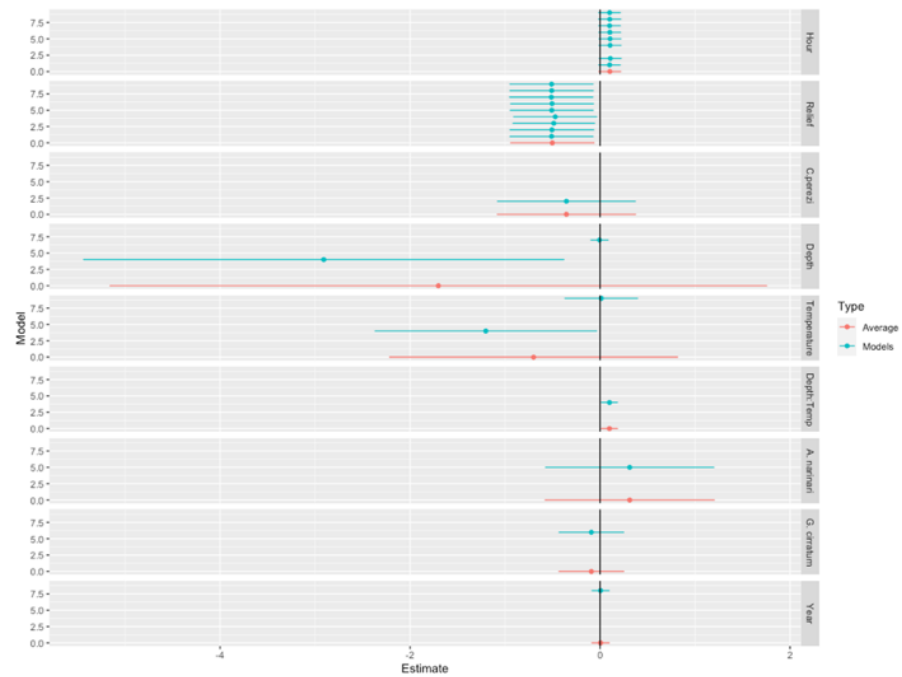
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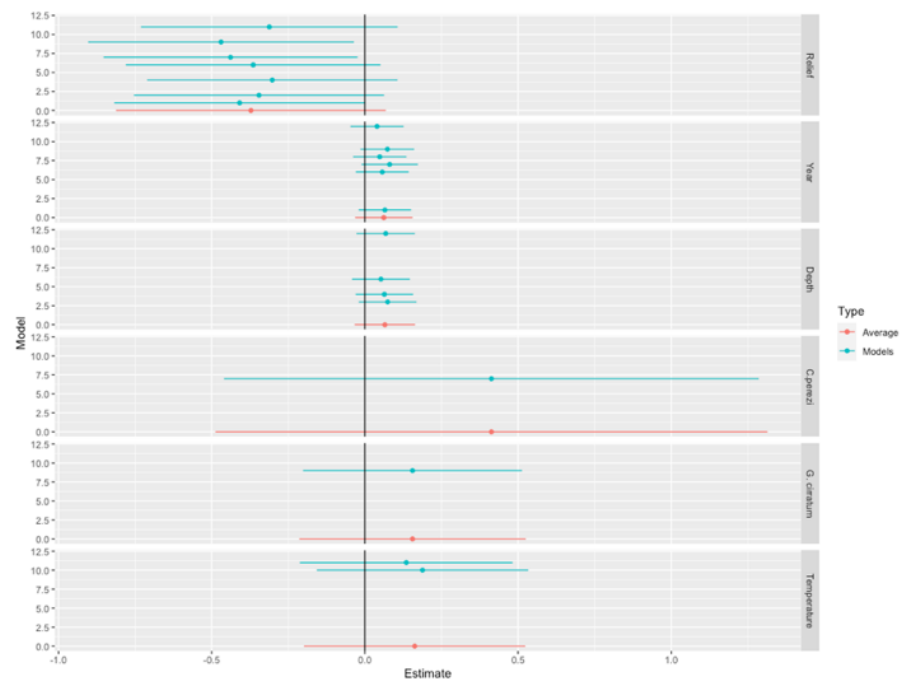
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SUPPLEMENTARY FIGURES FOR CHAPTER III

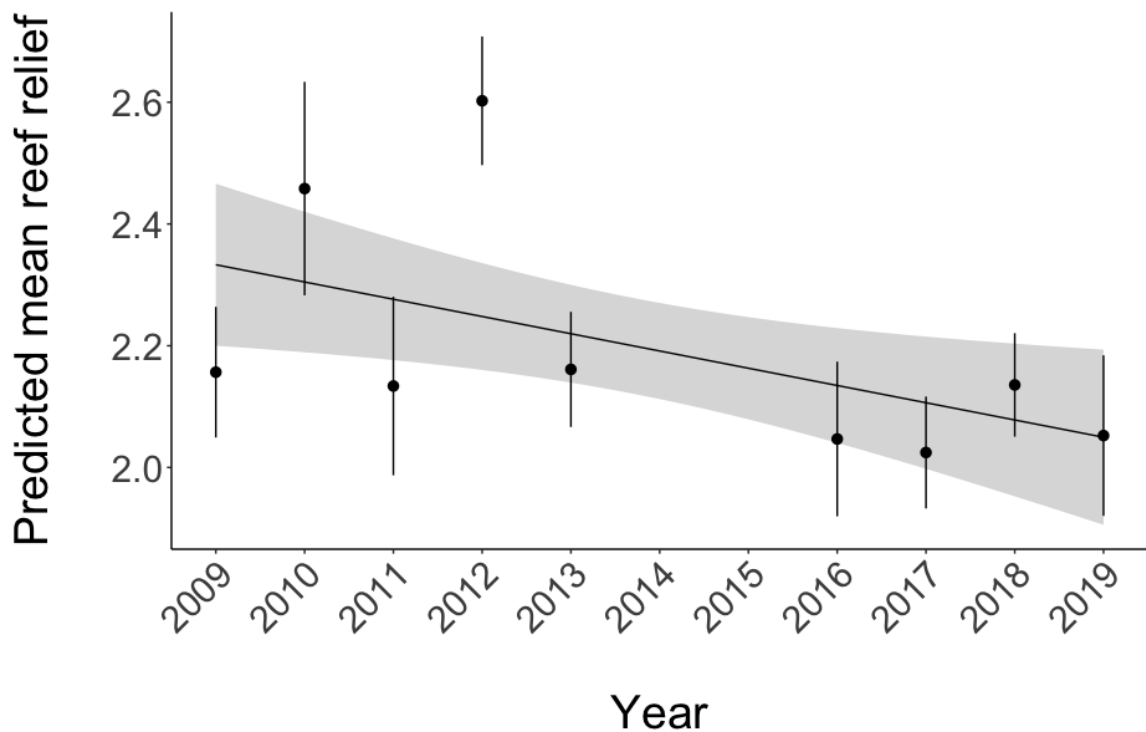
A) MaxN models



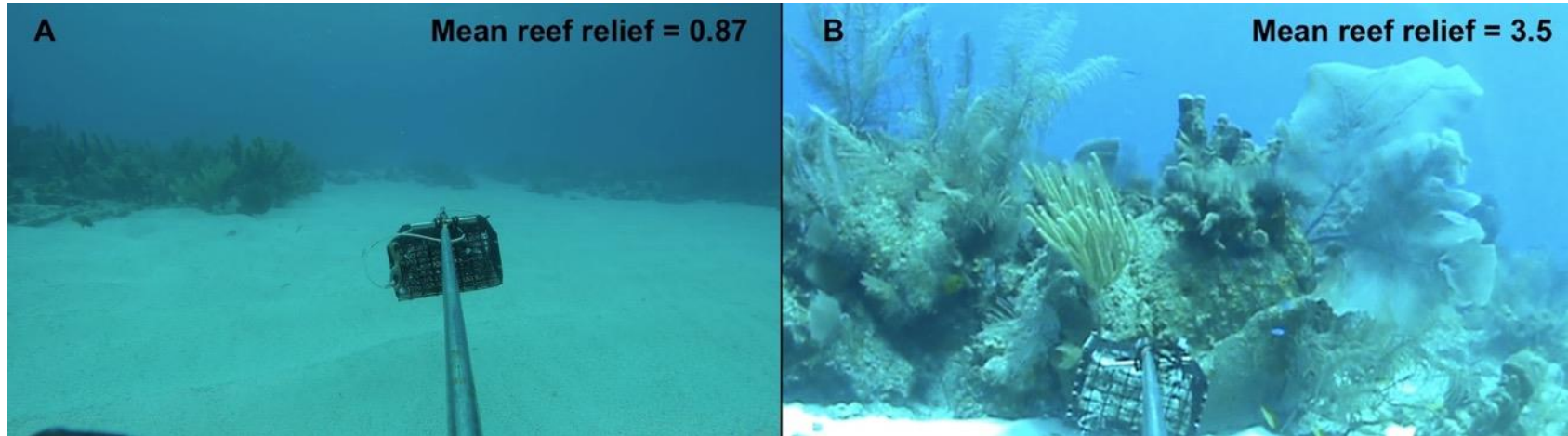
B) TIF models



Supplementary Figure 1: Coefficient estimates from model averaging for (A) southern stingray sightings (MaxN) models and (B) southern stingray behaviour (total time in frame) models (forereef data). Model averaging was selected for southern stingray sightings models because the coefficient estimates from the component models for predictor variables “Depth” and “Temperature” differed (A). Model averaging was not selected for the southern stingray behaviour models because the coefficient estimates were similar across all component models (B).



Supplementary Figure 2: Predicted decline in mean reef relief on the forereef inside the replenishment zone over time (black trendline) with 95% confidence intervals (grey shaded area). Points represent mean reef relief $\pm$ SE from observed data. Predictions were made from a linear regression model (reef relief $\sim$ year) using the R package “*jtools*” (Long 2020) and plotted with “*ggplot2*” (Wickham 2016).



Supplementary Figure 3: Baited remote underwater video station screenshots on the forereef comparing examples of low mean reef relief (A; 2018 deployment) and high mean reef relief (B; 2013 deployment). Southern stingrays may be more detectable when the video field of view (FOV) contains lower relief habitat (A). High reef relief in the FOV may be constraining our ability to detect rays if they swim or hide in or behind reef structure (B). The bait box location within the FOV may also affect southern stingray detectability.

CHAPTER IV

DIEL ACTIVITY PATTERNS OF A TROPICAL STINGRAY ACROSS DEPTH AND TEMPERATURE REVEALED BY HIDDEN MARKOV MODELS

ABSTRACT

Animals display a range of daily activity patterns that can be influenced by various biological and environmental factors. Elasmobranchs (rays and sharks) often have nocturnal or crepuscular peaks in activity. The advent of new tagging technologies in the last two decades has improved our ability to measure high resolution animal activity, yet biologging for rays remains in its infancy. Biologging can help us better understand how rays interact with their environment and other species. Here, I used accelerometry to calculate dynamic body acceleration and hidden Markov models (HMMs) to classify female southern stingray (*Hypanus americanus*) activity states across diel periods and environmental variables at a barrier reef site and an offshore coral reef atoll in Belize. Two (low and high activity) and three state (low, medium, and high activity) HMMs were constructed for all individuals combined and each individual separately (N = 9). When analyzed together, all stingrays demonstrated a high probability of being in a medium activity state around sunrise and a high probability of being in a high activity state post-sunset, likely representing crepuscular behaviour. Depth was an important predictor of changes in southern stingray activity, with stingrays being highly active in shallow water (<5 m) and

the deepest habitat used by one individual was at 19.8 m. The probability of being in a medium activity state increased with water temperature for all stingrays combined. There were individual differences in activity patterns across covariates, consistent with recent findings for several elasmobranch species. Southern stingray activity patterns and depth use are most likely related to foraging considerations; however, I cannot rule out that predation risk also plays a role in shaping southern stingray diel activity patterns.

INTRODUCTION

Animals exhibit a range of activity patterns in the wild that often follow daily cycles (Daan & Aschoff 1981). Activity can peak at night (nocturnal), during the day (diurnal), at dawn and/or dusk (crepuscular), be variable across a 24-hour period (cathemeral), and even occur constantly over time (ultradian) (e.g., DeCoursey & DeCoursey 1964, Nelson & Vance 1979, Odell & Mastro 1980, Bloch *et al.* 2013, Goldstein *et al.* 2015, Monette *et al.* 2020, Andreoni *et al.* 2021; but see Ito *et al.* 2022 for a more thorough list). Daily activity patterns can be endogenous (i.e., circadian rhythms), but are often influenced by external factors (Aschoff 1960, Daan & Aschoff 1981). The optimal time to be active can depend on prey activity and availability, environmental conditions, the need to avoid predators, and/or the need to reduce competition (e.g., Nelson & Vance 1979, Metcalfe *et al.* 1999, Reeb 2002, Kronfeld-Schor & Dayan 2003, Zhdanova & Reeb 2006, Bosiger & McCormick 2014, Courbin *et al.* 2019, Tatler

et al. 2021). Temperature dependent physiological processes, body condition, seasonal changes, and ontogeny also affect animal activity (e.g., Metcalfe *et al.* 1998, Matern *et al.* 2000, Reeb 2002, Houston & McNamara 2014, Tatler *et al.* 2021). Activity is often shaped by the multifaceted trade-offs that animals must manage in response to changes in internal and external biotic conditions and abiotic factors (e.g., Metcalfe *et al.* 1998, 1999, 2004). Animals can exhibit intraspecific and individual variation in activity (e.g., Fox & Bellwood 2011, Papastamatiou *et al.* 2022), therefore an adequate number of individuals and habitats need to be sampled to know how pervasive a pattern may be within a species or population.

The southern stingray (*Hypanus americanus*) is a large benthic stingray (Dasyatidae) common throughout its range in the Caribbean, the Gulf of Mexico, and along the eastern seaboard of the United States (Carlson *et al.* 2020, Chapter 2). Initial investigations into southern stingray movements in Puerto Rico and Grand Cayman Island suggested that they are primarily nocturnal (Clark *et al.* 2009, Corcoran *et al.* 2013). This nocturnal activity pattern was also supported by tri-axial acceleration data collected from southern stingrays in The Bahamas (Ward *et al.* 2019). Based on active tracking however, it is thought that southern stingrays at Glover's Reef Atoll in Belize may be diurnal, but with a high degree of individual variation (Tilley *et al.* 2013). Diurnal activity by small stingrays could be in response to increased predation risk from sharks at night; however, inferring activity from patterns of space use may be problematic, especially for benthic species which may be highly active over a small area. Therefore, the use

of acceleration loggers could improve our understanding of stingray activity (e.g., Payne *et al.* 2014, Whitney *et al.* 2018), but have rarely been used on Dasyatid stingrays (Otaki *et al.* 2015, Ward *et al.* 2019).

Acceleration measures a change in velocity over time and overall dynamic body acceleration (ODBA) represents the full scope of animal motion (activity), which is a proxy for energy expenditure (Wilson *et al.* 2006, Gleiss *et al.* 2011, Wilson *et al.* 2020). My research goal was to measure southern stingray activity, using ODBA, across diel periods, depths, and temperatures in Belize. To analyze patterns of ray activity, I used hidden Markov models (HMMs). HMMs can infer behavioural states in a time series dataset when the actual behaviours are unknown, using an unsupervised learning approach (Phillips *et al.* 2015, Zucchini *et al.* 2016, Leos-Barajas *et al.* 2017). If southern stingray activity is driven by predator avoidance (Tilley *et al.* 2013, Bond *et al.* 2019), I would expect peaks of activity to occur when predators are less active. The Caribbean reef shark (*Carcharhinus perezii*), the hypothesized main predator of southern stingrays at Glover's Reef Atoll, is more common in lagoon habitats at night, and exhibits post-sunset crepuscular activity (Chapman *et al.* 2007, Shipley *et al.* 2018, Bond *et al.* 2019). Therefore, sharks may be less likely to be encountered during the day, which would afford the stingrays the opportunity to feed in this period of relative safety. If southern stingray activity is instead based primarily on foraging considerations, I would expect peaks of activity to occur post-sunset and at night in shallow water in response to prey availability and activity patterns. Southern stingrays feed on invertebrates, many of which occur in shallow soft bottom

habitats and display post-sunset crepuscular and nocturnal activity (Bigelow & Schroeder 1953, Reynolds & Casterlin 1979, Snelson & Williams 1981, Stoner 1991, Smith & Herrnkind 1992, Gilliam & Sullivan 1993, De Grave *et al.* 2006, Hauser *et al.* 2007, Tilley 2011, Zantke *et al.* 2013).

METHODOLOGY

Data collection and animal handling

Two southern stingrays were captured on a shallow 20-hook longline using 16/0 circle hooks between Tobacco Caye and South Water Caye, Belize on 08 July 2017 (Figure1). Both cayes are part of the Mesoamerican Barrier Reef system, the second largest barrier reef in the world, located in the Caribbean Sea (Bland *et al.* 2017). Tobacco Caye is approximately 18 km offshore from Dangriga, Belize and South Water Caye is approximately 21 km offshore from Hopkins, Belize. Rays (superorder Batoidea) are relatively common on the forereef near South Water Caye, including southern stingrays (Clementi 2017). In June 2018, one southern stingray was captured on a shallow 20-hook longline using 16/0 hooks and one southern stingray was captured using a traditional Belizean handline with a 3/0 J hook in the shallow lagoon at Glover's Reef Atoll in Belize (Figure 1). An additional seven southern stingrays were captured in June 2019 using a 12-foot cast net with one inch mesh at Glover's Reef Atoll on shallow sandflat and seagrass beds inside the lagoon (Figure 1). Glover's Reef

Atoll is located approximately 45 km offshore from mainland Belize and makes up the marine protected area known as Glover's Reef Marine Reserve (Wildtracks & Wildlife Conservation Society 2007).



Figure 1: Map of study area with southern stingray capture locations represented by white circles with black dots in the middle. Two southern stingrays were caught near Tobacco Caye, Belize on the barrier reef and nine southern stingrays were caught in the southeast portion of Glover's Reef Atoll, Belize. All stingrays were captured in backreef habitat.

Southern stingrays were brought on the boat using a dipnet and workups lasted an average of 11 minutes and 24 seconds (± 3 minutes 33 seconds SD), during which time the spiracles were constantly flushed with seawater. Each stingray was scanned for an existing passive integrative transponder (PIT tag) and measured from wingtip to wingtip at the widest part of their pectoral fins (disc width, DW). New individuals had a PIT tag (Biomark, Inc. Mini HPT8) implanted near the base of the tail where it connects to the pelvic fin and no individual recaptures were made throughout the duration of this study. Small fin clips were

collected for genetic analyses and sex was recorded for each individual. All eleven southern stingrays captured for this study were females with DWs ranging from 63 cm to 85 cm (Table 1). Female southern stingrays mature between 75 and 80 cm, therefore it is likely most individuals in this study were maturing or mature (McEachran & de Carvalho 2002, Henningsen & Leaf 2010, Ramírez-Mosqueda *et al.* 2012). Two individuals were noted to be possibly gravid due to their convex dorsal surface above the uterine region (Stingray 1 [78 cm DW] and Stingray 9 [74 cm DW]).

Individual	Capture date (dd-mm-yy)	Capture time (hh:mm)	Location	Gear type	Sex	Disc width (cm)	Deployment duration	Data logger version
Stingray 1	08-07-17	20:01	BR	LL	F	78	54 hr 58 min	3
Stingray 2	08-07-17	22:15	BR	LL	F	81	56 hr 06 min	3
Stingray 3*	04-06-18	06:36	GRA	LL	F	85	24 hr 35 min	3
Stingray 4*	12-06-18	08:10	GRA	HL	F	75	50 hr 45 min	3
Stingray 5	08-06-19	06:56	GRA	CN	F	81	54 hr 20 min	4
Stingray 6	09-06-19	06:54	GRA	CN	F	63	54 hr 22 min	4
Stingray 7	10-06-19	06:45	GRA	CN	F	81	50 hr 23 min	4
Stingray 8	11-06-19	06:57	GRA	CN	F	81	53 hr 55 min	4
Stingray 9	12-06-19	08:20	GRA	CN	F	74	52 hr 44 min	4
Stingray 10	14-06-19	08:31	GRA	CN	F	71	55 hr 48 min	4
Stingray 11	20-06-19	07:16	GRA	CN	F	74	12 hr 08 min	4

Table 1: Southern stingrays included in this study. Individuals with an “*” were excluded from analyses. Deployment durations are approximations based on time stingray was released and near time tag package popped off (when depth became near zero and acceleration remained relatively constant across all three axes, representative of the tag floating at the surface). “BR” = barrier reef, “GRA” = Glover’s Reef Atoll, “LL” = longline, “HL” = handline, “CN” = cast net, “F” = female, “hr” = hours, “min” = minutes.

Tri-axial micro accelerometers with pressure sensors (AXY-Depth, TechnoSmArt Europe s.r.l.) were attached dorsally to southern stingrays within a float package. The float package was constructed from syntactic foam and contained the data logger and a VHF transmitter (Advanced Telemetry Systems, Inc.). Data loggers measured 3D acceleration (sampling frequency 25 Hz), depth

(1 Hz), and water temperature (1 Hz). The data loggers were programmed and downloaded using *Axy Manager 2* (TechnoSmArt Europe s.r.l.). Nylon-coated leader wire was inserted into the skin at the beginning of the pectoral fin musculature on the right shoulder using a 4" post-mortem curved surgical needle (Jorgensen Laboratories, Inc.) and subsequently wrapped tightly around the float package. The wire was secured to a galvanic timed release (72 hours) that corroded in saltwater to facilitate the release of the float package. Stingrays were released back into the sea immediately following attachment of the float package. Deployments lasted approximately 47 hours 17 minutes ($\pm$ 14 hours 41 minutes SD; Table 1). All eleven tags were successfully retrieved after pop-off inside the lagoon.

Data processing

I removed the first two hours of data post southern stingray release from each dataset to account for possible behavioural responses to capture and handling (Cartamil *et al.* 2003). The two individuals captured in 2018 were removed from the study: the float package of Stingray 3 popped off just after 24 hours and the data indicated she either did not recover from handling stress or her swimming was compromised from tag drag, and the pressure sensor failed on the data logger on Stingray 4. Tri-axial acceleration collected on the AXY-Depth version 4 was unexpectedly recorded as zero at each new record of depth and temperature (N stingrays = 7), therefore I interpolated acceleration for the

first row of each new second by calculating the average from the data in the row before and row after. I used the R package “*gRumble*” (White *et al.* 2022) to separate and smooth static and dynamic acceleration using a three second running average (Shepard *et al.* 2008) and to calculate ODBA (Gleiss *et al.* 2011). Subsequently, all data were averaged over three seconds for statistical analyses (Zucchini *et al.* 2016, Papastamatiou *et al.* 2022).

Statistical analyses

I used HMMs because they can identify unobserved (hidden) states from autocorrelated observed processes in time series data and are particularly useful for analysing unclassified acceleration data (Zucchini *et al.* 2016, Leos-Barajas *et al.* 2017, McClintock *et al.* 2020). In the unsupervised learning approach used here, underlying activity states are not labelled (i.e., not linked to a specific behaviour like foraging, travelling, or resting), which limits result interpretation but can help distinguish activity levels and infer how they vary across time and environmental conditions (Leos-Barajas *et al.* 2017). Due to the possibility of individual variation in activity patterns (e.g., Tilley *et al.* 2013, Papastamatiou *et al.* 2022) and that the two research sites likely have different physical and biological characteristics (e.g., Gibson 2011, Clementi 2017, Bond *et al.* 2019), models were built for each individual stingray separately using the R package “*momentuHMM*” (McClintock & Michelot 2018). A suite of HMMs were run on the full dataset as well (N individuals = 9) to look for general activity patterns within

the species. Two (low and high activity) and three (low, medium, and high activity) state models were considered for each stingray and for the full dataset (S1 Table). Conventional information theoretic approaches to model selection (e.g., Akaike's and Bayesian information criteria [AIC & BIC]) tend to favour models with the greatest number of states (i.e., higher complexity), therefore state selection was based on a combination of AIC and biological expertise (Leos-Barajas *et al.* 2017, Pohle *et al.* 2017, Adam *et al.* 2019). A previous study using accelerometry suggested that southern stingrays exhibit three possible activity states: one resting and two non-resting (Ward *et al.* 2019). Gamma distributions were used to describe each state. ODBA was the response variable, while hour of day, depth (m), water temperature (°C), and their interactions were considered as covariates (Table 2, S1 Table). Two cosinor models were considered to account for possible diel rhythms of 12 hour and 24 hour periods (Tong 1976, McClintock & Michelot 2017; Table 2, S1 Table). Pseudoresidual plots were checked for model fit and autocorrelation. State sequences were decoded using the Viterbi algorithm and added to the ODBA time series (Papastamatiou *et al.* 2022). The percentage of time each individual and all individuals combined spent in each state was calculated after states were decoded (McClintock & Michelot 2017).

Models	AIC preferred
Model 1 <i>depth * water temperature + hour</i>	Stingray 6 Stingray 11
Model 2 <i>depth * water temperature * cosinor(hour, period = 12)</i>	Stingray 8 Stingray 9 [†]
Model 3 <i>depth * water temperature * cosinor(hour, period = 24)</i>	All stingrays Stingray 1 Stingray 2 Stingray 5 Stingray 7 Stingray 10

[†] Models 1 & 3 repeatedly misclassified states for this individual by associating high activity with the lowest ODBA values, therefore Model 2 was selected based on exclusion of Models 1 & 3.

Table 2: Hidden Markov models used to describe southern stingray overall dynamic body acceleration. The second column lists Akaike's information criterion (AIC) preferred models (lowest AIC) for each individual and all stingrays combined. For all models considered, see Supplementary Table 1.

RESULTS

All stingray datasets combined

The highest mean ODBA occurred at 19:00 (0.08 ± 0.04 SD) and the lowest mean ODBA occurred at 08:00 (0.03 ± 0.01 SD) (Figure 2). Mean depth experienced by the stingrays was shallowest at 01:00 ($2.5 \text{ m} \pm 1.5$ SD) and deepest at 12:00 ($5.1 \text{ m} \pm 1.5$ SD) (Figure 2). Mean water temperature experienced by the stingrays was highest at 15:00 ($29.8^\circ\text{C} \pm 0.3$ SD) and lowest at 05:00 ($28.8^\circ\text{C} \pm 0.2$ SD) (Figure 2). The HMM with the lowest AIC included

three activity states (S1 Table, Appendix 2) and an interaction between depth, temperature, and a 24-hour time period (Table 2, S1 Table). The probability of all stingrays being in a low activity state remained relatively low and constant over time, with the highest probability occurring around 09:50 (P [low activity] = 0.19; Figure 3). The probability of being in a medium activity state peaked after sunrise around 06:40 (P [high activity] = 0.57) and the probability of being in a high activity state peaked after sunset around 19:00 (P [high activity] = 0.46; Figure 3). Stingrays spent most of their time in medium (46.2%) and high (37.6%) activity states. The probability of stingrays being in a high activity state was highest at 0.1 m (P [high activity] = 0.56) and declined with increasing depth (Figure 3). The probability of stingrays being in a medium activity state was lowest at 0.1 m (P [medium activity] = 0.32), increased with depth, and remained relatively stable between 10 and 20 m (Figure 3). Stingrays were most likely to be in a low activity state at 11.3 m (P [low activity] = 0.24; Figure 3). The probability that stingrays were in low and high activity states decreased with increasing temperature, and the probability of stingrays being in a medium activity state increased at higher temperatures (Figure 3).

