2022

Utilizing an Integrated Approach to Explore Niche in a Complex Equatorial System

Danielle Orrell
University of Windsor

Recommended Citation

Orrell, Danielle, "Utilizing an Integrated Approach to Explore Niche in a Complex Equatorial System" (2022). *Electronic Theses and Dissertations*. 9134.
https://scholar.uwindsor.ca/etd/9134

Utilizing an Integrated Approach to Explore Niche in a Complex Equatorial System

By

Danielle Orrell

A Dissertation

Submitted to the Faculty of Graduate Studies

through the Department of Integrative Biology and the Department of Biomedical Sciences

in Partial Fulfilment of the Requirements for the Degree of Doctor of Philosophy at the

University of Windsor

Windsor, Ontario, Canada

2022

Utilizing an Integrated Approach to Explore Niche in a Complex Equatorial System

by

Danielle Orrell

APPROVED BY:

M. Espinoza, External Examiner
Universidad de Costa Rica

C. Semeniuk
Great Lakes Institute for Environmental Research

O. Love
Department of Integrative Biology

D. Mennill
Department of Integrative Biology

N. E. Hussey, Advisor
Department of Integrative Biology

August 8th, 2022

Declaration of Co-Authorship/Previous Publication

I. Co-authorship

I hereby declare that this thesis incorporates material that is the result of joint research, as follows: I am the sole author of Chapter 1 (General Introduction) and Chapter 6 (General Discussion). I am the primary author of Chapters 2-5, and my supervisor, Dr. Nigel Hussey is a co-author on Chapter 2-5. Chapter 3 and 4 are co-authored by Dr. Dale Webber who provided technological guidance and input. Chapter 4 is also co-authored by Dr. Jack Hollins and Lauren McLean, who provided analytical and technological support, as well as co-authors from the Ascension Island Government Conservation and Fisheries Directorate (AIGCFD) including Daniel Sadd, Dr Tiffany Simpson and Darcy Philpott who provided logistical field support. Chapter 5 was also co-authored by Daniel Sadd, Kirsty Jones, Kate Chadwick, Dr. Tiffany Simpson and Darcy Philpott who provided logistical field support.

I am aware of the University of Windsor Senate Policy on Authorship, and I certify that I have properly acknowledged the contribution of other researchers to my thesis and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

II. Previous Publication

This thesis includes 2 original papers that have been previously published/submitted to journals for publication, as follows:

Thesis Chapter	Publication title/full citation	Publication status
Chapter 2	Orrell, D. L. Hussey, N. E. (2022) VEMCO Positioning System (VPS) to understand the fine-scale movements of aquatic species: Applications, analytical approaches and future directions. *MEPS*. 687: 195-216.	Published in Marine Ecology Progress Series
Chapter 3	Orrell, D. L. Webber, D. & Hussey, N. E. A standardised framework for the design and application of fine-scale acoustic tracking studies in aquatic environments.	In review

I certify that I have obtained a written permission from the copyright owner(s) to include the above published material(s) in my thesis. I certify that the above material describes work completed during my registration as a graduate student at the University of Windsor.

III. General

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone's copyright nor violate any proprietary rights and that any ideas, techniques, quotations, or any other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with the standard referencing practices. Furthermore, to the extent that I have included copyrighted material that surpasses the bounds of fair dealing within the meaning of the Canada Copyright Act, I certify that I have obtained a written permission from the copyright owner(s) to include such material(s) in my thesis.

I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution.

Abstract

Our ability to identify and understand the relationships and distributions of organisms in nature is key to exploring the rich tapestry of life seen on Earth. The term "niche" describes how animals partition resources in space and time, shaped by behavioural choices and environmental conditions. Iterations of niche over time have focused on different aspects of a species' ecological characteristics, from Grinnell's initial study of songbird distribution ('spatial niche') in 1917 to Elton's description of functional attributes shaping trophic position ('trophic niche'). The fusion of these niche definitions formed Hutchinson's *n*-dimensional niche hypervolume. The coexistence of species that utilize the same niche has been explained by a concept called 'niche partitioning', whereby species will differ in how they utilize resources (spatially, temporally or by the resources they acquire). Examples of niche partitioning include the selection of differing size spectra prey items, and differences in space use across diel or seasonal periods. Acoustic telemetry has been used to track the movements of aquatic species across a range of spatial scales and offers a powerful tool to estimate spatial niche and the mechanisms which facilitate coexistence. Additionally, trophic ecology is an important tool for understanding species interactions and the mechanisms that support coexistence, often explored using stomach content analysis and chemical tracers.

In this thesis, I explored the applications of acoustic telemetry, a forerunner in technology used to estimate the Grinnellian (spatial) niche of aquatic animals. Positioning algorithms shift the resolution of acoustic telemetry and the application of electronic tags from identifying the location of an animal within hundreds of metres to sub-metre precision. Through a systematic review of a commercial positioning system, I identified that this technology has been used to investigate fine-scale aquatic animal movement across a range of habitats, taxa and development stages. Analytical approaches to handling high precision datasets are adopting complex models which can accommodate a large quantity of contextual data to investigate facets of ecology including home range, habitat selection, activity and animal behaviour. The factors that shape the success of this fine-scale acoustic telemetry system can be grouped under factors relating to the study system, species studied, and logistical and technological constraints. Describing the steps that guide experimental design in fine-scale studies, as well as process to derive animal positions, is central to robust hypothesis testing and the identification of constraining factors which limit ecological inference. I use acoustic telemetry and dietary techniques (stomach content analysis and chemical tracers) to investigate coexistence of two abundant mesopredators in a nearshore environment. My findings suggest that the versatility of rock hind (*Epinephelus adscensionis*) and spotted moray eel (*Gymnothorax moringa*), including generalist dietary choices and individual differences in space use, facilitate their coexistence in a competitive high-biomass environment. Coexistence, particularly of species that perform similar trophic roles, provides ecosystem resilience in the wake of change, e.g., anthropogenic stressors or climate fluctuations, and contributes to the maintenance of biodiversity.

Dedication

I dedicate this thesis to my parents, who have supported my journey into science, the exploration of oceans and the transport of unusual fishy samples across continents. My mum, Ros, was the first in our family to pursue higher education, and her 2010 bachelor's graduation spurred my desire to earn one day "one of those funny hats" which she earnt while caring for four children, three grandchildren and a whole host of adoptive families. I also learnt the value of hard work from my dad who tirelessly cared for our family and fuelled my love of the ocean through his stories of being at sea, and even of exploring Ascension Island.

Acknowledgements

This thesis would not have come to be without the help and of my supervisor, Dr. Nigel Hussey. Thank you for ignoring my initial emails five years ago, and for your patience, motivation, and support in completing this research. Through sending me to remote research locations and facing the unique challenges that come with these field sites I feel I have grown tremendously as a person as well as a scientist. This project has been immensely challenging, and you have helped me navigate the many trials and tribulations that comes with chasing big dreams and testing ecological theory using field experiments.

I would also like to thank my committee members, Dr. Christina Semeniuk, Dr. Oliver Love and Dr. Daniel Mennill for their support and guidance on this journey. Tina, your support goes beyond this thesis and into the world of improving the EDI landscape at UWindsor. I greatly appreciate the strides you have made to encourage and support the next generation of scientists at Windsor. Oli, from taking your class back in 2018 I met many lifelong friends and learnt some valuable lessons in proposal writing and disseminating science. Your enthusiasm for scientific enquiry and supporting the wellbeing of the researchers behind the science is evident in the hundreds of grad students you have inspired to date. Dan, you have been a constant during my journey at UWindsor and I feel fortunate to have joined your Ecology teaching team back in 2021. Your ability to effectively manage your time, mentor your students, inspire young scientists, and support your family while maintaining your dazzling ecology-themed shirt game is truly inspiring.

My PhD and ultimately this thesis has been revised in the wake of COVID-19. The original field season was set for April 2020, fortunately through the help of Nigel, Isabel, Dan, Chris, and others I was able to continue with my proposed field season six months later. I will be forever grateful for their persistence in enabling this research to happen. While this journey has been far from smooth, this support offered a life raft during a storm.

I am incredibly fortunate to have had the support and unwavering friendships of many members of the Hussey Lab, past and present. Thank you to Ellyn, George, Eric and Brynn for becoming my Windsor family and support network during the pandemic. Jena and Laurissa, your presence never failed to brighten my day. Harri, our trip to the Arctic at the start of my PhD was incredibly inspiring and I learnt a lot from you on how to coordinate a remote field operation. Jack, your enthusiasm for science is infectious, and I am pleased you joined us in Canada so we could spend many hours puzzled over telemetric datasets. Teah, your help in the lab and friendship in my final year was an absolute godsend. Amanda, thank you for welcoming me into the lab and providing the glorious espresso machine. Kirsty and Blue, while you may have left Windsor your presence is greatly missed. To the Hussey Lab managers past and present, Steph, thank you for helping me find my feet when I first moved to Windsor and supporting lab logistics, and Reid thank you for your support on my return from island life. To my Biological Sciences friends, Nathan Tuck, Alyssa Eby, Rachel Pieniazek, Megan Mickle, Renada Hana, Vicky Heath, and countless more, thank you for making my experience at UWindsor memorable. Queer in STEM UWindsor came to be in December 2021 with the support of two incredible scientists and people, Teah Burke and Patricia Okpara, and we formed a beautiful community of likeminded people. It was an absolute joy to form this group, and I can’t wait to see this community continue to grow. The Ocean Tracking Network R support group has provided a lifeline at several times throughout my PhD, I am hugely thankful for the enthusiasm of its members and their insight on exploring animal movement data.

Thank you also extends to the communities which welcomed me and made this research possible. Ascension is a beautiful island in the South Atlantic but would not be half the place it is without you there. This project was facilitated by the Ascension Island Government Marine and Fisheries Directorate, without this partnership, this work would never have been possible. The Ascension Conservation team are a blessing, and I feel very fortunate to have met you all. Victoria, I am very glad we met and could not have achieved what I did without your continued support and morning cups of tea. You are my best friend, and I cannot imagine life without you. To the beach buoy girls, Kate and Kirsty, here is to peanut butter sandwiches and smooth jazz. Dan, your humour, and diving skills made you a key asset and friend during my PhD journey. Laura and Sophie, thank you for letting me litter your desks with coffee rings. Dee, Tiff, and Darcy, I am excited to hear of your future research endeavours on the island. Jolene, I am glad you are my wife's wife. Countless local fishers, their boats, equipment, and enthusiasm made this research possible. Special thanks to Jaco, Richie, Shaun, Alex, Clay, Eddie, Mike, Eugene, Siobhan, Rick, Tony, Jessie, Sunna, Adrienne, and Wayne. Your local knowledge, friendship, and gruelling hours of fishing with me and listening to classic rock in the tropical sunshine were not in vain.

From the tropics to the poles. Obrigado to Isabel, Tessa, Mark, Ryan, João for making my time in Mozambique truly memorable. Quana, Harri, Colin E-Coli-J, Ellen, Iceman, and Ross for teaching me so much about Arctic fisheries and ways of knowing. Iceman, your bannock will forever hold a place in my heart.

This project was supported by an NSERC Discovery Grant, the Ontario Trillium Scholarship, and an Animal Behaviour Society grant.

Contents

List of Tables

List of Figures

Chapter 1. General Introduction

The concept of ecological "niche" is central to understanding the distributions of species in space and time and the maintenance of biodiversity. Studying the ecological "niche" space an animal occupies has been explored by identifying behavioural and dietary choices and environmental conditions it experiences. Each iteration of niche and its defining parameters focus on different aspects of a species' ecological characteristics (Leibold 1995).

In 1917, Joseph Grinnell conceived "niche" as the biogeographic parameters and environmental conditions which enable population survival and continuance (Grinnell 1917). The conception of niche was spurred by the exploration of avian species distribution within vegetated landscapes, namely how the physical characteristics of the California thrasher ("…strong feet and legs, and muscular thighs, an equipment which betokens powers of running…") dictated its presence, and thus its observed "spatial" niche. In line with Grinnellian niche, a species ecological niche determines its geographic distribution and ecological distribution models can be used to predict its occurrence (Leitão & Santos 2019). Therefore, the scaling of spatial niche will depend on the distribution and range of the animal studied. Modern tools to assist with defining the spatial niche of aquatic animals include using electronic tags to identify animal space use and environmental data using indirect (satellite imagery, environmental loggers) and direct (observation surveys) sources to identify conditions that may facilitate its survival and limit a given animal's distribution.

Charles Elton later adapted the founding theory of niche in 1927. This iteration emphasized how functional attributes shape an organism's trophic position or "role" within an ecological community and its subsequent interactions (Elton 1927). Elton's definition of niche also aimed to quantify inter-and intra-specific competition between individuals who coexist in the same niche space. Elton explored this concept by describing two species of African rhinoceroses, whereby the white rhinoceros has wide mouthparts, which enable it to harvest grass efficiently. In contrast, the black rhinoceros has narrow pointed mouthparts, which allow it to feed on the foliage offered by thorny bushes. Eltonian (trophic) niche is commonly studied using stomach content analysis and, more recently, chemical tracers such as stable isotope analysis (Bolnick et al. 2002, Krebs 2014, Manlick et al. 2019), with dietary composition encapsulating an animal's trophic role and required sustenance for population continuance.

Hutchinson brought these two definitions together in 1957, describing niche as an "*n*-dimensional hypervolume" (Hutchinson 1957). In the *n*-hypervolume, a set of *n* variables represent biologically important and independent axes, defined by a set of *n*-dimensional space that reflects suitable ranges of these variables (e.g., temperature, salinity). This hypervolume, therefore, encompasses all points where a population can survive and persist. The concepts of "fundamental" and "realized" niche were also introduced, whereby "fundamental" niche is the theoretical conditions that an animal can use, and “realized niche” describes the constrained area that an animal actually occupies due to factors such as resource competition (food, mates) and predation. This transformation of niche into a hyperdimensional space enabled the representation of niche space (“biotope”) on two axes, one which represents a condition (“scenopoetic”) and the other a resource (“bionomic”) (Hutchinson 1957, Soberon & Nakamura 2009). This visualization was coined “Hutchinson’s duality” and explored the impact of limiting conditions on realized species distributions (“any point in niche space can correspond to many points in the biotope, but not all points in niche space are represented in any given biotope”). The scale of Hutchinson’s niche is still actively debated (Gómez et al. 2016) e.g., how do we define the niche space of a migratory species? Under Hutchinson’s definition of niche as a flexible hypervolume, migratory species have been described as following optimal climatic conditions (niche tracking) (Winger et al. 2014). In contrast, the changing climatic niche of animals between periods of the annual cycle has been coined niche switching (Joseph & Stockwell, 2000). Van Valen (1965) proposed that the variation in niche breath (e.g., dietary choice) could be reasoned by the "niche variation hypothesis" (NVH). Namely, that specialized or "specialist" populations are morphologically adapted to occupy a specific role will have a narrower niche (e.g., the thorny bushes consumed by black rhinoceros with narrow mouthparts) than "generalist" populations which occupy a broader niche space (e.g., capable of exploiting many food sources).

Attempts to explore the mechanisms that enable species to coexist in niche space have focused on concepts including functional redundancy and niche partitioning. Functional redundancy describes how two species can occupy the same "role" within a system and is thought to dictate ecosystem resilience (Peterson et al. 1998, Mouillot et al. 2013). Redundancy has been subsequently explained via niche (or resource) partitioning (Matich et al. 2017), which describes how species adapt to utilize the available resources in different ways, e.g. through spatial or temporal differences in resource use or selection of different size spectra of prey items (Bolnick et al. 2002). For example, Guzzo et al. (2016) used acoustic telemetry and stable isotope analysis to identify the habitat and dietary partitioning of three piscivorous fishes co-occurring in Canadian sub-Arctic lakes. While significant overlap was found in their spatial home range, species occupied different depths and utilized spatially diverse food sources. The advance of these acoustic telemetry has enhanced our understanding of animal movement, which is central to animal survival, structuring ecosystems, and defining Grinnellian (spatial) niche (Nathan et al. 2008).

1.0 Spatial niche and autonomous insight into our underwater world

Quantifying Grinnellian niche is both logistically and technologically challenging for aquatic animals. Aquatic species' distribution and demography (age, growth and sex) have been studied for decades using traditional methods, including netting, trawling, trapping, and electrofishing (Thorstad et al. 2013). These methods can glean information into life-history traits and animal behaviour (e.g., dietary choices and basic migration routes). External mechanical tags typically inserted just below the skin require animal capture for data generation (akin to bird rings, often called “mark-release-recapture”) and can also provide information on stock structure, growth, and mortality (Lees et al. 2021). However, mark-recapture techniques are highly influenced by the intensity of fishing effort, and this method requires a large number of individuals to be tagged, which can put a strain on stocks that may already be at risk (Thorstad et al. 2013).

The development of electronic tracking technology (acoustic, radio, satellite, and archival biologgers) has enabled the quasi-continuous positioning of multiple species, across diverse realms, from demersal fishes inhabiting the deep-sea 5900 m below the water's surface (Priede et al. 1994) to scyphozoan jellyfish floating on the ocean's waves (Hays et al. 2012). Several of these technologies do not require animal recapture for data collection, of which acoustic telemetry remains at the forefront given its affordability (ten times cheaper than satellite tags), miniaturization (smaller tags can be placed on smaller animals and thus earlier life stages), battery engineering (long lifetime), and flexibility of its application (Hussey et al. 2015). Acoustic telemetry requires an acoustic transmitter that emits a unique encoded signal to be externally attached or surgically implanted in a study organism. When within the range of an acoustic receiver, this signal is decoded into a unique identifier and associated timestamp of detection (Leander et al. 2019). By positioning single receivers at key features, the presence or absence of an animal can be determined from 50 to 2000 m from an acoustic receiver depending on the receiver detection range (Kessel et al. 2014). Acoustic receivers are often positioned at key landscape features of interest or in areas where animals are suspected to occur, such as on seamounts (Barnett et al. 2012), artificial structures (Piraino & Szedlmayer 2014), along pre-determined migration routes (Trancart et al. 2020), and at riverine barriers (Jellyman & Unwin 2019). Discontinuous strings of receivers, which describe receivers positioned in gates ("curtains") or point designs (see Heupel et al. 2006), can be used to calculate basic movement metrics, including turning angle (bearing between consecutive positions) and step length (distance between two detections) (Ironside et al. 2017). These units can be used to reconstruct an animal trajectory and estimate general space use, including residency and home range, over longitudinal timescales with minimal maintenance. This approach produces presence/absence data with a limited spatiotemporal resolution and, therefore cannot be used to infer fine-scale movement behaviour.

1.1 The next resolution of spatial niche

Acoustic telemetry systems which apply positioning algorithms to solve for the location of a tagged animal offer the opportunity to generate higher resolution foundational movement metrics and therefore offer a more accurate fine-scale reconstruction of an animal’s trajectory. In 1973 one of the first fine-scale positioning systems was developed; this system used the time of difference of arrival (TDOA) of an acoustic pulse within an array of omnidirectional hydrophones to position tagged cod (*Gadus morhua*), with information relayed using a cabled system to an on-shore laboratory (Hawkins et al. 1974). Unlike pre-existing passive acoustic systems, which could be used to record animal presence within several kilometres of an acoustic receiver, using the hyperbolic TDOA algorithm, an animal's position could be determined with sub-metre precision (Hawkins et al. 1974), significantly improving study resolution. Like modern-day commercial TDOA positioning systems, positioning required fixed deployed receivers to have an overlapping detection ("listening") range to enable a simultaneous detection to be recorded on three or more receivers. Using the TDOA algorithm, the difference in detection time between pairs of receivers is converted to a range difference using the speed of sound in water (using benchmark values for different water types, e.g., freshwater and saltwater) (Smith 2013). This results in three equations for each set of three receivers, which can be solved to find the transmitter's position along intersecting hyperbolas (Hawkins et al. 1974, Vergeynst et al. 2020). The TDOA algorithm is a point-by-point approach, with each position calculated independent of all others (Vergeynst et al 2020). Alternative positioning algorithms include the track-oriented approaches utilized by Yet Another Positioning Solver (YAPS; see Baktoft et al. 2017), which uses the time of arrival of a signal at fixed hydrophones integrated into a random walk model, an analysis the researcher can independently conduct. At present, the most popular commercial fine-scale positioning system is offered by Innovasea and is called the Vemco Positioning System ("VPS"; formerly VEMCO Ltd. now Innovasea, Boston, MA), which applies the original hyperbolic TDOA algorithm.

While the factors that can limit the performance of discontinuous acoustic receivers have been discussed in several seminal reviews and discussion papers (Heupel et al. 2006, Kessel et al. 2014), this has not been described in detail for fine-scale positioning. While there is overlap in these limiting factors as both techniques rely on the successful detection of an emitting transmitter (i.e., reduced detection range associated with environmental conditions and line-of-sight issues), TDOA systems require a detection to be simultaneously detected therefore identifying and accounting for limiting conditions is essential for effective array design. TDOA systems generate an associated error value with each derived position. At present, how these values are incorporated into the analysis of these datasets and how positioning erorr may impact the viability of results is poorly defined. Transparency in design considerations and subsequent positioning results is integral for robust ecological testing and advancement of this field.

The newest tracking technology iteration paired with the commercial analysis using the Time Difference of Arrival algorithm is called High Residence (“HR”) receivers and tags. Recently developed VEMCO high residence (HR) technology utilizes binary phase shift signalling to facilitate tag transmission rates several orders of magnitude greater than its predecessor while maintaining low collision rates. HR transmitter data (transmitter ID, timestamp of detection, and in specific models, sensor data) are encoded into a signal by modulating the phase of the wave tone being transmitted (binary phase shift key, BPSK), which is sent in a fraction of a second. The binary phase shift signal is received by an HR receiver, which receives the unique tag ID in a single transmission and can carry out fast Fourier transformations on the fly to decode the signal. In contrast, commonly used acoustic pulse per modulation (PPM) technology paired with the TDOA algorithm uses a code burst (series of 8 or 10 ping transmissions in 3-5 seconds) which contains a tag ID (unique identifier) code. If a part of this code burst is not received, a tag ID cannot be decrypted. Reduced HR signal arrival time decreases the incidence of signal collision and attenuation (VEMCO 2009, Leander et al. 2020) and allows for more transmitters within contained systems without the risk of losing data integrity. Using digital BPSK encoding, a digital listening receiver can determine very precise arrival time based on signal phase shifts (millisecond data), which, when combined with high-resolution receiver clocks, can generate sub-metre positions when HR receivers are deployed in triads to allow signal triangulation. At present, few studies have tested the feasibility of this new technology within the aquatic environment (Guzzo et al. 2018, Leander et al. 2019, 2020), and no studies have been conducted in the marine realm. Testing the applicability of HR technology which can be paired with the TDOA algorithm is key to assessing whether it is viable for investigating the spatial niche of marine animals. Increased data resolution has the potential to allow the identification of the fine-scale movement behaviour of fully aquatic animals, which could significantly improve our understanding of key areas in marine movement ecology and animal behaviour, including social and predatory intra- and interspecies interactions, schooling, behavioural idiosyncrasies and personality, and responses to recreational fishing activity.

1.2 Dietary niche: from the visible to the invisible

Estimating an aquatic animal's trophic (“Eltonian”) niche requires information on dietary composition. Lethal sampling techniques, including stomach content analysis, provide a valuable tool for identifying diet choices and the relative proportion of different prey items (Harmelin-Vivien et al. 1989). More recently, stomach content analysis has been successfully used to contextualize foraging behaviours observed using acoustic telemetry (Young & Winn 2003, Cunjak et al. 2005, Guzzo et al. 2016). While stomach sampling is a useful opportunistic tool for dietary analysis, it only captures a snapshot of dietary composition, requires lethal sampling of target species, and may be biased towards hard components that break down slower in the gut (Zacharia & Abdurahiman 2004). For these reasons, stable isotope analysis (SIA) has become increasingly popular as it provides insight into dietary composition across a range of timescales, from weeks to months, using tissues with different turnover rates, including fin clips, red blood cells, and mucus, and does not necessarily require lethal sampling (Heady & Moore 2013).