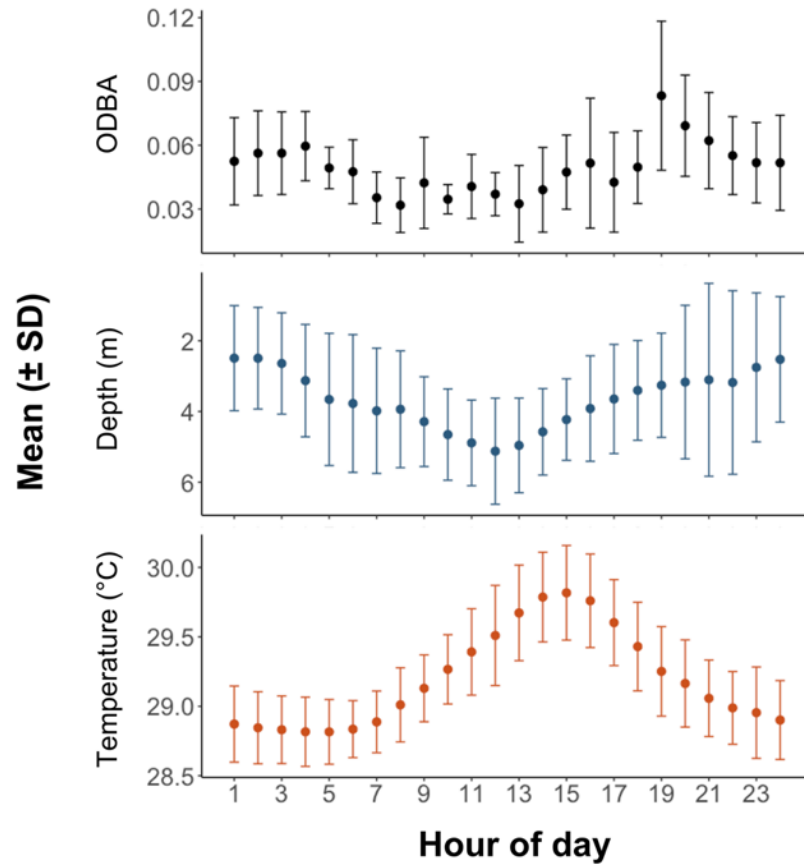


Figure 2: Grand means ($\pm$ standard deviations [SD]) of overall dynamic body acceleration (ODBA), depth, and water temperature for all stingrays combined ($N = 9$) across hour of the day.

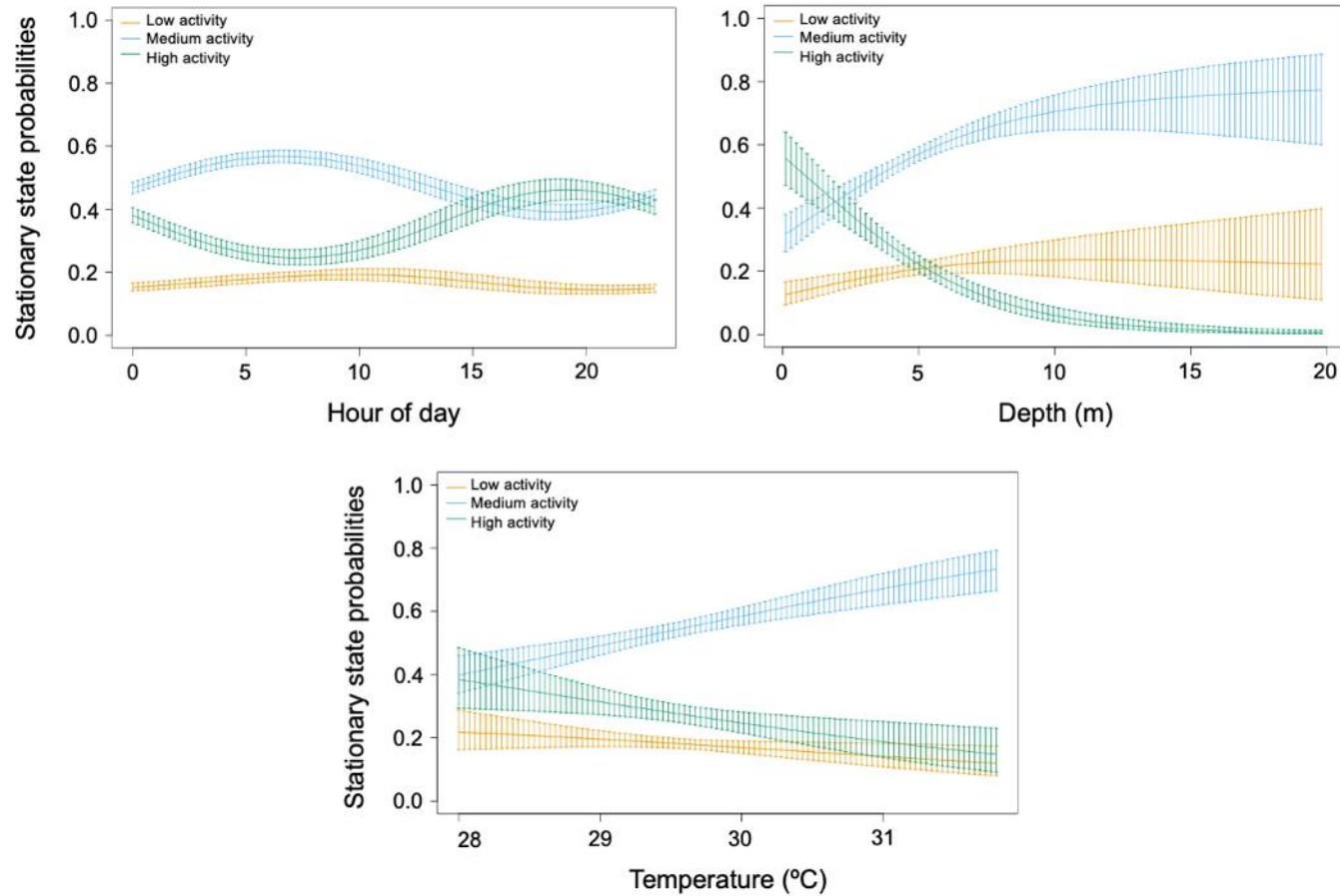


Figure 3: Stationary state probabilities (with 95% confidence intervals) from hidden Markov model with lowest Akaike's information criterion for all stingrays combined across hour of day, depth, and water temperature. Probabilities are calculated at mean values of the other covariates (hour = 11:24, depth = 3.69 m, temperature = 29.22 °C).

Individual stingrays

The AIC preferred model for all individuals included three activity states (Appendix 2, S1 Table) and for most individuals an interaction between depth, temperature, and time with a 24 hour cycle (Table 2, S1 Table). Diel activity patterns varied by individual stingray (Appendix 3). Stingray 5 had the highest probability of being highly active during the day and two stingrays had the highest probability of being highly active at night (Stingrays 2, 7) (Appendix 3). These three stingrays were the second largest individuals, all with an 81 cm DW. The probability of being in a highly active state fit an early diurnal pattern for Stingray 6 (Appendix 3). Stingray 8 exhibited a high probability of being in the most active state near midday and again throughout the night (Appendix 3). Stingray 9 showed a pre-sunrise crepuscular pattern of high activity, but also a late diurnal pattern of high activity (Appendix 3). Stingray 10 fit a late diurnal pattern with the highest probability of being in a high activity state between 14:00 and 20:00. Only one stingray did not appear to have a daily activity pattern and this individual remained in a state of medium activity for most of the deployment (60% of the time, Stingray 1, Appendix 3). Finally, the probability of being in a high activity state declined throughout the day for Stingray 11 from morning to post-sunset (Appendix 3). However, the tag deployment lasted just over 12 hours for Stingray 11, therefore it is not possible to classify the diel activity pattern for this individual. A consistent pattern that emerged for six of the nine individuals was that the probability of being in a high activity state was greatest in shallow water < 5 m

(Appendix 3), although most individuals remained in relatively shallow water throughout the course of the deployments (Figure 2). Additionally, when stingrays remained at a relatively constant depth over short and long periods of time, they were consistently in low and medium activity states (Figure 4; Appendix 4). Stingrays used depths between 0.1 m to 19.8 m, and the deepest part of the lagoon at Glover's Reef Atoll is approximately 20 m (McClanahan & Muthiga 1998). The probability of being in a high activity state decreased with increasing water temperature for most individuals (Stingrays 5, 7, 8, 9, 10, 11; Appendix 3). The opposite pattern emerged for two individuals (Stingrays 2 and 6; Appendix 3). The probability of being in a high activity state remained low and constant across temperature for Stingray 1; however, the probability that she was in a low activity state increased with increasing water temperature (Appendix 3). Ambient water temperature experienced by stingrays ranged from 28.0 °C to 31.8 °C.

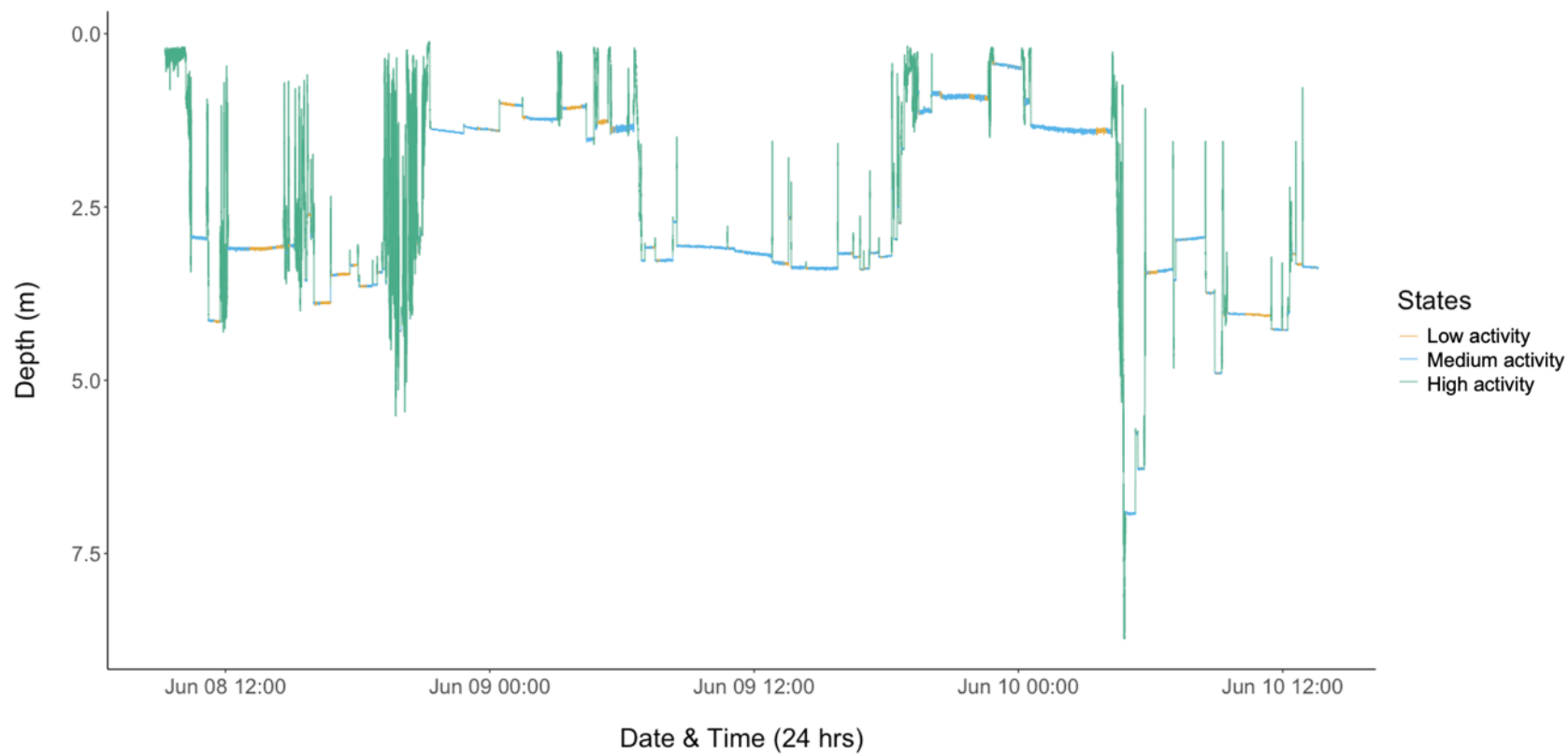


Figure 4: Depth over time plotted by activity states for Stingray 5. This plot represents a consistent pattern observed for all individuals: when a stingray remains at a relatively constant depth over time, they are in a low (yellow) or medium (blue) activity state.

DISCUSSION

When analyzed together, female southern stingray activity in Belize was primarily crepuscular and nocturnal. However, there was high individual variation in diel activity. Most elasmobranchs display crepuscular and/or nocturnal activity (Hammerschlag *et al.* 2017), therefore female southern stingray activity patterns in Belize may not align with a predator avoidance hypothesis. Potential predators of southern stingrays in Belize include several shark species, with the most likely being lemon sharks (*Negaprion brevirostris*), great hammerhead sharks (*Sphyrna mokarran*), tiger sharks (*Galeocerdo cuvier*), and Caribbean reef sharks (Pikitch *et al.* 2005, Chapman *et al.* 2011). Apart from tiger sharks, these shark species are most active at night (Nixon & Gruber 1988, Chapman *et al.* 2007, Shipley *et al.* 2018, Bond *et al.* 2019, Lear *et al.* 2021). The hypothesized key predator of southern stingrays at Glover's Reef Atoll is the Caribbean reef shark, which displays post-sunset crepuscular peaks in activity and moves into the lagoon at night (Chapman *et al.* 2007, Shipley *et al.* 2018, Bond *et al.* 2019). If southern stingrays were focusing activity in times that are less risky (e.g., Kohl *et al.* 2018), I would have expected a more diurnal signal across all individuals. However, I cannot fully rule out that state dependent factors are at play (e.g., Brown & Kotler 2004, Heithaus *et al.* 2007) given high individual variability in diel activity, although none of the stingrays had obvious visual signs of being in poor body condition upon capture. Future studies should seek to incorporate males and a

better representation of size classes, especially small juveniles and large mature adults.

Multiple lines of evidence instead point to a crepuscular - nocturnal activity pattern that may be driven more by foraging considerations rather than predator avoidance. For example, tourism operations often alter elasmobranch activity by increasing interest in foraging through provisioning (Gaspar *et al.* 2008, Corocoran *et al.* 2013, Huveneers *et al.* 2018), suggesting that food availability plays an important role in determining elasmobranch diel activity patterns. Shrimp are common prey for southern stingrays (Bigelow & Schroeder 1953, Snelson & Williams 1981, Smith & Herrnkind 1992, Gilliam & Sullivan 1993) and are nocturnal with crepuscular activity peaks (Reynolds & Casterlin 1979). Additionally, in a Caribbean seagrass bed, catch rates of multiple shrimp species peak within the first couple hours after sunset and decline thereafter (De Grave *et al.* 2006). Prey activity may explain southern stingray use of shallow water at night, a phenomenon documented in another durophagous ray species, the whitespotted eagle ray (*Aetobatus narinari*) (Ajemian *et al.* 2012, Brewster *et al.* 2021, DeGroot *et al.* 2020). Southern stingrays were most likely to be highly active in shallow water, which is where we would expect higher prey abundance and diversity inside the lagoon at Glover's Reef Atoll (Hauser *et al.* 2007, Tilley 2011). This is consistent with expectations of increasing the chances of encountering prey during peaks in prey activity. Southern stingray crepuscular activity peaks in this study align with times southern stingrays increase their movement rates in St. Thomas, United States Virgin Islands (Donihe 2018).

Although higher rates of movement may be directly related to foraging, they may also be due to fish shifting or moving through habitats (Cartamil *et al.* 2003, Donihe 2018, DeGroot *et al.* 2020, Meese & Lowe 2020). Southern stingrays move into seagrass habitats from the mangroves after sunset in Puerto Rico, which could be movement into foraging grounds (Clark *et al.* 2009).

Stingrays rest on the seafloor, often while buried in the sand, a behaviour that may help them avoid being detected by predators (e.g., Semeniuk & Dill 2005, Semeniuk & Rothley 2008, Vaudo & Heithaus 2013, Freitas *et al.* 2019, Meese & Lowe 2019). In Belize, southern stingrays were more likely to be in a state of low activity in deeper water (11.3 m) in the morning; however, it was not common for rays to be in this state. The probability of being in a low activity state increased slightly with depth, suggesting southern stingrays may rest in deeper areas away from where they forage. Since the southern stingrays were more likely to be in a state of low activity at lower temperatures, they may be using the deeper water to lower energy expenditure during digestion (Di Santo & Bennett 2011). Deeper lagoon habitat at Glover's Reef Atoll may also provide some refuge from lemon sharks, which commonly use the shallow sandflats (Chapter 3). Deeper lagoon habitat consists of seagrass beds, sand patches, and patch reefs. The patch reefs may help southern stingrays remain cryptic or evade predators (Tilley *et al.* 2013). However, Caribbean reef shark habitat use overlaps with southern stingrays in the lagoon (Chapter 3), so it remains unclear what role predator avoidance plays in driving southern stingray activity patterns across depth.

High and low southern stingray activity were most likely to occur in cooler water temperatures ($< 29^{\circ}\text{C}$). Stingrays, however, did not experience a wide variation in water temperature throughout the course of tag deployments, so temperature may be more important in areas with greater diel or spatial variability. Medium activity increased with temperature. It remains unclear, however, what behaviours are associated with a medium activity state. Southern stingrays were most likely to transition from high to medium activity states, but in water deeper than 10 m (Appendix 5). Southern stingrays rarely showed movements across depth while in low and medium activity states. These periods of remaining at depth occurred over long time periods (e.g., hours). Behavioural state classifications need to be verified using camera tags in the field (e.g., Papastamatiou *et al.* 2019) or in captive or semi-captive environments (e.g., Brewster *et al.* 2018) before conclusions related to specific behaviours can be made (Whitney *et al.* 2012).

Elasmobranchs commonly display high degrees of individual variability in activity patterns and depth use (e.g., Klimley *et al.* 2005, Brewster *et al.* 2021, Elston *et al.* 2022, Andrzejaczek *et al.* 2022, Papastamatiou *et al.* 2022). My results here support these findings along with previous work on southern stingrays at Glover's Reef Atoll (Tilley *et al.* 2013), emphasizing the need to account for individual variation when studying elasmobranch activity. It is possible that individual differences in activity in this study were due to short deployment durations and the time of day at which a ray was captured. Long-term deployments (e.g., Ward *et al.* 2019) may help elucidate the degree to

which individual variation occurs. Increasing the sample size and diversity to include both sexes and multiple size classes would also help elucidate the relative importance of ontogeny and sex in determining southern stingray activity. Lutz's stingrays (*Hypanus berthalutzae* sec. Petean *et al.* 2020) can display at least 21 unique behaviours related to foraging (Freitas *et al.* 2019), highlighting the complexity of stingray prey searching and handling techniques that may help explain high individual variation within my results. Linking these foraging behaviours with acceleration data could also help improve model fits through the identification of additional activity states. Some southern stingrays are more likely to be in a high activity state in higher water temperatures, suggesting that there is some intraspecific behavioural plasticity. These differences could be driven by the condition of each individual, for example, whether or not they are sated, gravid, or suffering from severe parasitic infections. Individual variation could also be due to individuals perceiving different levels of risk while balancing the need to forage and perform other primary biological functions.

Southern stingrays in Belize are highly active in shallow water post-sunset, likely related to foraging. Crepuscular-nocturnal activity patterns match those of their primary predators and prey, therefore it is unlikely that stingray activity is driven solely by the need to avoid predators. High individual variation in diel southern stingray activity may indicate state-dependent responses to predation risk and foraging decisions. Depth appears to be the most important predictor of stingray activity, which supports the prediction that southern stingray activity is based on foraging given that their prey are distributed in shallow water

in the lagoon and lemon sharks frequently use this habitat at night, making it a risky area rather than a refuge from predation (Chapter 3). Future research should attempt to clarify local abundance and activity patterns of invertebrate prey and shark predators across daily cycles in relation to southern stingray activity patterns (e.g., Kohl *et al.* 2018). In addition, it would be beneficial to estimate an appropriate smoothing window for acceleration values based on undulation frequency of the pectoral fins to avoid under or over smoothing the data (e.g., Shepard *et al.* 2008, Whitney *et al.* 2012). Finally, confirmation of behavioural states using camera tags (Watanabe and Takahashi 2013) and captive studies is imperative to understand the ecological and physiological significance of southern stingray activity states across daily cycles, environmental conditions, and interspecific interactions.

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SUPPLEMENTARY TABLE FOR CHAPTER IV

Hidden Markov model	Number of activity states	AIC	Δ AIC
<i>All stingrays combined</i>			
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-3939123	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-3937873	1250
ODBA ~ Hour + Depth * Temperature	3	-3937700	1423
ODBA ~ Hour + Depth + Temperature	3	-3925407	13716
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-3527698	411425
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-3527289	411834
ODBA ~ Hour + Depth * Temperature	2	-3527206	411917
<i>Stingray 1</i>			
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-531117	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-530911	206
ODBA ~ Hour + Depth + Temperature	3	-530749	368
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-497256	33861
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-497052	34065

ODBA ~ Hour + Depth * Temperature	2	-496846	34271
ODBA ~ Hour + Depth * Temperature	3	-490072	41045

Stingray 2

ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-476634	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-476459	175
ODBA ~ Hour + Depth * Temperature	3	-476392	242
ODBA ~ Hour + Depth + Temperature	3	-472798	3836
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-425828	50806
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-425801	50833
ODBA ~ Hour + Depth * Temperature	2	-425742	50892

Stingray 5

ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-512026	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-511888	138
ODBA ~ Hour + Depth * Temperature	3	-511836	190
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-454270	57756
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-454209	57817

ODBA ~ Hour + Depth * Temperature	2	-454206	57820

Stingray 6

ODBA ~ Hour + Depth * Temperature	3	-505831	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-502480	3351
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-502269	3562
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-457918	47913
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-457834	47997
ODBA ~ Hour + Depth * Temperature	2	-457758	48073

Stingray 7

ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-365910	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-363206	2704
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-322302	43608
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-322260	43650
ODBA ~ Hour + Depth * Temperature	2	-322257	43653
ODBA ~ Hour + Depth * Temperature	3	-322211	43699

Stingray 8

ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-421801	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-418694	3107
ODBA ~ Hour + Depth * Temperature	3	-374198	47603
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-373315	48486
ODBA ~ Hour + Depth * Temperature	2	-373291	48510
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-373290	48511

Stingray 9

ODBA ~ Depth * Temperature * cosinor(Hour, period = 24) [†]	3	-547580	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-547477	103
ODBA ~ Hour + Depth * Temperature [†]	3	-542939	4641
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-489276	58304
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-489274	58306
ODBA ~ Hour + Depth * Temperature	2	-489247	58333

Stingray 10

ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	3	-482705	0
ODBA ~ Hour + Depth * Temperature	3	-482604	101

ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-482599	106
ODBA ~ Depth * Temperature * cosinor(Hour, period = 24)	2	-431671	51034
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-431583	51122
ODBA ~ Hour + Depth * Temperature	2	-382206	100499

Stingray 11 [‡]

ODBA ~ Hour + Depth * Temperature	3	-122981	0
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	3	-122962	19
ODBA ~ Depth * Temperature * cosinor(Hour, period = 12)	2	-113292	9689
ODBA ~ Hour + Depth * Temperature	2	-113279	9702

Supplementary Table 1: Models used to describe overall dynamic body acceleration (ODBA) where model selection was based on delta Akaike's Information Criterion (ΔAIC) values. [‡] The tag deployment for Stingray 11 did not last a full 24 hour period, therefore only a 12 hour period was considered.

CHAPTER V

CONCLUSION

Top-down effects of sharks on stingrays

Our knowledge on the ecological roles of rays is rather extensive compared to our very limited understanding of the importance of rays in ecosystems (Chapter 1). An area that is particularly understudied is how rays may respond to changes in predator abundance and behaviour. Some evidence suggests that ray abundance or behaviour change when sharks are overexploited, although there is debate on the mechanisms that drive these changes (Myers *et al.* 2007, Pradervand *et al.* 2007, Ward & Myers 2005, Grubbs *et al.* 2016, Bond *et al.* 2019, Sherman *et al.* 2020). Recent studies focus on space for time models to understand how stingrays may respond to shark depletion (Bond *et al.* 2019, Sherman *et al.* 2020). However, environments are not static and may have legacies of priority effects (e.g., Pickett 1989, Damgaard 2019), and the extent to which local scale dynamics, like changes across environmental variables or biogeographical site differences, influence these patterns seen across large spatial scales is relatively unknown. Indeed, one of the more famous examples of top-down effects comes from Yellowstone National Park where the reintroduction of wolves was suggested to initiate a trophic cascade that ultimately benefitted riparian vegetation, among other things (Ripple & Beschta 2012, Ripple *et al.* 2014). Yet, alternative hypotheses were later explored and considered to be

plausible explanations for the observed vegetation changes previously attributed to wolves (Allen *et al.* 2018). Reaching conclusions about potential ray responses to predator declines and subsequent impacts on their infaunal prey can have unintended consequences for ray populations (Grubbs *et al.* 2016). Given the context dependent nature of risk effects (e.g., Mitchell & Harborne 2020, Wirsing *et al.* 2021, Heithaus *et al.* 2022), multimethod approaches will help predict what conditions need to be met for ray abundance or behaviour to change in response to direct predation and/or predation risk by sharks. For many ray species we do not yet have a solid grasp of their biology, behaviour, and habitat use (Frisk 2010, Simpfendorfer & Heupel 2012, Flowers *et al.* 2016, Last *et al.* 2016, Flowers *et al.* 2021). These knowledge gaps can limit our interpretations of ray responses to predators, especially using single method studies (i.e., baited remote underwater video station [BRUVS] surveys). This dissertation explored the possibility that stingray activity, behaviour, sightings, and habitat use across multiple spatial and temporal scales could be influenced by sharks or other environmental and anthropogenic factors.

What predicts ray sightings in the tropical Western Atlantic Ocean?