Stable isotope analysis can be used to measure the isotopic signal within an animal’s tissue and involves assessing the ratio of heavy to light stable isotopes of commonly occurring elements, including carbon and nitrogen. This paradigm works on the premise that most elements exist in two or more forms, known as isotopes. While isotopes have the same number of protons, they can differ in the number of neutrons, resulting in different masses for the same element (Hobson & Wassenaar 2008). Lighter forms are typically more common, forming weaker bonds and reacting faster than their heavier counterparts (Schoeninger 1995). Due to this, there is a tendency for retention of heavier isotopes and loss of lighter isotopes during processes including respiration, excretion, deamination and transamination (Fry 2006, Bowes & Thorp 2015). Trends in stable isotope values are based on the premise that “you are what you eat”, whereby consumer tissue reflects the prey they consume during the time of tissue synthesis (Hobson & Clark 1992, Bearhop et al. 2004, Bergmann et al. 2009). For example, the stepwise enrichment of nitrogen stable isotopes (^{15}N:^{14}N) of 2‰ to 5‰ per trophic level (‰ indicates parts per thousand) is commonly used to infer trophic position and food web length (Post 2002, Bearhop et al. 2004, Fry 2006), with the range of $\delta^{15}N$ values used to estimate trophic length of a community (Layman et al. 2007). Carbon (δ^{13}) stable isotopes are indicative of foraging location, for example, between inshore and offshore feeding areas (Bearhop et al. 2004), and undergoes a stepwise enrichment of 1‰ per trophic level (DeNiro & Epstein 1978). The range of $\delta^{13}C$ has been used to estimate the diversity of basal resources exploited by a given individual or population (Layman et al. 2007). Visualizing isotopes in multivariate (delta or "δ") space ($\delta^{13}C$ versus $\delta^{15}N$) has been likened to Hutchinson's *n*-dimensional niche space, as an animal's chemical composition directly relates to its diet (bionomic) and the habitat in which it resides (scenopoetic) (Genner et al. 1999, Newsome et al. 2007).

Initial visualizations of delta space included constructing a convex hull (ellipse) around datapoints to estimate niche width for an organism (Quevedo et al. 2009) or community (Layman et al. 2007). However, convex hull techniques are vulnerable to low sample sizes and outliers (Jackson et al. 2009). The application of Bayesian frameworks, which can account for uncertainty and error, are more resistant to sample size issues, mixing models with open access code, including (but not limited to) *SIBER* (Stable Isotope Bayesian Ellipses in R; (Jackson et al. 2011), and *nicheROVER* (Niche Region and Niche Overlap Metrics; Swanson et al. 2015). Mixing models such as nicheROVER use a probabilistic method to estimate niche regions and generate directional (asymmetric) metrics for estimating niche overlap of species. Pairing SIA with conventional techniques like stomach content analysis can generate more detailed dietary information (e.g. taxonomic identification) (Hobson & Clark 1992). This technique has been successfully used to study coexistence and dietary overlap in aquatic environments across a range of taxa, including freshwater fishes in lakes (Jensen et al. 2017) to penguins across the southern Indian Ocean (Thiebot et al. 2012).

1.3 An untouched study system to explore niche

Ascension Island is a young (1.25 Mya) remote volcanic island situated 1,500 km from Africa and 2,400 km from South America (Wirtz et al. 2017). Unlike other tropical islands, Ascension has no mangroves, coral reefs, or seagrass meadows. Instead, Ascension Island is fringed by nearshore volcanic rocky reefs punctuated by pockets of sand and rhodolith. Shallow water habitats host the highest levels of species endemism and biodiversity and are home to 133 coastal fish species, 11 endemic, and 20 fish species shared only with St Helena (1,295 km southeast) and St Peter and Paul's rocks (1,993 km north-west) (Wirtz et al. 2017, Ascension Island Government 2021). In 2019 the Ascension Island marine protected area (MPA) was designated, encompassing 445,000 km^2 of ocean, including the island's exclusive economic zone (Ascension Island Government 2021). This designation protects vast swaths of pelagic ocean, deepwater seamounts, and nearshore reefs and prohibits commercial fishing and resource extraction. Due to its small island population (826, June 2021 census; Ascension Island Government unpublished data) and limited access due to airport repairs, the nearshore waters are subject to low levels of reactional fishing pressure (there are no commercial fishing operators). Owing to these factors, Ascension offers an isolated and virtually untouched study system. At present, only a handful of published studies have been conducted within Ascension's marine environment, and the trophic structure of its incredibly high biomass waters remains poorly understood.

1.4 Two morphologically diverse mesopredators

Shallow nearshore habitats are an integral component of marine ecosystems and provide a wide range of provisioning and regulatory ecosystem services, including food, coastal protection and climate regulation (Wilson & Liu 2008). Medium-bodied mesopredators fishes that inhabit nearshore environments play a pivotal role in food web function and stability, for example, by transport of energy from herbivores to apex predators (Polovina 1984). These fishes are also commonly targeted by fisheries and occupy a habitat often subject to anthropogenic pressure, including coastal development and shifts in natural environment gradients (Lester & Halpern 2008, Seitz et al. 2014).

Murdaenidae, commonly known as moray eels, are an abundant and diverse family of over >200 species, with a widespread distribution across tropical waters and temperate seas (Smith 2012). Moray eels play a key role in shallow reef habitats as a nocturnal piscivorous predator (Almany 2003, Lamb & Johnson 2010) owing to their anguilliform body type, which facilitates their cryptic behaviour and ability to infiltrate small crevices used by prey (Hixon & Beets 1993). Despite their importance and ubiquity within reef systems, current research into the movement ecology of moray eels in a real-world setting is limited (Abrams et al. 1973, 1983, Bassett & Montgomery 2011). Research using visual census, baited remote underwater video and acoustic telemetry suggests that moray eels are transient and move from a central refuge every few days in search of a new den site (Abrams et al. 1973, 1983, Young & Winn 2003). Whether dens are cyclically occupied, routine movements are driven by the search for resources, or whether there are ontogenetic shifts in movement behaviour remains unclear. Of the three acoustic telemetry studies published to date, activity space estimates vary between species and locations and range from 0.002 km^2 – 0.010 km^2 home range estimates of *G. prasinus* tracked using acoustic telemetry during a six-month study period to 11 km traversed by Mediterranean moray (*Muraena helena*) across 60 days. Young & Winn (2003) tracked *G. moringa* and found individuals move as little as 115 m during nocturnal foraging trips. These studies' results suggest that the diet choice and movement behaviour of moray eels may be influenced by lunar illumination, circadian cycle and swell (Young & Winn 2003, Pereira et al. 2017).

There are 13 species of moray eels found in Ascension's waters (Wirtz et al. 2017). The sheer abundance of this mesopredator may be attributed to the fringing volcanic reef around the island, which offers refuge and abundant foraging grounds (Richardson & Brito 2015). The spotted moray (*G. moringa*) is the most commonly consumed moray species on Ascension Island. Studies of *G. moringa* elsewhere within its range, which extends across the Atlantic Ocean, have reported common prey items including fish, crustaceans, and cephalopods (Carvalho-Filho, 1999; Pimiento et al. 2013). Like other species of morays, *G. moringa* has a secondary set of jaws nested in its throat, which it can extend to draw prey back into the esophagus (Diluzio et al. 2017). While the recorded total length of *G. moringa* is between 60 cm (average; Bernardes et al. 2005) and 2 m (Cervigón et al. 1992), around Ascension Island, this species is reported to have lengths of 2-3 m (Lubbock, 1980). Despite their number and importance to recreational fishers (these fishes provide provisioning services including food, as well as cultural and recreational services), there has been no research to date on their ecology or movement in Ascension's waters.

The family Epinephelidae, or grouper, includes 163 species, ubiquitous across warm-water reef ecosystems, with unifying characteristics including slow growth, late maturity, long lifespan and aggregate spawning, making them vulnerable to overexploitation (Coleman et al. 2000). Groupers are thought to play a key role in moderating the abundance of prey species such as planktivorous fish (Hixon & Carr 1997, Stewart & Jones 2001) and are also documented to feed on crustaceans (Artero et al. 2015). At present, around 50 studies have explored grouper movement ecology, with patterns in ontogenetic habitat use (movements from shallow to deep water reefs by *E. striatus*, Tucker et al. 1993, Colin et al. 1997), documented larger home ranges in less structurally complex reefs with low resource availability (refuge and food; Bolden 2001) and increased emigration rates with higher conspecific density (manipulated field experiment; Amargós et al. 2010). Existing research in tropical climes suggests groupers have high site fidelity and small home ranges (0.018 km^2 home range of *E. striatus* in The Bahamas, Bolden 2001; <0.073 km^2 of *E. tauvina* in a MPA in eastern Africa, Kaunda-Arara & Rose 2004) with individuals more active diurnally.

Around Ascension, the rock hind grouper *Epinephelus adscensionis* is a common recreational fishery species. Around St Helena (the closest island to Ascension, 1293 km southeast), visual surveys identified that the majority of large adult *E. adscensionis* (>50 cm) are captured >100 m from the shore (Heemstra & Randall 1993). In the waters surrounding Ascension, populations show distinct life-history traits, including larger size at sexual maturity and recorded maximum size (Nolan et al. 2017). Research elsewhere in their range suggests these species are protogynous hermaphrodites, reaching sexual maturity at 20 cm (e. 4 years) with individuals transitioning from females to males around 20-33 cm total length (Marques & Ferreira 2017). The abundance of this species relative to other species within the simple nearshore food web (low biodiversity) suggests they likely play a pivotal role in the coastal food web dynamics and stability through their role as mesopredators (Menge 1992, Heemstra & Randall 1993, Sluka et al. 2005).

1.5 Thesis objectives

In my dissertation I aim to explore and apply technology and techniques that have been utilized to investigate different facets of niche, including spatial niche using acoustic telemetry and dietary niche through stomach content analysis and stable isotope analysis. I then aim to use these tools to demystify the mechanisms which support the coexistence of two morphologically diverse recreationally important fishery species that inhabit the nearshore waters of Ascension Island.

Chapter 1. General Introduction

Acoustic telemetry has provided unparalleled insight into the underwater world and the realized spatial niche of aquatic animals. In Chapters 2 and 3 of this thesis, I aim to synthesize and review current ecological applications of a fine-scale positioning system which uses the original Time Difference of Arrival algorithm. In Chapter 2, I address 4 research questions: What species and life histories have fine-scale telemetry studies focused on? What is the geographic distribution of these studies, and what systems and habitats have they been conducted in? What are the central questions in ecology answered using fine-scale telemetry? What are the commonly used analytical techniques used to study spatial niche using fine-scale telemetry?

In Chapter 3, I aim to identify key considerations and potential pitfalls faced when designing and conducting a fine-scale positioning study supported by a systematic review. To do this I address 2 research questions: What factors limit data acquisition and can introduce positioning error? What pre- in-situ and post-study assessment tools can be used to evaluate and assess system performance related to yield and error? With this knowledge, I aim to provide a comprehensive guiding framework for new and existing users of the technology to optimize data yield and accuracy and exemplify its use with a case study conducted on Ascension Island, which ultimately failed to collect ecologically meaningful data.

In Chapter 4 of this thesis, I aim to provide a primer for new and existing users aiming to utilize HR technology with the Time Difference of Arrival algorithm. This work aims to address two research questions: What steps can a user take to investigate the detection data yielded from an HR study and to assess potential limiting factors to positioning? What are the steps involved in generating positions using the Time Difference of Arrival algorithm? This recipe of user-led steps will be evidenced through the provision of a real-world case study, with experimental trials conducted in the nearshore waters of Ascension Island.

In Chapter 5, I aim to identify mechanisms that facilitate coexistence and resource partitioning of two abundant nearshore mesopredators in a remote equatorial volcanic system using acoustic telemetry (to study spatial or Grinnellian niche), and stomach content analysis and stable isotope analysis (to study Eltonian or dietary and isotopic niche). I address 4 key hypotheses: While both species will exhibit significant overlap in their observed spatial niche, the horizontal and vertical space over which they utilize resources (within and between species) will differ. There will be temporal differences in animal activity within and between species to facilitate coexistence i.e., across diurnal cycles. Due to high levels of resource competition among both predators, individuals will consume a wide variety of prey items, resulting in a broad trophic niche. Overlap in dietary niche will indicate a degree of functional redundancy. Residency and space use data will also directly inform the Ascension Island Government species management plans for these two recreationally important fishery species.

1.6 References

Abrams RW, Abrams MD, Schein MW (1973) Diurnal Observations on the Behavioral Ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean Coral Reef. Coral Reefs 1:185–192.

Abrams RW, Abrams MD, Schein MW (1983) Diurnal observations on the behavioral ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean coral reef. Coral Reefs 1:185–192.

Almany GR (2003) Priority effects in coral reef fish communities. Ecology 84:1920–1935.

Amargós FP, Sansón GG, del Castillo AJ, Fernández AZ, Blanco FM, de la Red WA (2010) An experiment of fish spillover from a marine reserve in Cuba. Environ Biol Fishes 87:363–372.

Artero C, Koenig CC, Richard P, Berzins R, Guillou G, Bouchon C, Lampert L (2015) Ontogenetic dietary and habitat shifts in goliath grouper *Epinephelus itajara* from French Guiana. Endangered Species Research.

Ascension Island Government (2021) The Ascension Island Marine Protected Area Management Plan.

Barnett A, AbrantesKá KG, Seymour J, Fitzpatrick R (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. PLOS ONE 7.

Bassett D, Montgomery J (2011) Home range use and movement patterns of the yellow moray eel Gymnothorax prasinus. J Fish Biol 79:520–525.

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: A novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012.

Bergmann M, Dannheim J, Bauerfeind E, Klages M (2009) Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. Deep Sea Research Part I: Oceanographic Research Papers 56:408–424.

Bolden SK (2001) Using Ultrasonic Telemetry to Determine Home Range of a Coral-Reef Fish. 167–168.

Bolnick DI, Svanback R, Araujo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences 104:10075–10079.

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. Ecology 83:2936–2941.

Bowes RE, Thorp JH (2015) Consequences of employing amino acid vs. bulk-tissue, stable isotope analysis: a laboratory trophic position experiment. Ecosphere 6:1–12.

Coleman F, Koenig CC, Musick JA (2000) Long-lived Reef Fishes: The Grouper-Snapper Complex. Fisheries 25:13–20.

Colin PL, Laroche WA, Brothers EB (1997) Ingress and settlement in the Nassau grouper, Epinephelus striatus (Pisces: Serranidae), with relationship to spawning occurence. Bull 60:656–667.

Cunjak RA, Roussel JM, Gray MA, Dietrich JP, Cartwright DF, Munkittrick KR, Jardine TD (2005) Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. Oecologia 144:636–646.

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506.

Diluzio AR, Baliga VB, Higgins BA, Mehta RS (2017) Effects of prey characteristics on the feeding behaviors of an apex marine predator, the California moray (*Gymnothorax mordax*). Zoology 122:80–89.

Elton CS (1927) Animal Ecology. Macmillan, New York.

Fry B (2006) Stable isotope ecology. Springer, New York, NY.

Genner MJ, Turner GF, Barker S, Hawkins SJ (1999) Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotope signatures. Ecology Letters 2:185–190.

Grinnell J (1917) The Niche-Relationships of the California Thrasher. The Auk 34:427–433.

Guzzo MM, Blanchfield PJ, Chapelsky AJ, Cott PA (2016) Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. J Great Lakes Res 42:276–285.

Guzzo MM, Van Leeuwen TE, Hollins J, Koeck B, Newton M, Webber DM, Smith FI, Bailey DM, Killen SS (2018) Field testing a novel high residence positioning system for monitoring the fine-scale movements of aquatic organisms. Methods Ecol Evol 9:1478–1488.

Harmelin-Vivien ML, Kaim-Malka RA, Ledoyer M, Jacob-Abraham SS (1989) Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. J Fish Biology 34:715–734.

Hawkins AD, MacLennan DN, Urquhart GG, Robb C (1974) Tracking cod Gadus morhua L. in a Scottish sea loch. J Fish Biology 6:225–236.

Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW (2012) High activity and Lévy searches: jellyfish can search the water column like fish. Proc Biol Sci 279:465–473.

Heady WN, Moore JW (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172:21–34.

Heemstra PC, Randall JE (1993) An annoted and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. FAO, Rome.

Heupel MR. et al. (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res 57:1.

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol Monogr 63:77–101.

Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. Science 277:946–949.

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: turnover of ^{13} C in Tissues. The Condor 94:181–188.

Hobson KA, Wassenaar LI (2008) Tracking Animal Migration with Stable Isotopes. Academic Press. ISBN: 9780123738677.

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Flemming JEM, Whoriskey FG (2015) Aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1255642.

Hutchinson GE (1957) Concluding Remarks. In: *Quantitive Biology*.

Ironside KE, Mattson DJ, Theimer T, Jansen B, Holton B, Arundel T, Peters M, Sexton JO, Edwards TC (2017) Quantifying animal movement for caching foragers: the path identification index (PII) and cougars, *Puma concolor*. Mov Ecol 5:24.

Jackson AL, Inger R, Bearhop S, Parnell A (2009) Erroneous behaviour of MixSIR, a recently published Bayesian isotope mixing model: a discussion of Moore & Semmens (2008). Ecology Letters 12:E1.

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R: Bayesian isotopic niche metrics. J Anim Ecol 80:595–602.

Jellyman DJ, Unwin MJ (2019) Fine-scale swimming movement and behaviour of female silver eels, *Anguilla dieffenbachii*, within a lake affected by hydro-power generation. Fish Manag Ecol 26:57–69.

Jensen H, Kiljunen M, Knudsen R, Amundsen P-A (2017) Resource partitioning in food, space and time between arctic charr (*salvelinus alpinus*), brown trout (*salmo trutta*) and european whitefish (*coregonus lavaretus*) at the southern edge of their continuous coexistence. PLoS ONE 12:e0170582.

Joseph L, Stockwell D. 2000. Temperature-based models of the migration of Swainson's flycatcher (*Myiarchus swainsoni*) across South America. A new use for museum specimens of migratory birds. Proc Acad Natl Sci Phila 150: 293–300.

Kaunda-Arara B, Rose GA (2004) Homing and site fidelity in the greasy grouper Epinephelus tauvina (Serranidae) within a marine protected area in coastal Kenya. Mar Ecol Prog Ser 277:245–251.

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218.

Krebs CJ (2014) Niche Measures and Resource Preferences. In: *Ecological Methodology*, 3rd ed. University of British Colummbia, Vancouver: Pearson, p 596–653

Lamb RW, Johnson DW (2010) Trophic restructuring of coral reef fish communities in a large Marine reserve. Mar Ecol Prog Ser 408:169–180.

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure? Ecology 88:42–48.

Leander J, Brodin T, Leonardsson K (2019) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. Can J Fish Aquat Sci.

Leander J, Klaminder J, Jonsson M, Brodin T, Leonardsson K, Hellström G (2020) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. Can J Fish Aquat Sci 77:177–187.

Lees KJ, MacNeil MA, Hedges KJ, Hussey NE (2021) Estimating demographic parameters for fisheries management using acoustic telemetry. Rev Fish Biol Fisheries 31:25–51.

Leibold MA (1995) The Niche Concept Revisited: Mechanistic Models and Community Context. Ecology 76:1371–1382.

Lester SE, Halpern BS (2008) Biological responses in marine no-take reserves versus partially protected areas. Mar Ecol Prog Ser 367:49–56.

Manlick PJ, Petersen SM, Moriarty KM, Pauli JN (2019) Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations. Funct Ecol 33:335–345.

Marques S, Ferreira BP (2017) Sexual development and demography of the rock hind *Epinephelus adscensionis*, a protogynous grouper, in the south-west Atlantic. Mar Freshwater Res 69:300–312.

Matich P, Ault JS, Boucek RE, Bryan DR, Gastrich KR, Harvey CL, Heithaus MR, Kiszka JJ, Paz V, Rehage JS, Rosenblatt AE (2017) Ecological niche partitioning within a large predator guild in a nutrient-limited estuary: Niche partitioning among estuarine predators. Limnol Oceanogr 62:934–953.

Menge BA (1992) Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765.

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059.

Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436.

Nolan ET, Downes KJ, Richardson A, Arkhipkin A, Brickle P, Brown J, Mrowicki RJ, Shcherbich Z, Weber N, Weber SB (2017) Life-history strategies of the rock hind grouper Epinephelus adscensionis at Ascension Island. J Fish Biol 91:1549–1568.

Pereira TJ, Silva AF, De Almeida PR, Belo AF, Costa JL, Castro N, Quintella BR (2017) Assessing the size adequacy of a small no-take marine protected area (MPA) for Mediterranean moray and European conger. Mar Ecol Prog Ser 584:213–227.

Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Piraino MN, Szedlmayer ST (2014) Fine-scale movements and home ranges of red snapper around artificial reefs in the Northern Gulf of Mexico. Trans Am Fish Soc 143:988–998.

Polovina JJ (1984) Model of a coral reef ecosystem. Coral Reefs 3:1–11.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Priede IG, Ragley PM, Smith KL (1994) Seasonal change in activity of abyssal demersal scavenging grenadiers *Coryphaenoides* (*Nematonums*) armatus in the eastern North Pacific Ocean. Limnol Oceanogr 39:279–285.

Quevedo M, Svanbäck R, Eklöv P (2009) Intrapopulation niche partitioning in a generalist predator limits food web connectivity. Ecology 90:2263–74.

Richardson AJ, Brito A (2015) The polygon moray, *Gymnothorax polygonius* (Poey, 1875): A new record from Ascension Island, South Atlantic. Arquipelago. ISSN: 0873-4704.

Schoeninger MJ (1995) Stable isotope studies in human evolution. Evol Anthropol: Issues, News, and Reviews 4:83–98.

Sluka R, Chiappone M, Sealey K (2005) Influence of habitat on grouper abundance in the Florida Keys, U.S.A. Journal of Fish Biology 58:682–700.

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological value of coastal habitats for commercially and ecologically important species. ICES J Mar Sci 71:648–665.

Smith D (2012) A checklist of the moray eels of the world (Teleostei: Anguilliformes: Muraenidae).

Soberon J, Nakamura M (2009) Niches and distributional areas: Concepts, methods, and assumptions. Proc Natl Acad Sci U.S.A 106:19644–19650.

Stewart BD, Jones GP (2001) Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. Mar Biol 138:383–397.

Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist JD (2015) A new probabilistic method for quantifying *n*-dimensional ecological niches and niche overlap. Ecology 96:318–324.

Thiebot J-B, Cherel Y, Trathan PN, Bost C-A (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. Ecology 93:122–130.

Thorstad EB, Rikardsen AH, Alp A, Økland F (2013) The use of electronic tags in fish research – an overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13:881–896.

Trancart T, Carpentier A, Acou A, Danet V, Elliott S, Feunteun É (2020) Behaviour of endangered European eels in proximity to a dam during downstream migration: Novel insights using high accuracy 3D acoustic telemetry. Ecol Freshw Fish 29:266–279.

Tucker JW, Bush PG, Slaybaugh ST (1993) Reproductive patterns of Cayman Islands Nassau grouper (*Epinephelus straitus*) populations. Bull Mar Sci 52:961–969.

Van Valen L (1965) Morphological variation and width of ecological niche. The American Naturalist 99:377–390.

VEMCO (2009) HR2 High Residence Receiver (Specification sheet).

Wilson M, Liu S (2008) Non-market value of ecosystem services provided by coastal nearshore marine systems. In: *Ecological Economics of the Oceans and Coasts*. Edward Elgar Publishing, Cheltenham, U.K., p 119–134.

Winger BM, Lovette IJ, Winkler DW. 2012. Ancestry and evolution of seasonal migration in the Parulidae. Proc R Soc B 279: 610–618.

Wirtz P, Bingeman J, Bingeman J, Fricke R, Hook TJ, Young J (2017) The fishes of Ascension Island, central Atlantic Ocean-new records and an annotated checklist. J Mar Biol Assoc UK 97:783–798.

Young RF, Winn HE (2003) Activity Patterns, Diet, and Shelter Site Use for Two Species of Moray Eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. American Society of Ichthyologists and Herpetologists 2003:44–55.

Zacharia PU, Abdurahiman KP (2004) Methods of stomach content analysis of fishes- Winter School on Towards Ecosystem Based Management of Marine Fisheries – Building

Mass Balance Trophic and Simulation Models. http://eprints.cmfri.org.in/5282/ (accessed December 30, 2021).