First, I wanted to test whether the spatial patterns observed in previous studies across large areas (Sherman *et al.* 2020) and nationwide in Belize (Bond *et al.* 2019) are observed in the tropical Western Atlantic Ocean (Chapter 2). This is a data-poor region for rays (e.g., Talwar *et al.* 2022), and we do not have a good

understanding of what affects ray abundance and distribution. I took advantage of a regional dataset provided by the Global FinPrint project to explore multiple possible predictors of ray sightings on coral reefs, including sharks, environmental, and anthropogenic factors. Consistent with the previous studies using BRUVS (Bond *et al.* 2019, Sherman *et al.* 2020), I found that across a large spatial scale southern sightings were influenced by shark abundance. I also discovered that fine scale habitat complexity was an important predictor of southern stingray sightings. When all species were combined, habitat structural complexity was the best predictor of ray sightings in the region, although the effect was weak and most model variance was explained by the random effect of country and territory. The finding that fewer stingrays are sighted in highly complex habitat complicates our interpretation of other predictive variable effects because we do not know if southern stingrays are simply selecting for soft bottom habitat, or if our ability to detect rays on BRUVS decreases in structurally complex areas. Although, it could be a combination of both due to cryptic stingray behaviour. Other predictors of southern stingray sightings included geomorphology, bottom fishing gear, and water temperature. These results highlight the complexities involved with understanding the variability in southern stingray sightings patterns across large spatial scales that sharks alone cannot explain. Seventy eight percent of the ray species observed on these BRUVS are threatened with extinction but were too rare in the dataset to look at species-specific patterns. Future research should be conducted in key ray habitats and

attempt to elucidate the possible differences in predation risk effects exerted by mesopredator sharks vs. apex shark species.

When Caribbean reef shark abundance declines, do southern stingray sightings, behaviour, and/or habitat use change?

Incorporating the element of time in our understanding of stingray responses to shark declines became possible when I detected a Caribbean reef shark decline at my main study site, Glovers Reef Atoll (Chapter 3). Previous work in Belize suggested that southern stingrays shift habitats due to predation risk induced by Caribbean reef sharks (Bond *et al.* 2019); however, I found that for a decade, southern stingray sightings remained stable in forereef habitat even while Caribbean reef shark abundance was declining. Southern stingray sightings were higher inside the lagoon than on the forereef in the beginning of the time series, and at the end of the time series when sharks had declined. The amount of time that southern stingrays spent in the field of view of the BRUVS camera also did not change over time. It is likely that southern stingrays prefer lagoon habitat based on the relative amount of prey available; however, it is not possible for me to rule out that not enough time has passed to detect a southern stingray habitat shift and that this survey may not have had the power to detect a Caribbean reef shark effect. Bond *et al.* (2019) assumed that the shallow lagoon was safer habitat for southern stingrays; however, I show that this was not the case during my study period because lemon sharks, Caribbean reef sharks, and female

southern stingrays all use shallow lagoon habitat. Female southern stingrays tagged inside the lagoon also rarely moved out onto the forereef. It remains unclear what is driving their use of lagoon habitat and whether individuals tagged on the forereef would remain in forereef habitat.

Does southern stingray activity make sense in the context of shark activity, behaviour, and habitat use?

Finally, female southern stingray activity appears to be crepuscular and nocturnal with high individual variation, which does not completely align with the hypothesis that predation risk is driving southern stingray behaviour (Chapter 4). At Glover's Reef Atoll, southern stingrays are most active at the same time as their main predators (lemon sharks and Caribbean reef sharks). Southern stingray activity patterns also follow those of their invertebrate prey. Southern stingrays are most active in very shallow water less than five meters deep, an area where their prey are distributed (Tilley 2011) and lemon sharks are common (Chapter 3).

Combined, these results suggest southern stingray activity is likely based on foraging decisions. Ultimately, there is a need to test the predation risk hypothesis across multiple temporal and spatial scales using well designed experiments and multiple survey techniques. Future research should track abundance and activity of ray prey and predators across daily cycles in relation to southern stingray activity patterns (e.g., Kohl *et al.* 2018).

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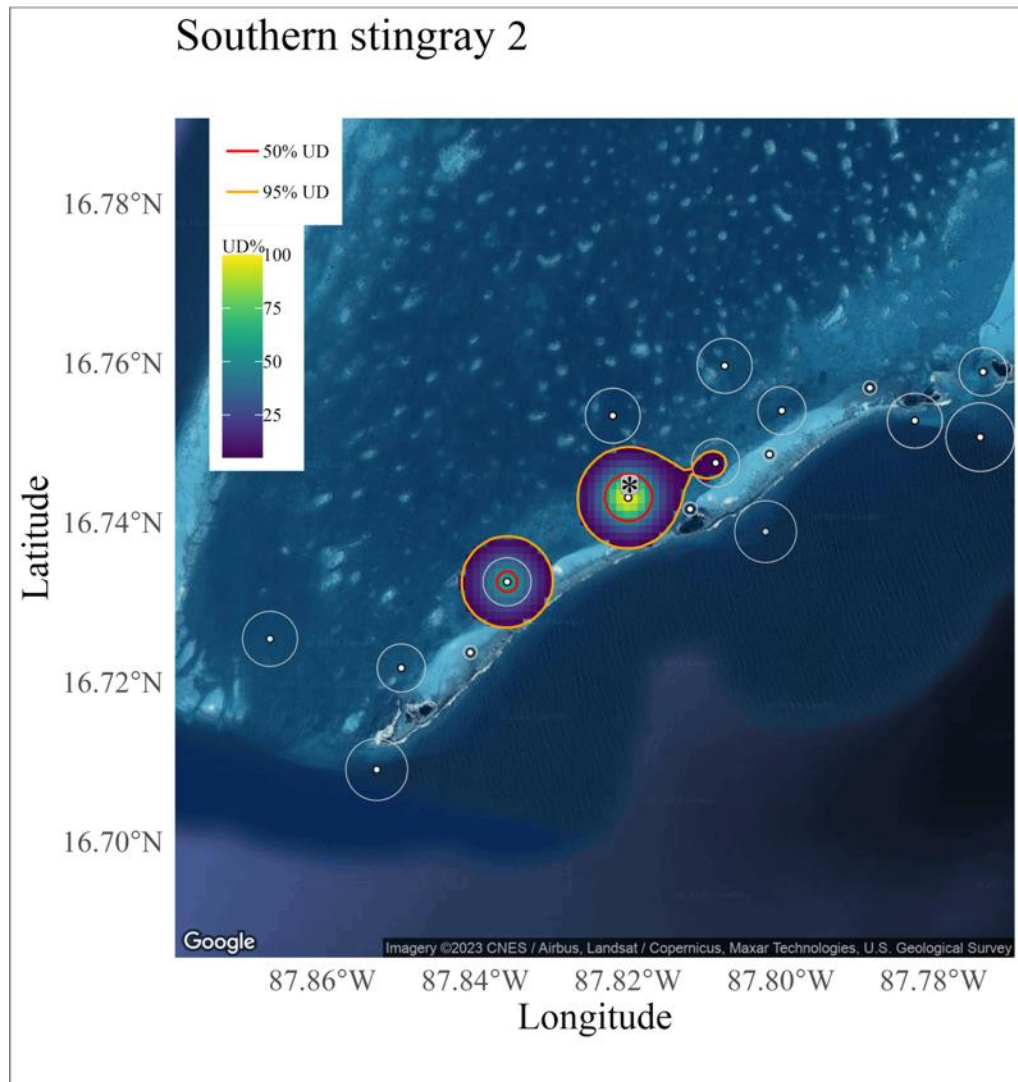
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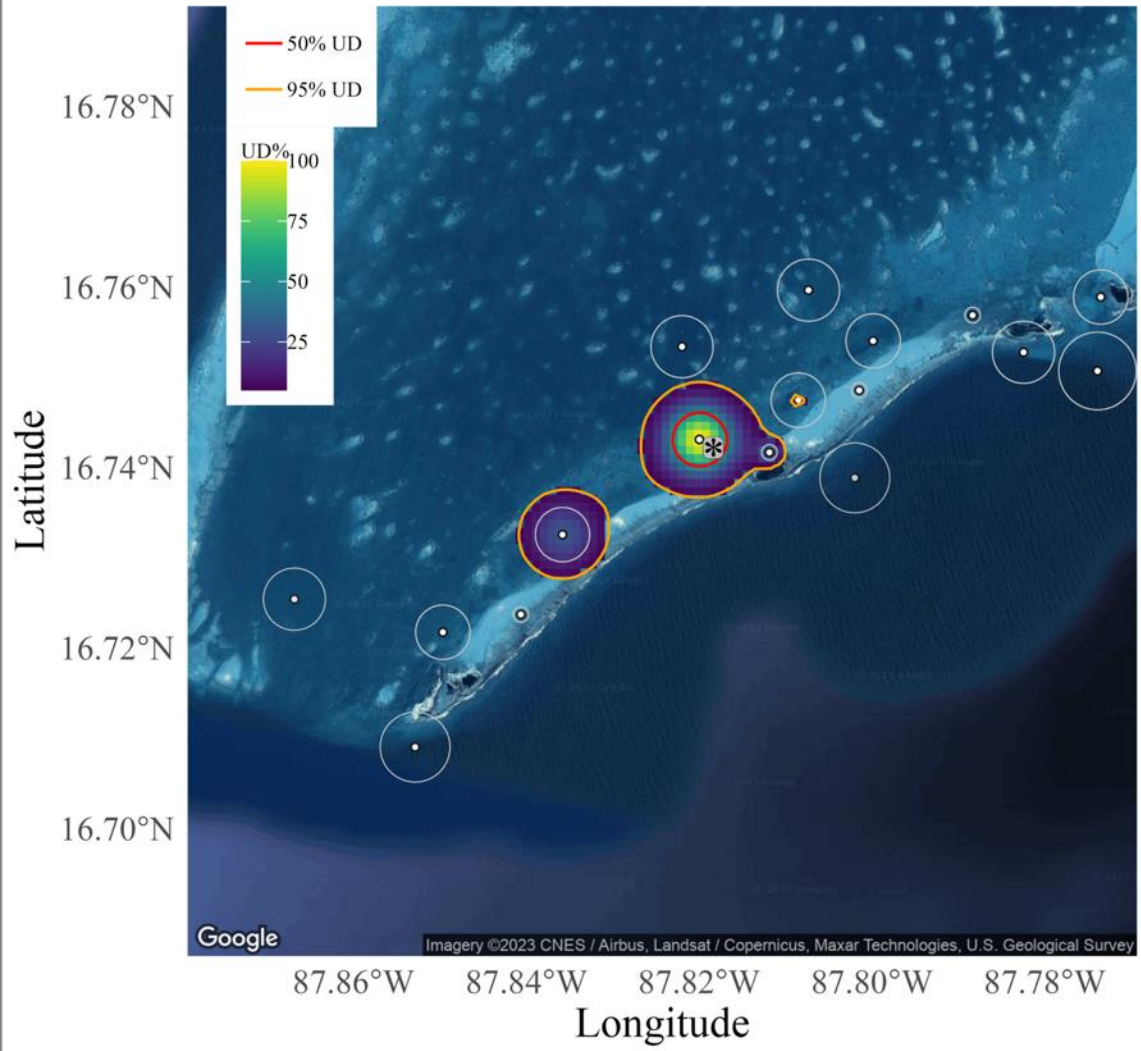
APPENDICES

APPENDIX I – CHAPTER III

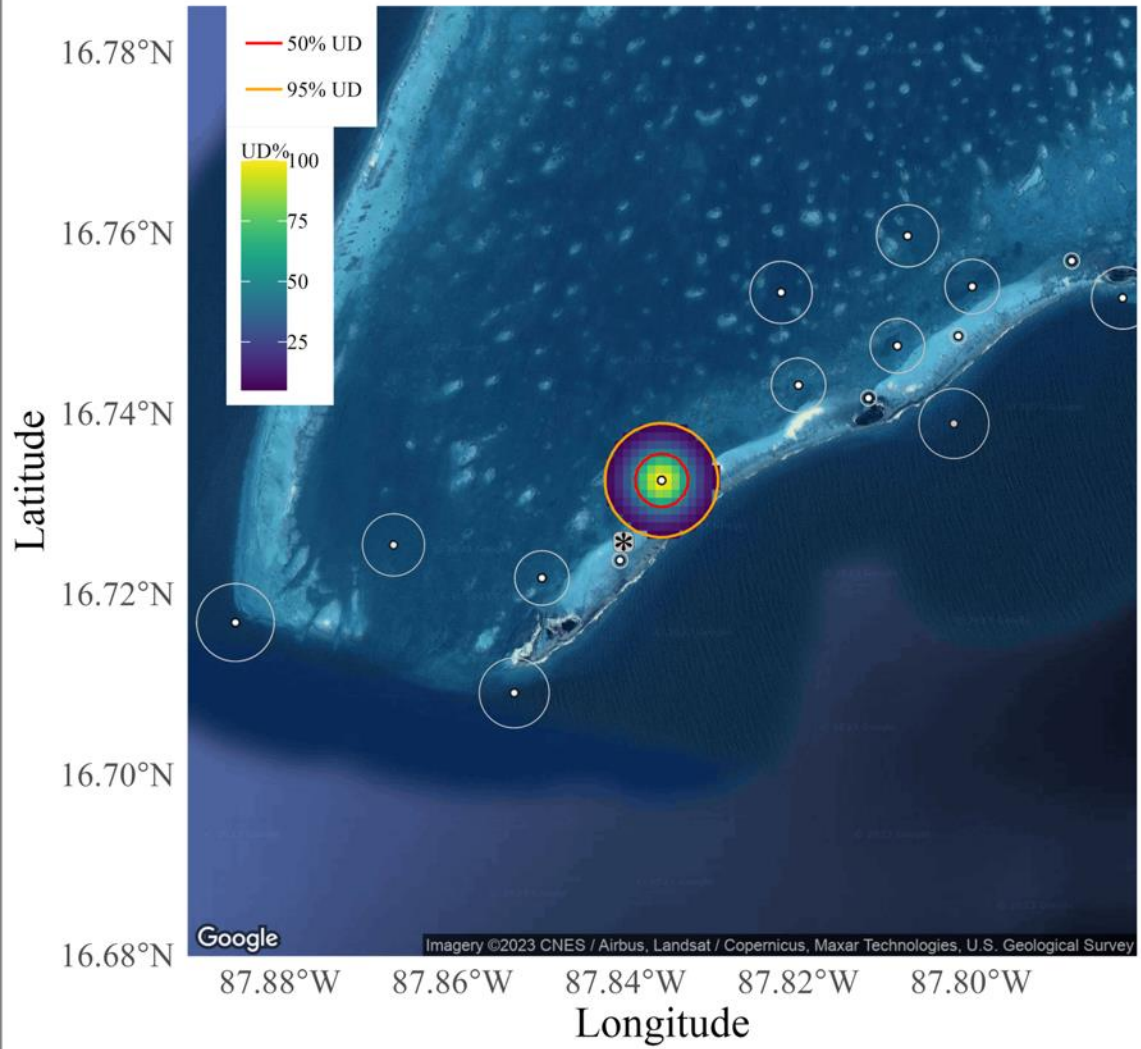
Individual southern stingray (*Hypanus americanus*) utilization distributions (UDs). 50% core use areas are outlined in red and 95% general use areas are outlined in orange. Receivers and their detection ranges are represented by white points and open white circles, respectively. Asterisks in grey boxes (*) represent approximate capture locations.



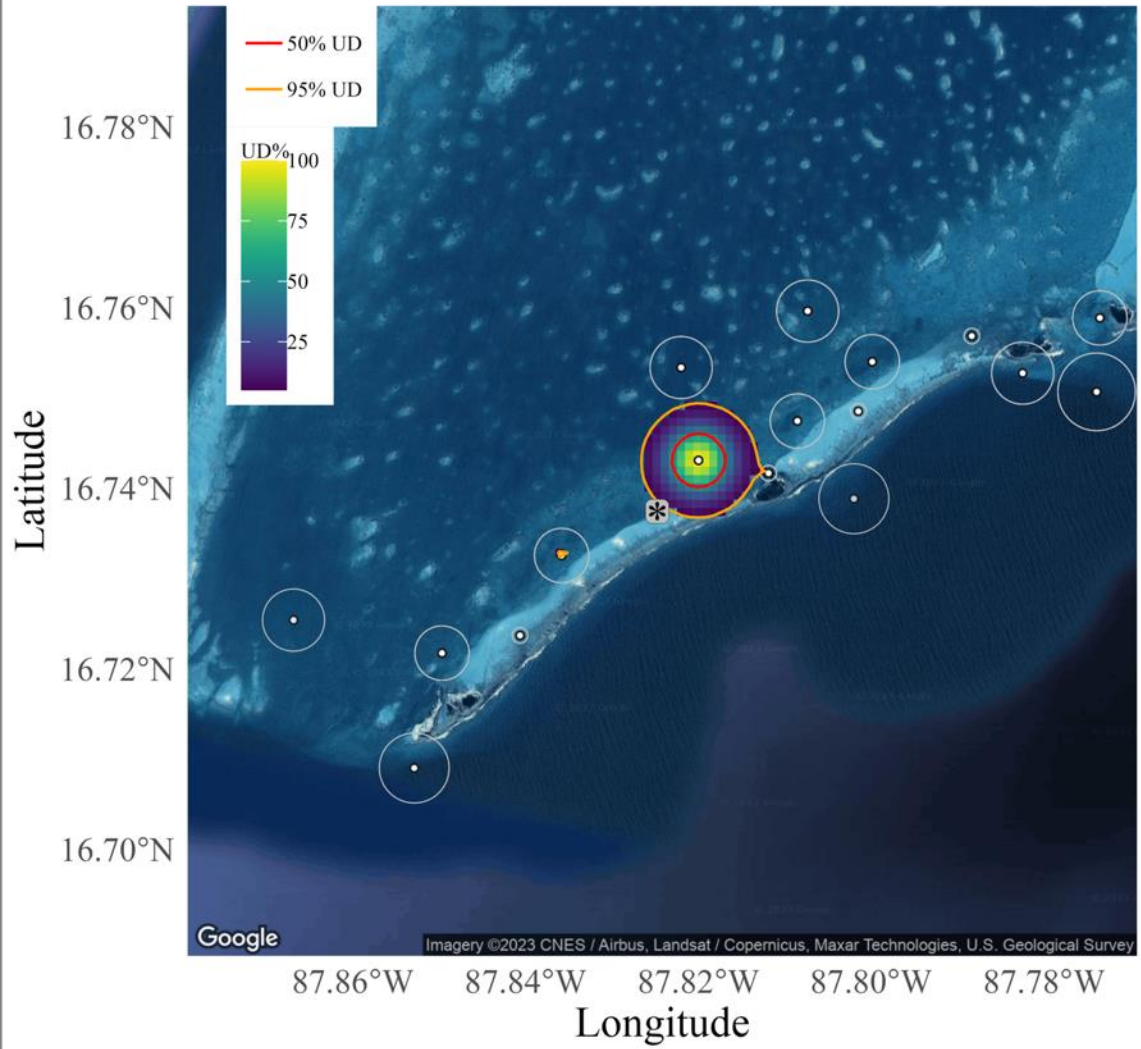
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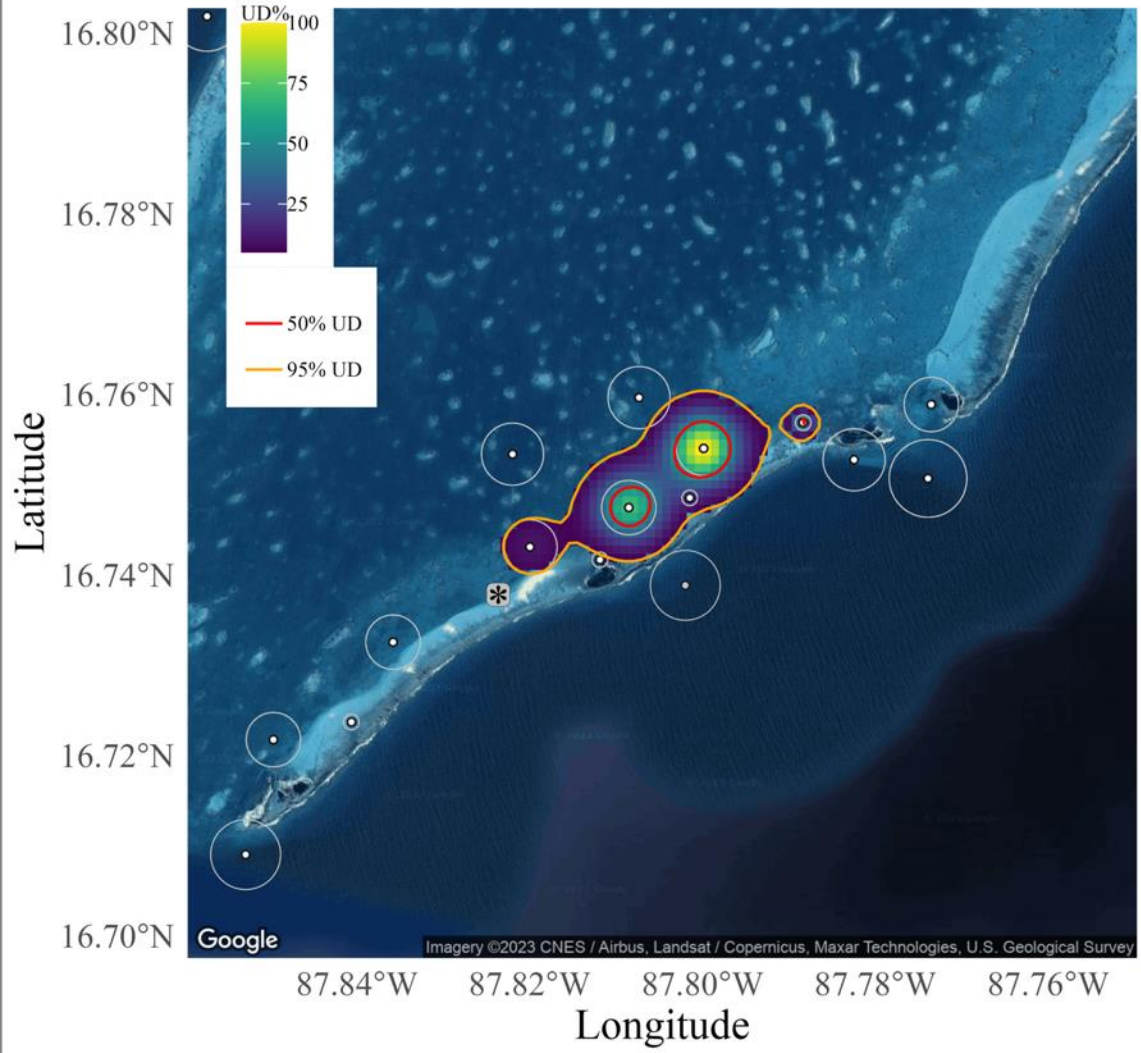
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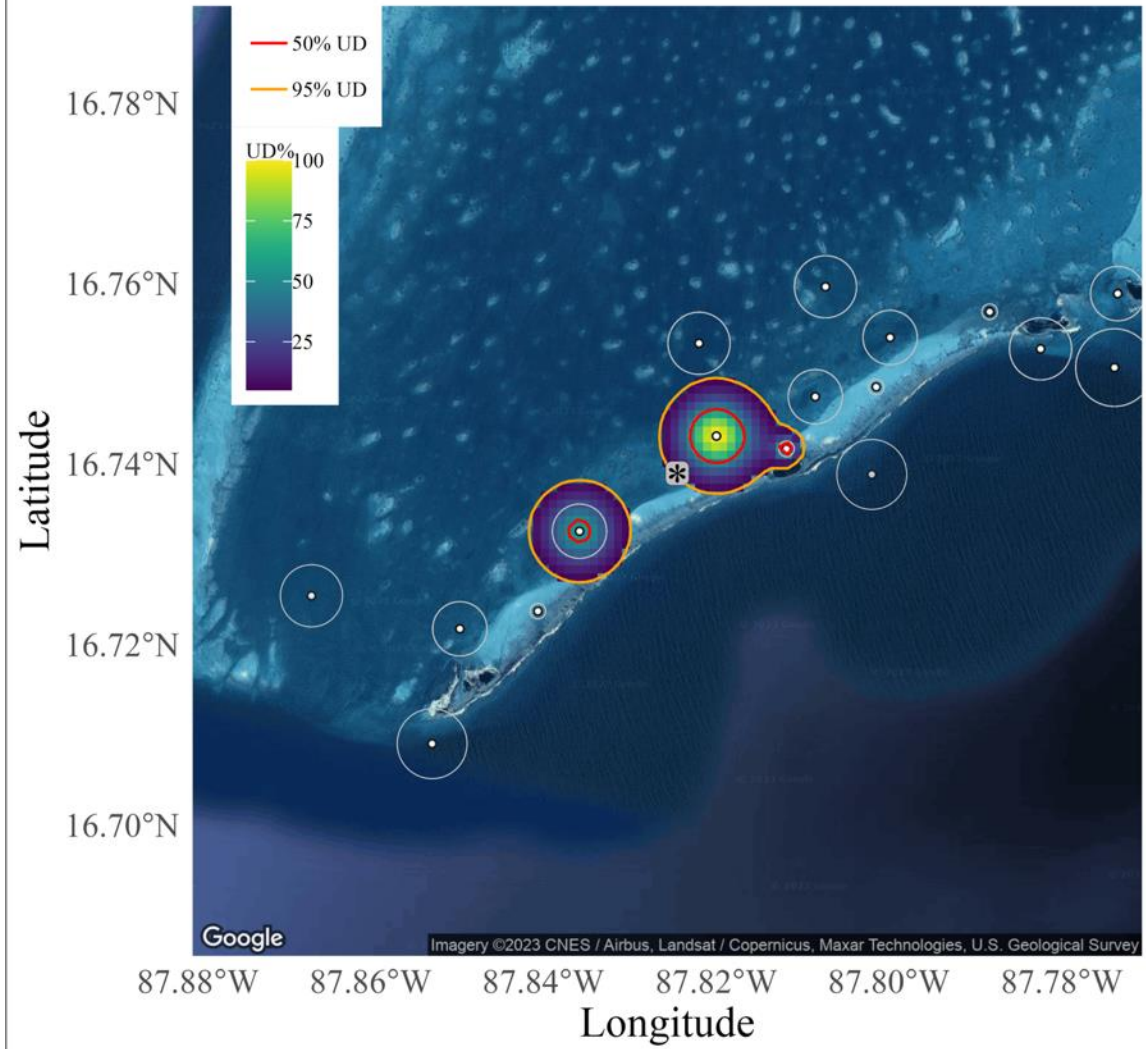
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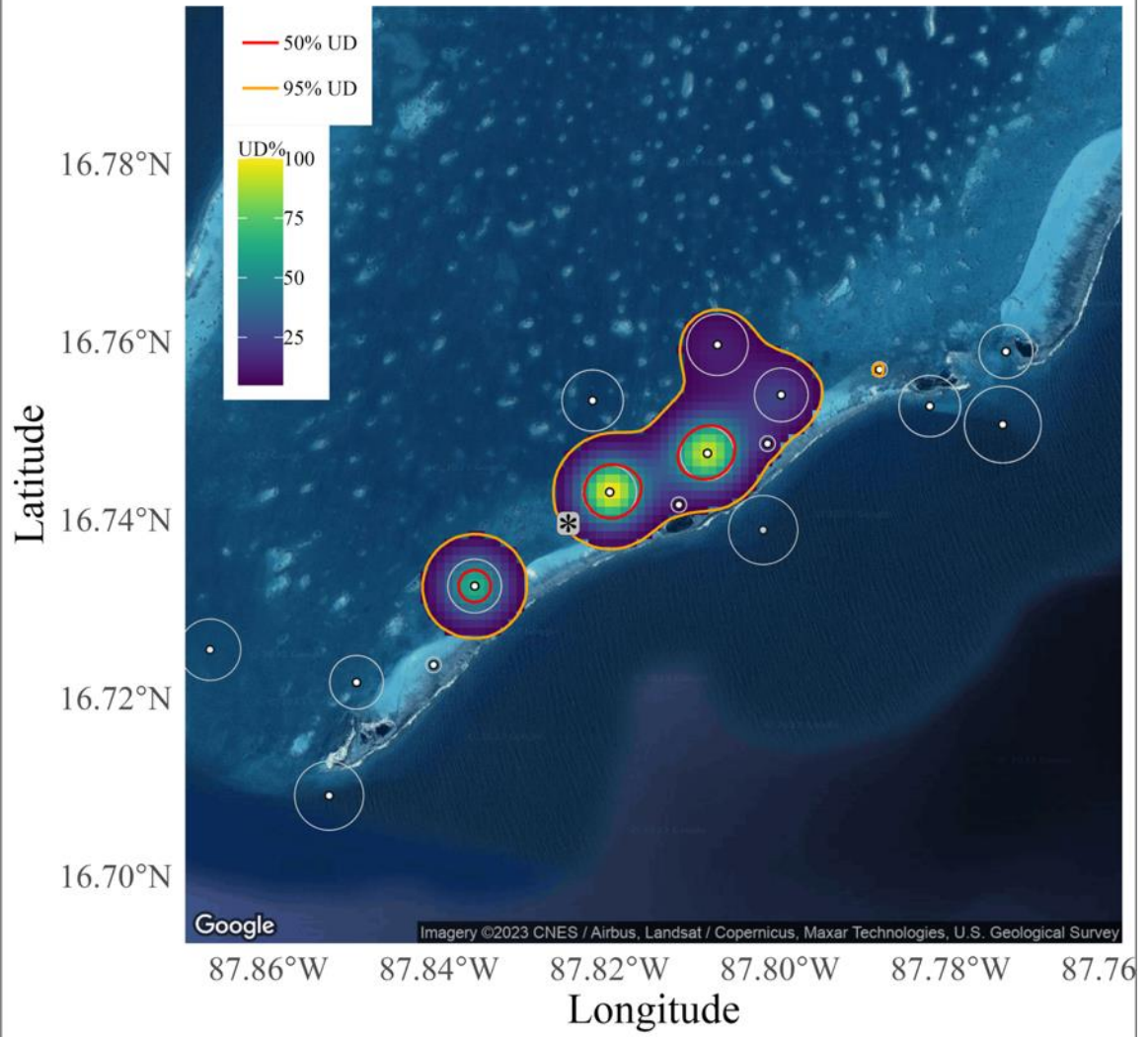
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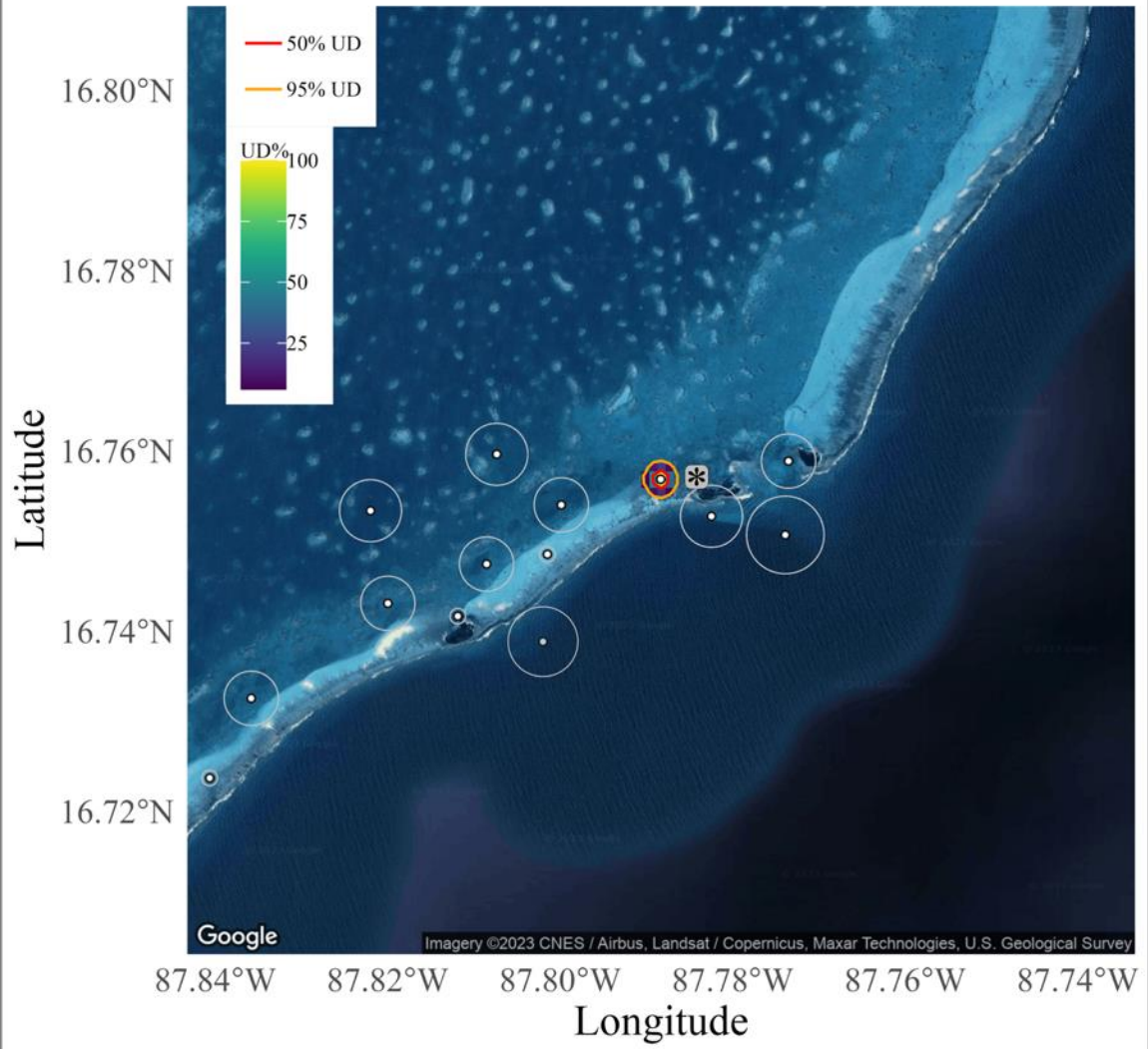
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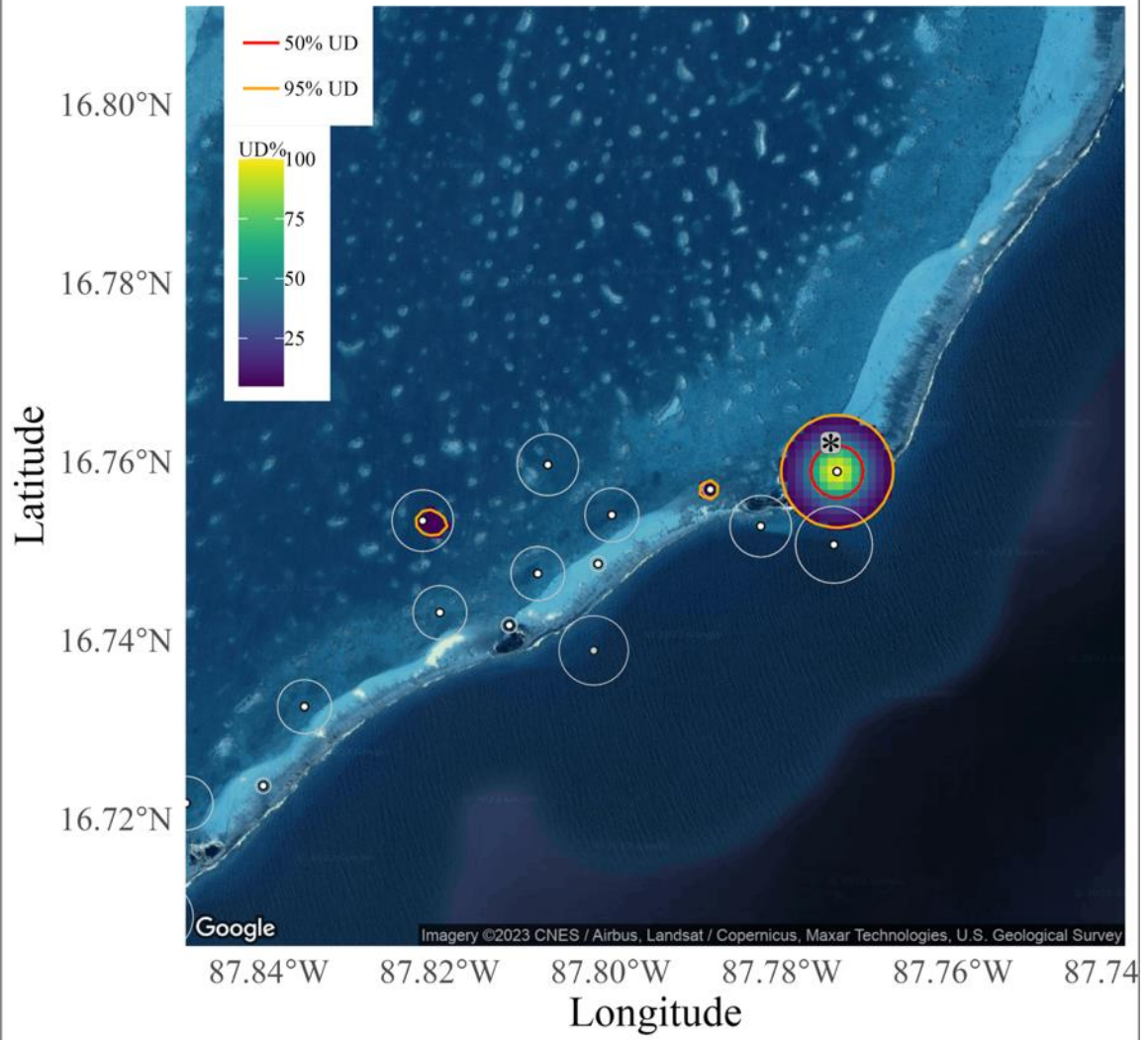
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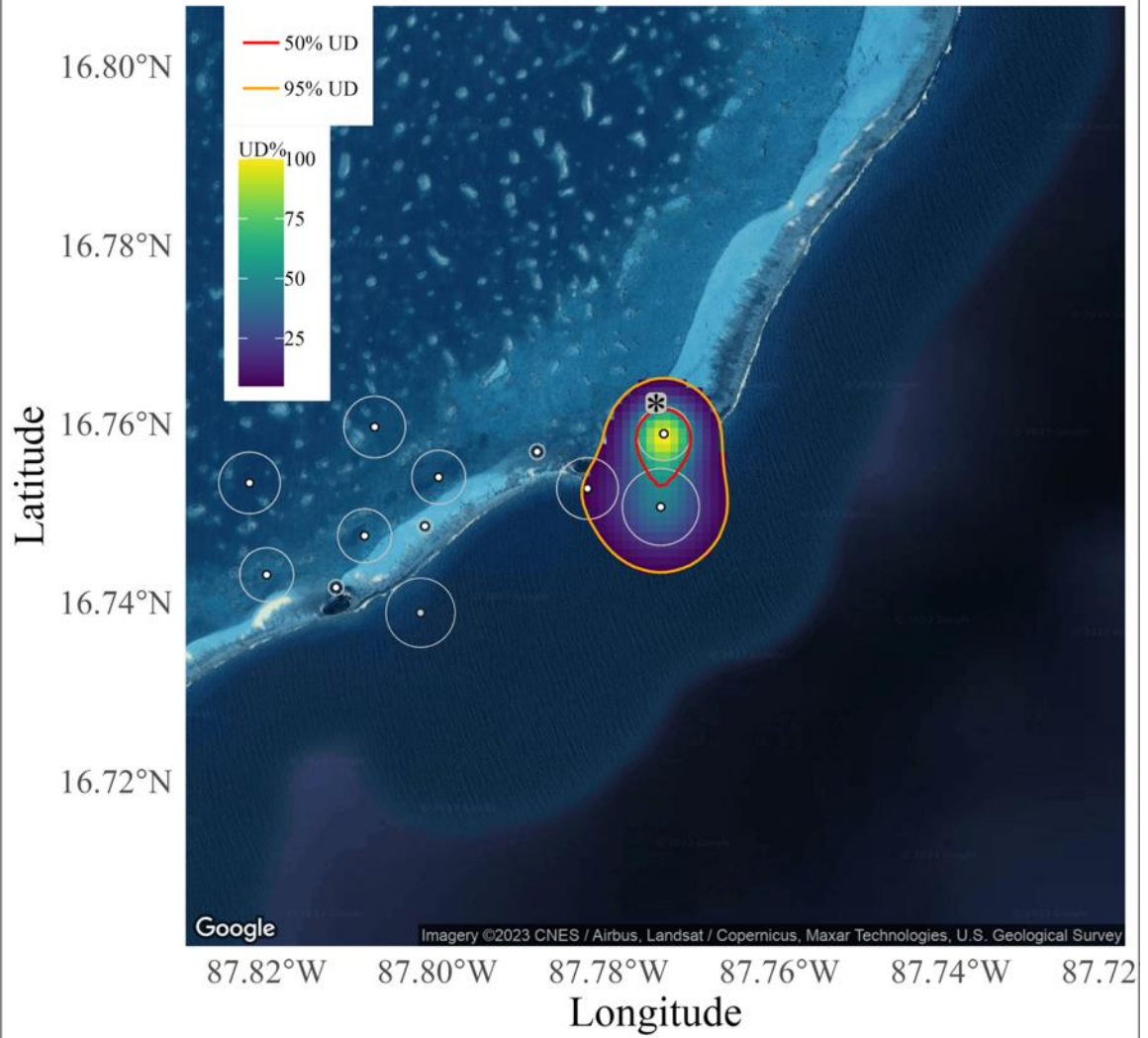
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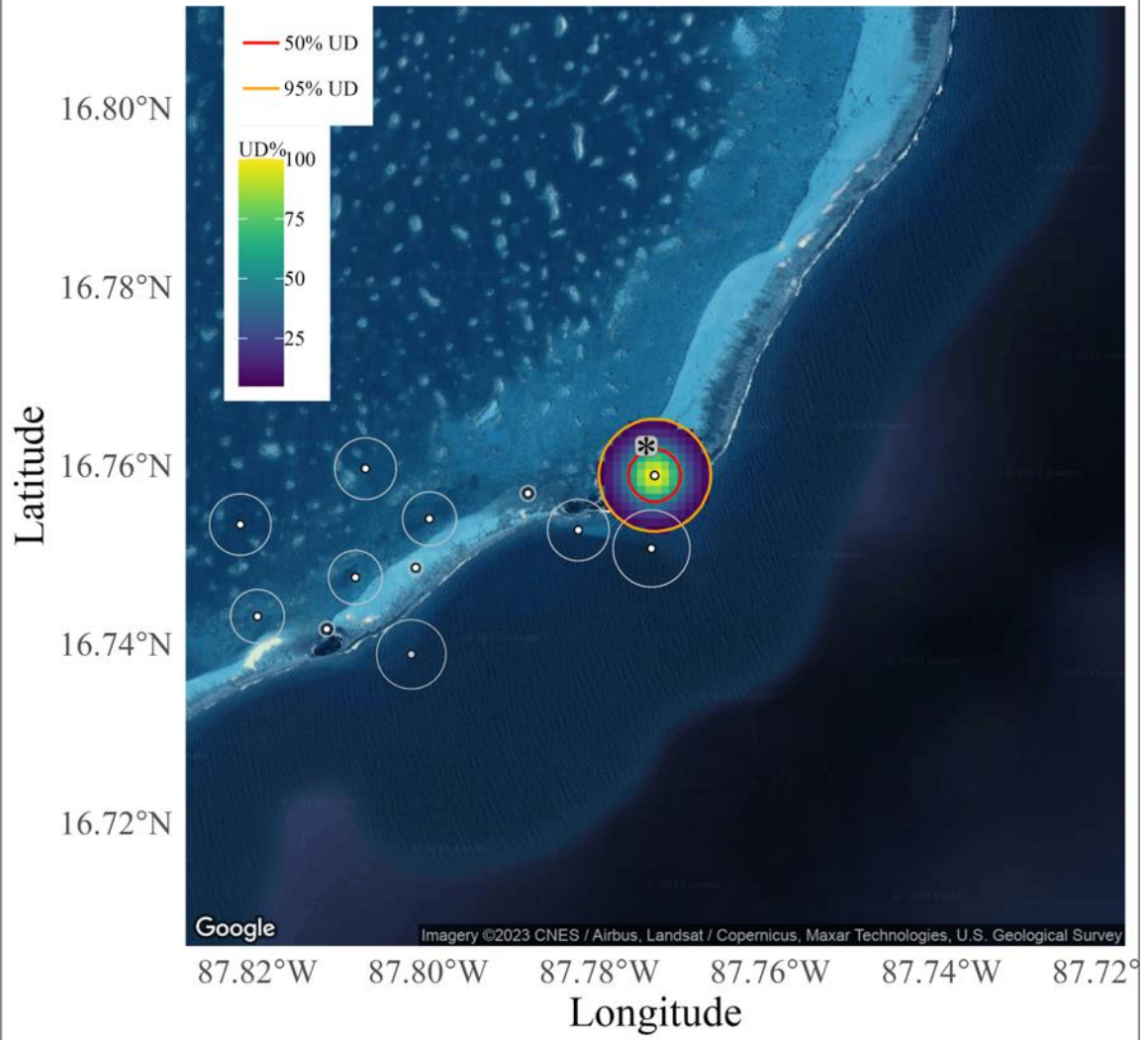
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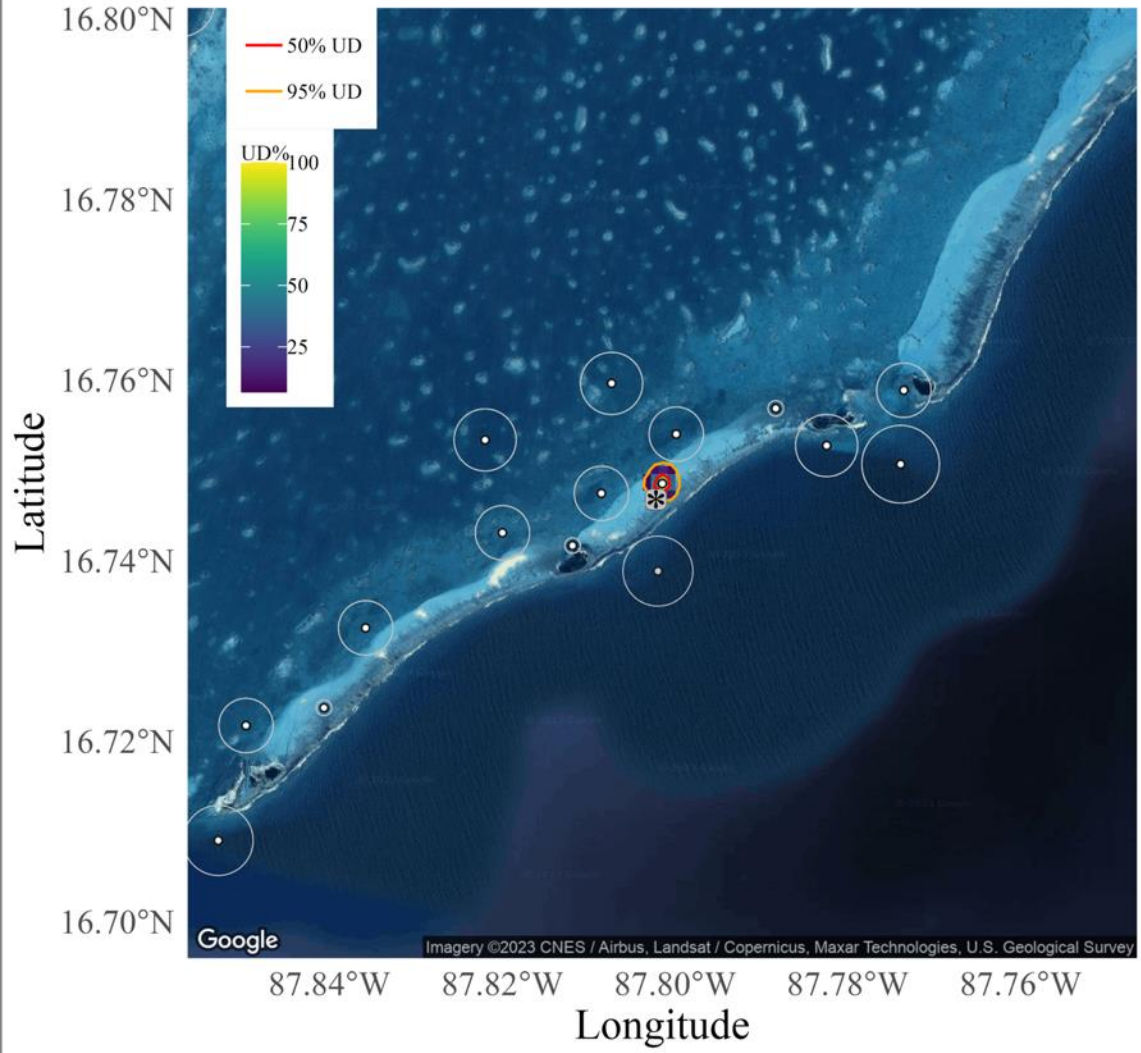
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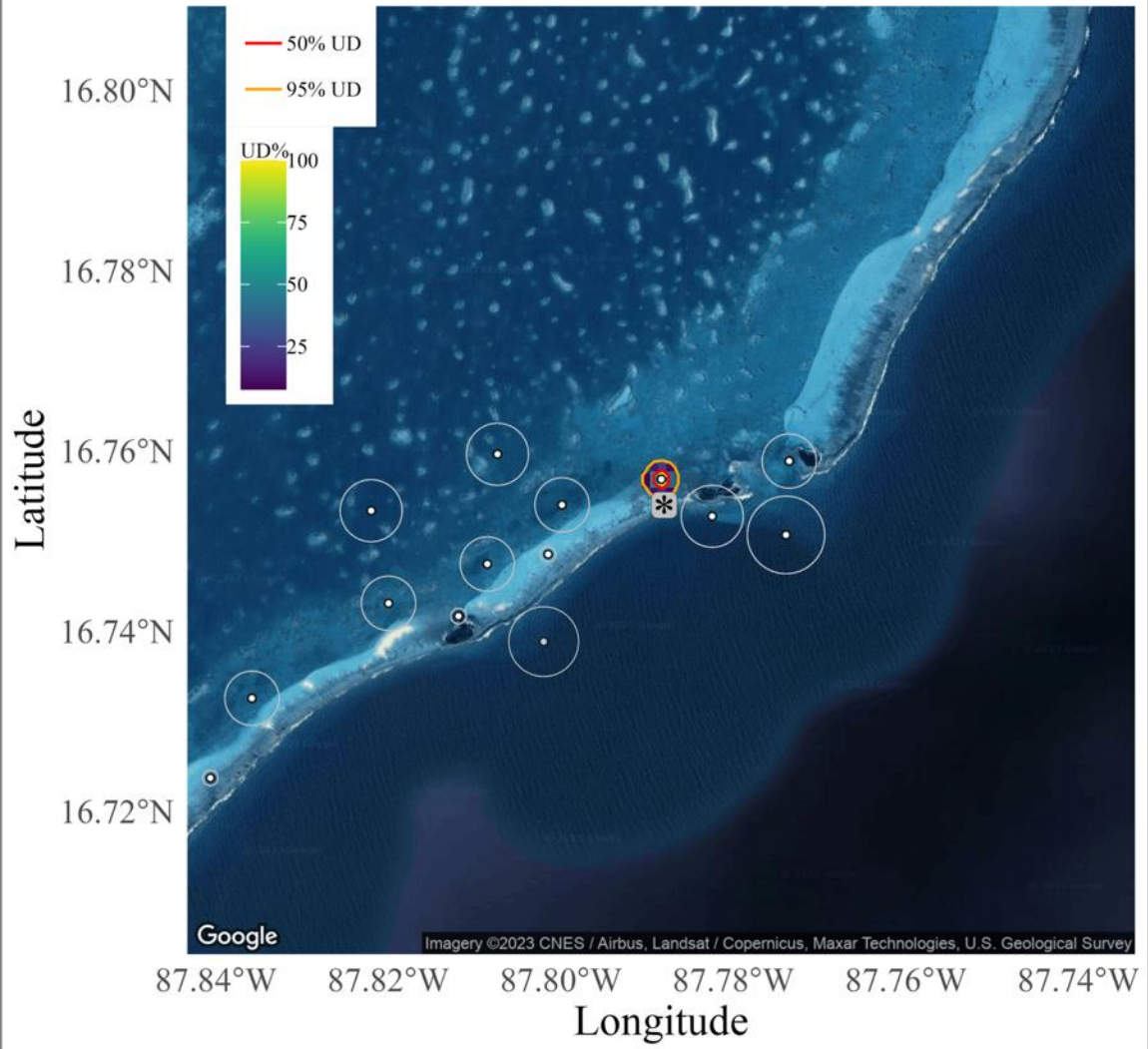
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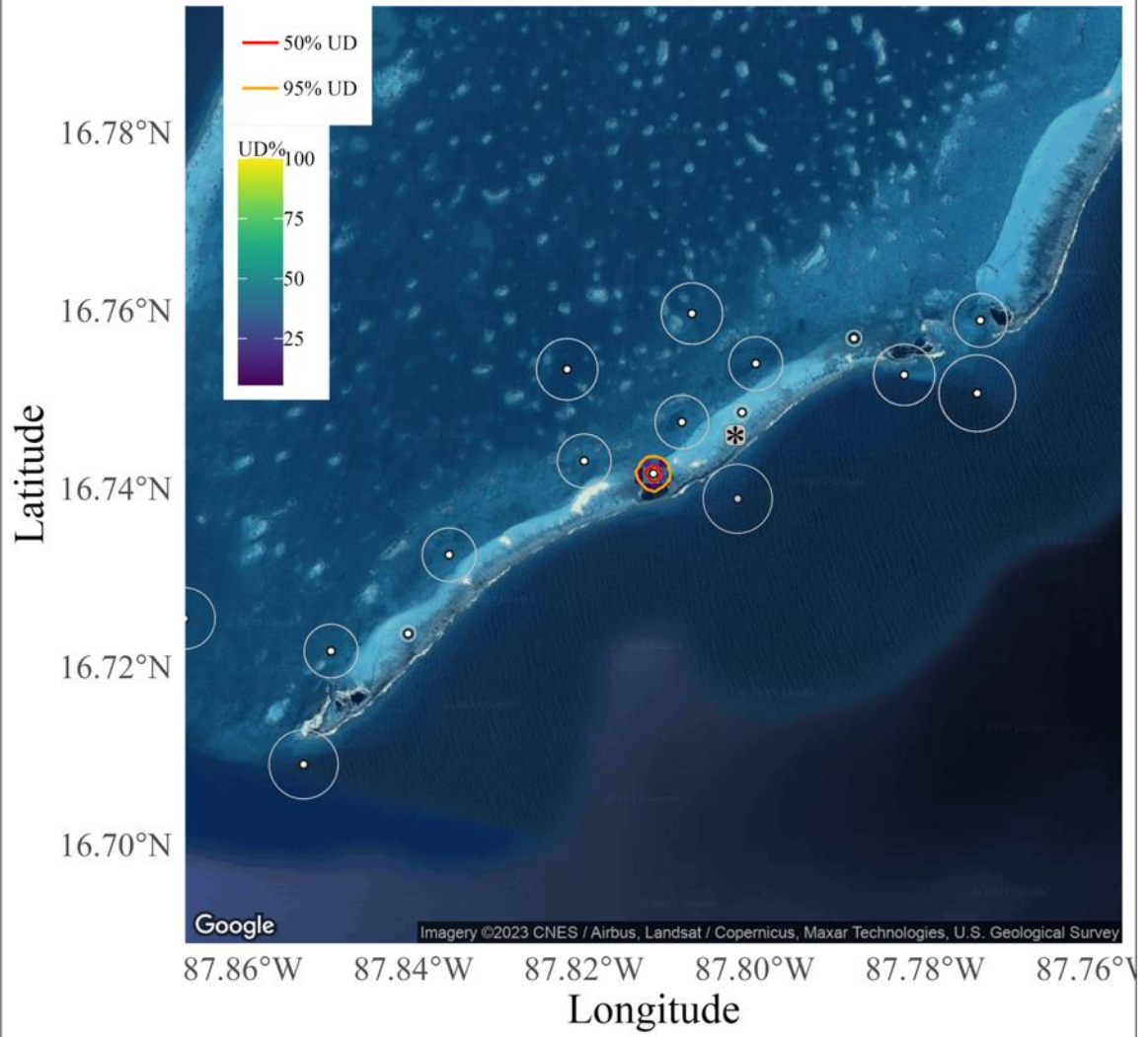
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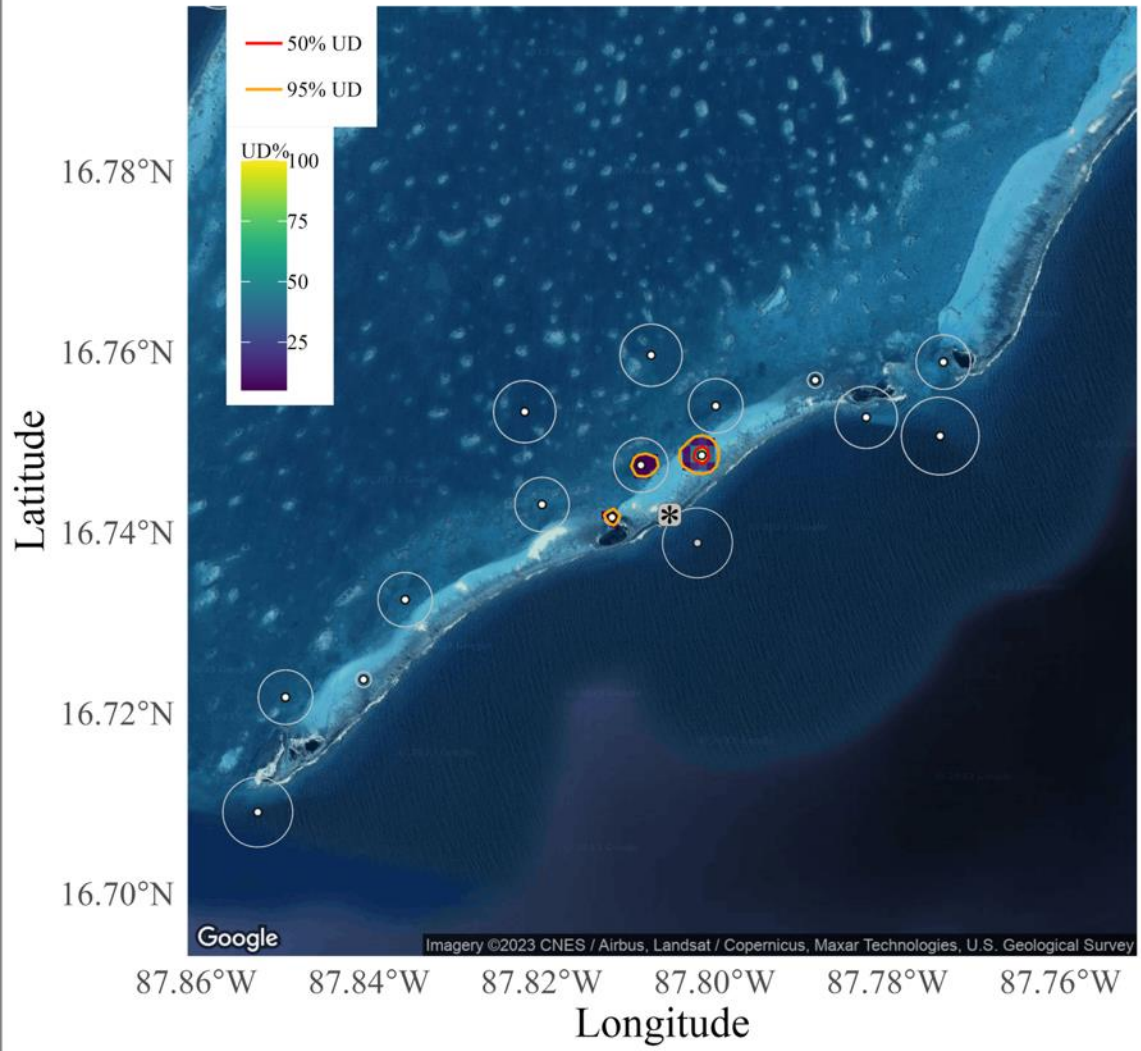
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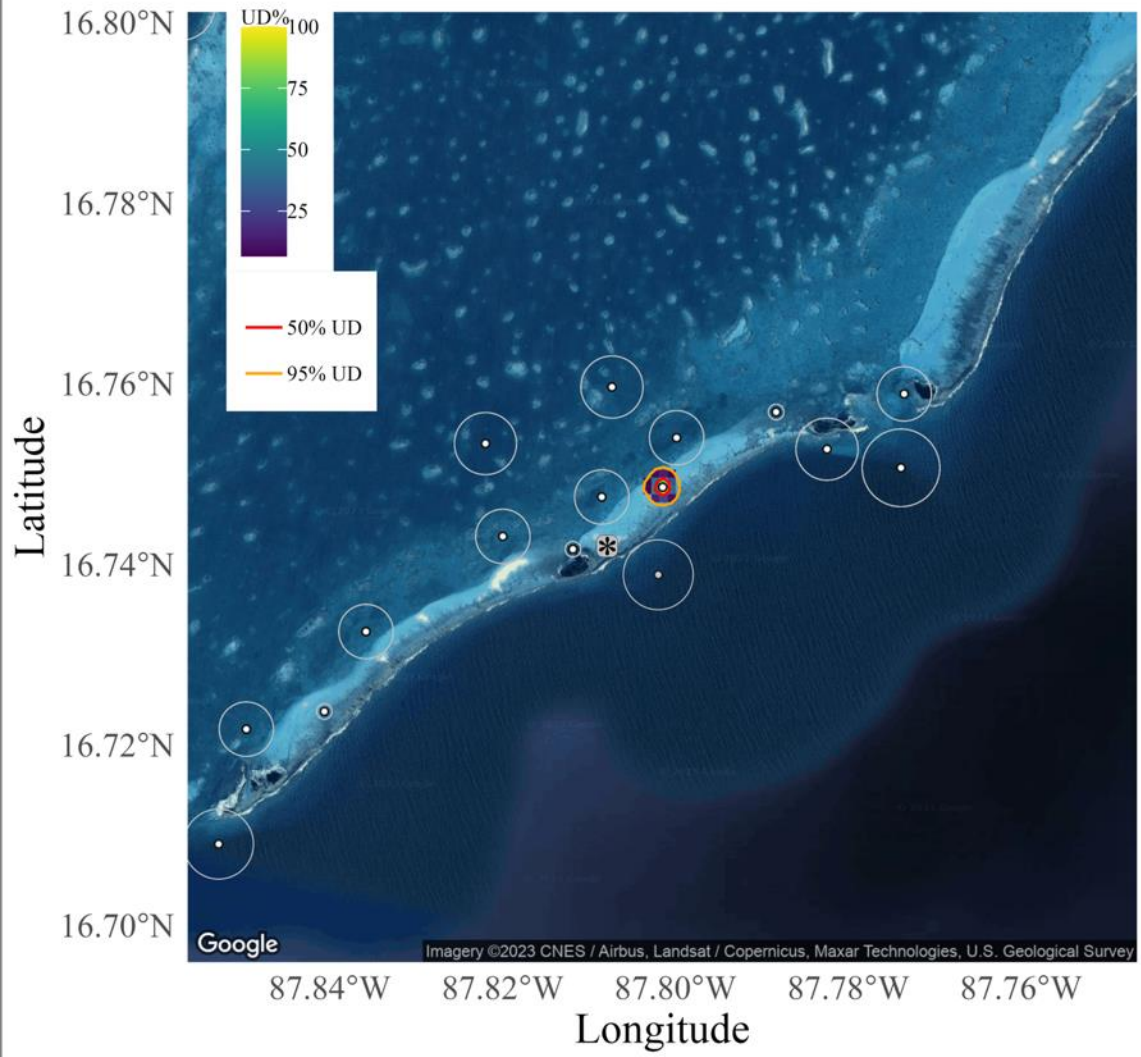
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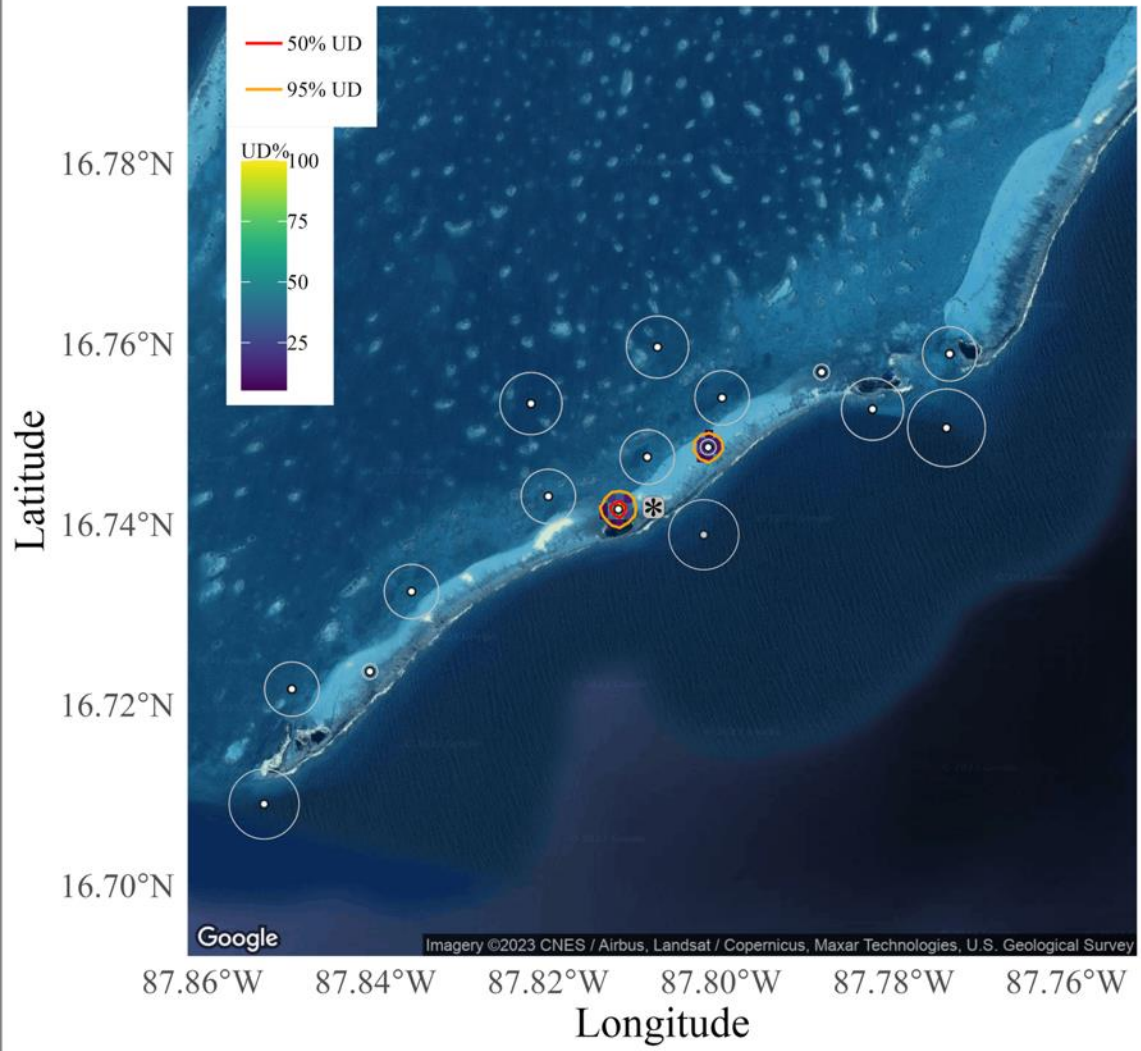
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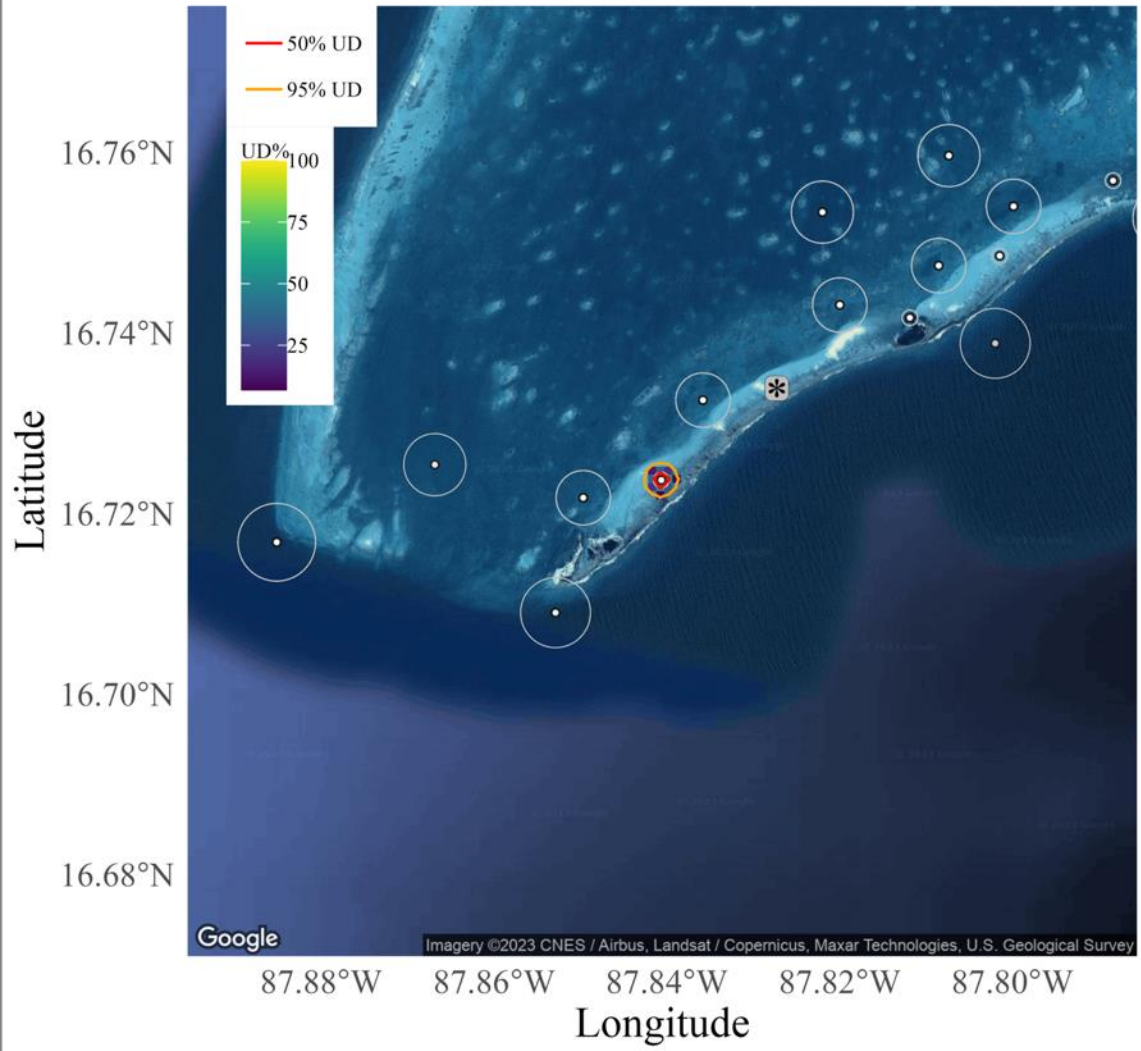
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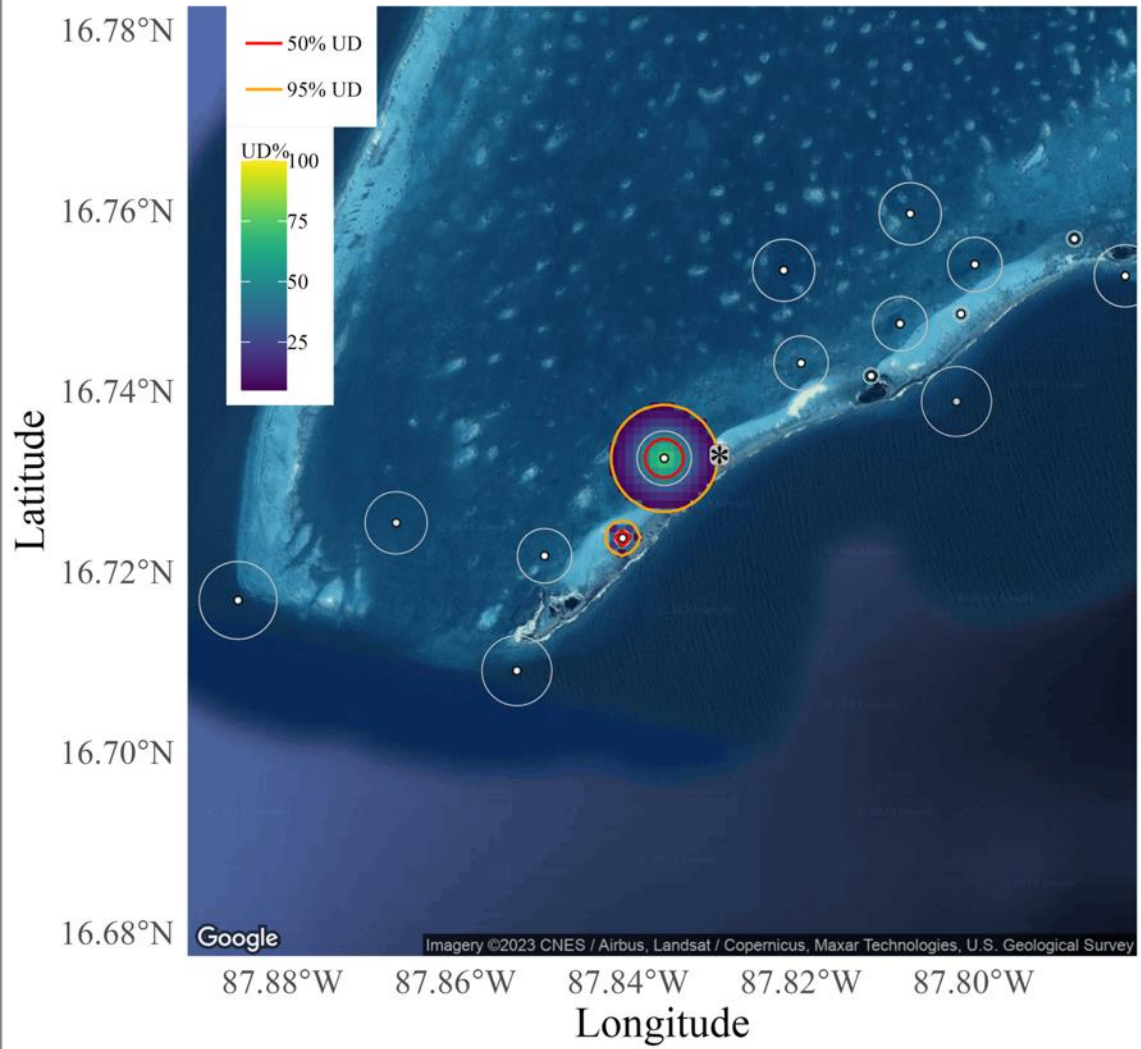
Southern stingray 28