Chapter 2. Using the VEMCO Positioning System (VPS) to explore fine-scale movements of aquatic species: applications, analytical approaches and future directions

2.0 Chapter summary

Recent advancements in telemetry have redefined our ability to quantify the fine-scale movements of aquatic animals and derive a mechanistic understanding of movement behaviours. The VEMCO Positioning System (VPS) is a fine-scale commercial positioning system used to generate highly accurate semi-continuous animal tracks. To date, VPS has been used to study 86 unique species, spanning 25 taxonomic orders. It has provided fine-scale movement data for critical life stages, from tracking day-old turtle hatchlings on their first foray into the sea to adult fish returning to natal rivers to spawn. These high-resolution tracking data have improved our understanding of the movements of species across environmental gradients within rivers, estuaries, and oceans, including species of conservation concern and commercial value. Existing VPS applications range from quantifying spatio-temporal aspects of animal space use and key aspects of ecology, such as rate of movement and resource use, to higher-order processes such as interactions among individuals and species. Analytical approaches have seen a move towards techniques that incorporate error frameworks such as autocorrelated kernel density estimators for home range calculations. VPS technology has the potential to bridge gaps in our fundamental understanding of fine-scale ecological and physiological processes for single and multi-species studies under natural conditions. Through a systematic review of the VPS literature, we focus on four principle topics; the diversity of species studied, current ecological- and ecophysiological applications, data analysis techniques and highlight future frontiers of exploration.

2.1 Introduction

Movement is pivotal to animal survival and the structuring of ecosystems by facilitating access to essential resources, including food, reproductive mates and refugia, which are regulated by external drivers active over a range of spatial and temporal scales (Nathan et al. 2008). The development of animal tracking technology (acoustic, radio and satellite telemetry and archival biologgers) has enabled the quasi-continuous positioning of diverse species, from those inhabiting the deep sea (Priede et al. 1990) to birds soaring thousands of metres above the earth's surface (Poessel et al. 2018).

In 1973, the first fine-scale aquatic telemetry positioning system study was published. This system used time difference of arrival (TDOA) of transmitted acoustic pulses within a grid array of omnidirectional hydrophones to position tagged cod (*Gadus morhua*), with information relayed using a cabled system to an on-shore laboratory (Hawkins et al. 1974). Unlike pre-existing passive acoustic systems, which could only identify animal presence with several hundred metres of accuracy, the hyperbolic TDOA algorithm provided sub-metre positioning accuracy (Hawkins et al. 1974). This innovation significantly improved the resolution and accuracy of underwater movement tracking. In 1989, the first commercially available positioning system called VRAP ("Vemco Radio Acoustic Positioning system") (Vemco Ltd., Nova Scotia, Canada) was released (O'Dor et al. 2001). The VRAP system consisted of a computer base station, three or four surface buoys that contained a receiver and hydrophone and a radio VHF modem (Klimley et al. 2001, Downey et al. 2011). The Vemco Positioning System (hereafter "VPS") (Innovasea, formerly Vemco Ltd., Nova Scotia, Canada) was released as a lower-cost alternative that had no upper limit on the number of incorporated receivers (Andrews et al. 2011). The VPS requires fixed deployed receivers to have an overlapping detection ("listening") range in order to record simultaneous detections of a tag on three or more receivers for positioning. Using the TDOA algorithm, the difference in tag detection time between pairs of receivers is converted to a range difference using the speed of sound in water (based on benchmark values for different water types, e.g. freshwater and saltwater) (Smith 2013). In simplest terms (two-dimensions), a range difference and the known locations of two receivers define one branch of a hyperbola (also referred to as a hyperbolic line of position) (Smith 2013). A third receiver provides an additional hyperbolic line of position, with the intersection of these providing the location of the transmitter (assuming no measurement error). In reality, TDOA is three-dimensional and uses receiver depth and tag depth (assumed if no depth sensor is present).

Unlike the original positioning systems, the VPS comprises of a network of time-synchronised acoustic receivers that are autonomous and do not require a computer base station or buoyed antennas (Espinoza et al. 2011, Smith 2013). For VPS, time synchronisation is achieved using integrated synchronisation (“sync”) tags (present in VEMCO VR2Tx, VR2AR or high residency receivers) or tags paired alongside older technologies (for example, VEMCO VR2W receivers). Sync tags are used to identify and account for clock drift between receivers that would otherwise impact calculated positions (Smith 2013). Reference tags are typically deployed within an array of listening receivers to evaluate spatiotemporal differences in system performance. Following data download on study completion, VEMCO provides a processed dataset of positions (and their associated accuracy). More recently, VEMCO has released licenced software and offers training to enable researchers to conduct autonomous TDOA positioning ‘in house’. The VPS system can be used to estimate the positions of multiple tagged animals within freshwater, brackish and saltwater environments (Espinoza et al. 2011, Farrugia et al. 2011, Guzzo et al. 2016, Logan & Lowe 2019). VPS has been used to study the fine-scale movements of diverse species across both natural and altered environmental settings (Wolfe & Lowe 2015, Veilleux et al. 2018).

Given the potential of VPS to advance our fundamental understanding of aquatic animal ecology, the objective of the current study was to undertake a systematic literature review focused on four key topics relevant to fine-scale acoustic telemetry positioning systems; (i) the diversity of species studied, (ii) experimental questions that can be addressed including conservation and management foci, (iii) common and emerging statistical techniques for handling VPS data, and (iv) contemporary areas of ecology which have yet to be explored, but where fine-scale acoustic telemetry approaches present novel opportunities.

2.2 Methods

To synthesise existing peer-reviewed VPS literature a global search was conducted in ISI Web of Science using the keywords "*VPS*" OR "*VEMCO Positioning System*" OR ("acoustic telemetry" AND "fine-scale"). Due to the number of extraneous results published in other fields, the resultant search output was filtered to categories including; "Environmental Sciences", "Environmental Studies". "Zoology", "Evolutionary Biology", "Marine Freshwater Biology", "Fisheries", "Ecology", "Biology", and "Oceanography". Searches were then repeated using SCOPUS and Google scholar to ensure all relevant studies were identified. Abstracts were screened for relevance, with duplicate articles removed and only studies that tagged animals included. In addition, relevant literature cited within these studies, not identified directly by the search, was also extracted. All studies identified before November 3, 2021, were included.

Data on the year, species studied, environment (habitat type, water body type, depth), geographic location of study, and key study objectives were extracted for each publication. Study objectives were then categorised under seven broad topics following an evaluation of all extracted manuscripts; behavioural ecology, conservation measures and assessments, fisheries management, land use management, methodological testing, reproductive ecology, and the study of other drivers of movement (e.g. oceanographic conditions, temporal and seasonal drivers and extreme weather events). The order of information in the abstract and final objective statement of the introduction was used to categorise each study within these defined topics. The majority of studies addressed several core objectives; therefore, their order of importance was defined according to the abstract.

2.3 Results

Using Web of Science, 188 articles were identified, of which 26 were deemed relevant i.e. studies acoustically tagged animals and deployed a Vemco Positioning System to track their movements. A duplicate search using SCOPUS identified 167 articles; following abstract screening, 26 unique articles remained. A replicated search in Google scholar yielded 2270 articles, of which 60 unique articles were directly relevant. An additional four articles were identified from in-text citations. In total, combined searches yielded 116 peer-reviewed articles published between 2011 and 2021, which analyzed data from 140 unique species datasets (full list of articles in Supplementary Material S2.1).

2.3.1 The diversity of life: species studied over time

Since 2011, VPS has been used to track the movements of 86 unique species, spanning 25 taxonomic orders. This diversification over time (Fig. 2.1) has been facilitated by tag miniaturisation, enabling the tracking of smaller species and earlier life stages. Key groups studied include morphologically diverse species ranging from bony and cartilaginous fishes to echinoderms and reptiles. The type of tag chosen by a study remains a trade-off between tag size and battery life. The smallest animal tagged to date is a juvenile European eel (*Anguilla anguilla*, Bašić et al. 2019) measuring 37 mm in total length internally implanted with a VEMCO V5 tag (0.65 g in air, 5 mm diameter, 12 mm length). Smaller tags are limited in life span due to the power and capacity required to transmit acoustic signals; therefore, studies tracking juvenile fishes (*n* unique datasets = 27; 19%) have typically spanned up to six months (*n* unique datasets = 19; 70%). Adult life stages remain the most commonly tagged (*n* = 61; 44%), with few studies tracking multiple life stages (adult and juvenile) (*n* = 16; 11%). Note, over a quarter of all tracking studies (*n* = 36; 26%) did not describe the species life stage or provide identifiable biometrics. The increased battery life of large acoustic tags (up to 10 years) has generated multi-year VPS data, with the longest VPS study to date spanning over four years (lake trout *Salvelinus namaycush* tracked for 1569 days, Binder et al. 2018).

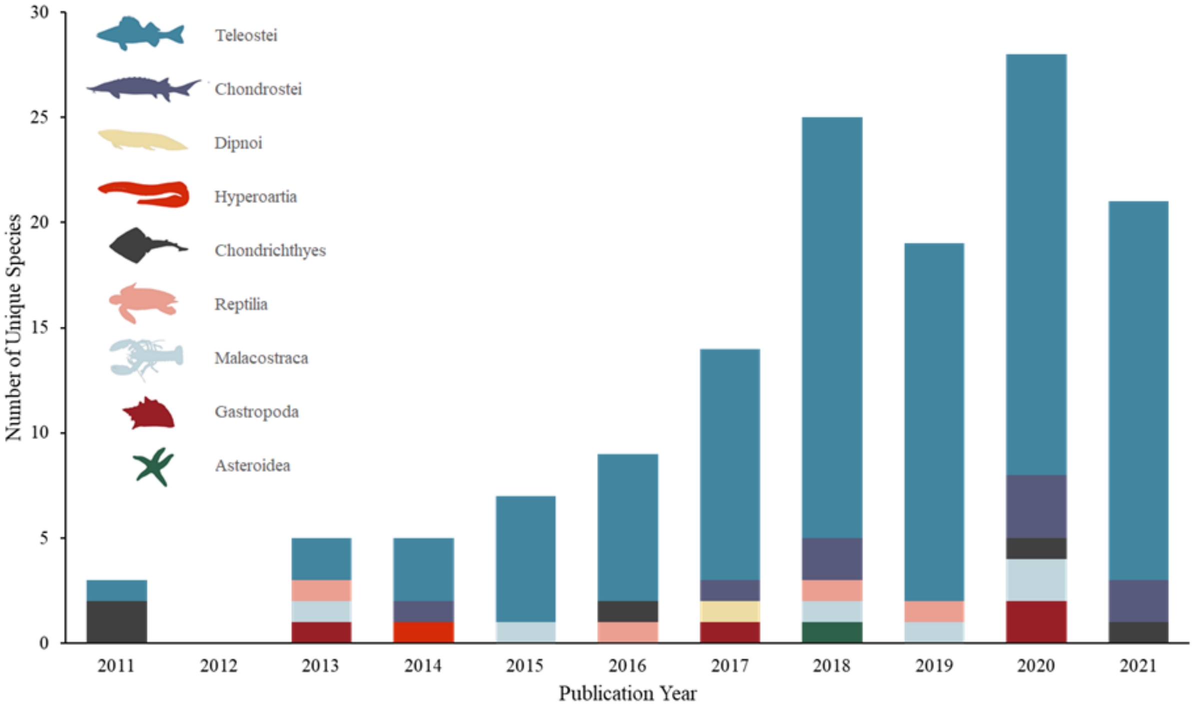


Figure 2.1 The diversity of taxa studied using the VEMCO positioning system (VPS) in literature published between 2011 and 2021. Includes fishes such as Teleostei (bony fishes), Chondrostei (sturgeons and paddlefishes), Dipnoi (lungfish), Hyperoartia (lampreys), Chondrichthyes (cartilaginuous fishes such as sharks, skates and rays), as well as reptiles (Reptilia), shellfish (Malacostraca and Mollusca), and echinoderms (Asteroidea).

2.3.1.1 Fishes

Teleosts are the most widely studied taxonomic group of fishes using VPS, with 85 articles published since 2011, representing 11 taxonomic orders and 66 unique species. Species include a diverse morphological spectrum, from eel-like body morphs (Anguilliformes, *n* species = 5) to depressiform benthic flatfish (Pleuronectiformes, *n* species = 5). As well as species that occupy a range of functional roles and trophic levels, from key mesopredators in coastal ecosystems such as the great barracuda (*Sphyraena barracuda*) (Becker et al. 2020) and carnivorous fishes in freshwater systems (northern pike, *Esox lucius*, Roy et al. 2018), to abundant mid-level consumers which link lower and upper trophic levels; the shorthorn sculpin (*Myoxocephalus scorpius*) in marine systems (Ivanova et al. 2018), and the white sucker (*Catostomus commersonii*) in freshwater reservoirs (Veilleux et al. 2018). Perciformes, the largest order of fish containing ~41% of all teleosts (Pandey & Marthur 2018), are the most studied group (*n* fish tagged = 1702; 40% of all tagged teleosts).

Prehistoric lineages of fishes, including Chondrosteans (subclass Chondrostei), lungfish (subclass Dipnoids), and Hyperoartia (lamprey) have received some attention. Three species of primitive ray-finned bony fishes, including Atlantic sturgeon (*Acipenser oxyrinchus*), lake sturgeon (*A. fulvescens*), and green sturgeon (*A. medirostris*), have been studied under the lens of reproductive ecology, space use and the influence of anthropogenic stressors (*n* articles = 5). These studies include one of the largest fish tagged in a VPS study, a 96 kg Atlantic sturgeon (*A. oxyrinchus*) measuring 216 cm fork length (Balazik et al. 2020). Lungfish (subclass Dipnoids), the closest living relatives to tetrapods (Irisarri & Meyer 2016), are uniquely adapted to hypoxic conditions through the presence of one or two primitive lungs derived from the swim bladder. Through contextualising 3D-space movements of freshwater Australian lungfish (*Neoceratodus forsteri*) derived from VPS with environmental data, it was possible to identify how this ancient lineage has adapted to survive in an altered riverine system (Roberts et al. 2017).

Chondrichthyans (class Chondrichthyes) contain cartilaginous fishes, including sharks, batoids (rays, skates, guitarfish, and sawfishes) and chimaeras, and are comprised of over 1,100 living species (Weigmann 2016). Despite this, only four species of elasmobranch have been studied using VPS; the grey-smooth hound (*Mustelus californicus*, Espinoza et al. 2011), the shovelnose guitarfish (*Rhinobatos productus*, Farrugia et al. 2011, Espinoza et al. 2011), the spotted wobbegong (*Orectolobus maculatus*, Armansin et al. 2016) and the reef manta ray (*Mobula alfredi*, Armstrong 2020). These studies include the first published study using the VPS system by Espinoza et al. (2011), which tagged grey-smooth hound (*n* = 1) and shovelnose guitarfish (*n* = 2) and tested the feasibility of this technology as well as associated positional accuracy and precision.

2.3.1.2 Reptiles

Two species of reptile have been studied using VPS, hatchling flatback turtles (*Natator depressus*) at two nesting sites in Western Australia (Eco Beach, Thums et al. 2013; Thevenard Island, Wilson et al. 2018), and juvenile green turtle (*Chelonia mydas*) in Culebra, Puerto Rico. Both studies aimed to identify tagged hatchling direction and swim speed on their first foray from their natal beaches. These data are important given that the mortality rate of sea turtle hatchlings is ~25% in the first 24 h (Gryuis 1994), and the IUCN Red List classifies all seven species of sea turtle as Threatened (Critically Endangered, *n* species = 2; Endangered, *n* species = 1; Vulnerable, *n* species = 3) or Data Deficient (*n* species = 1). VPS has provided an approach to elucidate data on a poorly understood developmental stage with a crucial mortality bottleneck.

2.3.1.3 Shellfish and echinoderms

VPS studies have focused on lobsters (Malacostraca, *n* articles = 6, *n* tagged individuals = 543), molluscs (Gastropoda, *n* articles = 4, *n* tagged individuals = 109), and echinoderms (Asteroidea, *n* articles = 1, *n* tagged individuals = 18). Malacostraca research has included three important commercial species, the European lobster (*Homarus gammarus;* Skerritt et al. 2015, Lees et al. 2018) off the northeast coast of England, and the American lobster (*H. americanus*; McMahan et al. 2013) and snow crab in (*Chinoecetes opilio*) (Cote et al. 2019,

2020) in North America. Gastropoda studies have investigated movement related to population recovery following intensive fishing activity (pink abalone, *Haliotis corrugata*; Coates et al. 2013), habitat use under suboptimal conditions (Caribbean queen conch, *Aliger gigas;* Stieglitz & Dujon 2017), as well as the movements of mariculture pests, the Northern Pacific seastar (*Asterias amurensis;* Miyoshi et al. 2018) and pest removers (*Charonia tritonis*; Schlaff et al. 2020).

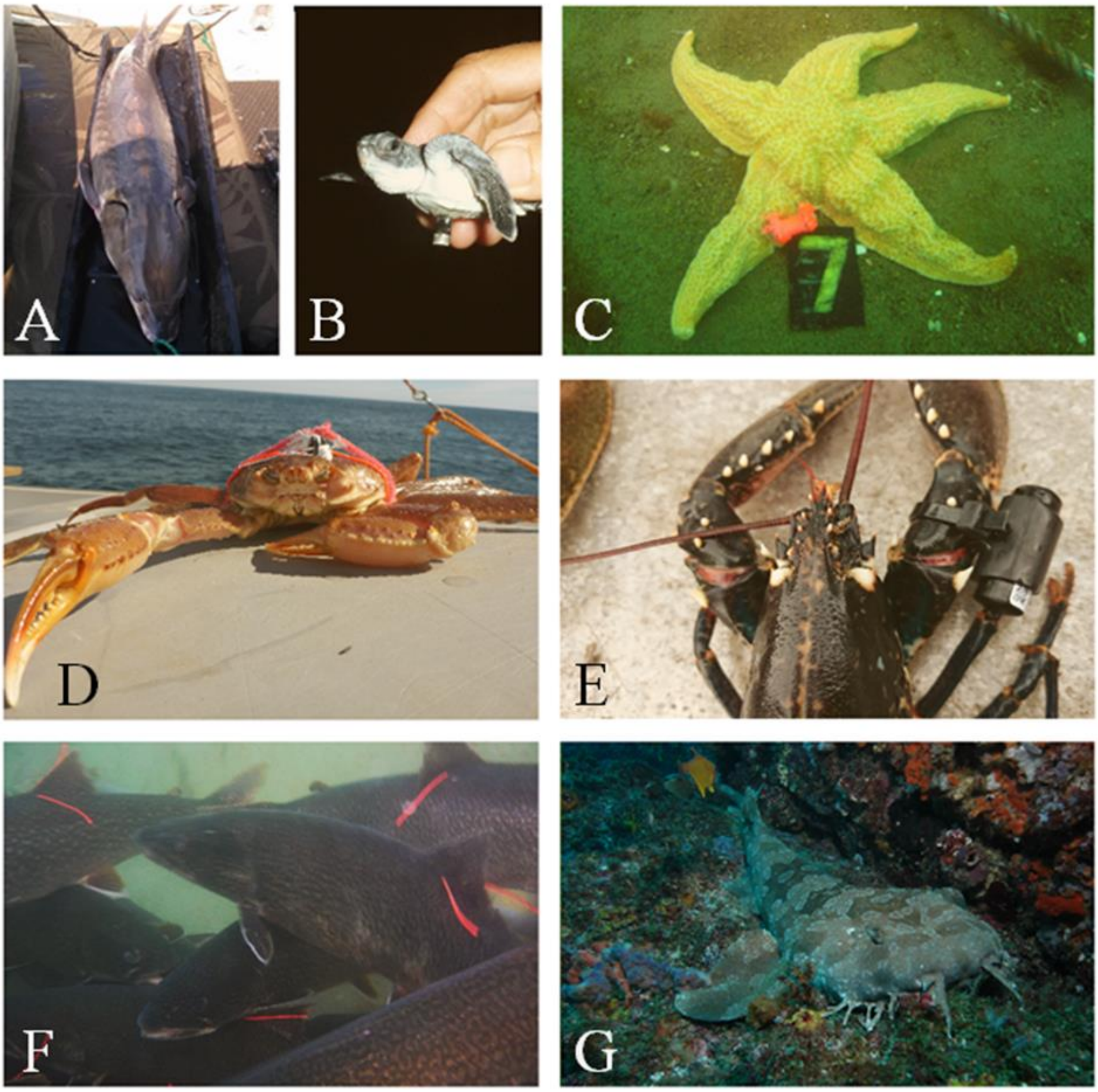


Figure 2.2 Diversity of species studied using the Vemco Positioning System (VPS). (A) The largest fish tagged for a VPS study to date, a 96 kg Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) tracked by Balazik *et al.* (2020). (photo credit Matthew Balazik). (B) The smallest animal externally tagged for a VPS study to date, a 31.1 g hatchling flatback turtle (*Natator depressus*) tracked by Thums *et al.* (2013) (photo credit: Michelle Thums). (C) A tagged Northern Pacific sea star (*Asterias amurensis*) tracked in northern Japan to identify its seasonal movements within maricultural fields in Miyoshi *et al.* (2018) (photo credit: Koji Miyoshi). (D) A snow crab (*Chionocetes opilio*) tagged to study fundamental deep-water movement characteristics of this commercial fishery resource in Cote *et al*. (2019) (photo credit: David Cote). (E) A European lobster (*Homarus gammarus*) tagged to investigate free-ranging animal behaviour and movements in relation to baited commercial traps (photo credit Kirsty Lees). (F) The largest tagged cohort to date, with 390 lake trout *Salvelinus namaycush* tracked in Lake Huron, Canada to investigate habitat use during spawning (Riley et al. 2014, Binder et al. 2017) (photo credit: Thomas Binder). (G) An internally tagged spotted wobbegong shark (*Orectolobus maculatus*) tracked to study inter-sociality in Armansin *et al.* (2016) (photo credit Robert Harcourt).

2.3.2 Conservation status of species studied using VPS

The majority of species studied to date using VPS are considered low conservation risk by the IUCN Red List (i.e., Least Concern or Near Threatened), with far fewer Threatened (Vulnerable, Endangered and Critically Endangered), Data Deficient or Not Evaluated tracked (Fig. 2.2). The trend of studying low conservation risk species is likely a result of reduced administrative barriers (i.e., ease of securing a scientific permit), availability of funding for commercially or recreationally fished species (e.g. industry and Governmental partnerships), as well as practicality (species with known distribution and ease of capture). Despite these factors, improving our understanding of Threatened, Data Deficient, and Not Evaluated species remains critical to conservation management.

2.3.3 The global distribution, habitats and functional roles of species studied

VPS studies have spanned 120 degrees of latitude, ranging from tracking Endangered silver eels (*Anguilla dieffenbachii)* occupying a freshwater reservoir in New Zealand (Jellyman & Unwin 2019) to studying movement trajectories of the abundant shorthorn sculpin (*M. scorpius*) in the Canadian High Arctic (Ivanova et al. 2018, Landry et al. 2019). Tagging effort has been focused in North America (*n* unique articles = 49; 49% articles), followed by Europe (*n* = 21; 21%), Oceania (*n* = 16; 16%), with less research undertaken in the Caribbean (*n* = 5; 5%), East Asia (*n* = 5; 5%), West and Central Asia (*n* = 3; 3%), and Central America (*n* = 1; 1%) (Fig. 2.3). No published VPS studies have been conducted in South America, Northern Asia, Antarctica or Africa.

The evident geographic gap in applying this technology could be due to several reasons; the search criteria used in this review, the acquisition and distribution of equipment, the applicability of this equipment (i.e., coverage required and expected scale of animal movements) mechanisms of knowledge transfer, available funding, and geopolitical factors. Firstly, this review only incorporated literature published in journals that accept the English language, which in some cases is not the official language of countries situated within the regions mentioned above e.g., Russia's official language is Russian. A duplicate search was run using eLIBRARY.ru, a popular Russian literature search engine that contains over 29 million Russian scientific articles and publications, to assess the impact of this factor on the review output. Using the search term "VEMCO Positioning System" yielded three results that had been identified using our selected search engines. While this search engine did not provide any unique articles relevant to this review, the use of more inclusive search engines should not be overlooked. It should be noted that technical reports were not included in this review, which may be a more popular form of science communication in some regions.

The global distribution of VPS studies mirrors that of acoustic and satellite telemetry studies (see Hussey et al. 2015) (Fig. 2.3). This pattern may in part be due to regional telemetry networks. Well-established networks and centralised databases are present across many regions, including but not limited to, North America, Europe, Australia, southern Africa and Eastern Tropical Pacific that facilitate equipment sharing and knowledge transfer within these regions. Furthermore, Innovasea (the manufacturer of the VPS, formerly manufactured by VEMCO Ltd.) is based in Canada. The cost of procuring equipment outside of North America increases further from the source, which may deter researchers from using this technology. This disparity is likely further amplified by the limited funding and capacity in developing countries (Hussey et al. 2015; Barkley et al. 2019). Geopolitical boundaries may also present a challenge. Of all studies conducted to date, only one compared the fine-scale movement metrics of an invasive species across two distinct geographic locations (see Pickholtz et al. 2018). This apparent shortfall in VPS applications across certain regions does not reflect the distribution of unique habitats or species present, which do not conform to sociopolitical boundaries.

Fine-scale tracking studies have predominantly focused on the marine biome (*n* unique datasets = 73; 52% of all unique datasets) within coastal (*n* coastal marine datasets = 42; 67% of unique marine datasets) habitats. VPS technology has been used to track aquatic species across a range of unique coastal habitats, including, but not limited to, restored wetlands (Farrugia et al. 2011), giant kelp forests (Coates et al. 2013), artificial reef systems (Logan & Lowe 2019), and mangroves (Rooker et al. 2018). Offshore marine habitats (>2 km from land) have received some attention (*n* unique offshore marine datasets = 21; 29%) and have investigated species movements around unique features, including offshore wind farms (van der Knaap et al. 2021), subsea cables (Cote et al. 2019), marine canyons (Cote et al. 2020), and around wastewater outflow sites (Burns et al. 2019). Studies within freshwater environments (*n* unique datasets = 52; 37%), and brackish environments (*n* = 17; 12%), have focused on studying lakes (Buchinger et al. 2017, Guzzo et al. 2018), natural flowing rivers (Espinoza et al. 2020), impounded waterways (Whitmore & Litvak 2018, Baker et al. 2020, Fahlman et al. 2021), shipping canals (Vergeynst et al. 2019) and harbours (Teesdale et al. 2015).

Of the species targeted in VPS studies, the majority typically occupy the lower water column (*n* unique demersal species = 54, 63%; *n* unique reef-associated species = 16; 19%), followed by those found in the benthopelagic zone (*n* = 16; 25%). Animals inhabiting the pelagic zone are the least studied (*n* = 1; 1%) (*n* = 3; 3% not described). This application gap results from the relative ease of studying species that occupy the lower water column relative to pelagic, highly mobile (horizontally and vertically) species. VPS studies provide detection coverage over relatively small areas (<5 km^2) compared to coarse-scale linear strings of acoustic receivers with non-overlapping detection ranges. Therefore, adequately capturing the range of movement that a pelagic species performs is a challenge.

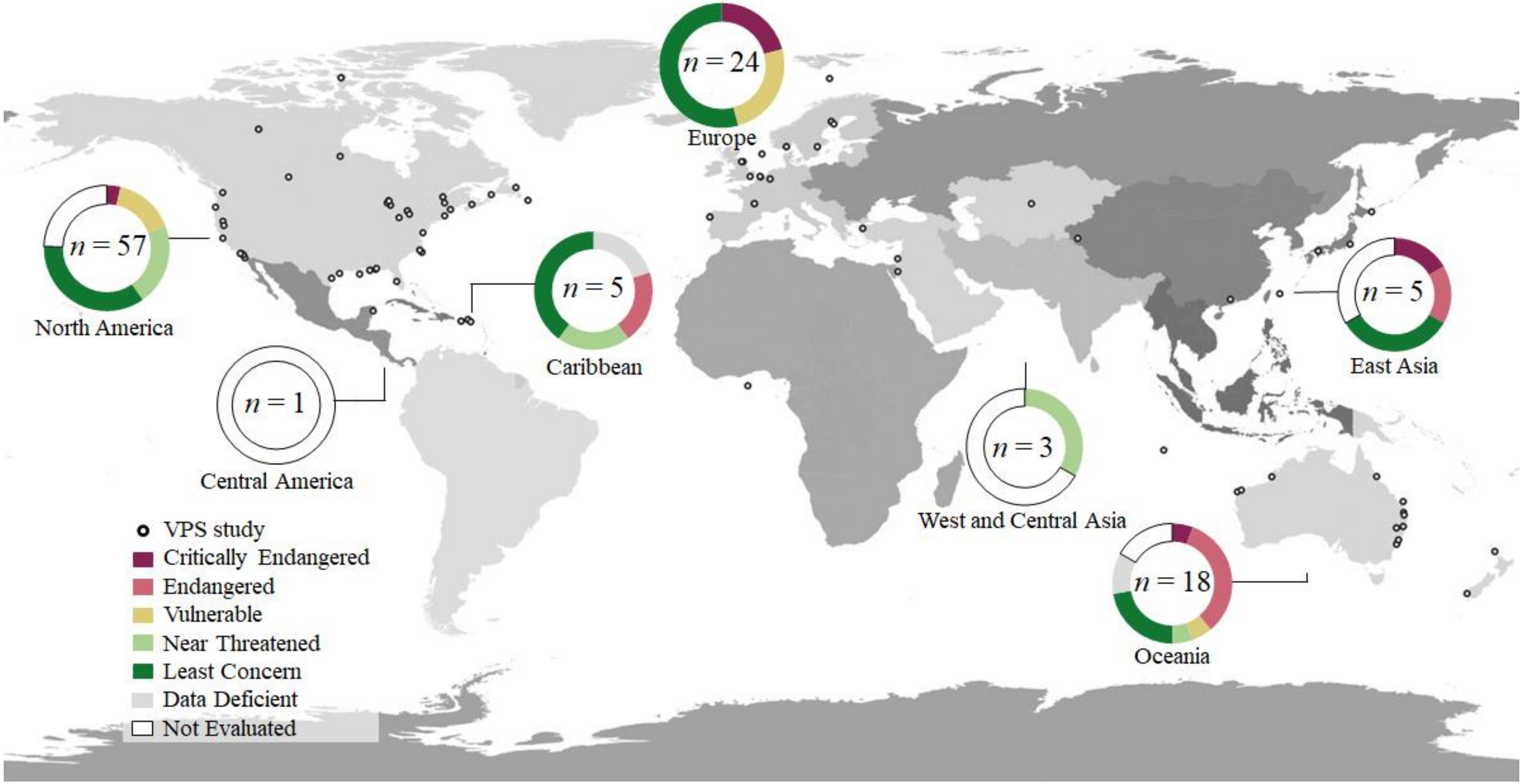
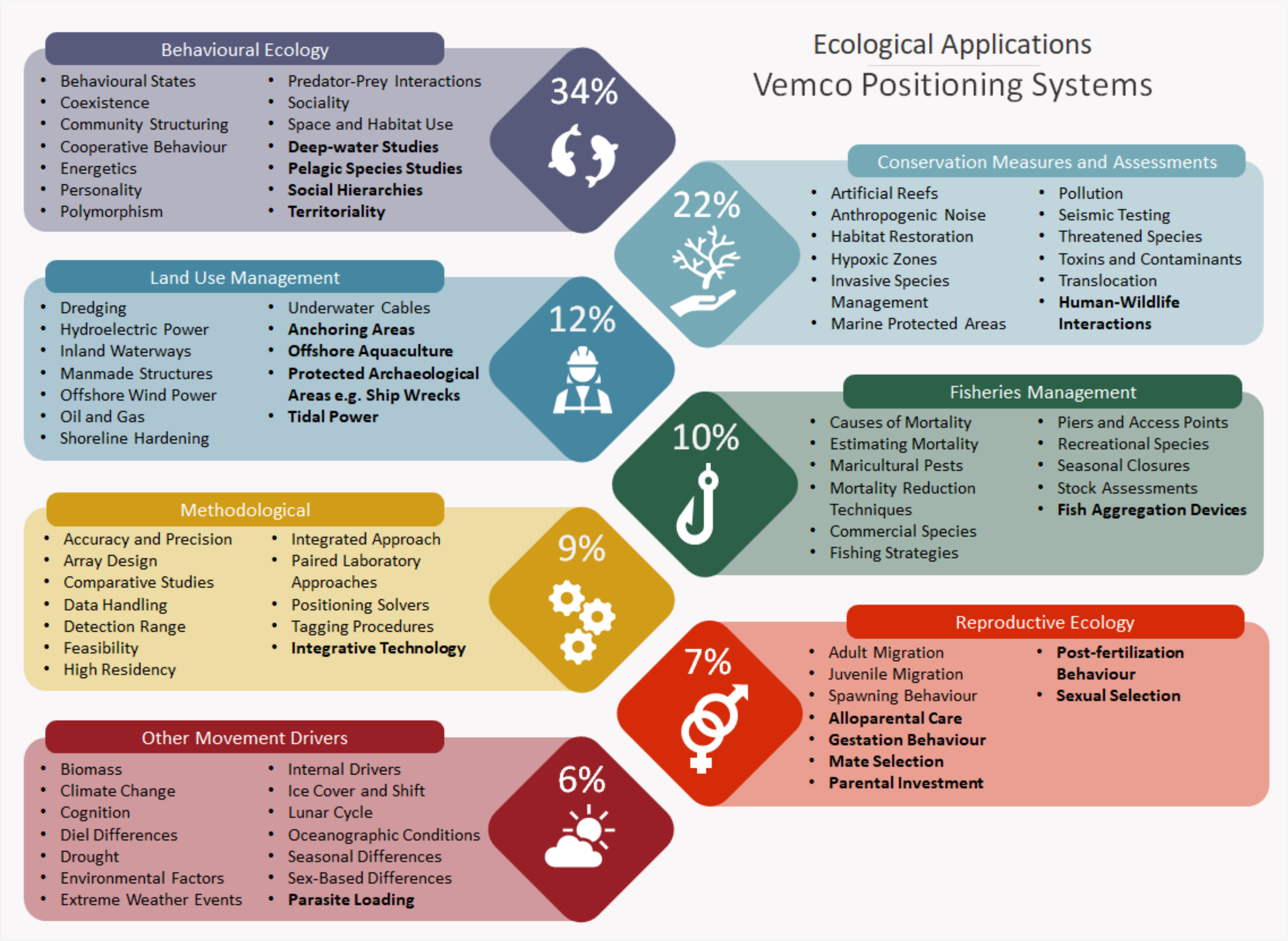


Figure 2.3 Global distribution of Vemco Positioning System (VPS) tagging studies (points). Colour wheels reflect the IUCN Red List Categories and Criteria of study species relative to the total number of unique species tracked (*n*) within each region (monochromatic shade).

2.4 Using VPS to address ecological questions

Primary ecological themes addressed using VPS can be categorised under seven overarching topics; behavioural ecology (*n* articles = 40; 35% articles), conservation measures (*n* = 25; 22%), land use management (*n* = 14; 12%), fisheries management (*n* = 12; 10%), methodological testing (*n* = 11; 9%), reproductive ecology (8; 7%), and the influence of other movement drivers (*n* = 7; 6%). In addition, 70 fine-scale categories were identified within these core topics, ranging from assessing the impact of boat noise to applying mortality reduction techniques to assist fisheries management (Fig. 2.4). Over time, these central themes and subsidiary aims have diversified, facilitated in part by technological progress. Technological advances include the enhanced resolution offered by VEMCO High Residency equipment. In conjunction, statistical progress has been driven by the ease of conducting different analyses via the availability of open-access computational packages (Joo et al. 2019) and “big” data via data sharing (Thums et al. 2018).

As new statistical approaches emerge in ecology, existing data can be used to drive a new wave of understanding of animal ecology and behaviour. VPS data have been analyzed and published utilizing different timeframes, subsets of animals, and types of analysis to answer diverse ecological questions. For example, of the five articles studying red snapper (*L. camperchanus*), four articles used different combinations of data generated from a single VPS array (differing time frames and data generated by different tagged individuals) to identify 2D (Piraino & Szedlmayer 2014, Williams-Grove & Szedlmayer 2016a) and 3D (Williams-Grove & Szedlmayer 2017) movements of this species, and the leading causes of mortality (Williams-Grove & Szedlmayer 2016b).



Ecological Applications
Vemco Positioning Systems

Behavioural Ecology
34%

- Behavioural States
- Coexistence
- Community Structuring
- Cooperative Behaviour
- Energetics
- Personality
- Polymorphism
- Predator-Prey Interactions
- Sociality
- Space and Habitat Use
- **Deep-water Studies**
- **Pelagic Species Studies**
- **Social Hierarchies**
- **Territoriality**

Conservation Measures and Assessments
22%

- Artificial Reefs
- Anthropogenic Noise
- Habitat Restoration
- Hypoxic Zones
- Invasive Species Management
- Marine Protected Areas
- Pollution
- Seismic Testing
- Threatened Species
- Toxins and Contaminants
- Translocation
- **Human-Wildlife Interactions**

Land Use Management
12%

- Dredging
- Hydroelectric Power
- Inland Waterways
- Manmade Structures
- Offshore Wind Power
- Oil and Gas
- Shoreline Hardening
- Underwater Cables
- **Anchoring Areas**
- **Offshore Aquaculture**
- **Protected Archaeological Areas e.g. Ship Wrecks**
- **Tidal Power**

Fisheries Management
10%

- Causes of Mortality
- Estimating Mortality
- Maricultural Pests
- Mortality Reduction Techniques
- Commercial Species
- Fishing Strategies
- Piers and Access Points
- Recreational Species
- Seasonal Closures
- Stock Assessments
- **Fish Aggregation Devices**

Methodological
9%

- Accuracy and Precision
- Array Design
- Comparative Studies
- Data Handling
- Detection Range
- Feasibility
- High Residency
- Integrated Approach
- Paired Laboratory Approaches
- Positioning Solvers
- Tagging Procedures
- **Integrative Technology**

Reproductive Ecology
7%

- Adult Migration
- Juvenile Migration
- Spawning Behaviour
- **Alloparental Care**
- **Gestation Behaviour**
- **Mate Selection**
- **Parental Investment**
- **Post-fertilization Behaviour**
- **Sexual Selection**

Other Movement Drivers
6%

- Biomass
- Climate Change
- Cognition
- Diel Differences
- Drought
- Environmental Factors
- Extreme Weather Events
- Internal Drivers
- Ice Cover and Shift
- Lunar Cycle
- Oceanographic Conditions
- Seasonal Differences
- Sex-Based Differences
- **Parasite Loading**

Figure 2.4 Key ecological themes addressed using fine-scale Vemco Positioning Systems (VPS) to date, with future directions highlighted in bold.

While technological advancement and statistical approaches have the potential to improve our understanding of mechanistic animal behaviour, disseminating these results effectively to non-specialized users is critical. At present, VPS data visualizations are similar to those selected for coarse-scale animal tracking data. From the use of abacus plots to identify animal fate and highlight presence/absence from the study area (Williams-Grove & Szedlmayer 2016b, Carpenter-Bundhoo et al. 2020), to visualization of 2D home range (Schlaff et al. 2020) along *x, y* coordinates. High-resolution data have been paired with environmental data to generate detailed visualizations of space use, for example, by matching water temperature recordings and high-resolution animal depth data (from pressure tags) through time series plots (Freitas et al. 2021) and 3D visualizations of space use during stratification (Roberts et al. 2017). Visualising VPS results is critical to disseminating data to non-technical stakeholders, including natural resource managers, policymakers, and the public.

We highlight the need for validation techniques throughout this section and offer common techniques and technologies that can be used. For example, a key validation and cross-comparison technique that VPS studies have not fully taken advantage of are controlled experiments in laboratory settings. Laboratory experiments can be highly effective at testing study design features, including tag retention and responses to novel olfactory stimuli; only four VPS studies reported running additional or parallel laboratory studies. These parallel applications have investigated barrier avoidance (Leander et al. 2019), spawning behaviour (Buchinger et al. 2017), personality (Villegas-Ríos et al. 2018), and common behavioural traits (Fahlman et al. 2020). While most VPS studies use field study components alone, there is also the potential to validate and support field observations using controlled environments such as isolated lakes or controlled flumes (Lennox et al. 2021).

2.3.4.1 Behavioural Ecology

Most behavioural-focused studies have used VPS data to investigate space use metrics, including residency, activity space, core, and extended home range. Other applications include studies using VPS data to investigate coexistence (Guzzo et al. 2016, Becker et al. 2020, Freitas et al. 2021), sociality (measured as the persistence of social networks over time) (Armansin et al. 2016), and physiological drivers (Brownscombe et al. 2017; Fig. 2.4). Secondary to understanding these characteristics is identifying the drivers of animal movement, for example, abiotic factors such as salinity, temperature, ice cover, seasonal productivity, and weather extremes. The majority of studies have used data collected over longitudinal time scales to identify periodicities of movement characteristics, e.g. across diel periods, within and between seasons and over annual timescales (the secondary focus of 50% of articles with a primary focus on behavioural ecology). For example, Moulton et al. (2017) examined the periodicity of movements of two sympatric gamefishes, the red drum (*Sciaenops ocellatus*) and the spotted seatrout (*Cynoscion nebulosus*), on both a localised and bay-wide scale. Over two years, animals were tracked using a smaller VPS grid array to identify fine-scale movements and across discontinuous strings of receivers that captured movements within the broader bay. Habitat use of sea trout shifted from seagrass during the day to bare substrate at night indicative of nocturnal foraging and potential predator avoidance, given seagrass can attenuate high-frequency vocalisations which dolphins use to echolocate prey (Wilson et al. 2013). Nocturnal foraging was also indicated by the higher calculated rate of movement (ROM) at night (3.4 m min^{-1}) versus day (0.95 m min^{-1}).

VPS studies have used additional data streams from a variety of sources to advance understanding of behaviour including, animal-borne accelerometers to measure activity, environmental sensors to measure abiotic parameters (dissolved oxygen, salinity, temperature, light, current speed and direction, wind speed) and anthropogenic effects such as noise and artificial light. For example, Brownscombe *et al.* (2017) were able to study the spatiotemporal energy expenditure of bonefish (*Albula vulpes*) in the wild by pairing swim tunnel respirometers with accelerometers to estimate metabolic rate across several habitat types and behavioural states. Using these techniques, Brownscombe *et al.* (2017) estimated energy expenditure across a heterogeneous reef flat and identified environmental drivers of movement. One such driver included the avoidance of nearshore areas during temperature extremes.

The ability to track multiple species simultaneously has facilitated an understanding of species interactions and the testing of traditional ecological theory or concepts, including coexistence, niche and resource partitioning (Guzzo et al. 2016). With the acquisition of depth data, there is potential to estimate the degree of spatial overlap in 3D space among individuals and species to reveal a deeper understanding of their co-occurrence and mechanisms driving species interactions. There is also the possibility to incorporate 3D models of space use with autonomous cameras and deep learning models to capture the diversity of non-tagged life and conspecifics on reefs (Villon et al. 2018).

Future applications of VPS could include the study of predator-prey interactions that shape ecosystems over varying scales, from individual decision making and predator avoidance to trophic cascades and food web restructuring (Smith et al. 2020). While joint space use has been studied under the lens of resource partitioning, coexistence and sociality, it also has relevance for epidemiology via disease transmission (Schauber et al. 2007, Gilbertson et al. 2020) as well as population genetics and gene flow (Roffler et al. 2012, Hahn et al. 2019).

2.3.4.2 Conservation Measures

Conservation driven VPS studies have primarily focused on the behavioural responses of animals to ameliorative measures (*n* articles = 13; Fig. 2.4), as well as noise pollution and contaminants (*n* = 3), seismic testing (*n* = 1), hypoxia (*n* = 1), as well as studying the movements of threatened (*n* = 2) and invasive species (*n* = 2).

Artificial reefs are the most commonly studied ameliorative conservation measures, with studies focusing on their influence on species' site fidelity, residency and home range (*n* = 7) and community structuring (*n* = 1). The geographic scale of artificial reef studies has ranged from deploying VPS arrays around discrete reef units and clusters in coastal marine environments (*n* receivers = 15; Piraino & Szedlmayer 2014) to a grid of receiver grids across a freshwater bay (*n* receivers = 27; Marsden et al. 2016). For example, Marsden et al. (2016) studied the relative attraction of tagged spawning lake trout (*S. namaycush*) to natural and artificial reefs using an integrated VPS approach in Lake Huron, Canada. Surface- and diver deployed egg and fry traps were used to validate spawning behaviours identified by a lake deployed VPS. Using these integrative techniques revealed that the proximity of a new artificial reef to an existing natural reef increased spawning activity. Moreover, by conducting a longitudinal study across three spawning seasons, the use of new reefs was initially low but increased over the assessment period.

The benefits of conservation strategies, including habitat restoration (*n* articles = 1), marine protected areas (*n* = 2), and translocation (*n* = 3), have also been studied. For example, Farrugia et al. (2011) investigated the use of a restored habitat by the shovelnose guitarfish (*R. productus*) to mitigate habitat loss from the expansion of the Port of Los Angeles, California, USA. In terms of understanding the benefits of marine protected areas (*n* = 2), Stieglitz & Dujon (2017) paired data from environmental loggers (measuring salinity, temperature, dissolved oxygen, and ambient light levels) with telemetered Caribbean queen conch, which spanned a range of developmental stages (*L. gigas*, *n* tagged = 38). This study aimed to assess the use of marginal atypical estuarine environment by this species and found space use was comparable to marine habitats, highlighting the conservation need for this potential nursery habitat.

2.3.4.3 Land Use Management

Land use management-focused VPS studies have primarily investigated the behavioural response of teleosts (*n* species = 16, *n* articles = 12) and chondrosteans (*n* species = 2, *n* articles = 2) within modified systems including reservoirs, harbours, and those influenced by sewage outflows and dredging. These studies typically incorporate multiple data sources such as habitat type from bathymetric surveys (multibeam sonar), vegetation surveys, fish community surveys and categorisation of substrate type. For example, Veilleux et al. (2018) assessed the use of harbour slips in the Inner Harbour of Toronto, two of which were "enriched" to increase habitat complexity (i.e. increased over-head cover and presence of in-water structures) and two deeper slips with no enrichment.

VPS is often paired with discontinuous strings or gates of receivers. While this trait is not unique to land use management-focused studies, creating "checkpoints" to identify animals that emigrate or exit a fine-scale study area is vital to identifying the relative impact of habitat modification and anthropogenic structures. For example, Vergeynst et al. (2019) deployed a VPS within the Albert Canal in Belgium to investigate the impact of intermediate-head navigation locks on downstream migration success of European eel (*A. anguilla*) and Atlantic salmon (*Salmo salar*). While this VPS array was positioned at the entrance to a single navigation lock, it formed part of a more extensive acoustic network that validated the tagged fish exiting the study system.

Mortality within aquatic systems is currently identified from patterns observed within telemetric data. Common techniques include identifying; rapid changes in vertical profile across a range of depths atypical of the species behaviour, a continuous depth profile or detection at a single receiver station (cessation of movement), or abnormal swim speeds outside the range of expected values (Everett et al. 2020, Bacheler et al. 2021). A unifying aspect of these techniques is that species ecology is well known and the study system well understood. The recent advent of the “predation tag” presents a new frontier to integrate within VPS applications in land use management studies, for example, in impounded systems that experience population bottlenecks, e.g. high-risk areas for juvenile fish migrating out to sea (Boulêtreau et al. 2020). These predation tags are coated in a biologically inert polymer. When a predator consumes a tagged animal, the biologically inert polymer that coats the tag breaks down, triggering a change in the tag’s emitted identification code (Halfyard et al. 2017). While no published VPS studies to date have utilized this technology, this will likely become a important tool in fisheries and land management research. These predation tags also present opportunities to estimate biomass structuring in ecosystems through determining natural predation rates across functional groups.

While VPS have shed light on the influence of riverine and coastal structures on fish movement, future research could explore the association of aquatic animals with structures, including tidal power and protected archaeological areas such as shipwrecks. For example, one avenue of inquiry could include research into the link between tidal power, altered bottom substrates in locations downstream of tidal energy installation, and subsequent changes in plant and animal community composition and abundance (DOE 2009, Frid et al. 2012).

2.3.4.4 Fisheries Management

Fisheries VPS management studies have investigated a range of topics from testing techniques to reduce discard mortality (Bohaboy et al. 2019), to bait attraction and catchability (Bacheler et al. 2018, Lees et al. 2018), causes of mortality (Williams-Grove & Szedlmayer 2016b) to general movements of species of commercial value within offshore (defined here as >2 km from shore, Skerritt et al. 2015) and aquaculture pests within culture areas (Miyoshi et al. 2018).

VPS data has direct applications for improving existing fisheries management tools, for example, by collecting data to inform catch per unit effort (CPUE) estimates. CPUE is a metric used to understand species distribution and abundance (Hinton & Maunder 2003). Lees *et al.* (2018) used VPS to identify localised behaviours of an important recreationally and commercially fished species, the European lobster (*H. gammarus*), in response to baited traps. This study aimed to understand the probability of attraction to a bait source and quantify the proportion of the population targetted. Understanding the fine-scale behavioural response of animals to different fishing practices has vast potential to aid our understanding of fishing induced evolution (Uusi-Heikkilä et al. 2008), as well as the design of effective protected areas (Lennox et al. 2017) and improving current estimates of population dynamics (i.e. survivorship/mortality) (Langrock et al. 2012, Lees et al. 2021).