Southern stingray 29

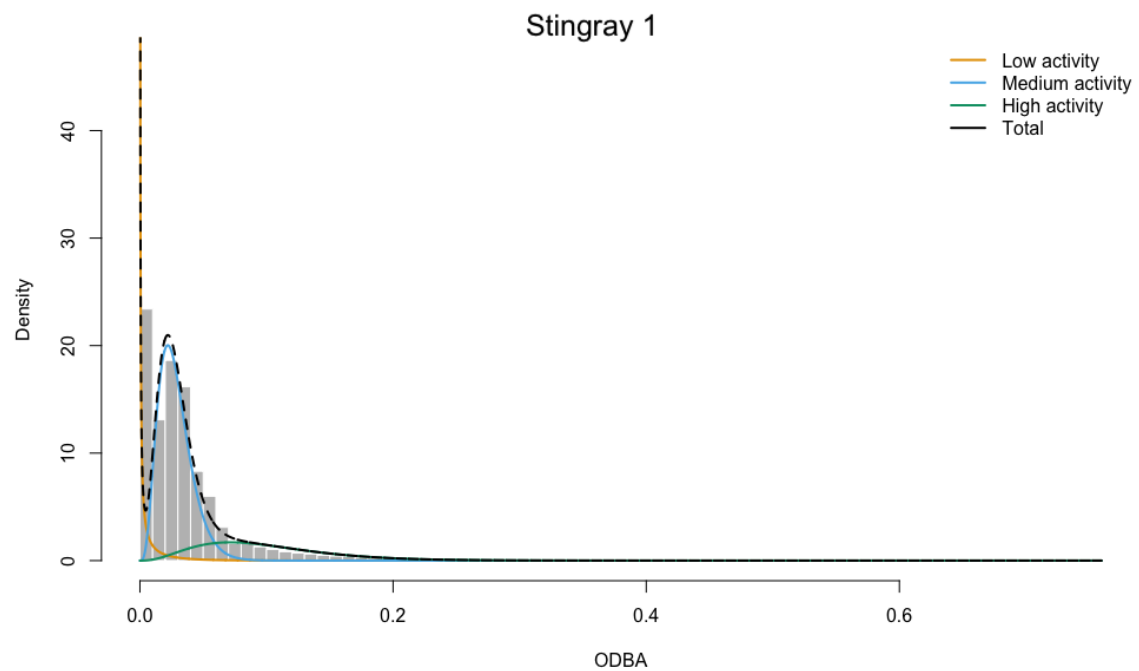
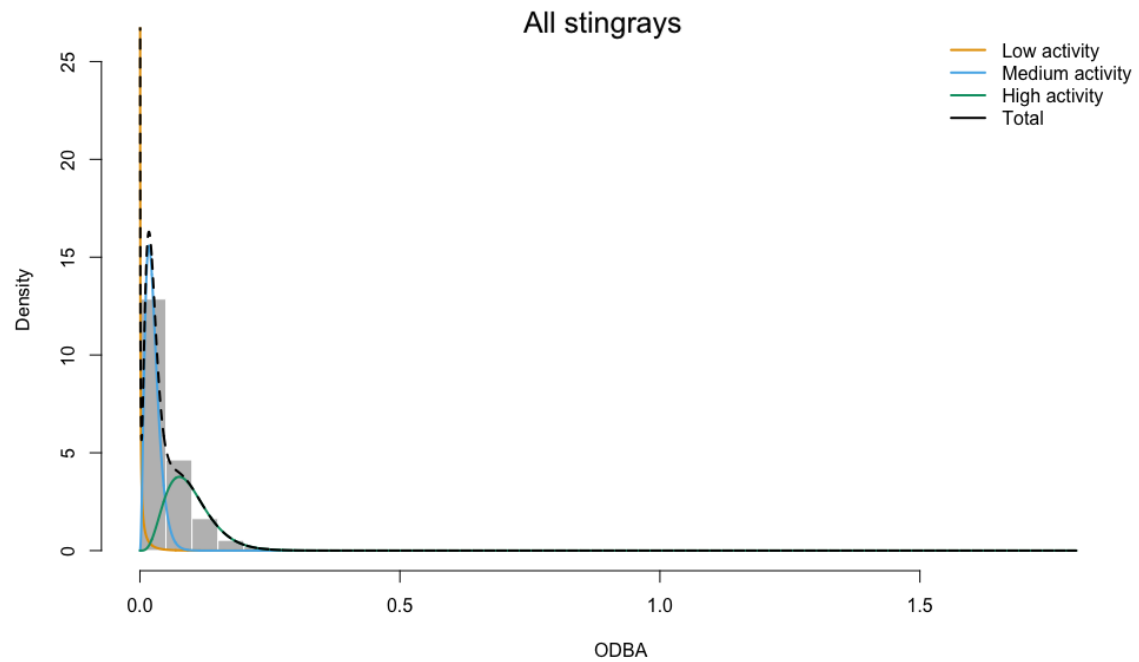