Techniques to validate fisheries management VPS studies have included the use of underwater cameras. When investigating post-release survivorship, Bohaboy et al. (2019) affixed an underwater camera above descender devices to record fish descent and release to evaluate the performance of descender devices to capture possible predator interactions and behaviour of released fish. While no fish were predated during descent, three predation events were captured on video post-release, including consumption by a shark (n predated = 2) and a dolphin (n predated = 1), validating the removal of these fish from subsequent analysis. By incorporating complementary technology such as remote underwater video, there is potential to confirm mortality estimates and behavioural modes speculated from positional data (as seen using other biologging techniques, see Nakamura et al. 2015).

2.3.4.5 Methodological testing

Methodological VPS articles (*n* articles = 11) have shifted from initial work testing the feasibility and accuracy of VPS technology (Andrews et al. 2011, Espinoza et al. 2011, Ozgul et al. 2015) to those assessing the complementarity of high-resolution spatiotemporal models to support VPS findings (Goulon et al. 2018, Guénard et al. 2020), and testing of new VPS-compatible technology (Guzzo et al. 2018, Leander et al. 2019). It should be noted that the current review only incorporated VPS studies that had directly tagged animals as part of the study. During this search, nine articles were identified which tested the mechanics of VPS (Supplementary Material S2.2), including the factors influencing detection performance (Roy et al. 2014, Steel et al. 2014, Binder et al. 2014, 2016, Swadling et al. 2020). One additional article was feasibility-driven and studied the potential application of VPS to track turtle hatchlings (Thums et al. 2013); however, screening criteria identified understanding behavioural ecology as a primary focus. The first feasibility studies demonstrated the ability of VPS to accurately and precisely generate continuous positioning data (Espinoza et al. 2011) and its improved performance relative to existing VEMCO positioning technology (VRAP; Andrews et al. 2011).

Recently developed VEMCO High Residency (HR) equipment uses binary phase shift signalling to facilitate tag transmission rates several orders of magnitude greater than its predecessor and at a higher resolution. Data loss using this technology is less likely than traditional pulse-per-modulation (PPM) acoustic telemetry, which uses a code burst (8 or 10 ping signal that takes 3 to 5 seconds to transmit) transmission type. Due to a reduction in the propensity of signal collision, studies can track larger cohorts of animals. Initial testing by Guzzo et al. (2018) in a freshwater lake in Scotland, UK, revealed that the higher transmission interval attainable with HR tags (mean = 4 s) could more accurately determine complex path tortuosity as a result of higher data yield. Tortuosity characteristics, including turning angles and speed, are key characteristics for deciphering behavioural modes which drive movement choices (Gurarie et al. 2016). In addition, a comparison between traditional PPM and HR transmissions conducted by Leander et al. (2019) found that the higher transmission rates achieved by HR enabled the generation of 12 times more positions for tagged European eels (*A. anguilla*) navigating the Motala River in Sweden using a tag transmitting both signal types (1.1 s nominal HR transmission rate versus 37.5 s with PPM). It should be noted that while HR can generate a significant volume of data, these positions require careful evaluation to assess whether positions are ecologically meaningful, particularly in cases where the error associated with a position exceeds the scale of movement studied (C. H. Fleming et al. preprint; https://doi.org/10.1101/2020.06.12.130195).

2.3.4.6 Reproductive Ecology

VPS articles primarily focusing on reproductive ecology (*n* articles = 8) have investigated key characteristics, including spawning cues and sex-based differences in behaviour. These studies have incorporated large sample sizes (mean *n* animals tagged = 147, unique datasets = 7), including the largest cohort of animals tagged within a single VPS study (lake trout *S. namaycush*, *n* = 390; Riley et al. 2014, Binder et al. 2017). Often studies addressing this theme incorporate abiotic data streams, including habitat mapping using high resolution multibeam bathymetric surveys (Riley et al. 2014, Binder et al. 2018, unique datasets = 1) and habitat flow models (Wyman et al. 2018). A novel multifaceted study by Buchinger et al. (2017) used chemical analyzes, electro-olfactogram recordings, and behavioural assays to evaluate the persistence of fry odours during a spawning season coupled with the installation of a 27-receiver VPS array. While laboratory components of this study supported the theory that lake trout use fry odours as cues of past reproductive success, these results were not replicated in the natural VPS experiment (Buchinger et al. 2017). This example highlights how a multifaceted study design, with both laboratory and in-field components, can identify differences in observed behaviours dependent on the environmental setting.

2.3.4.7 Other Drivers of Movement

Aquatic environments are highly dynamic with the scale of movement necessary to acquire essential resources and undertake life history processes in part modulated by abiotic conditions (Jackson et al. 2001). Vast expanses of the aquatic realm are physiologically challenging to occupy, and therefore it is critical to identify environmental and oceanographic conditions which drive movement behaviours and intimately link with individual performance and fitness (Madigan et al. 2020). While only seven articles focused primarily on abiotic environmental variables, it should be noted that a large proportion of remaining articles listed this as a secondary (*n* articles = 23; 21%) or tertiary (*n* = 33; 38%) aim.

Environmental sensors are often deployed alongside VPS to measure the temporal and seasonal change in the ambient environment, including: temperature, salinity, dissolved oxygen and photosynthetically active radiation. Aside from using these data to identify environmental drivers of movement, it can also provide indicators of conditions that may impede system performance. For example, weather extremes such as hurricanes can reduce data acquisition due to animal displacement, while increased turbidity and wave action can limit signal propagation (Dahl & Patterson 2020, Bacheler et al. 2021). Ivanova et al. (2018) provide an applied example of using environmental sensors to explore the drivers of movements. To disentangle whether the movements of the shorthorn sculpin (*M. scorpious*) in Resolute Bay, Nunavut, Canada, were driven by vessel presence and/or abiotic factors, environmental loggers were installed to record salinity, water temperature, and dissolved oxygen. Additional environmental covariates, including mean wind speed, air temperature and photoperiod were retrieved from online archives. Using fine-scale VPS data, trajectories were broken into bursts containing discrete successive VPS positions which were then clustered into three movement types. Models were subsequently run to examine the influence of ship traffic and environmental variables on the three defined movement behaviours.

Given the forecasted increase in the frequency of extreme weather events with climate change (National Academies of Sciences 2016, Knutson et al. 2020), it is likely that future studies will unwittingly capture these events, which will improve our fundamental understanding of behavioural responses and potential plasticity of species' movements. Future work is also required to capture the influence of other environmental extremes, including El Niño, La Niña and flooding on animal movement (Wilson et al. 2001, Campbell et al. 2012, Briscoe et al. 2021).

2.4.1 Analytical approaches for VPS data

Increased transmission rates and encoding options (with reduced transmission intervals and multiple steps of programming) have the potential to yield an unprecedented quantity of high accuracy positions using VPS technology (Espinoza et al. 2011). VPS studies using traditional pulse per modulation (PPM) VEMCO technology typically generate upward of 500 positions a day (*n* unique species datasets with nominal transmission rate detailed = 109, median nominal transmission rate = 120 s, range of nominal delay = 7.5 – 4800 s). The new age of enhanced positioning accuracy, precision and tracking resolution offered by VEMCO High Residency (HR) equipment can generate over 20,000 positions a day for a single animal (*n* HR-VPS species datasets = 6) with sub-metre accuracy. With this volume of data, there are two integral steps to ensure data integrity is maintained. Firstly, the error associated with a position does not exceed the scale of movement studied. VPS positions include a Horizontal Positioning Error or 'HPE', a form of dimensionless error analogous to GPS horizontal dilution of precision (HDOP) (C. H. Fleming et al. preprint; https://doi.org/10.1101/2020.06.12.130195). HPE values are unique to each application of VPS, with fixed reference tags used to compare location error with calculated animal positions (Smith 2013). Identifying associated error is key to selecting an appropriate analytical technique. For example, Fleming et al. (preprint;

https://doi.org/10.1101/2020.06.12.130195) identified that a per unit increase in HPE equated to 3-9 m of location error. Given this scale of error, if step lengths (distance between two consecutive positions) were calculated at <9 m subsequent calculations would be contaminated by location error as the error associated exceeds the scale of movement studied. Secondly, it is key that for high-resolution tracking data, analytical techniques that account for autocorrelation are selected (Gurarie et al. 2009). Autocorrelation describes positions that are not independent in time or space, which is the case for consecutive telemetric datapoints (Gurarie et al. 2009).

On a foundational level, consecutive detections can be used to calculate basic metrics, including step length and turning angle (bearing between consecutive positions) (Ironside et al. 2017). Using these foundational units of movement, metrics including tortuosity (degree of turning across the movement path) and total distance travelled (Euclidean distance between first and last points or within a user-determined time frame) can be calculated for a given trajectory. Trajectories are often used to investigate species distribution metrics such as space and habitat use, including home range, site fidelity and residency. By incorporating potential drivers of movement, for example, environmental and oceanographic conditions, these covariates can be used to explore animal movement as a community-level process and identify underlying behavioural patterns (Schick et al. 2008). While VPS-compatible technology advances and user-friendly data handling and modelling techniques are explored in seminal papers and guides (e.g. a continuous-time correlated random walk model, Johnson et al. 2008; state space models, Auger-Méthé et al. 2021), the variety of analytical techniques used to explore fine-scale movement will continue to diversify.

2.3.5.1 Home range

A fundamental characteristic of an animal’s movement trajectory is its home range. Information on animal home ranges can be used in conjunction with broader ecosystem models to develop and assess conservation strategies such as protected areas (Andrzejaczek et al. 2020). Home range describes the area in which an animal travels to acquire the resources it needs for survival and reproduction (Burt 1943). Despite the simplicity of this definition, defining this statistically is challenging (Dougherty et al. 2017). Common approaches to estimate home range can be grouped in two different ways. Firstly, those that aim to estimate an animal's range distribution and its long-term area requirements (as per the definition provided in Burt 1943) which commonly include minimum convex polygon ("MCP"), and kernel-density estimators ("KDE") (Fleming et al. 2015). Alternatively, techniques that estimate occurrence distributions through interpolation of the observed data during the study period include Brownian bridge density estimators (BBDE) and Time Local Convex Hull ("T-LoCoh") which do not link to Burt's (1943) conceptualisation of home range. As detailed in Fleming et al. (2015), these approaches can also be viewed in terms of their methods as either (i) geometric (lacking an underlying probabilistic model, includes MCP, T-LoCoh), or (ii) statistical (KDE and BBDE). Choice of statistical approach depends on the study question at hand and can differ in their fundamental framework; therefore, comparisons between fine-scale telemetry studies that utilize different methods should be made with caution.

Early techniques of home-range analysis were devised to quantify two dimensional (i.e. horizontal) space use, such as 100% minimum convex polygons (MCP; Blair 1940, Odum & Kuenzler 1955). MCP (also called a convex hull) is a simple technique that draws the smallest possible convex polygon around point locations (*x*, y). Despite the well-published limitations of this technique (Worton 1987, 1995, Börger et al. 2006), it is still used today in VPS studies (*n* articles = 14).

Home range is often analyzed as the relative frequency (probability) distribution of an animal's location in space, also known as a utilisation distribution (UD) (French et al. 2019).

A common form of UD estimation uses a KDE. While initially not intended for telemetric datasets, this technique is very popular (*n* VPS articles = 41). Kernel Uds or “KUDs” often use the 50% and 95% isopleths of the probability distribution of locations to estimate an animal’s core and extended home range (see Worton 1989). This technique relies on the assumption that data is independent and identically distributed (Silverman 1983). High-resolution telemetric data does not meet this assumption as it is intrinsically autocorrelated and nonstationary (Fleming et al. 2015). Autocorrelated KDE (“AKDE”) is a generalisation of KDE which incorporates an autocorrelation function (“ACF”) and is derived from a fitted model or directly from the data (see Fleming et al. 2015). The only example of its application to VPS data to date is provided by Bašić et al. (2019), wherein this technique was used to determine the home range and core areas used by tracked European eels (*A. anguilla)*.

Three VPS articles used BBDE (for method see Horne et al. 2007), an approach originally devised for occurrence distributions that is not a home-range estimator (see Fleming et al. 2015 for further details). This technique uses an underlying movement model to create a smooth bridge between animal relocations (Kranstauber et al. 2012). The driving parameter in Brownian Bridge Movement Models (“BBMMs”) is the Brownian motion variance, which describes the irregularity of the path of an animal track (Byrne et al. 2014, Kranstauber 2019). Adaptations of BBMMs include dynamic BBMMs, which calculate the Brownian motion variance for each behavioural track segment (Kranstauber et al. 2012, Silva et al. 2018) with the aim of improving estimator accuracy.

The T-LoCoH technique is a occurrence distribution estimator which generalises the MCP method (see Getz et al. 2007, Kie et al. 2010) and incorporates time (Lyons et al. 2013) (*n* = 1). Whitmore & Litvak (2018) used T-LoCoH to study the space use and aggregation behaviour of juvenile Atlantic sturgeon (*A. oxyrinchus*) and constructed isopleths incorporated point density, directional movement, revisitation and residency time to identify pathways and activity space across two seasons.

2.3.5.2 Habitat selection

Habitat selection describes the process by which an animal chooses a resource, and habitat preference indicates the likelihood that an animal selects a resource given equal availability (Johnson 1980). The ability to identify preferred or critical habitats which support vital life-history stages, including spawning, is central to conservation (Caro 1999). Two common techniques used to quantify microhabitat selection using VPS data include Compositional Analysis (classification based) and Euclidean Distance Analysis (EDA, distance-based; Degregorio et al. 2011).

Compositional Analysis classifies animal locations by a single habitat type to determine proportional use (Aebischer et al. 1993). The method relies on several assumptions: (i) each animal provides an independent measure of habitat use within the population, e.g. no gregarious behaviour, (ii) all animals select habitat in the same way, e.g. all have equal access to resources and exhibit no territoriality, and (iii) habitat use by different animals is equally accurate, e.g. not dependent on “detectability” such as reduced detection likelihoods in complex habitats, and (iv) the more available a resource, the more likely an animal is to use it (Garshelis 2000).

The Habitat Selection Index (HSI), a type of Compositional Analysis, has been used to estimate the preference or avoidance for a given habitat (*n* articles = 5), with resultant values >1 used to indicate preference and <1 indicate avoidance (Manly 1972). To calculate I, the proportion of positions within each habitat type is divided by the proportion of available habitat. For example, Özgül et al. (2019) used I to evaluate the conservation benefit of artificial reefs, with habitat selection by two species of scorpionfish (*Scorpaena*) identified within a 15 m spatial buffer generated around twelve artificial reef sets within a 0.28 km^2 VPS array.

Resource selection functions (“RSFs”, *n* articles = 2) are often favoured as they yield statistical rankings among habitats (Garshelis 2000). Data are arranged similar to an ANOVA whereby between-group variation can be tested against within-group variation among individuals. RSFs can also incorporate covariates such as temporal scale (diurnal, seasonal and annual differences) and study areas (such as differing biomass and animal densities) (Garshelis 2000, Boyce et al. 2002, McLoughlin et al. 2010). For example, Freitas et al. (2016) used VPS to identify habitat selection of Atlantic cod (*Gadus morhua*) within a Norwegian fjord across seasons and temperature ranges. Habitat selected by tagged cod were coded as one while an equal number of theoretical random locations were generated and coded as zeros (see the detailed method in Johnson et al. 2006).

In contrast to Compositional Analysis, EDA (*n* articles = 15) is a multivariate distance-based approach that computes the distance between each animal position and the nearest occurrence of each habitat type (Conner et al. 2003). Random points are simulated, which present the expected distances to each habitat type (the null distribution). If an individual’s habitat use is random, then the distance calculated for the null distribution and animal positions should be equal for a given habitat type (Novak et al. 2020). EDA is preferable in incidences where an area is classified as two habitat types simultaneously, whereas compositional analysis requires a single discrete categorisation for each area (Conner & Plowman 2001). Novak et al. (2020) used EDA to investigate fine-scale habitat use of the yellowtail snapper (*Ocyurus chrysurus*) within a nearshore marine protected area. Results suggested that EDA is a valuable tool when looking at population-level habitat preference, but differences in individual preference or avoidance in habitat use were masked.

It should be noted that if receivers are unevenly spaced or prone to reduced detection efficiency due to physical barriers, the perceived time spent across different portions of the array (particularly in truncated systems) may be inaccurate. These approaches assume that all habitat is equally available, regardless of distance and animal speed (Forester et al. 2009). Alternate habitat selection methods using telemetry data, but not yet VPS, include Step Selection Functions (SSF) which are similar mathematically in structure to a Resource Selection Function (Fortin et al. 2005). The main difference is that SSFs account for distance (defined as step length) and turning angle. In addition, there is potential for the use of non-Euclidean distances to assign a cost to movements across habitats, which is used in metapopulation ecology (Wiens et al. 1993).

Habitat connectivity and use have been studied primarily through the use of multiple installed VPS arrays (*n* articles = 21) and the integration of additional gates of receivers across broad-scale habitat features (*n* = 39). For example, Dance & Rooker (2015) examined movements of two co-occurring juveniles fishes, southern flounder (*Paralichthys lethostigma*) and red drum (*Sciaenops ocellatus*), across a range of spatial scales. Movement was studied at a habitat scale using a VPS (*n* receivers = 10; coverage = 1 km^2), and bay scale using a grid of receivers with non-overlapping detection ranges (*n* receivers = 17; coverage = 20 km^2). It was found that environmental factors did not affect red drum movement on a habitat scale, but on a broader bay-wide scale, movement increased in response to decreasing salinity and lower temperatures.

2.3.5.3 Activity

Animal movements, behaviour and energetics vary across habitats, landscapes and climes. Consequently, quantifying spatiotemporal variation in animal activity is key to understanding energetic budgets (Wilson et al. 2011). The activity of tracked animals within VPS is predominantly calculated using basic calculations generated from animal relocations, including the rate of movement (“ROM”, estimated by dividing the distance between detections by the elapsed time, *n* articles = 42). Straight-line displacement (SLD) estimates (typically used for ROM calculations) are susceptible to errors associated with the scale of measurement, sampling frequency, and path tortuosity (Rowcliffe et al. 2012, Noonan et al. 2019).

While not yet applied in VPS studies, continuous-time speed and distance (CTSD) estimation methods may offer greater accuracy for mean speed estimates from fine-scale positioning data (Noonan et al. 2019). This approach uses measurement and process models estimated from tracking and preferably calibration data (from fixed-location tags). A trajectory is then simulated as conditioned by the data, fitted movement model, and aforementioned calibrated error model (see Noonan et al. 2019 for further details). The distance/speed of that trajectory is then calculated, and the process is repeated through multiple simulations to create a point estimate and confidence intervals that come directly from the sampling distribution (Noonan et al. 2019).

The integration of an acceleration sensor in tags has allowed the identification of animal behaviours (feeding, foraging, transiting) (Cott et al. 2015) and estimates of energy expenditure (Brownscombe et al. 2017). VEMCO acoustic triaxial accelerometers can either log data at high frequencies (>100 Hz; but require animal recapture) or transmit data less frequently in the form of a summarised activity value (5-10 Hz; “SI” units). SI units are calculated from measuring acceleration over two (“tailbeat algorithm” uses lateral [*x*] and vertical [*z*] axes) or three axes (“activity algorithm” uses lateral [*x*], forward [*y*] and vertical axes [*z*]) (InnovaSea Systems Inc. 2018). For the “activity algorithm”, the root mean square of acceleration is calculated and averaged over a given sampling period, e.g. 25 s (Brownscombe et al. 2017). As with positioning data, sampling frequency directly determines the scale of inference, e.g. identification of fast-action feeding events and burst swimming to escape predation (Broell et al. 2013). While these intensive movement events often last seconds, they constitute an important component of an animal's energy budget. Low-frequency accelerometer sampling is often selected due to constraints on battery life and data-archiving and can record for >1 year. Paired laboratory trials provide a crucial tool to validate assumptions of animal energetics from accelerometers (Broell et al. 2013, Brownscombe et al. 2017, InnovaSea Systems Inc. 2018). While high-frequency sampling is feasible with an acoustic tag, this equates to a larger battery and storage requirement, increasing tag dimensions. Alternatively, developments in tags could allow the recording and transmission of each triaxial axis of acceleration independently. With future advances in microprocessors, battery power and storage or data compression capabilities (Lennox et al. 2017), integrated high-resolution accelerometers offer a tool to identify animal activity rates outside of simplified point-by-point calculations used to estimate the rate of movement or current combined triaxial metrics.

2.3.5.4 Behavioural patterns

Behavioural states which drive movement choices, such as foraging, feeding and transiting, are often assumed from systematic patterns and structures observed in telemetric data (Gurarie et al. 2016). Enhanced resolution of VPS positions enabled by higher transmission rates and typically lower probable error bounds can equate to a trajectory that better reflects the true path of an animal, and thus its behaviour. There are four broad categories of behavioural movement analysis techniques: metric-based, classification and segmentation techniques, phenomenological time-series analysis, and mechanistic movement models (Gurarie et al. 2016).

Metric-based analytical techniques use movement path characteristics estimated from variables such as distance, speed, turning angles and residency to classify behaviours or distinct movement trajectories. This method is often paired with classification and segmentation techniques, for example, *k*-means cluster-based analysis (*n* articles = 3). To conduct *k*-means clustering, "*k*" describes the number of centroids (clusters) to group the data, with each location allocated to the nearest randomly generated centroid in *n*-dimensional space. The cluster is then recalculated using the mean of all vectors in the group and reiterated until the centroids show minimal change (Zhang et al. 2014). For example, Landry et al. (2019) identified periods of activity of the shorthorn sculpin (*M. 55corpius*) using the *adehabitatLT* package in *R* (Calenge 2006), which groups detections into bursts identified as continuous consecutive detections terminated by 30-minutes of no consecutive detections. To distinguish between movement trajectory types, metrics including (but not limited to) mean turning angle, mean bearing, mean depth, mean ROM, and path linearity were classified using *k*-means cluster analysis (Landry et al. 2019). Using this technique three behavioural types were identified from the shorthorn sculpin data. Feeding behaviour was identified by quick turns within a small area, with foraging classified by a higher sum of distance and mean ROM than the speculated feeding cluster. Transiting was identified by large, straight movements across deeper waters identifiable by a higher cumulative distance travelled, rate of movement and linearity ratios.

Phenomenological time-series models are used to identify relationships observed within time-series data without exploring the underlying drivers of changes in detection sequence indicative of a behavioural change (Hilborn & Mangel 1997, Zhang et al. 2014). An example of this model type used in VPS studies includes behavioural change point analysis (BCPA) (*n* articles = 1). BCPA uses a likelihood-based method to identify changes in movement parameter values by identifying likely behavioural changepoints from abrupt changes in the underlying autocorrelation structure, and then testing if they occurred using Bayesian Inference Criterion or "BIC" (Gurarie 2013, Zhang et al. 2014). Cote et al. (2019) used the *BCPA* package in *R* (Gurarie 2013) to calculate metrics of snow crab (*C. opilio*) movement behaviour, including velocity and changes in movement direction for each track segment (successive positions) within a state-space modelled track.

Mechanistic movement models used in VPS studies include hierarchical models such as State-space models (“SSM”, *n* articles = 1) and Hidden Markov models (“HMM”, *n* articles = 4). These time-series models predict the future “state” (e.g. location, behavioural state, physiological or energetic condition) based on its previous states in a probabilistic manner using a process model (Patterson et al. 2008). A HMM is an SSM, where the states are discrete rather than continuous (Auger-Méthé et al. 2021). Random walks are a form of process model often used as a foundational step for generating complex, multistate models, such as state-state models. A random walk is a mathematical description that is often a Markov process (a stochastic process in which the probability of a future state is a function of its current and past states, Patterson et al. 2008). For example, Cote et al. (2019) used a one-behavioural first difference correlated random walk (DCRW) state-space model to generate movement tracks which were then integrated into a generalized additive mixed model (GAMM) to understand snow crab (*C. opilio*) movement behaviour in a deep offshore environment. A key advantage of using an SSM is that it integrates error correction into the modelling process, rather than relying on pre-processing and subjective data cleaning prior to modelling (Patterson et al. 2008).

A promising technique that has yet to be utilized with VPS data is the time-varying move persistence model (Jonsen et al. 2019). This approach identifies “move persistence”, which describes autocorrelation in both animal speed and duration, by identifying variance in move persistence along a movement trajectory and indexing behaviour from 0 (low movement persistence) to 1 (high movement persistence).