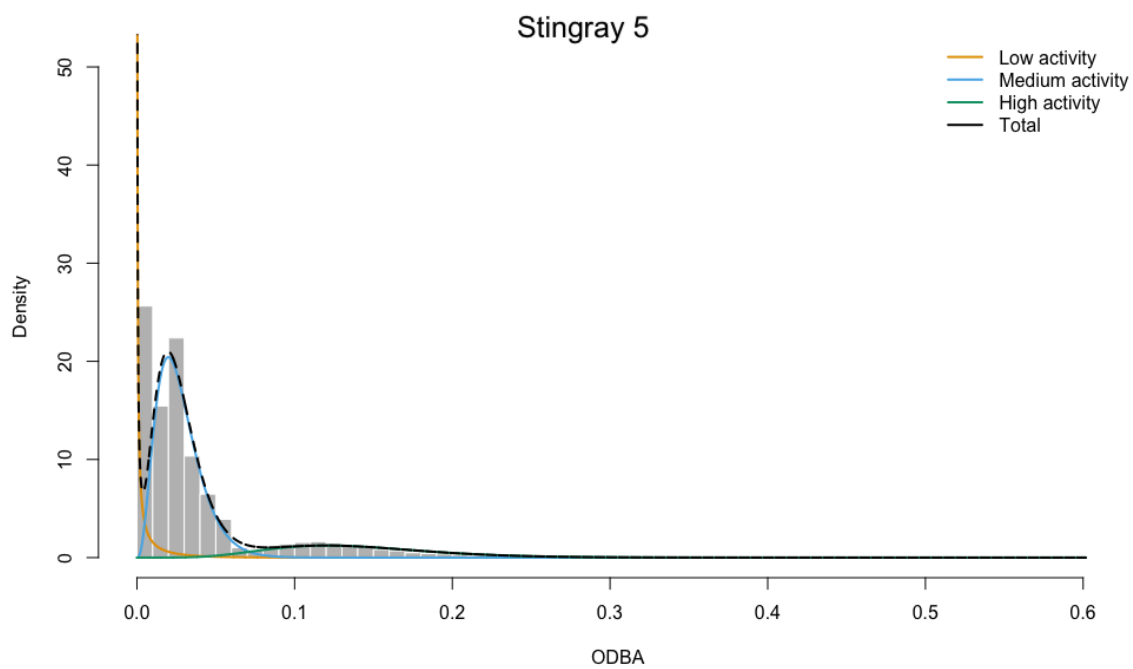
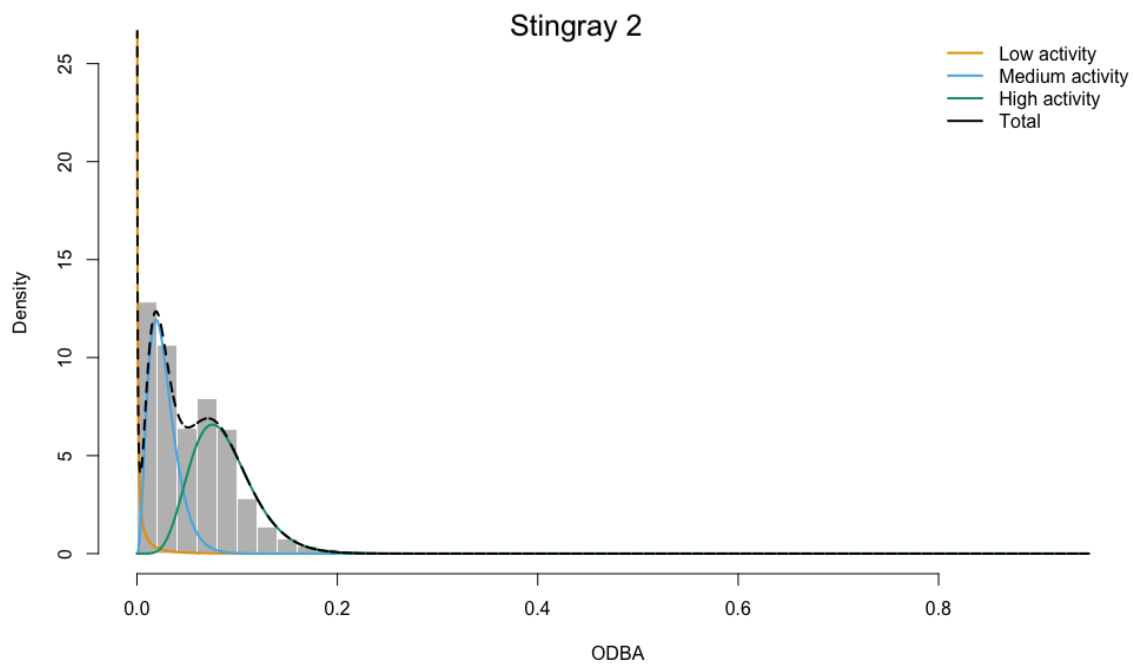
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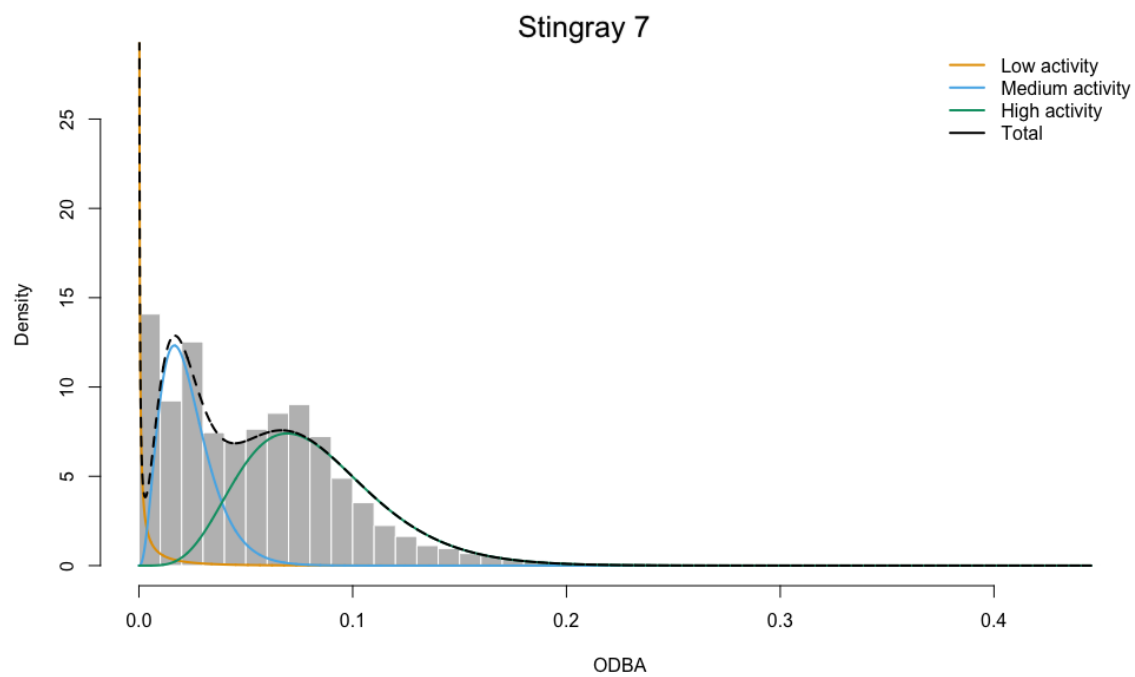
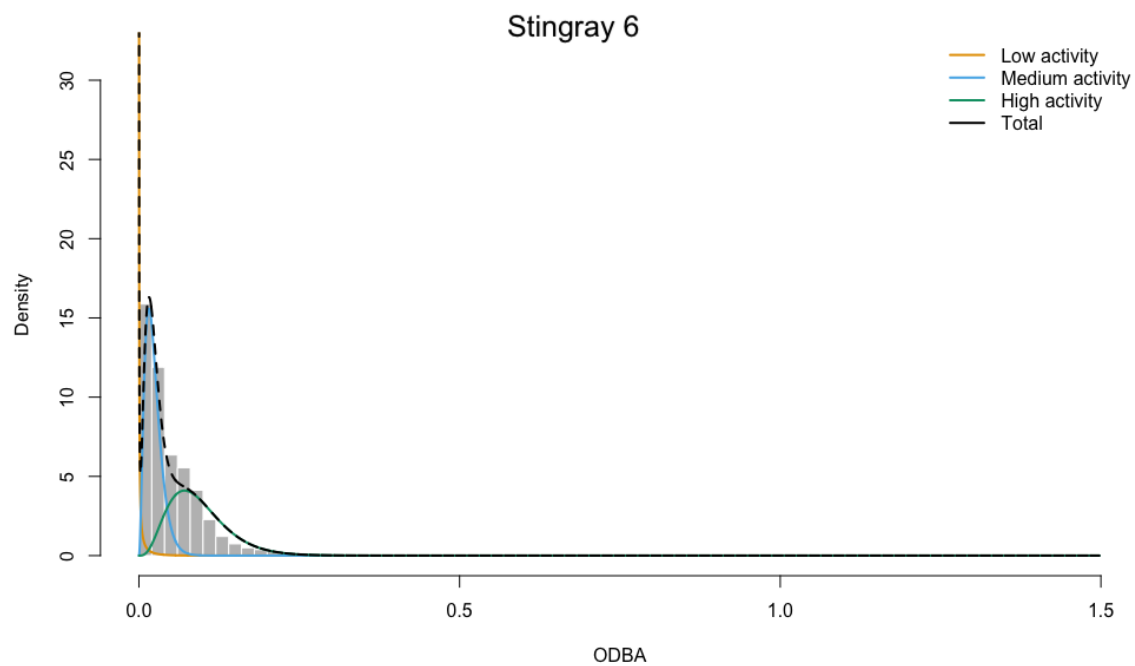


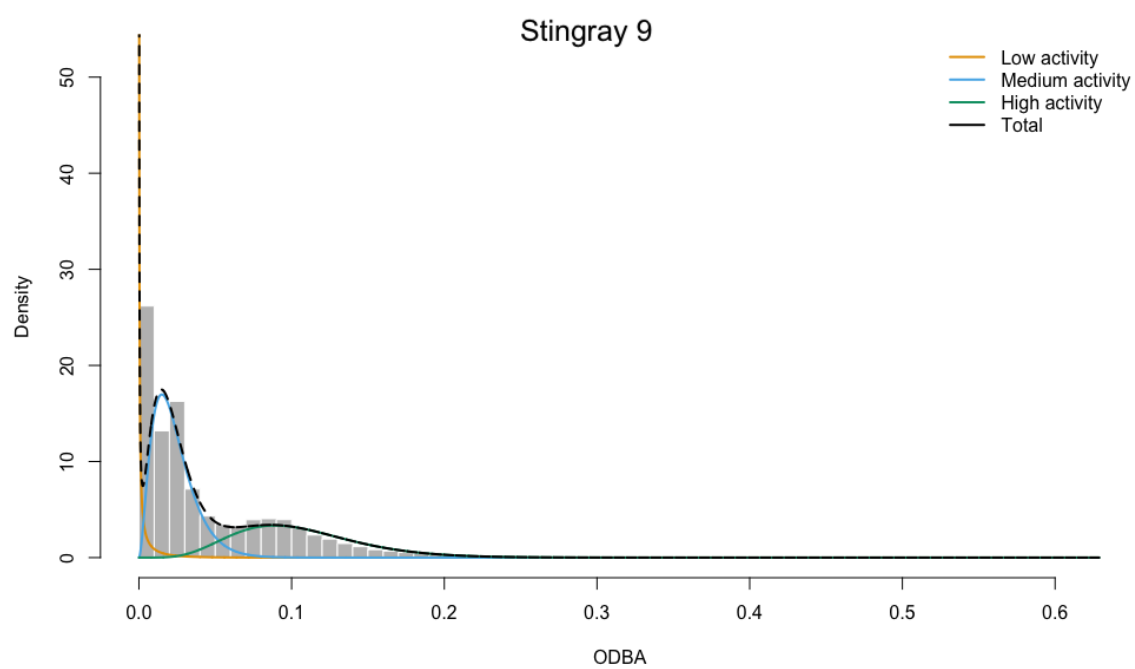
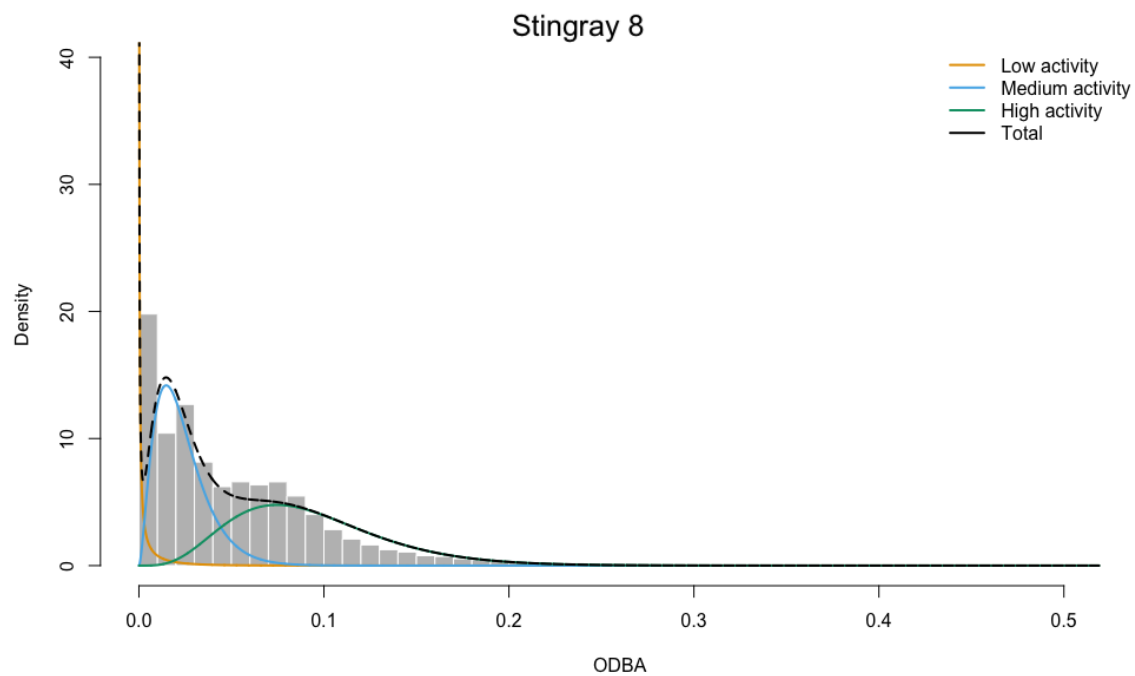
APPENDIX II – CHAPTER IV

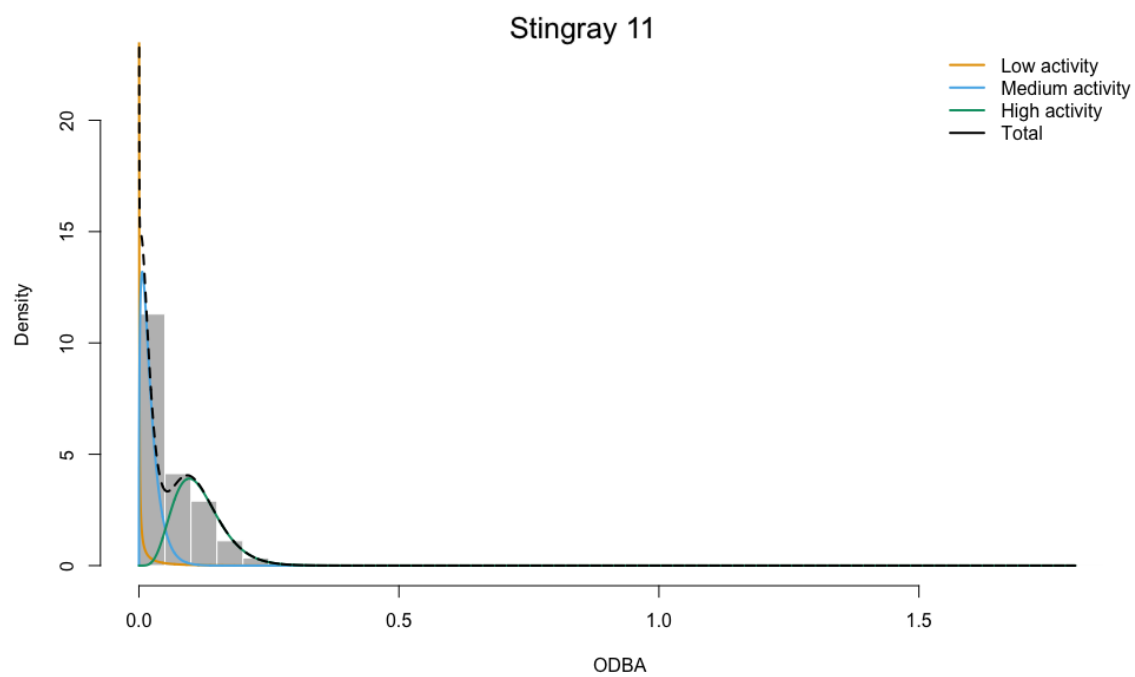
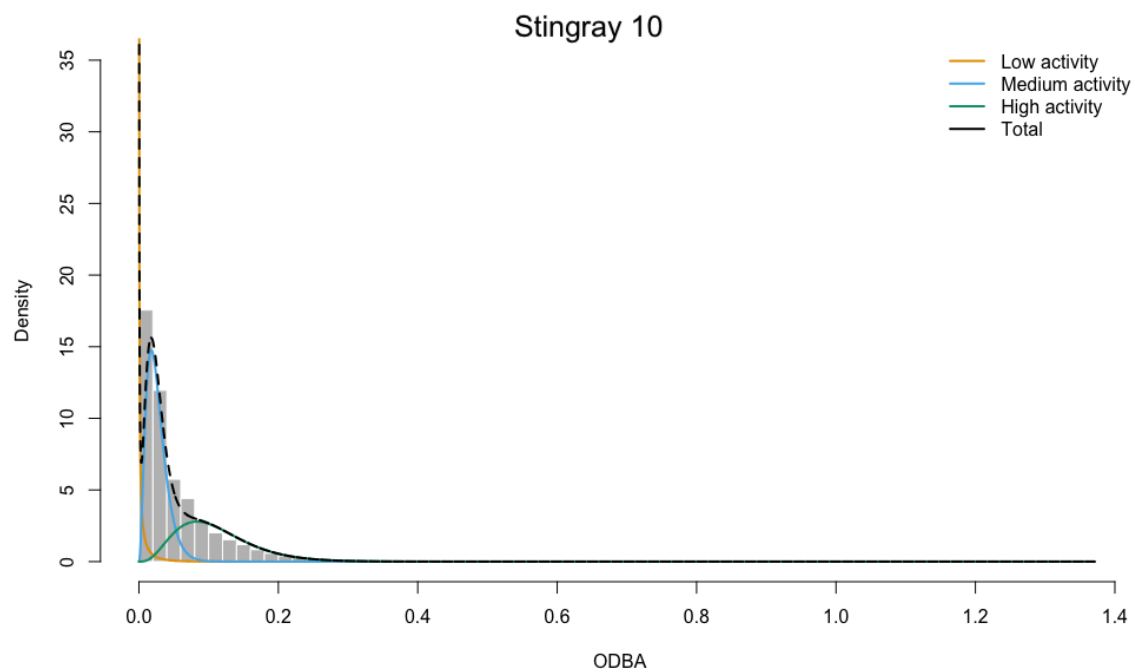
Estimated state-dependent probability distributions of overall dynamic body acceleration (ODBA) from the AIC preferred hidden Markov models.







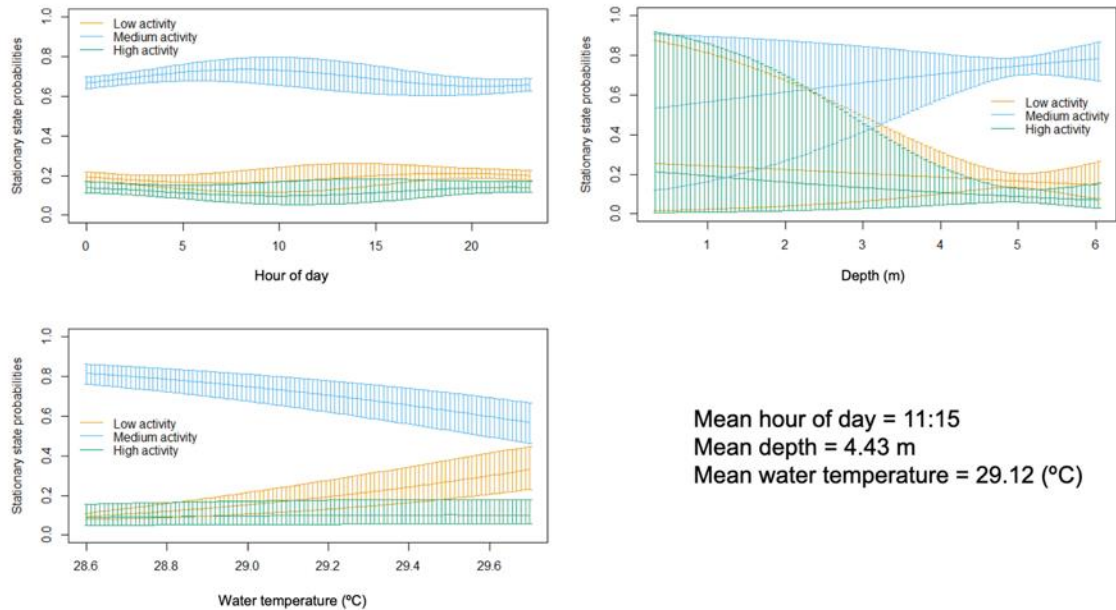




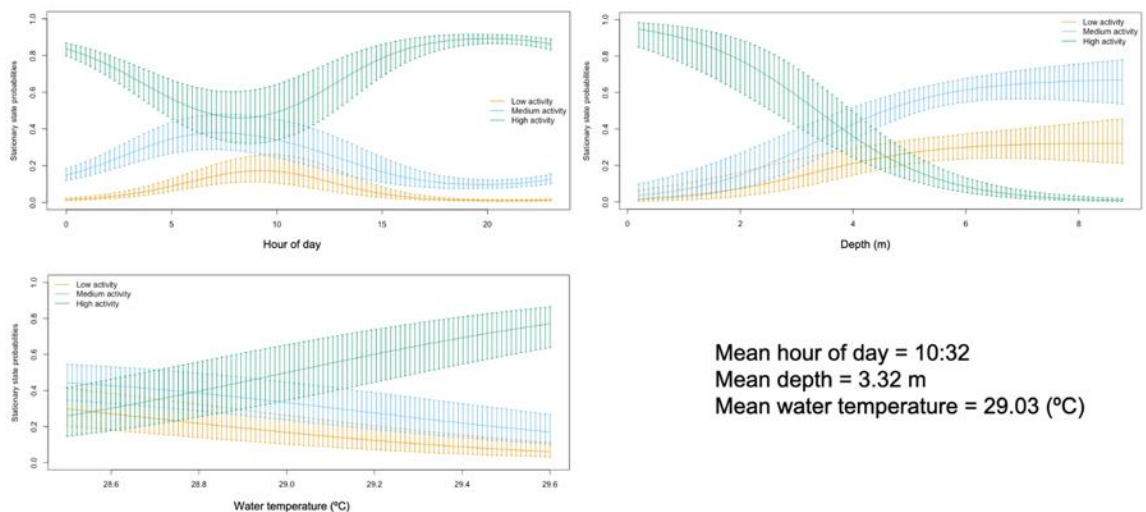
APPENDIX III – CHAPTER IV

Stationary state probabilities (with 95% confidence intervals) from hidden Markov models with lowest Akaike's information criterion for individual stingrays across hour of day, depth, and water temperature. Probabilities are calculated at mean values of the other covariates. Stingrays 1 and 2 were captured along the Belize barrier reef in 2017 and Stingrays 5 – 11 were captured at Glover's Reef Atoll in 2019.

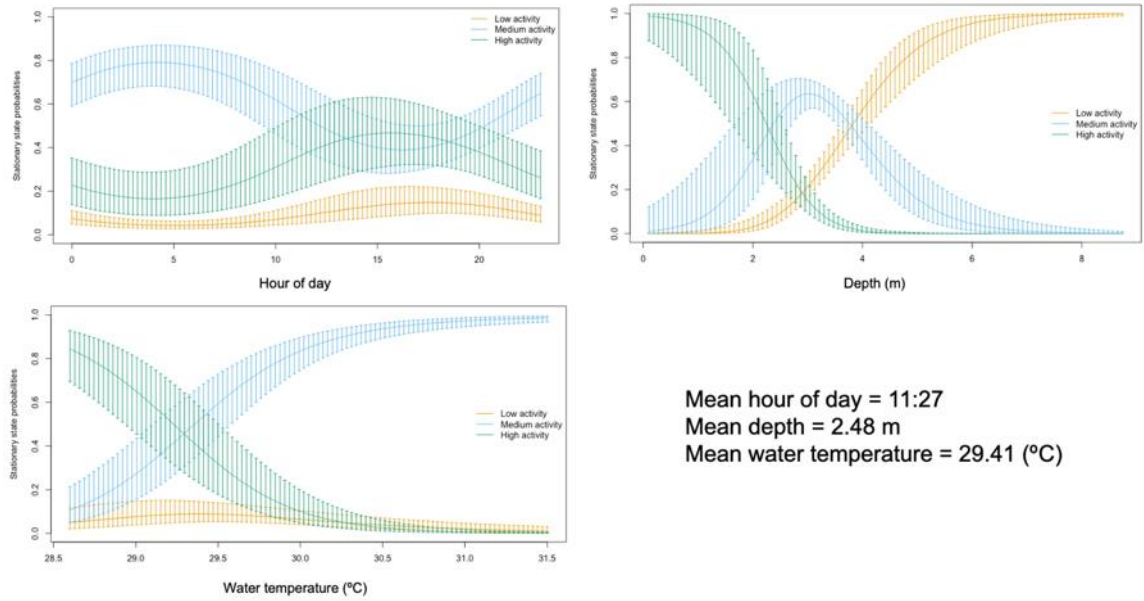
Stingray 1



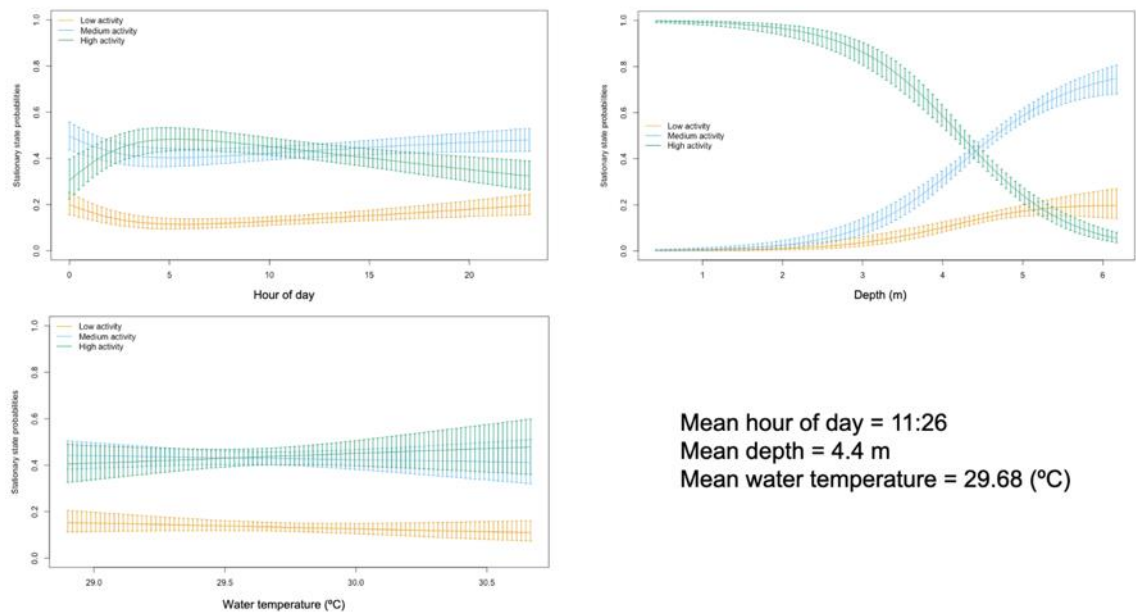
Stingray 2



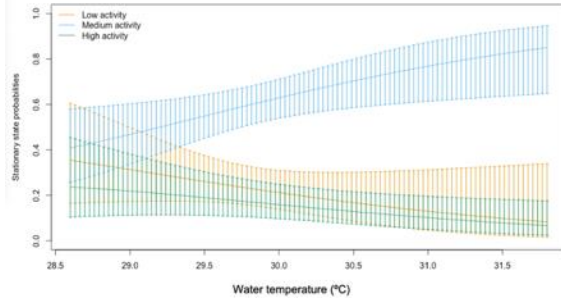
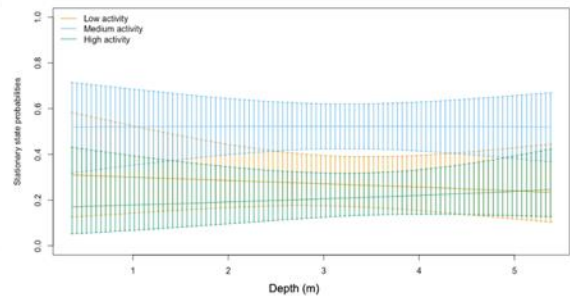
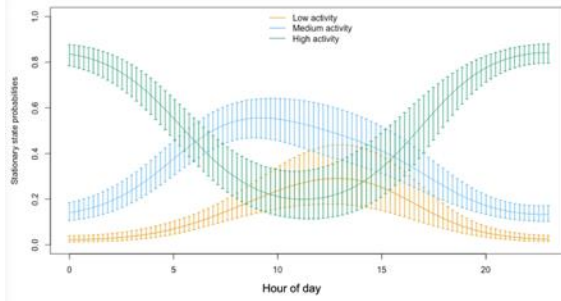
Stingray 5



Stingray 6

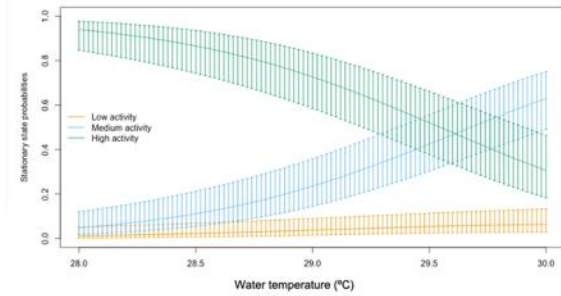
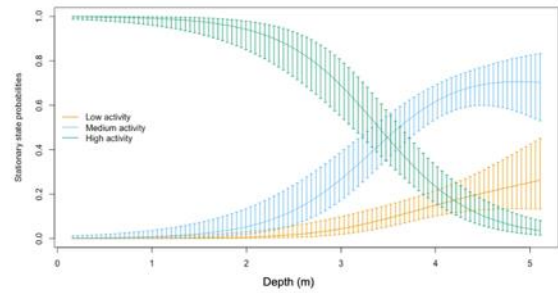
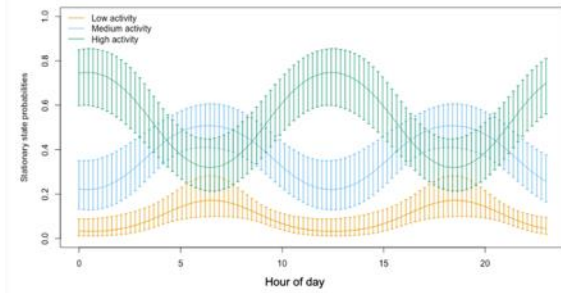


Stingray 7



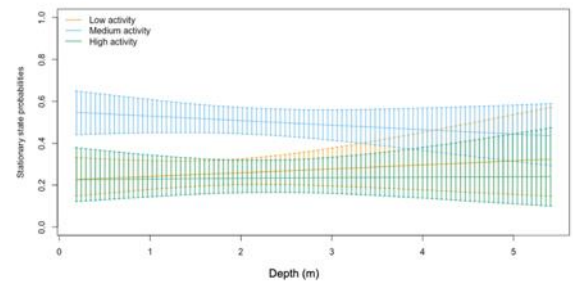
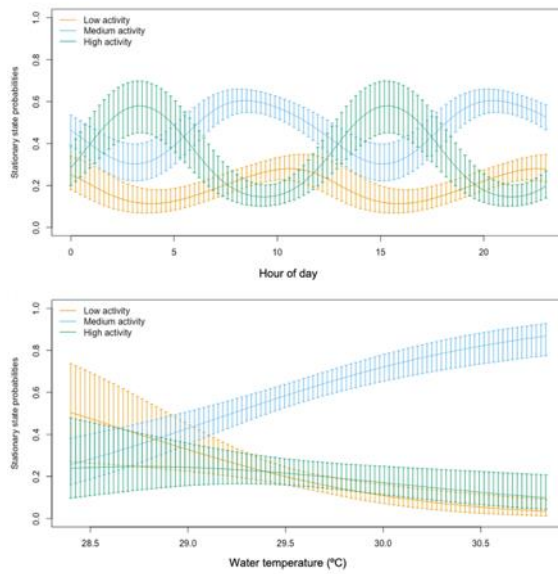
Mean hour of day = 11:29
Mean depth = 2.58 m
Mean water temperature = 29.34 (°C)

Stingray 8



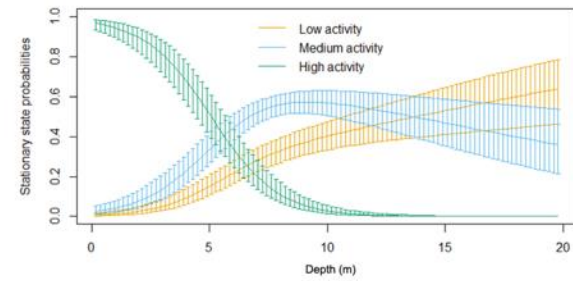
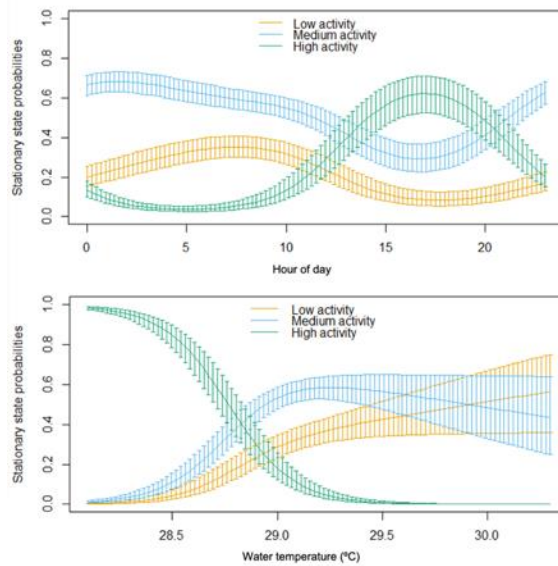
Mean hour of day = 11:26
Mean depth = 2.91 m
Mean water temperature = 29.01 (°C)

Stingray 9



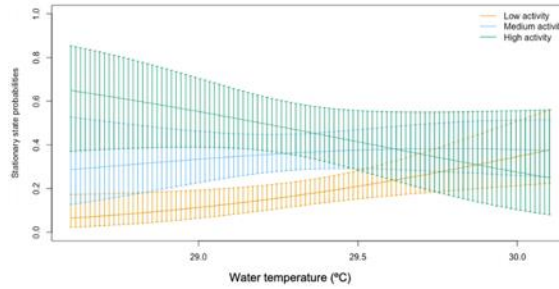
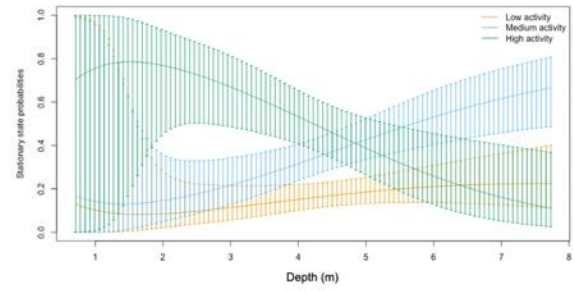
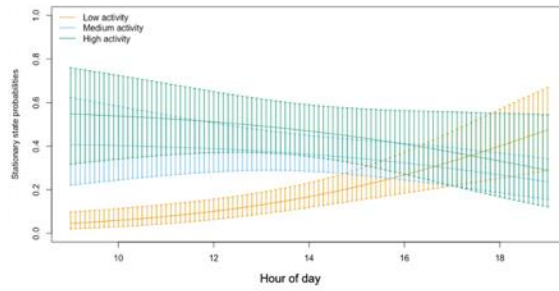
Mean hour of day = 11:30
Mean depth = 2.5 m
Mean water temperature = 29.22 (°C)

Stingray 10



Mean hour of day = 11:40
Mean depth = 6.54 m
Mean water temperature = 28.93 (°C)

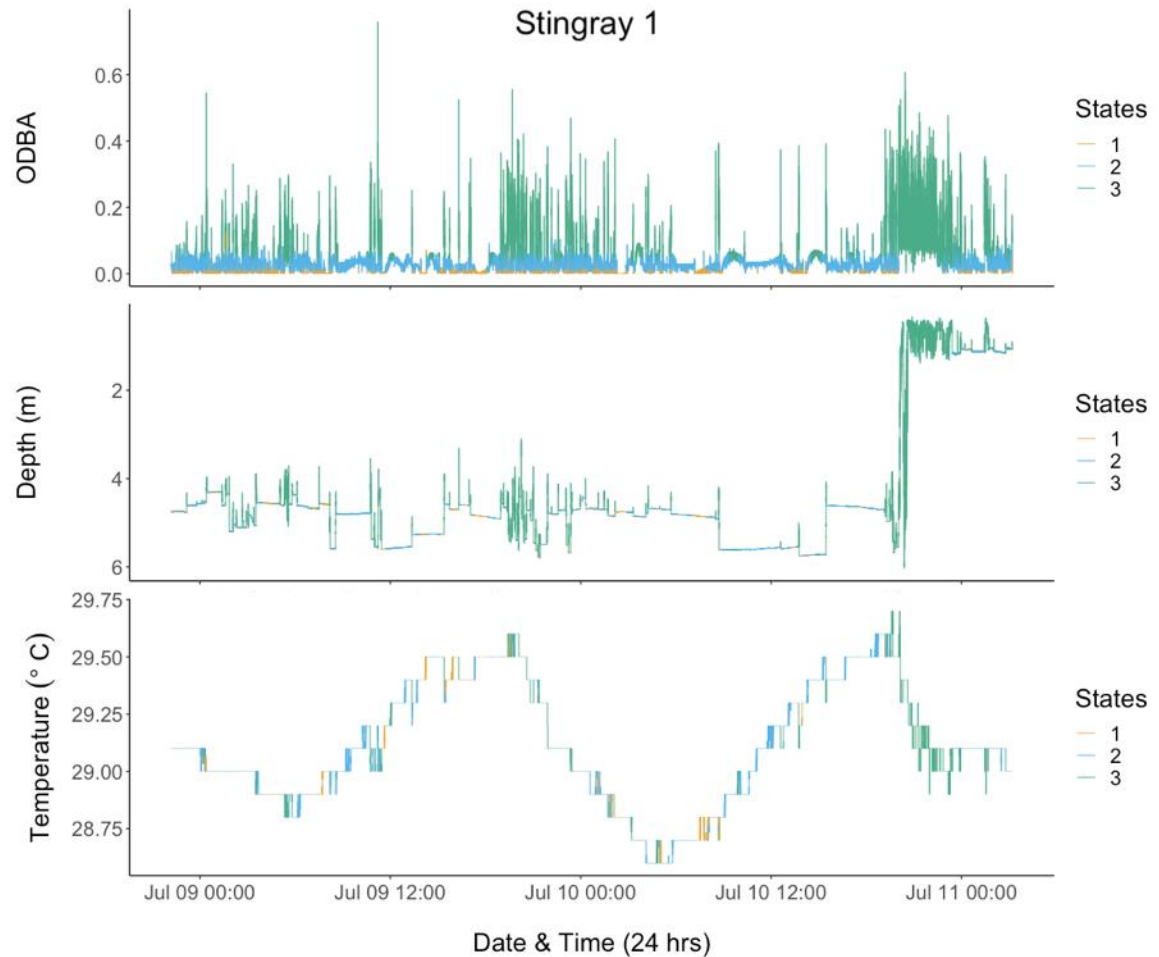
Stingray 11

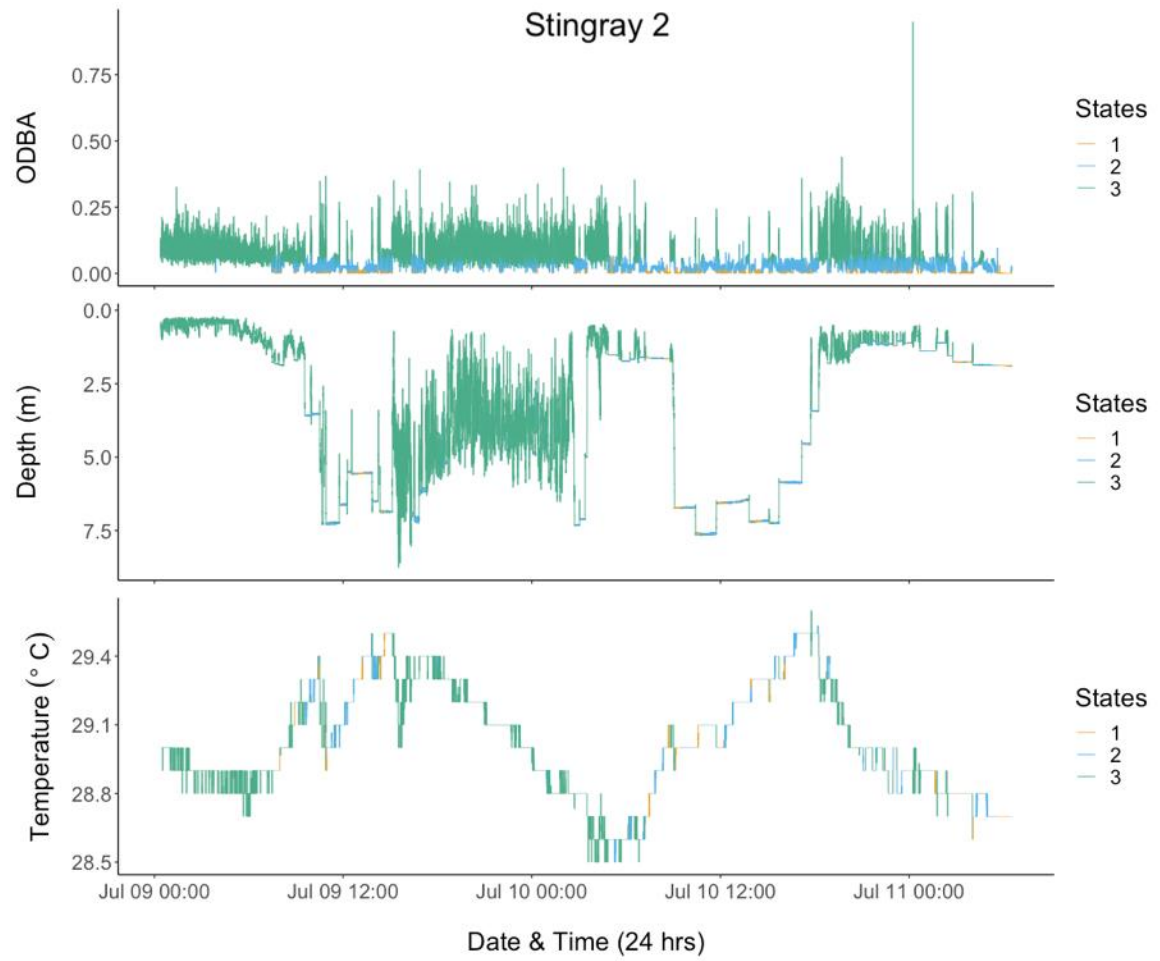


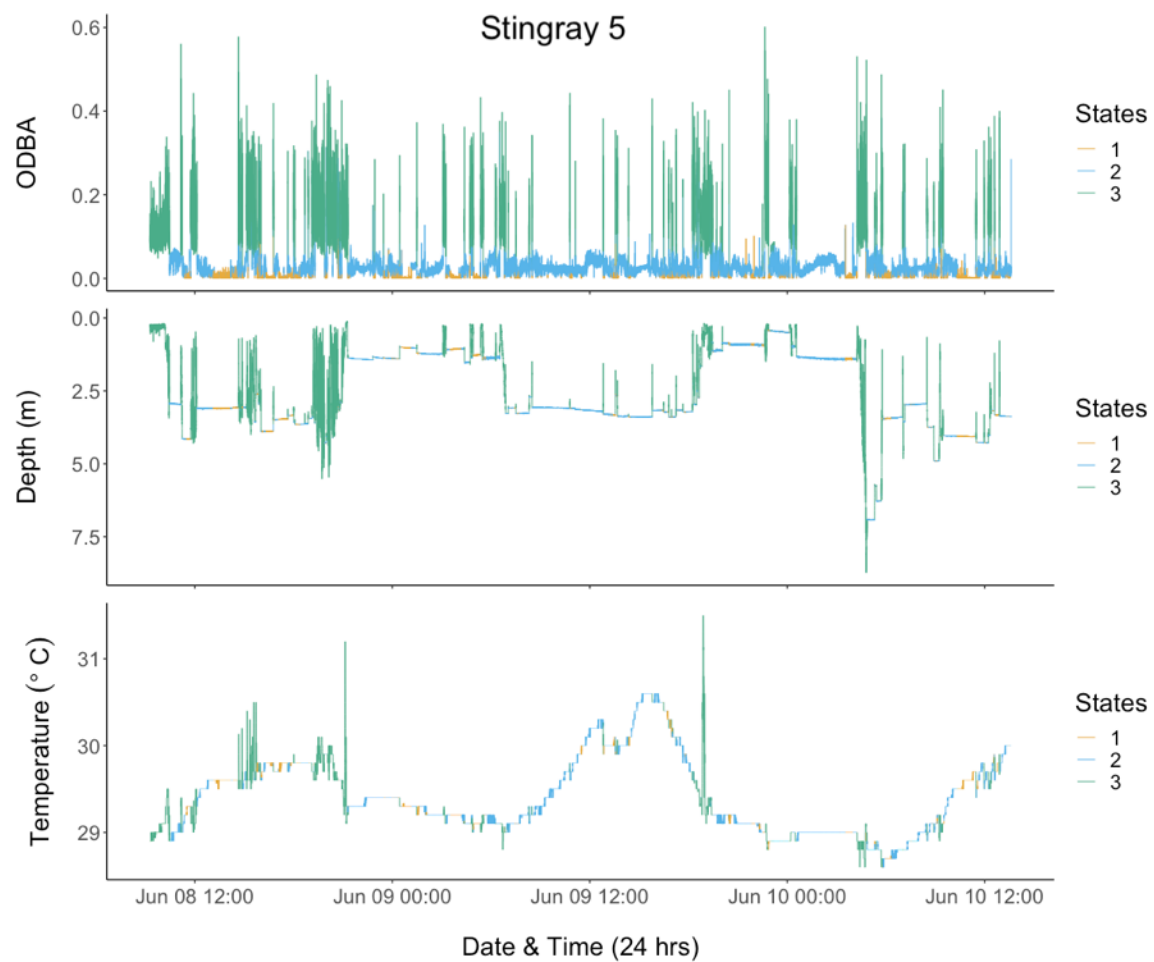
Mean hour of day = 13:58
Mean depth = 4.43 m
Mean water temperature = 29.3 (°C)

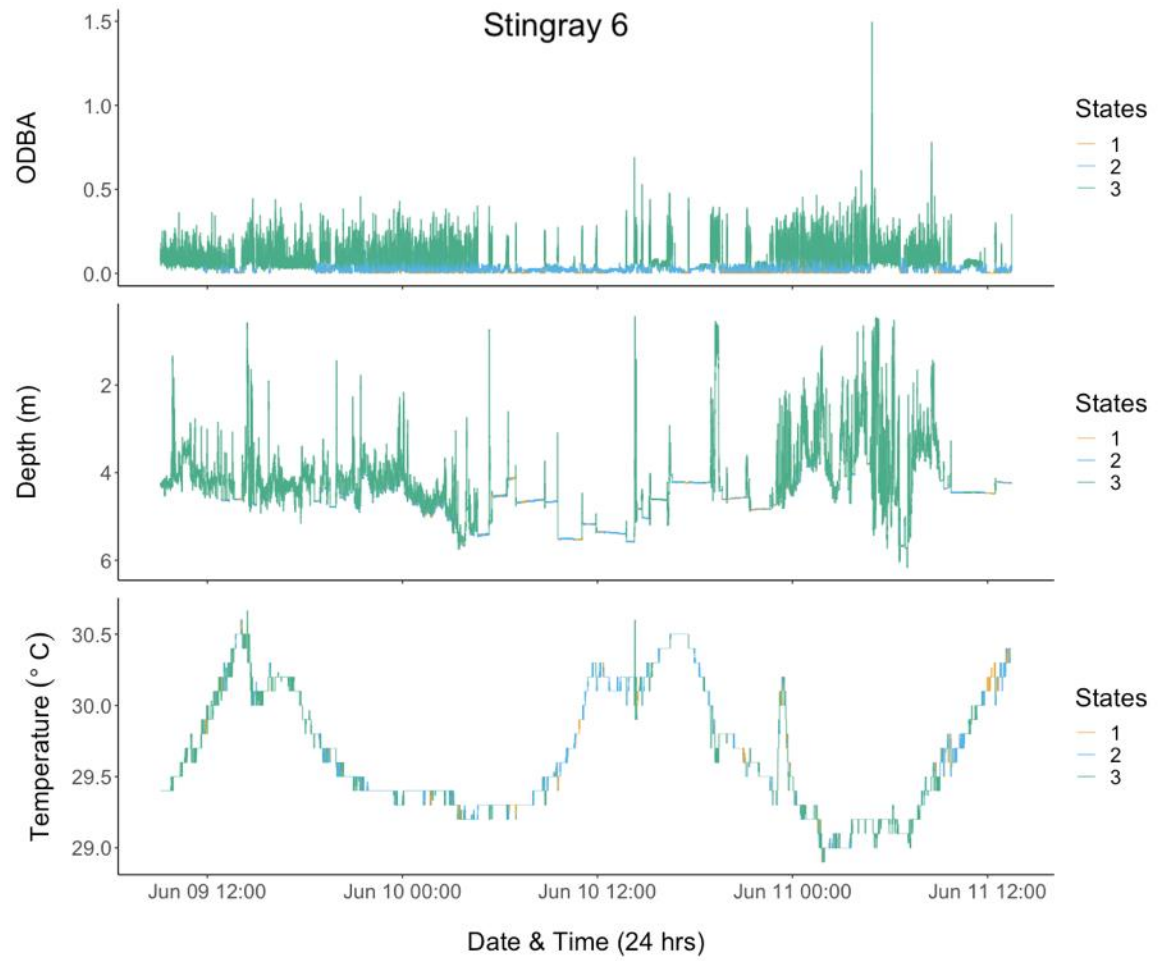
APPENDIX IV – CHAPTER IV

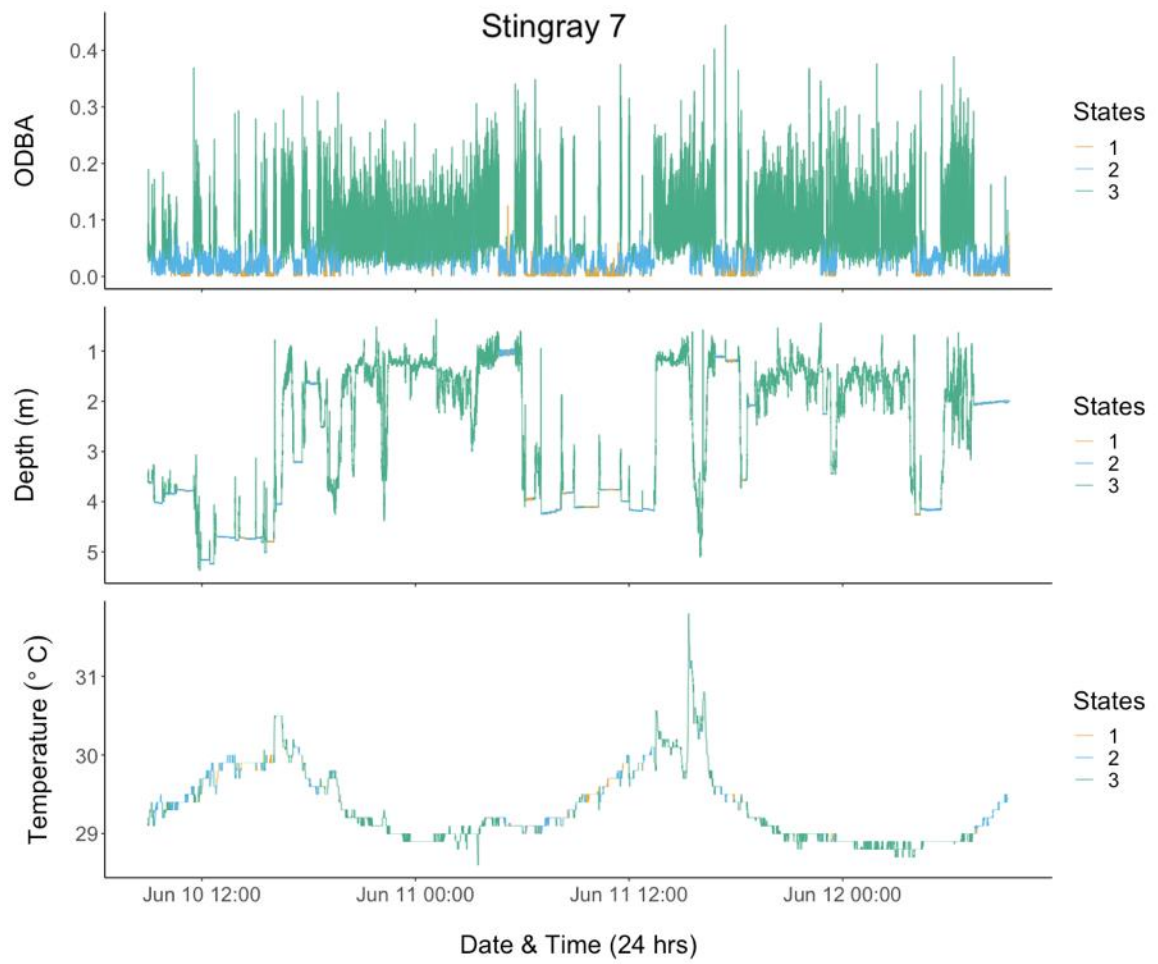
Model variables plotted over time for each southern stingray and coloured by activity state (state 1 = low activity, state 2 = medium activity, state 3 = high activity). “ODBA” = overall dynamic body acceleration. Stingrays 1 and 2 were captured along the Belize barrier reef in 2017 and Stingrays 5 – 11 were captured at Glover’s Reef Atoll in 2019. Stingray 11 did not record data during a full 24-hour period, therefore only time is represented on the x-axis for June 20, 2019.