2.3.5.5 Species interactions

As the resolution and accuracy of positioning multiple individuals and species improves, so is our ability to identify the fine-scale movement behaviours associated with species interactions. Movement behaviour is shaped by intra- and inter-species interactions that directly influence individuals' fate, from competing for resources to predator avoidance. On a finer scale, species interactions also include symbiotic relationships such as cleaning behaviour, parasitism, and cooperative feeding (Henry 1966). Identifying species interactions and testing of classic ecological theory, including coexistence, has been conducted by comparing species overlap using measures of space use (EDA and residency) and movement metrics such as ROM. For example, Moulton et al. (2017) used VPS positioning data to study habitat-scale space use (using EDA, residency, ROM metrics) of two teleost species over diel and seasonal scales and subsequently compared within and between species differences using t-tests. Additionally, this study combined stable isotope and VPS data to identify differences in spatial (telemetric) niche and dietary niche, with data-rich mixed effect models used to examine coexistence (Guzzo et al. 2016).

Identifying sociality from tracking data requires careful consideration of an animal's ecology and the systems positioning accuracy. For example, Armansin et al. (2016) studied the sociality of the spotted wobbegong (*O. maculatus*, *n* tagged = 23) within a coastal protected reserve with the aim of identifying associations between both juveniles and adults over a 15-month period. This study used social network analysis which can be used to characterise the social structure of a population by identifying associations and interactions suggested by closely associated positioning data (Godde et al. 2013). The maximum distance which wobbegongs impact each other's movements and share information socially was defined as the combined value of one body length (148 cm, the max recorded total length of all tagged sharks) and the median positional error calculated for VPS positions (280 cm). In this case, a half-weight-index (HWI) was used to estimate the proportion of time individuals spent together over a dyadic scale whereby “0” represents individuals never observed together and “1’ describes continuous individual association. In addition, simple ratio indices (SRI) were also used to calculate the probability that two individuals were observed together, given that one has been detected. Dyadic data was then compiled into symmetric and weighted association matrices for the 15-month study period to assess how the dynamics of individual associations changed over time (Armansin et al. 2016).

At present, the ability to quantitively describe how a network changes over time is limited. For example, can temporal shifts in network use by an animal be used to understand changes in the navigational abilities of tracked animals under differing environmental conditions or scenarios (Jacoby & Freeman 2016)? Direct comparisons of network analysis conducted across different locations are not feasible as the network structure itself is dependent on the deployment design of a receiver network. Improvements in the predictive power of social network analysis within VPS have vast potential in understanding sociality, which forms the building blocks of animal societies, and our ability to estimate the resilience of animals to disturbances (Silk et al. 2018).

2.5 Conclusion

VPS allows the study of the fine-scale movements of aquatic animals across a size spectra and developmental stages, offering unique behavioural insights into a range of behaviours, including coexistence, sociality and predator-prey interactions. VPS has been used to investigate key ecological themes that shape environmental policy and management across local and regional scales. A plethora of topics within these broad ecological themes remains to be investigated, and this technology could provide unique insights into species under real-world experimental settings. Moreover, such fine-scale positioning systems and current developments (i.e. High Residency) can generate big data allowing the use and further development of advanced analytical techniques to characterize the intrinsic (physical state; memory, perception and energetics) and extrinsic drivers of animal behaviour. However, as the volume of data continues to increase, robust ecological grounding is required to determine meaningful data standards, from filtering, cleaning, pre-processing (e.g. position filtering) to modelling positioning data and integrating multiplex data streams. Continued efforts to identify and incorporate error will facilitate the next frontier of ecological inference from high-resolution telemetric data, which has vast potential to improve our understanding of fundamental aspects of animal ecology in the aquatic realm.

2.6 References

Abrams RW, Abrams MD, Schein MW (1973) Diurnal Observations on the Behavioral Ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean Coral Reef. Coral Reefs 1:185–192.

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional Analysis of Habitat Use From Animal Radio-Tracking Data. Ecology 74:1313–1325.

Andrews KS, Tolimieri N, Williams GD, Samhouri JF, Harvey CJ, Levin PS (2011) Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. Mar Biol 158:2377–2387.

Andrzejaczek S, Chapple TK, Curnick DJ, Carlisle AB, Castleton M, Jacoby DMP, Peel LR, Schallert RJ, Tickler DM, Block BA (2020) Individual variation in residency and regional movements of reef manta rays Mobula alfredi in a large marine protected area. Mar Ecol Prog Ser 639:137–153.

Armansin NC, Lee KA, Huveneers C, Harcourt RG (2016) Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark. Anim Behav 115:245–258.

Armstrong AO (2021) Mutualism promotes site selection in a large marine planktivore. 11:5606–5623.

Ascension Island Government (2021) The Ascension Island Marine Protected Area Management Plan. Available from: https://www.ascension.gov.ac.

Auger-Méthé M, Newman K, Cole D, Empacher F, Gryba R, King AA, Leos-Barajas V, Flemming JM, Nielsen A, Petris G, Thomas L (2021) A guide to state-space modeling of ecological time series. arXiv 2002.02001.

Bacheler N, Shertzer K, Buckel J, Rudershausen P, Runde B (2018) Behavior of gray triggerfish *Balistes capriscus* around baited fish traps determined from fine-scale acoustic tracking. Mar Ecol Prog Ser 606:133–150.

Bacheler NM, Shertzer KW, Runde BJ, Rudershausen PJ, Buckel JA (2021) Environmental conditions, diel period, and fish size influence the horizontal and vertical movements of red snapper. Sci Rep 11:9580.

Baker NJ, Boubée J, Lokman PM, Bolland JD (2020) Evaluating the impact of hydropower on downstream migrating anguillid eels: Catchment-wide and fine-scale approaches to identify cost-effective solutions. Sci Total Environ 748:141111.

Balazik M, Barber M, Altman S, Reine K, Katzenmeyer A, Bunch A, Garman G (2020) Dredging activity and associated sound have negligible effects on adult Atlantic sturgeon migration to spawning habitat in a large coastal river. PLoS ONE 15:e0230029.

Barkley AN, Gollock M, Samoily M, Llewellyn F, Shivji M, Wetherbee B, Hussey NE (2019) Complex transboundary movements of marine megafauna in the Western Indian Ocean. Anim Conserv 22:1–12.

Barnett A, AbrantesKá KG, Seymour J, Fitzpatrick R (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. PLOS ONE 7.

Bašić T, Aislabie L, Ives M, Fronkova L, Piper A, Walker A (2019) Spatial and temporal behavioural patterns of the European eel *Anguilla anguilla* in a lacustrine environment. Aquat Sci 81:73.

Bassett D, Montgomery J (2011) Home range use and movement patterns of the yellow moray eel *Gymnothorax prasinus.* J Fish Biol 79:520–525.

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: A novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012.

Becker SL, Finn JT, Novak AJ, Danylchuk AJ, Pollock CG, Hillis-Starr Z, Lundgren I, Jordaan A (2020) Coarse- and fine-scale acoustic telemetry elucidates movement patterns and temporal variability in individual territories for a key coastal mesopredator. Environ Biol Fishes.

Bergmann M, Dannheim J, Bauerfeind E, Klages M (2009) Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. Deep Sea Res Part I Oceanogr Res Pap 56:408–424.

Binder TR, Farha SA, Thompson HT, Holbrook CM, Bergstedt RA, Riley SC, Bronte CR, He J, Krueger CC (2017) Fine-scale acoustic telemetry reveals unexpected lake trout, *Salvelinus namaycush*, spawning habitats in northern Lake Huron, North America. Ecol Freshwat Fish 27:594–605.

Binder TR, Holbrook CM, Hayden TA, Krueger CC (2016) Spatial and temporal variation in positioning probability of acoustic telemetry arrays : fine-scale variability and complex interactions. Animal Biotelemetry 4:1–15.

Binder TR, Holbrook CM, Miehls SM, Thompson HT, Krueger CC (2014) Use of oviduct-inserted acoustic transmitters and positional telemetry to estimate timing and location of spawning: a feasibility study in lake trout, *Salvelinus namaycush*. Anim Biotelemetry 2:1–14.

Blair W (1940) A study of prairie deer-mouse populations in southern Michigan. American Midland Naturalist 24:273–305.

Bohaboy E, Guttridge TL, Hammerschlag N, Van Zinnicq Bergman MPM, Patterson W F (2019) Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality. ICES J Mar Sci 77:83–96.

Bolden SK (2001) Using Ultrasonic Telemetry to Determine Home Range of a Coral-Reef Fish. 167–168.

Bolnick DI, Svanback R, Araujo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences 104:10075–10079.

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. Ecology 83:2936–2941.

Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T (2006) Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecology 75:1393–1405.

Briscoe DK, Turner Tomaszewicz CN, Seminoff JA, Parker DM, Balazs GH, Polovina JJ, Kurita M, Okamoto H, Saito T, Rice MR, Crowder LB (2021) Dynamic thermal corridor may connect endangered loggerhead sea turtles across the Pacific Ocean. Front Mar Sci 8.

Broell F, Noda T, Wright S, Domenici P, Steffensen JF, Auclair J-P, Taggart CT (2013) Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. J Exp Biol 216:1522–1522.

Brownscombe JW, Cooke SJ, Danylchuk AJ (2017) Spatiotemporal drivers of energy expenditure in a coastal marine fish. Oecologia 183:689–699.

Buchinger TJ, Marsden JE, Binder TR, Huertas M, Bussy U, Li K, Hanson JE, Krueger CC, Li W, Johnson NS (2017) Temporal constraints on the potential role of fry odors as cues of past reproductive success for spawning lake trout. Ecol Evol 7:10196–10206.

Burns ES, Armstron J, Tang D, Sakamoto K, Lowe CG (2019) The residency, movement patterns and habitat association of several demersal fish species to the Orange County Sanitation District wastewater outfall. Mar Pollut Bull 149:UNSP 110638.

Burt WH (1943) Territoriality and Home Range Concepts as Applied to Mammals. J Mammal 24:346–352.

Byrne ME, Clint McCoy J, Hinton JW, Chamberlain MJ, Collier BA (2014) Using dynamic Brownian bridge movement modelling to measure temporal patterns of habitat selection. J Anim Ecol 83:1234–1243.

Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519.

Campbell HA, Hewitt M, Watts ME, Peverell S, Franklin CE (2012) Short- and long-term movements patterns in the freshwater whipray (*Himantura dalyensis*) determined by the signal processing of passive acoustic telemetry data. Mar Freshw Res 63:341–350.

Caro T (1999) The behaviour-conservation interface. Trends Ecol Evol 14:366–369.

Carpenter-Bundhoo L, Butler GL, Bond NR, Bunn SE, Reinfelds IV, Kennard MJ (2020) Effects of a low-head weir on multi-scaled movement and behavior of three riverine fish species. Sci Rep 10:6817.

Coates J, Hovel K, Butler J, Klimley A, Morgan S (2013) Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery. Mar Ecol Prog Ser 486:189–201.

Conner LM, Plowman BW (2001) Using Euclidean Distances to Assess Nonrandom Habitat Use. In: *Radio Tracking and Animal Populations*. Elsevier, 275–290

Conner LM, Smith MD, Burger LW (2003) A comparison of distance-based and classification-base analyses of habitat use. Ecology 84:526–531.

Cote D, Nicolas J-M, Whoriskey F, Cook AdamM, Broome J, Regular PM, Baker D (2019) Characterizing snow crab (*Chionoecetes opilio*) movements in the Sydney Bight (Nova Scotia, Canada): A collaborative approach using multiscale acoustic telemetry. Can J Fish Aquat Sci 76:334–346.

Cote D, Tibble B, Curry RA, Peake S, Adams BK, Clarke KD, Perry R (2020) Seasonal and diel patterns in activity and habitat use by brook trout (*Salvelinus fontinalis*) in a small Newfoundland lake. Environ Biol Fishes 103:31–47.

Cott PA, Guzzo MM, Chapelsky AJ, Milne SW, Blanchfield PJ (2015) Diel bank migration of Burbot (*Lota lota*). Hydrobiologia 757:3–20.

Cunjak RA, Roussel JM, Gray MA, Dietrich JP, Cartwright DF, Munkittrick KR, Jardine TD (2005) Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. Oecologia 144:636–646.

Dahl KA, Patterson WF (2020) Movement, home range, and depredation of invasive lionfish revealed by fine-scale acoustic telemetry in the northern Gulf of Mexico. Mar Biol 167:111.

Dance MA, Rooker JR (2015) Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. Estuar Coast Shelf Sci 167:447–457.

Degregorio BA, Putman BJ, Kingsbury BA (2011) Which habitat selection method is most applicable to snakes? Case studies of the eastern massasauga (*Sistrurus catenatus*) and eastern fox snake (*Pantherophis gloydi*). Herpetol Conserv Biol 6:372–382.

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495–506.

DOE (2009) Report to Congress on the Potential Environmental Effects of Marine and Hydrokinetic Energy Technologies: Prepared in Response to the Energy Independenc e and Security Act of 2007, Section 633(B). Wind and Hydropower Technologies Program, Energy Efficiency and Renewable Energy, U.S. Department of Energy.

Dougherty ER, Carlson CJ, Blackburn JK, Getz WM (2017) A cross-validation-based approach for delimiting reliable home range estimates. Mov Ecol 5:19.

Downey N, Webber D, Roberts M, Smale M, Sauer W, Singh L (2011) The Use of Acoustic Telemetry in South African Squid Research (2003-2010). In: *Modern Telemetry*. Krejcar O (ed) InTech

Elton CS (1927) Animal Ecology. Macmillan, New York.

Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res 108:364–371.

Espinoza T, Burke C, Carpenter-Bundhoo L, Marshall S, Roberts D, Kennard M (2020) Fine-scale acoustic telemetry in a riverine environment: movement and habitat use of the endangered Mary River cod *Maccullochella mariensis*. Endang Species Res 42:125–131.

Everett A, Szedlmayer S, Gallaway B (2020) Movement patterns of red snapper Lutjanus campechanus based on acoustic telemetry around oil and gas platforms in the northern Gulf of Mexico. Mar Ecol Prog Ser 649:155–173.

Fahlman J, Hellström G, Jonsson M, Fick JB, Rosvall M, Klaminder J (2021) Impacts of oxazepam on perch (*Perca fluviatilis*) behavior: fish familiarized to lake conditions do not show predicted anti-anxiety response. Environ Sci Technol 55:3624–3633.

Fahlman J, Hellström G, Jonsson M, Veenstra A, Klaminder J (2020) Six common behavioral trials and their relevance for perch performance in natural lakes. Sci Total Environ 732:139101.

Farrugia TJ, Espinoza M, Lowe CG (2011) Abundance, habitat use and movement patterns of the shovelnose guitarfish (*Rhinobatos productus*) in a restored southern California estuary. Mar Freshw Res 62:648.

Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96:1182–1188.

Forester JD, Im HK, Rathouz PJ (2009) Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Freitas C, Olsen EM, Knutsen H, Albretsen J, Moland E (2016) Temperature-associated habitat selection in a cold-water marine fish. J Anim Ecol 85:628–637.

Freitas C, Villegas-Ríos D, Moland E, Olsen EM (2021) Sea temperature effects on depth use and habitat selection in a marine fish community. J Anim Ecol:1365-2656.13497.

French JT, Wang H-H, Grant WE, Tomeček JM (2019) Dynamics of animal joint space use: a novel application of a time series approach. Mov Ecol 7:38.

Frid C, Andonegi E, Depestele J, Judd A, Rihan D, Rogers SI, Kenchington E (2012) The environmental interactions of tidal and wave energy generation devices. Environ Impact Assess Rev 32:133–139.

Fry B (2006) Stable isotope ecology. Springer, New York, NY.

Garshelis D (2000) Delusions in habitat evaluation: measuring use, selection, and importance. In: Boitani L, Fuller TK In: *Research Techniques in Animal Ecology: Controversies and Consequences*, Columbia University Press, New York. 111–164.

Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC (2007) LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLOS ONE 2:e207.

Gilbertson MLJ, White LA, Craft ME (2020) Trade-offs with telemetry-derived contact networks for infectious disease studies in wildlife. Methods Ecol Evol:2041–210X.13355.

Godde S, Humbert L, Côté SD, Réale D, Whitehead H (2013) Correcting for the impact of gregariousness in social network analyses. Anim Behav 85:553–558.

Goulon C, Westrelin S, Samedy V, Roy R, Guillard J, Argillier C (2018) Complementarity of two high-resolution spatiotemporal methods (hydroacoustics and acoustic telemetry) for assessing fish distribution in a reservoir. Hydroécol Appl 20:57–84.

Griffin L, Finn J, Diez C, Danylchuk A (2019) Movements, connectivity, and space use of immature green turtles within coastal habitats of the Culebra Archipelago, Puerto Rico: implications for conservation. Endang Species Res 40:75–90.

Grinnell J (1917) The Niche-Relationships of the California Thrasher. The Auk 34:427–433.

Guénard G, Morin J, Matte P, Secretan Y, Valiquette E, Mingelbier M (2020) Deep learning habitat modeling for moving organisms in rapidly changing estuarine environments: A case of two fishes. Estuar Coast Shelf Sci 238:106713.

Gurarie E (2013) Behavioral Change Point Analysis in R: The bcpa package.

Gurarie E, Andrews RD, Laidre KL (2009) A novel method for identifying behavioural changes in animal movement data. Ecol Lett 12:395–408.

Gurarie E, Bracis C, Delgado M, Meckley TD, Kojola I, Wagner CM (2016) What is the animal doing? Tools for exploring behavioural structure in animal movements. J Anim Ecol 85:69–84.

Guzzo MM, Blanchfield PJ, Chapelsky AJ, Cott PA (2016) Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. J Great Lakes Res 42:276–285.

Guzzo MM, Van Leeuwen TE, Hollins J, Koeck B, Newton M, Webber DM, Smith FI, Bailey DM, Killen SS (2018) Field testing a novel high residence positioning system for monitoring the fine-scale movements of aquatic organisms. Methods Ecol Evol 9:1478–1488.

Gyuris E (1994) The rate of predation by fishes on hatchlings of green turtle (*Chelonia mydas*). Coral Reefs 13:137–144.

Hahn L, Silva PC, Malabarba MC, Malabarba LR, Câmara LFD, Nunes LD, Machado LS, Martins EG, Barthem RB (2019) Genetics and telemetry indicate unexpected movements among structured populations for *Brachyplatystoma platynemum* in the Amazon. J Fish Biol 95:633–637.

Halfyard EA, Webber D, Papa JD, Leadley T, Kessel ST, Colborne SF, Fisk AT (2017) Evaluation of an acoustic telemetry transmitter designed to identify predation events. Methods Ecol Evol 8:1063–1071.

Harmelin-Vivien ML, Kaim-Malka RA, Ledoyer M, Jacob-Abraham SS (1989) Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. J Fish Biology 34:715–734.

Hawkins AD, MacLennan DN, Urquhart GG, Robb C (1974) Tracking cod *Gadus morhua* L. in a Scottish sea loch. J Fish Biology 6:225–236.

Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW (2012) High activity and Lévy searches: jellyfish can search the water column like fish. Proc Biol Sci 279:465–473.

Heady WN, Moore JW (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. Oecologia 172:21–34.

Henry SM (1966) Symbiosis: Associations of invertebrates, birds, ruminants, and other biota. Academic Press.

Heupel MR et al. (2006) Automated Acoustic Tracking of Aquatic Animals: Scales, Design and Deployment of Listening Station Arrays. Mar Freshw Res 57:1.

Hilborn R, Mangel M (1997) The Ecological Detective: Confronting Models With Data. Princeton University Press. ISBN:9870691034973.

Hinton MG, Maunder MN (2003) Methods for standardizing CPUE and how to select among them. Inter-American Tropical Tuna Commission, USA. doi:10.13140/2.1.4433.2164.

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. The Condor 94:181–188.

Hobson KA, Wassenaar LI (2008) Tracking animal migration with stable isotopes. Academic Press. ISBN:9780128147245.

Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using Brownian Bridges. Ecology 88:2354–2363.

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Flemming JEM, Whoriskey FG (2015) Aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1255642.

Hutchinson GE (1957) Concluding Remarks. In: *Quantitive Biology*.

InnovaSea Systems Inc. (2018) V13AP Coded Transmitters Datasheet (5249-12).

Irisarri I, Meyer A (2016) The identification of the closest living relative(s) of tetrapods: phylogenomic lessons for resolving short ancient internodes. Syst Biol 65:1057–1075.

Ironside KE, Mattson DJ, Theimer T, Jansen B, Holton B, Arundel T, Peters M, Sexton JO, Edwards TC (2017) Quantifying animal movement for caching foragers: the path identification index (PII) and cougars, Puma concolor. Mov Ecol 5:24.

Ivanova SV, Kessel ST, Landry J, O’Neill C, McLean MF, Espinoza M, Vagle S, Hussey NE, Fisk AT (2018) Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. Can J Fish Aquat Sci 75:2390–2400.

Jackson JBC, Kirby MX, Berger WH, A. BjorndalK, Botsford LW, Bourque BJ, Bradbury RH (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637.

Jacoby DMP, Freeman R (2016) Emerging network-based tools in movement ecology. Trends Ecol Evol 31:301–314.

Jellyman DJ, Unwin MJ (2019) Fine-scale swimming movement and behaviour of female silver eels, *Anguilla dieffenbachii*, within a lake affected by hydro-power generation. Fish Manag Ecol 26:57–69.

Jensen H, Kiljunen M, Knudsen R, Amundsen P-A (2017) Resource partitioning in food, space and time between Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*) and European whitefish (*Coregonus lavaretus*) at the southern edge of their continuous coexistence. PLoS ONE 12:e0170582.

Johnson CJ, Nielsen SE, Merrill EH, Mcdonald TL, Boyce MS (2006) Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. J Wildl Manag 70:347–357.

Johnson DH (1980) The Comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson DS, London JM, Lea M-A, Durban JW (2008) Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215.

Jonsen ID, McMahon CR, Patterson TA, Auger-Méthé M, Harcourt R, Hindell MA, Bestley S (2019) Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model. Ecology 100:e02566.

Joo R, Boone ME, Clay TA, Patrick SC, Clusella-Trullas S, Basille M (2019) Navigating through the R packages for movement. J Anim Ecol 89(10).

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218.

Kie JG, Matthiopoulos J, Fieberg J, Powell RA, Cagnacci F, Mitchell MS, Gaillard J-M, Moorcroft PR (2010) The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philos Trans R Soc Lond, B 365:2221–2231.

Klimley AP, Burney, J. LB, Cantara KM, Richert JE, Davis SF, Sommeran SV (2001) Radio-acoustic positioning as a tool for studying site-specific behavior of the white shark and other large marine species. Mar Biol 138:18.

van der Knaap I, Slabbekoorn H, Winter HV, Moens T, Reubens J (2021) Evaluating receiver contributions to acoustic positional telemetry: a case study on Atlantic cod around wind turbines in the North Sea. Anim Biotelemetry 9:14.

Knutson T, Camargo SJ, Chan JCL, Emanuel K, Ho C-H, Kossin J, Mohapatra M, Satoh M, Sugi M, Walsh K, Wu L (2020) Tropical Cyclones and Climate Change Assessment: Part II: Projected Response to Anthropogenic Warming. Bull Am Meteorol Soc 101:E303–E322.

Kranstauber B (2019) Modelling animal movement as Brownian bridges with covariates. Mov Ecol 7:1–10.

Kranstauber B, Kays R, LaPoint SD, Wikelski M, Safi K (2012) A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. J Anim Ecol 81:738–746.

Krebs CJ (2014) Niche Measures and Resource Preferences. In: *Ecological Methodology,* 3rd ed. University of British Colummbia, Vancouver: Pearson, p 596–653

Landry JJ, Kessel ST, McLean MF, Ivanova SV, Hussey NE, O'neill C, Vagle S, Dick TA, Fisk AT (2019) Movement types of an arctic benthic fish, shorthorn sculpin (*Myoxocephalus scorpius*), during open-water periods in response to biotic and abiotic factors1. Can J Fish Aquat Sci 76:626–635.

Langrock R, King R, Matthiopoulos J, Thomas L, Fortin D, Morales JM (2012) Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology 93:2336–2342.

Leander J, Brodin T, Leonardsson K (2019) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. Can J Fish Aquat Sci.

Leander J, Klaminder J, Jonsson M, Brodin T, Leonardsson K, Hellström G (2020) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. Can J Fish Aquat Sci 77:177–187.

Lees KJ, MacNeil MA, Hedges KJ, Hussey NE (2021) Estimating demographic parameters for fisheries management using acoustic telemetry. Rev Fish Biol Fisheries 31:25–51.