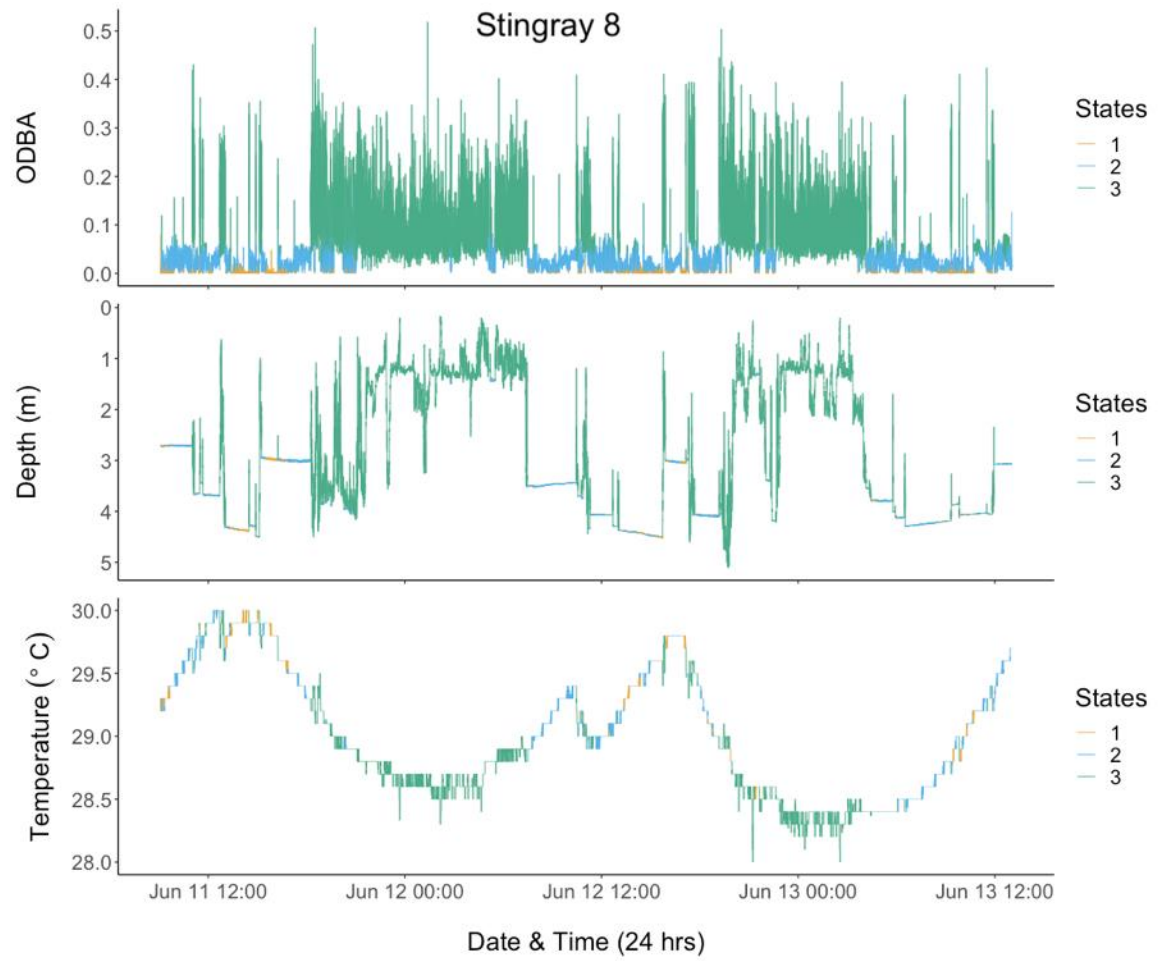


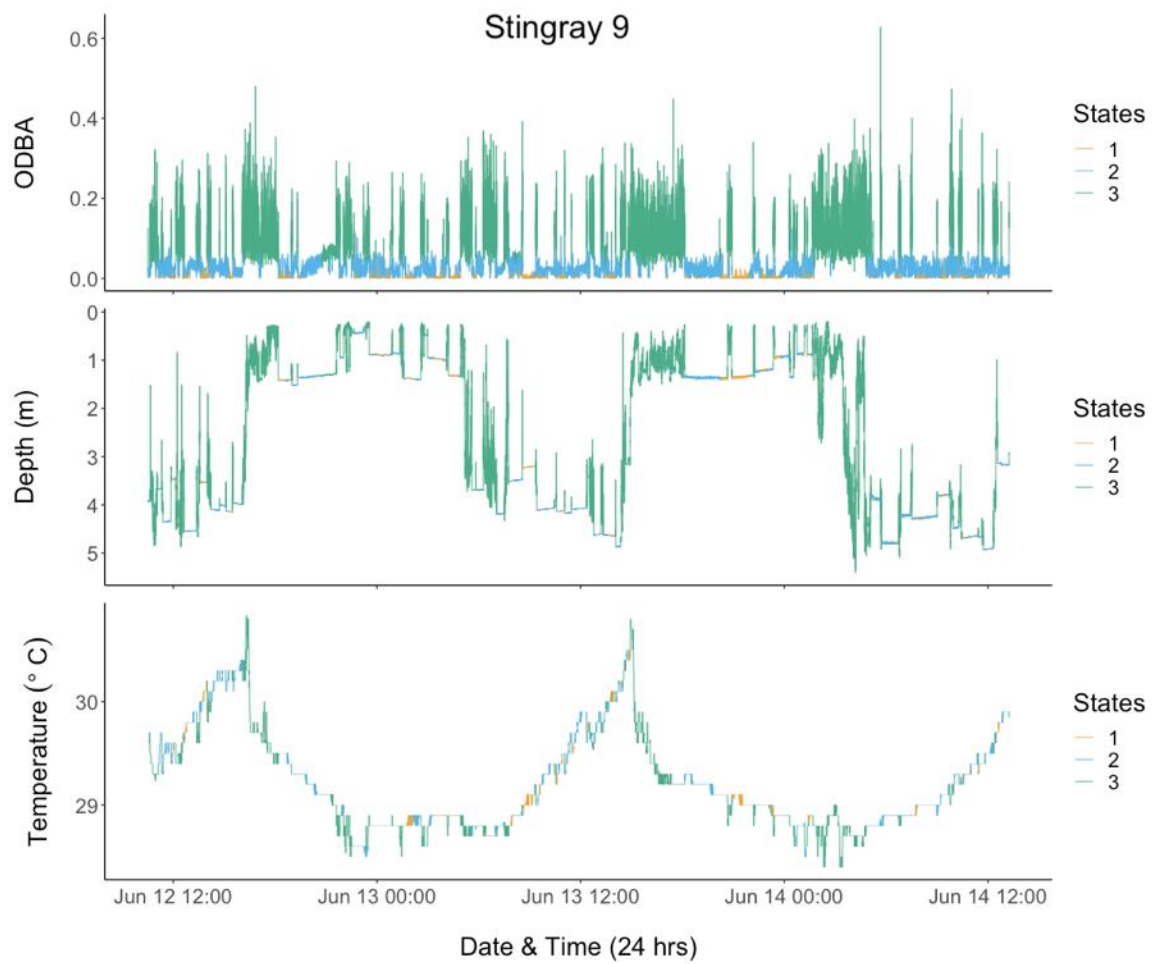


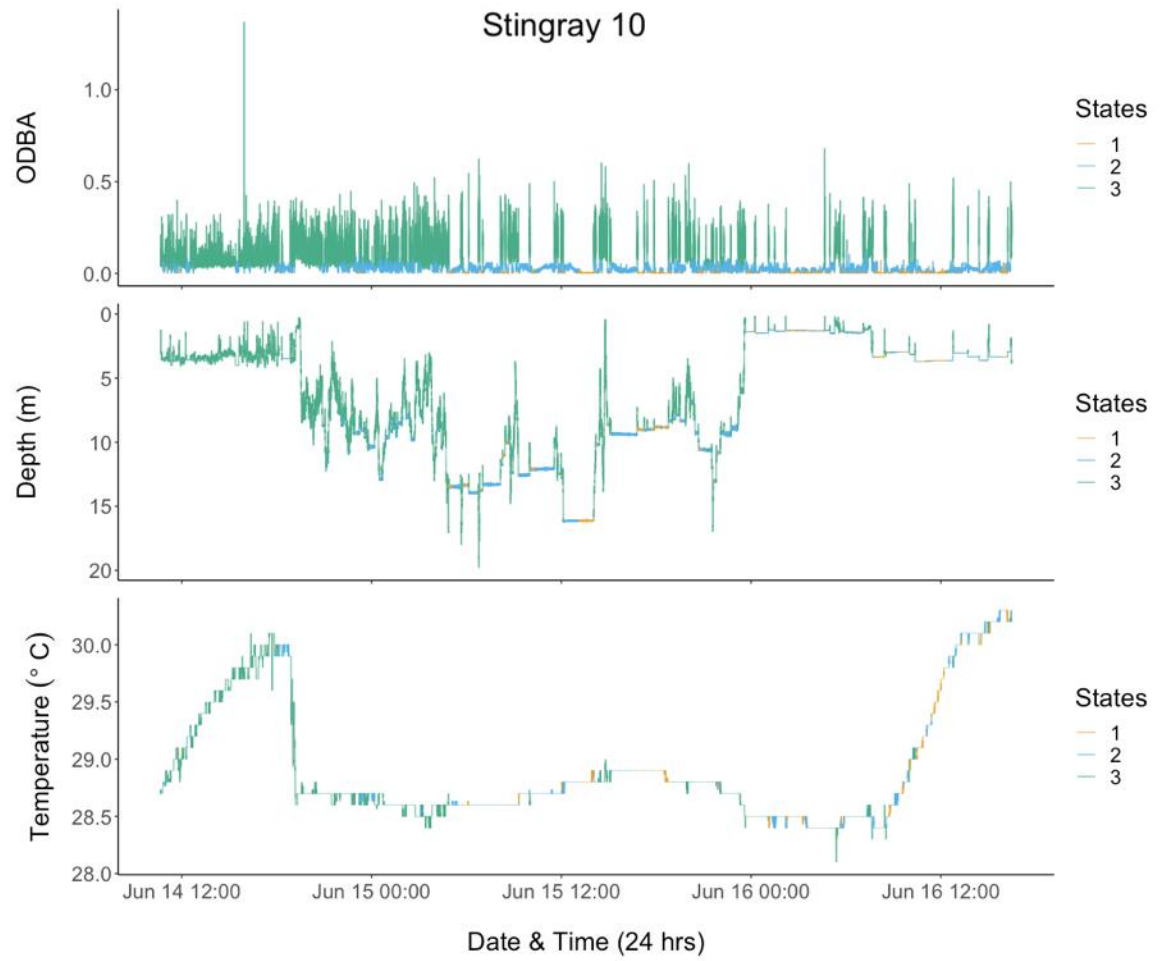


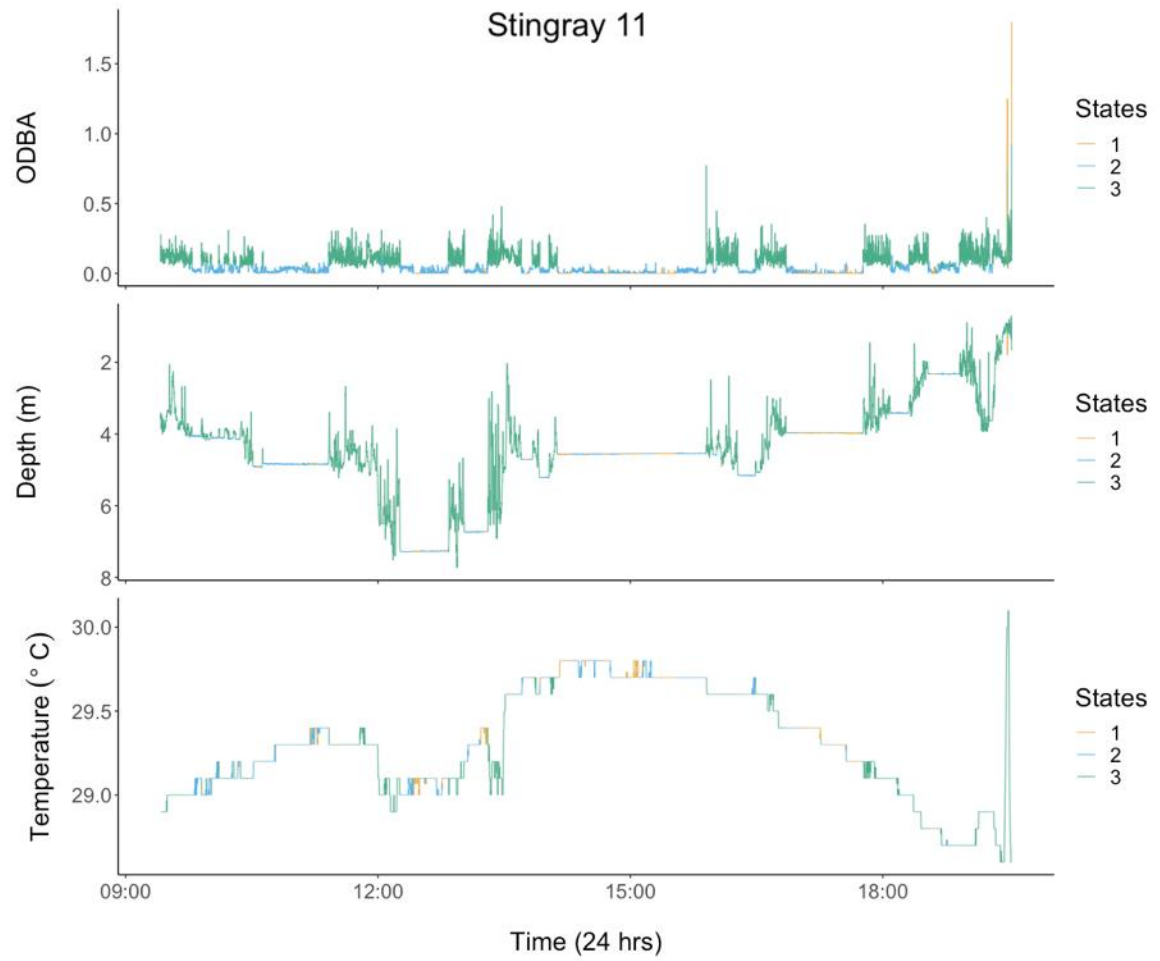








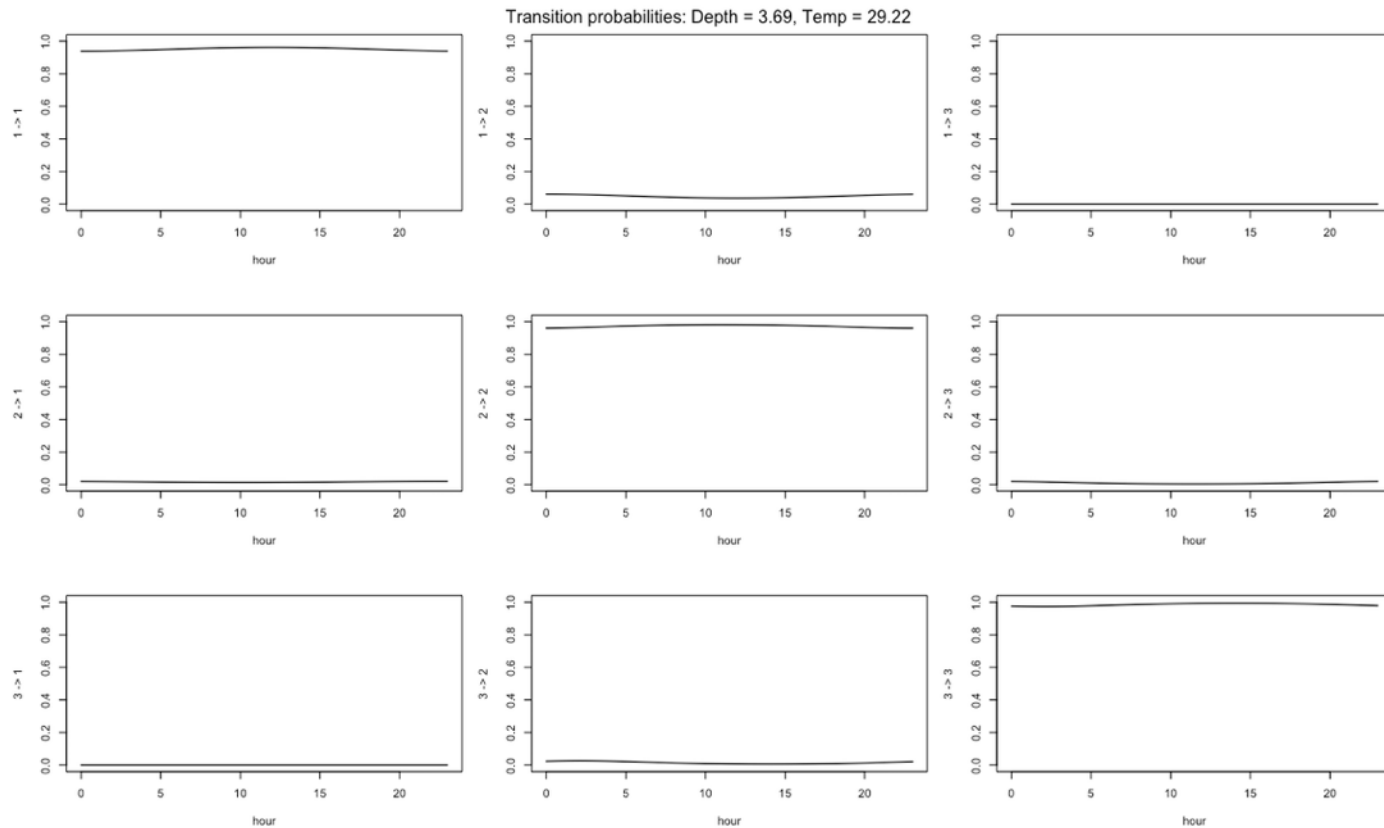




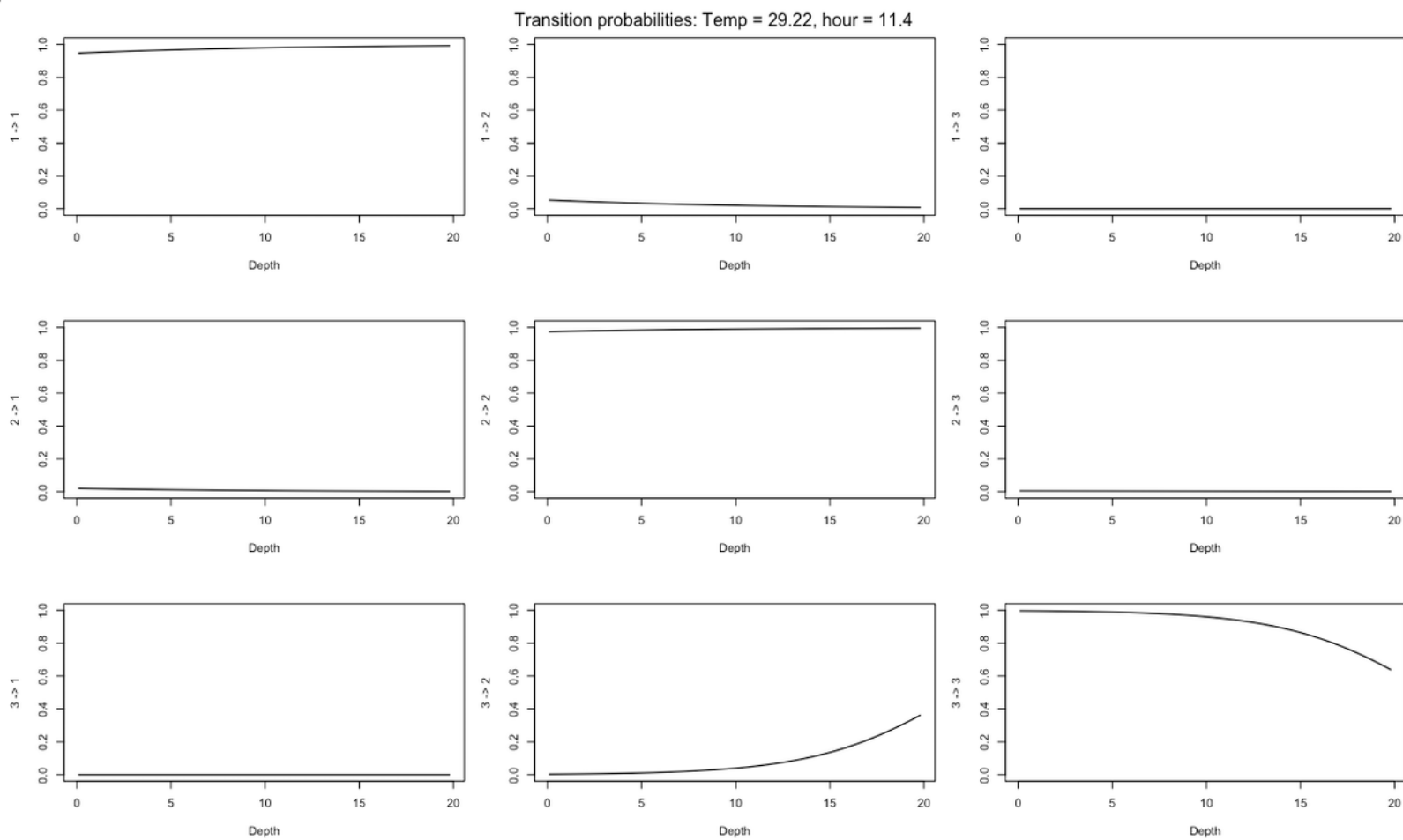
APPENDIX V – CHAPTER IV

State transition probabilities across (A) hour of day, (B) depth (in meters), and (C) temperature (“Temp”) in degrees Celsius for all southern stingrays combined. Estimated across mean values of the other covariates listed at the top of each panel. “1” = low activity, “2” = medium activity, “3” = high activity.

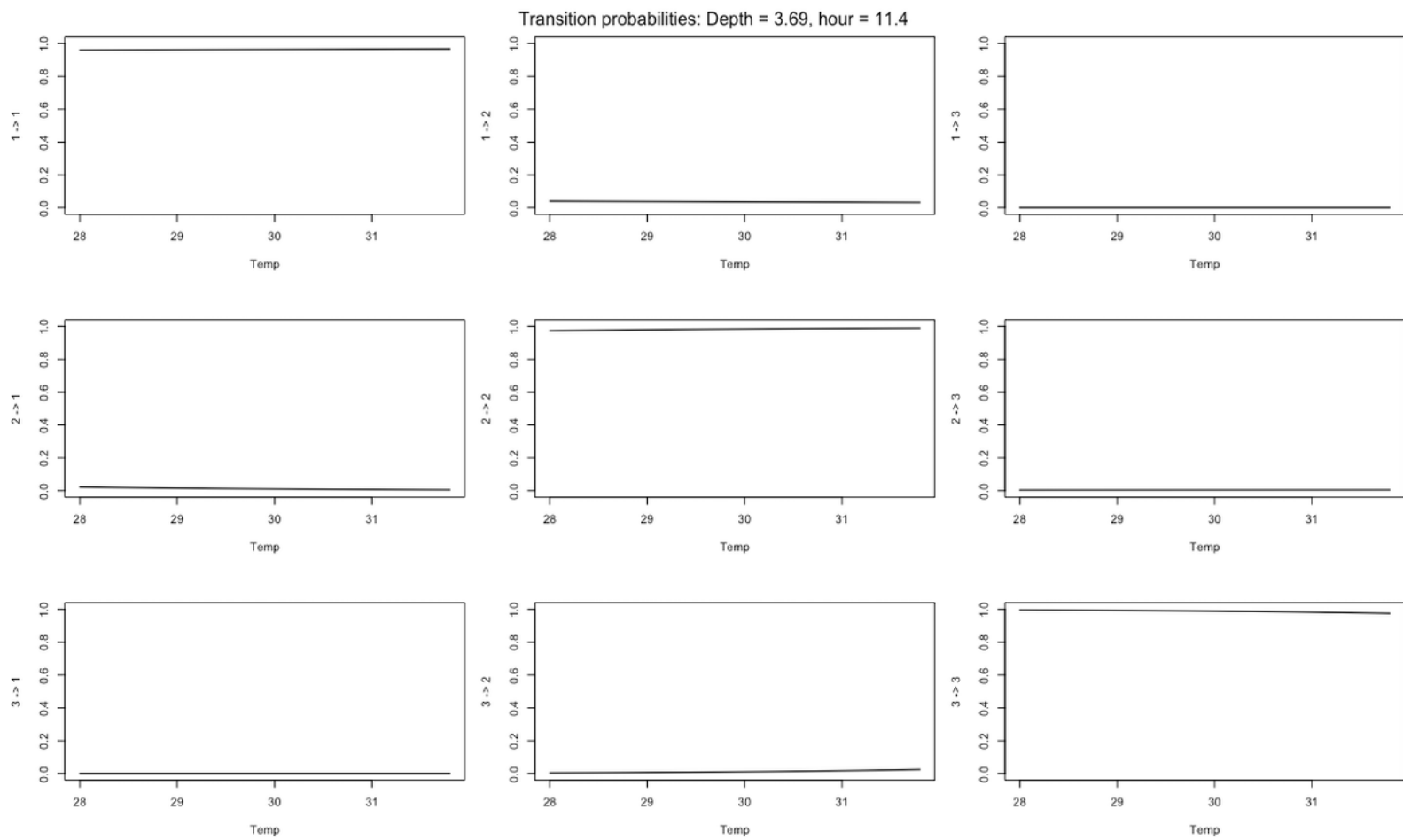
A



B



C



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PUBLICATIONS AND PRESENTATIONS

Flowers KI, Ajemian MJ, Bassos-Hull K, Feldheim KA, Hueter RE, Papastamatiou YP, Chapman DD (2016) A review of batoid philopatry, with implications for future research and population management. *Marine Ecology Progress Series* 562: 251-261.

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Clark-Shen N, Tinting KX, Rao M, Cosentino-Roush S, Sandrasegeren R, Gajanur AR, Chapman DD, Ying ELX, Flowers KI, Feldheim KA, Manjaji-Matsumoto BM, Hui SNZ (2021) The sharks and rays at Singapore's fishery ports. *Fisheries Research* 235: 105805.

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