Lees KJ, Mill AC, Skerritt DJ, Robertson PA, Fitzsimmons C (2018) Movement patterns of a commercially important, free-ranging marine invertebrate in the vicinity of a bait source. Anim Biotelemetry 6:8.

Leibold MA (1995) The niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382.

Lennox RJ *et al.* (2017) Envisioning the future of aquatic animal tracking: Technology, science, and application. BioScience.

Lennox RJ *et al.* (2021) A role for lakes in revealing the nature of animal movement using high dimensional telemetry systems. Mov Ecol 9:1–28.

Logan RK, Lowe CG (2019) Space use and inferred spawning activity of three exploited gamefish species on a large artificial reef. Fish Manag Ecol 26:558–569.

Lyons A, Turner WC, Getz WM (2013) Home range plus: A space-time characterization of movement over real landscapes. BMC Movement Ecology 1.

Madigan DJ, Richardson AJ, Carlisle AB, Weber SB, Brown J, Hussey NE (2020) Water column structure defines vertical habitat of twelve pelagic predators in the South Atlantic. ICES J Mar Sci.

Manlick PJ, Petersen SM, Moriarty KM, Pauli JN (2019) Stable isotopes reveal limited Eltonian niche conservatism across carnivore populations. Funct Ecol 33:335–345.

Marsden JE, Binder TR, Johnson J, He J, Dingledine N, Adams J, Johnson NS, Buchinger TJ, Krueger CC (2016) Five-year evaluation of habitat remediation in Thunder Bay, Lake Huron: Comparison of constructed reef characteristics that attract spawning lake trout. Fish Res 183:275–286.

Matich P, Ault JS, Boucek RE, Bryan DR, Gastrich KR, Harvey CL, Heithaus MR, Kiszka JJ, Paz V, Rehage JS, Rosenblatt AE (2017) Ecological niche partitioning within a large predator guild in a nutrient-limited estuary: Niche partitioning among estuarine predators. Limnol Oceanogr 62:934–953.

McMahan MD, Brady DC, Cowan DF, Grabowski JH, Sherwood GD (2013) Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). Can J Fish Aquat Sci 70:1625–1634.

Menge BA (1992) Community Regulation: Under What Conditions Are Bottom-Up Factors Important on Rocky Shores? Ecology 73:755–765.

Mitchenson YS, Craig MT, Cheung W, Choat JH, Mitcheson YSD, Craig MT, Bertoncini AA, Carpenter KE, William WL (2011) Fishing groupers towards extinction: A global assessment of threats and extinction risks in a billion dollar fishery. Fish Fish 14:119–136.

Miyoshi K, Kuwahara Y, Miyashita K (2018) Tracking the Northern Pacific sea star *Asterias amurensis* with acoustic transmitters in the scallop mariculture field of Hokkaido, Japan. Fish Sci 84:349–355.

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177.

Moulton DL, Dance MA, Williams JA, Sluis MZ, Stunz GW, Rooker JR (2017) Habitat partitioning and seasonal movement of red drum and spotted seatrout. Estuar Coasts 40:905–916.

Nakamura I, Goto Y, Sato K (2015) Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. J Anim Ecol 84:590–603.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059.

National Academies of Sciences E and Medicine (2016) Attribution of extreme weather events in the context of climate change. The National Academies Press, Washington, DC.

Noonan MJ, Fleming CH, Akre TS, Drescher-lehman J, Gurarie E, Kays R, Calabrese JM (2019) Scale-insensitive estimation of speed and distance traveled from animal tracking data. Mov Ecol 7:1–15.

Novak AJ, Becker SL, Finn JT, Pollock CG, Hillis-Starr Z, Jordaan A (2020) Scale of biotelemetry data influences ecological interpretations of space and habitat use in yellowtail snapper. Mar Coast Fish 12:364–377.

O’Dor RK, Aitken JP, Babcock RC, Bolden SK, Seino S, Zeller DC, Jackson GD (2001) Using Radio-Acoustic Positioning and Telemetry (RAPT) to define and assess marine protected areas (MPAs). In: *Electronic Tagging and Tracking in Marine Fisheries*. Reviews: Methods and Technologies in Fish Biology and Fisheries, Sibert JR, Nielsen JL (eds) Springer Netherlands, Dordrecht, 147–166.

Odum EP, Kuenzler EJ (1955) Measurement of Territory and Home Range Size in Birds. The Auk 72:128–137.

Özgül A, Lök A, Tansel Tanrıkul T, Alós J (2019) Home range and residency of *Scorpaena porcus* and *Scorpaena scrofa* in artificial reefs revealed by fine-scale acoustic tracking. Fish Res 210:22–30.

Ozgul A, Lok A, Ulas A, Duzbastilar FO, Tanrikul TT, Pelister C (2015) Preliminary study on the use of the Vemco Positioning System to determine fish movements in artificial reef areas: A case study on Sciaena umbra Linnaeus, 1758. J Appl Ichthyol 31:41–47.

Pandey BN, Marthur V (2018) Biology of Chordates. PHI Learning.

Patterson T, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State–space models of individual animal movement. Trends Ecol Evol 23:87–94.

Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. Ecosystems 1:6–18.

Pickholtz RSM, Kiflawi M, Friedlander AM, Belmaker J (2018) Habitat utilization by an invasive herbivorous fish (*Siganus rivulatus*) in its native and invaded range. Biol Invasions 20:3499–3512.

Piraino MN, Szedlmayer ST (2014) Fine-scale movements and home ranges of red snapper around artificial reefs in the Northern Gulf of Mexico. Trans Am Fish Soc 143:988–998.

Poessel SA, Brandt J, Miller TA, Katzner TE (2018) Meteorological and environmental variables affect flight behaviour and decision-making of an obligate soaring bird, the California Condor *Gymnogyps californianus*. Ibis 160:36–53.

Post DM (2002) Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. Ecology 83:703–718.

Priede IG, Smith KL, Armstrong JD (1990) Foraging behavior of abyssal grenadier fish: inferences from acoustic tagging and tracking in the North Pacific Ocean. Deep-Sea Res I: Oceanogr Res Pap 37:81–101.

Riley SC *et al.* (2014) Lake trout in northern Lake Huron spawn on submerged drumlins. J Great Lakes Res 40:415–420.

Roberts DT, Udyawer V, Franklin C, Dwyer RG, Campbell HA (2017) Using an acoustic telemetry array to assess fish volumetric space use: A case study on impoundments, hypoxia and an air-breathing species (*Neoceratodus forsteri*). Mar Freshw Res 68:1532.

Roffler GH, Adams LG, Talbot SL, Sage GK, Dale BW (2012) Range overlap and individual movements during breeding season influence genetic relationships of caribou herds in south-central Alaska. J Mammal 93:1318–1330.

Rooker JR *et al.* (2018) Seascape connectivity and the influence of predation risk on the movement of fishes inhabiting a back-reef ecosystem. Ecosphere 9.

Rowcliffe JM, Carbone C, Kays R, Kranstauber B, Jansen PA (2012) Bias in estimating animal travel distance: the effect of sampling frequency. Methods Ecol Evol 3:653–662.

Roy R, Beguin J, Argillier C, Tissot L, Smith F, Smedbol S, De-Oliveira E (2014) Testing the VEMCO Positioning System: spatial distribution of the probability of location and the positioning error in a reservoir. Anim Biotelem 2:1.

Roy R, Tissot L, Argillier C (2018) Environmental drivers of fish spatial distribution and activity in a reservoir with water level fluctuations. Hydroécol Appl.

Schauber EM, Storm DJ, Nielsen CK (2007) Effects of joint space use and group membership on contact rates among white-tailed deer. J Widlife Manage 71:155–163.

Schick RS, Loarie SR, Colchero F, Best BD, Boustany A, Conde DA, Halpin PN, Joppa LN, McClellan CM, Clark JS (2008) Understanding movement data and movement processes: current and emerging directions. Ecol Lett 11:1338–1350.

Schlaff A, Menéndez P, Hall M, Heupel M, Armstrong T, Motti C (2020) Acoustic tracking of a large predatory marine gastropod, *Charonia tritonis*, on the Great Barrier Reef. Mar Ecol Prog Ser 642:147–161.

Schoeninger MJ (1995) Stable isotope studies in human evolution. Evolutionary Anthropology: Issues, News, and Reviews 4:83–98.

Silk MJ, Finn KR, Porter MA, Pinter-Wollman N (2018) Can multilayer networks advance animal behavior research? Trends Ecol Evol 33:376–378.

Silva I, Crane M, Suwanwaree P, Strine C, Goode M (2018) Using dynamic Brownian Bridge Movement Models to identify home range size and movement patterns in king cobras. PLoS ONE 13:e0203449.

Silverman BW (1983) Some properties of a test for multimodality based on kernel density estimates. In: *Probability, Statistics and Analysis*. London Mathematical Society Lecture Note Series, Cambridge University Press

Skerritt D, Robertson P, Mill A, Polunin N, Fitzsimmons C (2015) Fine-scale movement, activity patterns and home-ranges of European lobster Homarus gammarus. Mar Ecol Prog Ser 536:203–219.

Smith F (2013) Understanding HPE in the VEMCO Positioning System (VPS). Available from http://www.oceans-research.com.

Smith JA *et al.* (2020) Zooming in on mechanistic predator–prey ecology: Integrating camera traps with experimental methods to reveal the drivers of ecological interactions. J Anim Ecol:1365-2656.13264.

Soberon J, Nakamura M (2009) Niches and distributional areas: Concepts, methods, and assumptions. Proceedings of the National Academy of Sciences 106:19644–19650.

Steel AE, Coates JH, Hearn AR, Klimley AP (2014) Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim Biotelem 2:15.

Stieglitz TC, Dujon AM (2017) A groundwater-fed coastal inlet as habitat for the Caribbean queen conch *Lobatus gigas* - an acoustic telemetry and space use analysis. Mar Ecol Prog Ser 571:139–152.

Swadling DS, Knott NA, Rees MJ, Pederson H, Adams KR, Taylor MD, Davis AR (2020) Seagrass canopies and the performance of acoustic telemetry: implications for the interpretation of fish movements. Anim Biotelemetry 8:8.

Teesdale G, Wolfe B, Lowe C (2015) Patterns of home ranging, site fidelity, and seasonal spawning migration of barred sand bass caught within the Palos Verdes Shelf Superfund Site. Mar Ecol Prog Ser 539:255–269.

Thiebot J-B, Cherel Y, Trathan PN, Bost C-A (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. Ecology 93:122–130.

Thorstad EB, Rikardsen AH, Alp A, Økland F (2013) The use of electronic tags in fish research – an overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13:881–896.

Thums M, Fernández-Gracia J, Sequeira AMM, Eguíluz VM, Duarte CM, Meekan MG (2018) How big data fast tracked human mobility research and the lessons for animal movement ecology. Front Mar Sci 5:21.

Thums M, Whiting SD, Reisser JW, Pendoley KL, Pattiaratchi CB, Harcourt RG, McMahon CR, Meekan MG (2013) Tracking sea turtle hatchlings - A pilot study using acoustic telemetry. J Exp Mar Biol Ecol 440:156–163.

Trancart T, Carpentier A, Acou A, Danet V, Elliott S, Feunteun É (2020) Behaviour of endangered European eels in proximity to a dam during downstream migration: Novel insights using high accuracy 3D acoustic telemetry. Ecol Freshw Fish 29:266–279.

Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R (2008) A behavioral perspective on fishing-induced evolution. Trends Ecol Evol 23:419–421.

Van Valen L (1965) Morphological variation and width of ecological niche. The American Naturalist 99:377–390.

Veilleux MAN, Midwood JD, Boston CM, Lapointe NWR, Portiss R, Wells M, Doka SE, Cooke SJ (2018) Assessing occupancy of freshwater fishes in urban boat slips of Toronto Harbour. Aquatic Ecosystem Health & Management 21:331–341.

Vergeynst J, Pauwels I, Baeyens R, Coeck J, Nopens I, De Mulder T, Mouton A (2019) The impact of intermediate-head navigation locks on downstream fish passage. River Res Appl 35:224–235.

Villegas-Ríos D, Réale D, Freitas C, Moland E, Olsen EM (2018) Personalities influence spatial responses to environmental fluctuations in wild fish. J Anim Ecol 87:1309–1319.

Villon S, Mouillot D, Chaumont M, Darling ES, Subsol G, Claverie T, Villéger S (2018) A Deep learning method for accurate and fast identification of coral reef fishes in underwater images. Ecol Inform 48:238–244.

Weigmann S (2016) Annotated checklist of the living sharks, batoids and chimaeras (Chondricthyes) of the world, with a focus on biogeographical diversity. J Fish Biol 88:837–1037.

Whitmore MM, Litvak MK (2018) Fine-scale movement of juvenile Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) during aggregations in the lower Saint John River Basin, New Brunswick, Canada. Can J Fish Aquat Sci 75:2332–2342.

Wiens JA, Stenseth NChr, Van Horne B, Ims RA (1993) Ecological Mechanisms and Landscape Ecology. Oikos 66:369–380.

Williams-Grove LJ, Szedlmayer ST (2016a) Acoustic positioning and movement patterns of red snapper *Lutjanus campechanus* around artificial reefs in the northern Gulf of Mexico. Mar Ecol Prog Ser 553:233–251.

Williams-Grove LJ, Szedlmayer ST (2016b) Mortality estimates for red snapper based on ultrasonic telemetry in the Northern Gulf of Mexico. N Am J Fish Manage 36:1036–1044.

Williams-Grove LJ, Szedlmayer ST (2017) Depth preferences and three-dimensional movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Fish Res 190:61–70.

Wilson CJ, Wilson PS, Greene CA, Dunton KH (2013) Seagrass meadows provide an acoustic refuge for estuarine fish. Mar Ecol Prog Ser 472:117–127.

Wilson P, Thums M, Pattiaratchi C, Meekan M, Pendoley K, Fisher R, Whiting S (2018) Artificial light disrupts the nearshore dispersal of neonate flatback turtles *Natator depressus*. Mar Ecol Prog Ser 600:179–192.

Wilson R, Wilson RP, Quintana F, Hobson VJ (2011) Construction of energy landscapes can clarify the movement and distribution. Proc R Soc B 279:975-980.

Wilson SG, Taylor JG, Pearce AF (2001) The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Niño/ Southern Oscillation. Environ Biol Fishes 61:1–11.

Wirtz P, Bingeman J, Bingeman J, Fricke R, Hook TJ, Young J (2017) The fishes of Ascension Island, central Atlantic Ocean - new records and an annotated checklist. J Mar Biol Assoc UK 97:783–798.

Wolfe BW, Lowe CG (2015) Movement patterns, habitat use and site fidelity of the white croaker (*Genyonemus lineatus*) in the Palos Verdes Superfund Site, Los Angeles, California. Mar Environ Res 109:69–80.

Worton BJ (1995) A convex hull-based estimator of home-range size. Biometrics 51:1206–1215.

Worton BJ (1987) A review of models of home range for animal movement. Ecol Modell 38:277–298.

Worton BJ (1989) Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. Ecology 70:164–168.

Wyman MT, Thomas MJ, McDonald RR, Hearn AR, Battleson RD, Chapman ED, Kinzel P, Minear JT, Mora EA, Nelson JM, Pagel MD, Klimley AP (2018) Fine-scale habitat selection of green sturgeon (*Acipenser medirostris*) within three spawning locations in the Sacramento River, California. Can J Fish Aquat Sci 75:779–791.

Young RF, Winn HE (2003) Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. Copeia. 2003(1):44–55.

Zacharia PU, Abdurahiman KP (2004) Methods of stomach content analysis of fishes- Winter School on Towards Ecosystem Based Management of Marine Fisheries – Building Mass Balance Trophic and Simulation Models. http://eprints.cmfri.org.in/5282/ (accessed December 30, 2021)

Zhang J, O'Reilly KM, Perry GLW, Taylor GA, Dennis TE (2014) Extending the functionality of Behavioural Change-Point Analysis with k-Means clustering: a case study with the little penguin (*Eudyptula minor*). PLOS ONE 10.

Zhang Y, Li Y, Zhang L, Wu Z, Zhu S, Li J, Li X (2020) Site fidelity, habitat use, and movement patterns of the common carp during its breeding season in the pearl river as determined by acoustic telemetry. Water 12:2233.

Supplementary Material for Chapter 2

S2.1 VPS articles reference list

Includes all VPS articles identified using the search terms described in the manuscript. Numbers in superscript indicate data used by multiple articles, note article may still contain unique species datasets if multiple species were tagged. Ordinal number determined by timeline of search and is therefore non-alphabetical.

Andrews KS, Tolimieri N, Williams GD, Samhouri JF, Harvey CJ, Levin PS (2011) Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. Mar Biol 158:2377–2387.

Armansin NC, Lee KA, Huveneers C, Harcourt RG (2016) Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark. Anim Behav 115:245–258.

Armstrong AO (2021) Mutualism promotes site selection in a large marine planktivore. 11:5606–5623.

[1]Bacheler N, Shertzer K, Buckel J, Rudershausen P, Runde B (2018) Behavior of gray triggerfish *Balistes capriscus* around baited fish traps determined from fine-scale acoustic tracking. Mar Ecol Prog Ser 606:133–150.

[1]Bacheler NM, Michelot T, Cheshire RT, Shertzer KW (2019a) Fine-scale movement patterns and behavioral states of gray triggerfish *Balistes capriscus* determined from acoustic telemetry and hidden Markov models. Fish Res 215:76–89.

[1]Bacheler NM, Shertzer KW, Cheshire RT, MacMahan JH (2019b) Tropical storms influence the movement behavior of a demersal oceanic fish species. Sci Rep 9:1481.

[12]Bacheler NM, Runde BJ, Shertzer KW, Buckel JA, Rudershausen PJ (2021a) Fine-scale behavior of red snapper (*Lutjanus campechanus*) around bait: approach distances, bait plume dynamics, and effective fishing area. Can J Fish Aquat Sci:cjfas-2021-0044.

[12]Bacheler NM, Shertzer KW, Runde BJ, Rudershausen PJ, Buckel JA (2021b) Environmental conditions, diel period, and fish size influence the horizontal and vertical movements of red snapper. Sci Rep 11:9580.

Bade AP, Binder TR, Faust MD, Vandergoot CS, Hartman TJ, Kraus RT, Krueger CC, Ludsin SA (2019) Sex-based differences in spawning behavior account for male-biased harvest in Lake Erie walleye (*Sander vitreus*). Can J Fish Aquat Sci 76:2003–2012.

Baker NJ, Boubée J, Lokman PM, Bolland JD (2020) Evaluating the impact of hydropower on downstream migrating anguillid eels: Catchment-wide and fine-scale approaches to identify cost-effective solutions. Sci Total Environ 748:141111.

Baker NJ, Wright RM, Cowx IG, Murphy LA, Bolland JD (2021) Downstream passage of silver European eel (*Anguilla anguilla*) at a pumping station with a gravity sluice. Ecol Eng 159:106069.

Balazik M, Barber M, Altman S, Reine K, Katzenmeyer A, Bunch A, Garman G (2020) Dredging activity and associated sound have negligible effects on adult Atlantic sturgeon migration to spawning habitat in a large coastal river. PLoS ONE 15:e0230029.

Barilotti AA, White CF, Lowe CG (2020) Are Fishes Attracted to Piers? Movements and Association of Marine Fishes to a Public Fishing Pier within a Commercial Harbor. Bulletin, Southern California Academy of Sciences 119:18.

Bašić T, Aislabie L, Ives M, Fronkova L, Piper A, Walker A (2019) Spatial and temporal behavioural patterns of the European eel *Anguilla anguilla* in a lacustrine environment. Aquat Sci 81:73.

Becker SL, Finn JT, Novak AJ, Danylchuk AJ, Pollock CG, Hillis-Starr Z, Lundgren I, Jordaan A (2020) Coarse- and fine-scale acoustic telemetry elucidates movement patterns and temporal variability in individual territories for a key coastal mesopredator. Environ Biol Fishes.

[8]Binder TR, Farha SA, Thompson HT, Holbrook CM, Bergstedt RA, Riley SC, Bronte CR, He J, Krueger CC (2018) Fine-scale acoustic telemetry reveals unexpected lake trout, *Salvelinus namaycush*, spawning habitats in northern Lake Huron, North America. Ecol Freshwat Fish 27:594–605.

Bohaboy E, Guttridge TL, Hammerschlag N, Van Zinnicq Bergman MPM, Patterson W F (2019) Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality. ICES J Mar Sci 77:83–96.

[13]Brownscombe JW, Cooke SJ, Danylchuk AJ (2017) Spatiotemporal drivers of energy expenditure in a coastal marine fish. Oecologia 183:689–699.

[13]Brownscombe JW, Griffin LP, Gagne TO, Haak CR, Cooke SJ, Finn JT, Danylchuk AJ (2019) Environmental drivers of habitat use by a marine fish on a heterogeneous and dynamic reef flat. Mar Biol 166:18.

[6]Buchinger TJ, Marsden JE, Binder TR, Huertas M, Bussy U, Li K, Hanson JE, Krueger CC, Li W, Johnson NS (2017) Temporal constraints on the potential role of fry odors as cues of past reproductive success for spawning lake trout. Ecol Evol 7:10196–10206.

[10]Burns ES, Armstrong J, Tang D, Sakamoto K, Lowe CG (2019) The residency, movement patterns and habitat association of several demersal fish species to the Orange County Sanitation District wastewater outfall. Mar Pollut Bull 149:110638.

Burns ES, Clevenstine AJ, Logan RK, Lowe CG (2020) Evidence of artificial habitat use by a recovering marine predator in southern California. J Fish Biol 97:1857–1860.

[10]Burns ES, Wolfe BW, Armstrong J, Tang D, Sakamoto K, Lowe CG (2021) Using acoustic telemetry to quantify potential contaminant exposure of Vermilion Rockfish (*Sebastes miniatus*), Hornyhead Turbot (*Pleuronichthys verticalis*), and White Croaker (*Genyonemus lineatus*) at wastewater outfalls in southern California. Mar Environ Res 170:105452.

Caldwell TJ, Chandra S, Feher K, Simmons JB, Hogan Z (2020) Ecosystem response to earlier ice break-up date: Climate-driven changes to water temperature, lake-habitat-specific production, and trout habitat and resource use. Glob Change Biol 26:5475–5491.

Carpenter-Bundhoo L, Butler GL, Bond NR, Bunn SE, Reinfelds IV, Kennard MJ (2020) Effects of a low-head weir on multi-scaled movement and behavior of three riverine fish species. Sci Rep 10:6817.

Carpenter-Bundhoo L, Butler GL, Espinoza T, Bond NR, Bunn SE, Kennard MJ (2020) Reservoir to river: Quantifying fine-scale fish movements after translocation. Ecol Freshw Fish 29:89–102.

Coates J, Hovel K, Butler J, Klimley A, Morgan S (2013) Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery. Mar Ecol Prog Ser 486:189–201.

Cote D, Morris CJ, Regular PM, Piersiak MG (2020a) Effects of 2D Seismic on Snow Crab Movement Behavior. Fish Res 230:105661.

Cote D, Nicolas J-M, Whoriskey F, Cook AdamM, Broome J, Regular PM, Baker D (2019) Characterizing snow crab (*Chionoecetes opilio*) movements in the Sydney Bight (Nova Scotia, Canada): A collaborative approach using multiscale acoustic telemetry. Can J Fish Aquat Sci 76:334–346.

Cote D, Tibble B, Curry RA, Peake S, Adams BK, Clarke KD, Perry R (2020b) Seasonal and diel patterns in activity and habitat use by brook trout (*Salvelinus fontinalis*) in a small Newfoundland lake. Environ Biol Fishes 103:31–47.

Cott PA, Guzzo MM, Chapelsky AJ, Milne SW, Blanchfield PJ (2015) Diel bank migration of burbot (*Lota lota*). Hydrobiologia 757:3–20.

Dahl KA, Patterson WF (2020) Movement, home range, and depredation of invasive lionfish revealed by fine-scale acoustic telemetry in the northern Gulf of Mexico. Mar Biol 167:111.

Dance MA, Rooker JR (2015) Habitat- and bay-scale connectivity of sympatric fishes in an estuarine nursery. Estuar Coast Shelf Sci 167:447–457.

[11]Dean MJ, Hoffman WS, Zemeckis DR, Armstrong MP (2014) Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine. ICES J Mar Sci 71:1474–1489.

Espinoza M, Farrugia TJ, Lowe CG (2011a) Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. Journal of Experimental Marine Biology and Ecology 401:63–74.

Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011b) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res 108:364–371.

Espinoza T, Burke C, Carpenter-Bundhoo L, Marshall S, Roberts D, Kennard M (2020) Fine-scale acoustic telemetry in a riverine environment: movement and habitat use of the endangered Mary River cod *Maccullochella mariensis*. Endang Species Res 42:125–131.

Everett A, Szedlmayer S, Gallaway B (2020) Movement patterns of red snapper Lutjanus campechanus based on acoustic telemetry around oil and gas platforms in the northern Gulf of Mexico. Mar Ecol Prog Ser 649:155–173.

[3]Fahlman J, Hellström G, Jonsson M, Fick JB, Rosvall M, Klaminder J (2021) Impacts of Oxazepam on Perch (*Perca fluviatilis*) Behavior: Fish Familiarized to Lake Conditions Do Not Show Predicted Anti-anxiety Response. Environ Sci Technol 55:3624–3633.

[3]Fahlman J, Hellström G, Jonsson M, Veenstra A, Klaminder J (2020) Six common behavioral trials and their relevance for perch performance in natural lakes. Sci Total Environ 732:139101.

Farrugia TJ, Espinoza M, Lowe CG (2011) Abundance, habitat use and movement patterns of the shovelnose guitarfish (*Rhinobatos productus*) in a restored southern California estuary. Mar Freshw Res 62:648.

Freitas C, Olsen EM, Knutsen H, Albretsen J, Moland E (2016) Temperature-associated habitat selection in a cold-water marine fish. J Anim Ecol 85:628–637.

Freitas C, Villegas-Ríos D, Moland E, Olsen EM (2021) Sea temperature effects on depth use and habitat selection in a marine fish community. J Anim Ecol:1365-2656.13497.

Furey NB, Dance MA, Rooker JR (2013) Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape. J Fish Biol 82:1469–1483.

[7]Goulon C, Westrelin S, Samedy V, Roy R, Guillard J, Argillier C (2018) Complementarity of two high-resolution spatiotemporal methods (hydroacoustics and acoustic telemetry) for assessing fish distribution in a reservoir. Hydroécol Appl 20:57–84.

Graham J, Kroetz A, Poulakis G, Scharer R, Carlson J, Lowerre-Barbieri S, Morley D, Reyier E, Grubbs R (2021) Large-scale space use of large juvenile and adult smalltooth sawfish *Pristis pectinata*: implications for management. Endang Species Res 44:45–59.

Griffin L, Finn J, Diez C, Danylchuk A (2019) Movements, connectivity, and space use of immature green turtles within coastal habitats of the Culebra Archipelago, Puerto Rico: implications for conservation. Endang Species Res 40:75–90.

Guénard G, Morin J, Matte P, Secretan Y, Valiquette E, Mingelbier M (2020) Deep learning habitat modeling for moving organisms in rapidly changing estuarine environments: A case of two fishes. Estuar Coast Shelf Sci 238:106713.

Guzzo MM, Blanchfield PJ, Chapelsky AJ, Cott PA (2016) Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. J Great Lakes Res 42:276–285.

Guzzo MM, Van Leeuwen TE, Hollins J, Koeck B, Newton M, Webber DM, Smith FI, Bailey DM, Killen SS (2018) Field testing a novel high residence positioning system for monitoring the fine-scale movements of aquatic organisms. Methods Ecol Evol 9:1478–1488.

Hawley KL, Rosten CM, Christensen G, Lucas MC (2016) Fine-scale behavioural differences distinguish resource use by ecomorphs in a closed ecosystem. Sci Rep 6:24369.

Herbig JL, Szedlmayer ST (2016) Movement patterns of gray triggerfish, *Balistes capriscus*, around artificial reefs in the northern Gulf of Mexico. Fish Manag Ecol 23:418–427.

Hrenchuk CL, McDougall CA, Nelson PA, Barth CC (2017) Movement and habitat use of juvenile Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in a large hydroelectric reservoir (Nelson River, Canada). Journal of Applied Ichthyology 33:665–680.

Huber ER, Carlson SM (2020) Environmental correlates of fine-scale juvenile steelhead trout (*Oncorhynchus mykiss*) habitat use and movement patterns in an intermittent estuary during drought. Environ Biol Fishes 103:509–529.

Itakura H, Miyake Y, Kitagawa T, Kimura S (2018) Site fidelity, diel and seasonal activities of yellow-phase Japanese eels (Anguilla japonica) in a freshwater habitat as inferred from acoustic telemetry. Ecology of Freshwater Fish 27:737–751.

Ivanova SV, Kessel ST, Espinoza M, McLean MF, O’Neill C, Landry J, Hussey NE, Williams R, Vagle S, Fisk AT (2020) Shipping alters the movement and behavior of Arctic cod (*Boreogadus saida*), a keystone fish in Arctic marine ecosystems. Ecol Appl 30.

[9]Ivanova SV, Kessel ST, Landry J, O’Neill C, McLean MF, Espinoza M, Vagle S, Hussey NE, Fisk AT (2018) Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. Can J Fish Aquat Sci 75:2390–2400.

Jellyman DJ, Unwin MJ (2019) Fine-scale swimming movement and behaviour of female silver eels, *Anguilla dieffenbachii,* within a lake affected by hydro-power generation. Fish Manag Ecol 26:57–69.

[4]Klimley AP, McDonald R, Thomas MJ, Chapman E, Hearn A (2020) Green sturgeon habitat suitability varies in response to drought related flow regimes. Environ Biol Fishes 103:425–435.

van der Knaap I, Reubens J, Thomas L, Ainslie MA, Winter HV, Hubert J, Martin B, Slabbekoorn H (2021a) Effects of a seismic survey on movement of free-ranging Atlantic cod. Current Biology 31:1555-1562.e4.

van der Knaap I, Slabbekoorn H, Winter HV, Moens T, Reubens J (2021b) Evaluating receiver contributions to acoustic positional telemetry: a case study on Atlantic cod around wind turbines in the North Sea. Anim Biotelemetry 9:14.

Konzewitsch N, Evans SN (2020) Examining the Movement of the Common Spider Conch Lambis lambis in Shallow Water of a Northeastern Indian Ocean Atoll Using Passive Acoustic Tracking. J Shellfish Res 39:389.

[9]Landry JJ, Kessel ST, McLean MF, Ivanova SV, Hussey NE, O'neill C, Vagle S, Dick TA, Fisk AT (2019) Movement types of an arctic benthic fish, shorthorn sculpin (*Myoxocephalus scorpius*), during open-water periods in response to biotic and abiotic factors1. Can J Fish Aquat Sci 76:626-635

[2]Leander J, Klaminder J, Hellström G, Jonsson M (2021) Bubble barriers to guide downstream migrating Atlantic salmon (*Salmo salar*): An evaluation using acoustic telemetry. Ecol Eng 160:106141.

[2]Leander J, Klaminder J, Jonsson M, Brodin T, Leonardsson K, Hellström G (2020) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. Can J Fish Aquat Sci 77:177–187.

[14]Lees K, Mill A, Skerritt D, Robertson P, Fitzsimmons C (2020) Spatial overlap, proximity, and interaction between lobsters revealed using acoustic telemetry. Mar Ecol Prog Ser 645:109–124.

Lees KJ, Mill AC, Skerritt DJ, Robertson PA, Fitzsimmons C (2018) Movement patterns of a commercially important, free-ranging marine invertebrate in the vicinity of a bait source. Anim Biotelemetry 6:8.

Logan RK, Lowe CG (2019) Space use and inferred spawning activity of three exploited gamefish species on a large artificial reef. Fish Manag Ecol 26:558–569.

[6]Marsden JE, Blanchfield PJ, Brooks JL, Fernandes T, Fisk AT, Futia MH, Hlina BL, Ivanova SV, Johnson TB, Klinard NV, Krueger CC, Larocque SM, Matley JK, McMeans B, O'Connor LM, Raby GD, Cooke SJ (2021) Using untapped telemetry data to explore the winter biology of freshwater fish. Rev Fish Biol Fish 31:115–134.

McLean M, Simpfendorfer C, Heupel M, Dadswell M, Stokesbury M (2014) Diversity of behavioural patterns displayed by a summer feeding aggregation of Atlantic sturgeon in the intertidal region of Minas Basin, Bay of Fundy, Canada. Mar Ecol Prog Ser 496:59–69.

McMahan MD, Brady DC, Cowan DF, Grabowski JH, Sherwood GD (2013) Using acoustic telemetry to observe the effects of a groundfish predator (Atlantic cod, *Gadus morhua*) on movement of the American lobster (*Homarus americanus*). Can J Fish Aquat Sci 70:1625–1634.

Meckley TD, Holbrook CM, Wagner CM, Binder TR (2014) An approach for filtering hyperbolically positioned underwater acoustic telemetry data with position precision estimates. Animal Biotelemetry 2:7.

Miyoshi K, Kuwahara Y, Miyashita K (2018) Tracking the Northern Pacific sea star Asterias amurensis with acoustic transmitters in the scallop mariculture field of Hokkaido, Japan. Fish Sci 84:349–355.

Moulton DL, Dance MA, Williams JA, Sluis MZ, Stunz GW, Rooker JR (2017) Habitat Partitioning and Seasonal Movement of Red Drum and Spotted Seatrout. Estuar Coasts 40:905–916.

Mucientes G, Leeb K, Straßer F-E, Villegas-Ríos D, Alonso-Fernández A (2021) Short-term survival, space use and diel patterns of coastal fish species revealed from 'solo datasets.' Mar Freshwat Behav Physiol 54:87–95.

Nanami A, Mitamura H, Sato T, Yamaguchi T, Yamamoto K, Kawabe R, Soyano K, Arai N, Kawabata Y (2018) Diel variation in home range size and precise returning ability after spawning migration of coral reef grouper *Epinephelus ongus*: Implications for effective marine protected area design. Mar Ecol Prog Ser 606:119–132.

Novak AJ, Becker SL, Finn JT, Pollock CG, Hillis-Starr Z, Jordaan A (2020) Scale of biotelemetry data influences ecological interpretations of space and habitat use in yellowtail snapper. Mar Coast Fish 12:364–377.

Özgül A, Lök A, Tansel Tanrıkul T, Alós J (2019) Home range and residency of *Scorpaena porcus* and *Scorpaena scrofa* in artificial reefs revealed by fine-scale acoustic tracking. Fish Res 210:22–30.

Özgül A, Lök A, Ulaş A, Düzbastılar FO, Tanrıkul TT, Pelister C (2015) Preliminary study on the use of the Vemco Positioning System to determine fish movements in artificial reef areas: a case study on *Sciaena umbra* Linnaeus, 1758. J Appl Ichthyol 31:41–47.

Pickholtz RSM, Kiflawi M, Friedlander AM, Belmaker J (2018) Habitat utilization by an invasive herbivorous fish (*Siganus rivulatus*) in its native and invaded range. Biol Invasions 20:3499–3512.

[5]Piraino MN, Szedlmayer ST (2014) Fine-Scale Movements and Home Ranges of Red Snapper around Artificial Reefs in the Northern Gulf of Mexico. Trans Am Fish Soc 143:988–998.

Puckeridge A, Becker A, Taylor M, Lowry M, McLeod J, Schilling H, Suthers I (2021) Foraging behaviour and movements of an ambush predator reveal benthopelagic coupling on artificial reefs. Mar Ecol Prog Ser 666:171–182.

Rasmuson LK, Blume MTO, Rankin PS (2021) Habitat use and activity patterns of female Deacon Rockfish (*Sebastes diaconus*) at seasonal scales and in response to episodic hypoxia. Environ Biol Fishes 104:535–553.

Reubens JT, Pasotti F, Degraer S, Vincx M (2013) Residency, site fidelity and habitat use of Atlantic cod (Gadus morhua) at an offshore wind farm using acoustic telemetry. Marine Environmental Research 90:128–135.

[8]Riley SC, Binder TR, Wattrus NJ, Faust MD, Janssen J, Menzies J, Marsden JE, Ebener MP, Bronte CR, He JX, Tucker TR, Hansen MJ, Thompson HT, Muir AM, Krueger CC (2014) Lake trout in northern Lake Huron spawn on submerged drumlins. J Great Lakes Res 40:415–420.

Roberts DT, Udyawer V, Franklin C, Dwyer RG, Campbell HA (2017) Using an acoustic telemetry array to assess fish volumetric space use: a case study on impoundments, hypoxia and an air-breathing species (Neoceratodus forsteri). Mar Freshw Res 68:1532.

Rooker JR, Dance MA, Wells RJD, Quigg A, Hill RL, Appeldoorn RS, Padovani Ferreira B, Boswell KM, Sanchez PJ, Moulton DL, Kitchens LL, Rooker GJ, Aschenbrenner A (2018) Seascape connectivity and the influence of predation risk on the movement of fishes inhabiting a back-reef ecosystem. Ecosphere 9.

[7]Roy R, Tissot L, Argillier C (2018) Environmental drivers of fish spatial distribution and activity in a reservoir with water level fluctuations. Hydroécol Appl.

[12]Runde BJ, Bacheler NM, Shertzer KW, Rudershausen PJ, Sauls B, Buckel JA (2021) Discard Mortality of Red Snapper Released with Descender Devices in the U.S. South Atlantic. Marine and Coastal Fisheries 13:478–495.

Schlaff A, Menéndez P, Hall M, Heupel M, Armstrong T, Motti C (2020) Acoustic tracking of a large predatory marine gastropod, *Charonia tritonis*, on the Great Barrier Reef. Mar Ecol Prog Ser 642:147–161.

Secor DH, O’Brien MHP, Coleman N, Horne A, Park I, Kazyak DC, Bruce DG, Stence C (2021) Atlantic Sturgeon Status and Movement Ecology in an Extremely Small Spawning Habitat: The Nanticoke River-Marshyhope Creek, Chesapeake Bay. Reviews in Fisheries Science & Aquaculture:1–20.

[1]Shertzer KW, Bacheler NM, Pine WE, Runde BJ, Buckel JA, Rudershausen PJ, MacMahan JH (2020) Estimating population abundance at a site in the open ocean: combining

information from conventional and telemetry tags with application to gray triggerfish (*Balistes capriscus*). Can J Fish Aquat Sci 77:34–43.

Shoji J, Mitamura H, Ichikawa K, Kinoshita H, Arai N (2017) Increase in predation risk and trophic level induced by nocturnal visits of piscivorous fishes in a temperate seagrass bed. Sci Rep 7:3895.

[14]Skerritt D, Robertson P, Mill A, Polunin N, Fitzsimmons C (2015) Fine-scale movement, activity patterns and home-ranges of European lobster *Homarus gammarus*. Mar Ecol Prog Ser 536:203–219.

Stieglitz TC, Dujon AM (2017) A groundwater-fed coastal inlet as habitat for the Caribbean queen conch *Lobatus gigas*-an acoustic telemetry and space use analysis. Mar Ecol Prog Ser 571:139–152.

Taylor MD, Becker A, Lowry MB (2018) Investigating the functional role of an artificial reef within an estuarine seascape: a case study of yellowfin bream (*Acanthopagrus australis*). Estuar Coasts 41:1782–1792.

Taylor MD, Payne NL, Becker A, Lowry MB (2017) Feels like home: Homing of mature large-bodied fish following translocation from a power-station canal. ICES J Mar Sci 74:301–310.

Teesdale G, Wolfe B, Lowe C (2015) Patterns of home ranging, site fidelity, and seasonal spawning migration of barred sand bass caught within the Palos Verdes Shelf Superfund Site. Mar Ecol Prog Ser 539:255–269.

Thayer D, Ruppert JLW, Watkinson D, Clayton T, Poesch MS (2017) Identifying temporal bottlenecks for the conservation of large-bodied fishes: Lake Sturgeon (*Acipenser fulvescens*) show highly restricted movement and habitat use over-winter. Global Ecology and Conservation 10:194–205.

Thums M, Whiting SD, Reisser J, Pendoley KL, Pattiaratchi CB, Proietti M, Hetzel Y, Fisher R, Meekan MG (2016) Artificial light on water attracts turtle hatchlings during their near shore transit. Royal Society Open Science 3:160142.

Thums M, Whiting SD, Reisser JW, Pendoley KL, Pattiaratchi CB, Harcourt RG, McMahon CR, Meekan MG (2013) Tracking sea turtle hatchlings — A pilot study using acoustic telemetry. J Exp Mar Biol Ecol 440:156–163.

Veilleux MAN, Midwood JD, Boston CM, Lapointe NWR, Portiss R, Wells M, Doka SE, Cooke SJ (2018) Assessing occupancy of freshwater fishes in urban boat slips of Toronto Harbour. Aquatic Ecosystem Health & Management 21:331–341.

Vergeynst J, Pauwels I, Baeyens R, Coeck J, Nopens I, De Mulder T, Mouton A (2019) The impact of intermediate-head navigation locks on downstream fish passage. River Res Appl 35:224–235.

Vergeynst J, Vanwyck T, Baeyens R, De Mulder T, Nopens I, Mouton A, Pauwels I (2020) Acoustic positioning in a reflective environment: going beyond point-by-point algorithms. Anim Biotelemetry 8:1–17.

Villegas-Ríos D, Réale D, Freitas C, Moland E, Olsen EM (2018) Personalities influence spatial responses to environmental fluctuations in wild fish. J Anim Ecol 87:1309–1319.

[7]Westrelin S, Roy R, Tissot-Rey L, Bergès L, Argillier C (2018) Habitat use and preference of adult perch (*Perca fluviatilis* L.) in a deep reservoir: variations with seasons, water levels and individuals. Hydrobiologia 809:121–139.

Whitmore MM, Litvak MK (2018) Fine-scale movement of juvenile Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) during aggregations in the lower Saint John River Basin, New Brunswick, Canada. Can J Fish Aquat Sci 75:2332–2342.

[5]Williams-Grove L, Szedlmayer S (2016a) Acoustic positioning and movement patterns of red snapper, *Lutjanus campechanus*, around artificial reefs in the northern Gulf of Mexico. Mar Ecol Prog Ser 553:233–251.

[5]Williams-Grove LJ, Szedlmayer ST (2017) Depth preferences and three-dimensional movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Fish Res 190:61–70.

[5]Williams-Grove LJ, Szedlmayer ST (2016b) Mortality Estimates for Red Snapper Based on Ultrasonic Telemetry in the Northern Gulf of Mexico. N Am J Fish Manage 36:1036–1044.

Wilson P, Thums M, Pattiaratchi C, Meekan M, Pendoley K, Fisher R, Whiting S (2018) Artificial light disrupts the nearshore dispersal of neonate flatback turtles *Natator depressus*. Mar Ecol Prog Ser 600:179–192.

Withers JL, Takade-Heumacher H, Davis L, Neuenhoff R, Albeke SE, Sweka JA (2021) Large- and small-scale movement and distribution of acoustically tagged lake sturgeon (*Acipenser fulvescens*) in eastern Lake Erie. Anim Biotelemetry 9:40.

Wolfe BW, Lowe CG (2015) Movement patterns, habitat use and site fidelity of the white croaker (*Genyonemus lineatus*) in the Palos Verdes Superfund Site, Los Angeles, California. Mar Environ Res 109:69–80.

[4]Wyman MT, Thomas MJ, McDonald RR, Hearn AR, Battleson RD, Chapman ED, Kinzel P, Minear JT, Mora EA, Nelson JM, Pagel MD, Klimley AP (2018) Fine-scale habitat selection of green sturgeon (*Acipenser medirostris*) within three spawning locations in the Sacramento River, California. Can J Fish Aquat Sci 75:779–791.

[11]Zemeckis DR, Hoffman WS, Dean MJ, Armstrong MP, Cadrin SX (2014) Spawning site fidelity by Atlantic cod (*Gadus morhua*) in the Gulf of Maine: implications for population structure and rebuilding. ICES Journal of Marine Science 71:1356–1365.

Zhang Y, Li Y, Zhang L, Wu Z, Zhu S, Li J, Li X (2020) Site Fidelity, Habitat Use, and Movement Patterns of the Common Carp during Its Breeding Season in the Pearl River as Determined by Acoustic Telemetry. Water 12:2233.

S2.2 VPS methodological article list

Includes VPS methodological studies identified using the search terms and subsequently excluded from the review as they did not directly tag any animals or utilize animal tracking data

Binder TR, Holbrook CM, Hayden TA, Krueger CC (2016) Spatial and temporal variation in positioning probability of acoustic telemetry arrays: fine-scale variability and complex interactions. Animal Biotelemetry 4:4.

Binder TR, Holbrook CM, Miehls SM, Thompson HT, Krueger CC (2014) Use of oviduct-inserted acoustic transmitters and positional telemetry to estimate timing and location of spawning: a feasibility study in lake trout, *Salvelinus namaycush*. Anim Biotelemetry 2:1–14.

Cho S, Zhang F, Edwards C (2016) Tidal Variability of Acoustic Detection. In: *2016 IEEE International Conferences on Big Data and Cloud Computing (BDCloud), Social Computing and Networking (SocialCom), Sustainable Computing and Communications (SustainCom) (BDCloud-SocialCom-SustainCom)*. 431–436

Farmer NA, Ault JS, Smith SG, Franklin EC (2013) Methods for assessment of short-term coral reef fish movements within an acoustic array. Mov Ecol 1:7.

Reubens J, Verhelst P, van der Knaap I, Deneudt K, Moens T, Hernandez F (2019) Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup. Hydrobiologia 845:81–94.

Roy R, Beguin J, Argillier C, Tissot L, Smith F, Smedbol S, De-Oliveira E (2014) Testing the VEMCO Positioning System: spatial distribution of the probability of location and the positioning error in a reservoir. Anim Biotelem 2:1.

Steel AE, Coates JH, Hearn AR, Klimley AP (2014) Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim Biotelemetry 2:1–17.

Swadling DS, Knott NA, Rees MJ, Pederson H, Adams KR, Taylor MD, Davis AR (2020) Seagrass canopies and the performance of acoustic telemetry: implications for the interpretation of fish movements. Anim Biotelemetry 8:8.

Vergeynst J, Baktoft H, Mouton A, De Mulder T, Nopens I, Pauwels I (2020) The influence of system settings on positioning accuracy in acoustic telemetry, using the YAPS algorithm. Anim Biotelemetry 8:1–12.

Chapter 3. A standardised framework for the design and application of fine-scale acoustic tracking studies in aquatic environments

3.0 Chapter summary

Fine-scale tracking technology has advanced our understanding of aquatic animal behaviour by deriving near-continuous movements of invertebrates to large predatory fish. Commercial fine-scale positioning systems, such as the VEMCO Positioning System (VPS), can pinpoint an animal's location within metres of its true position. While methodological applications of commonly used presence-absence acoustic telemetry have identified factors that can limit-improve array performance, the factors that influence position yield and accuracy and introduce error in fine-scale positioning systems have yet to be synthesised. Evidenced through a systematic review of VPS literature, we highlight key considerations and potential pitfalls faced when designing and conducting a fine-scale tracking study. Key factors that can impact data acquisition are grouped under four key categories linked to the study system, species studied, and logistical and technological constraints. Thereafter, in-line with these categories we provide a framework that can be used prior, during, and post-study to identify sources of error and data loss to optimize VPS design and acquired results. We provide details on user assessment tools that include, a pre-study trial period using fixed tags to assess array geometry and data yield, an in-situ checkpoint data download, and post-study assessment of fixed transmitter performance. We highlight the utility of this framework and integrated assessment tools by presenting a real-world VPS study that ultimately was compromised. We anticipate that this framework can be used to standardize reporting of essential steps and checks that will generate comparable data for future synthesis, which will further advance VPS and other fine-scale tracking approaches.

3.1 Introduction

Given the widespread availability of commercial acoustic positioning systems in the modern era, this technology has vast potential to identify fine-scale movements which shape fundamental aspects of aquatic animal behaviour (Orrell & Hussey 2022). Acoustic fine-scale tracking systems that use a positioning algorithm to estimate an animal's location and allow the reconstruction of semi-continuous movement tracks offer the best lens of resolution to elucidate the fine-scale movements of fully aquatic species in their natural environment with high accuracy (Espinoza et al. 2011). This technology has been used to address critical conservation issues and inform fisheries management strategies. For example, to investigate the behavioural responses of species to anthropogenic stressors such as noise (Ivanova et al. 2018), artificial light (Wilson et al. 2018), contaminants (Wolfe 2013) and human-made barriers (Bašić et al. 2019). Fine-scale positioning systems have also shaped our understanding of behavioural responses to ameliorative conservation measures, such as artificial reefs (Piraino & Szedlmayer 2014, Herbig & Szedlmayer 2016, Özgül et al. 2019) and habitat enrichment (Veilleux et al. 2018).

Fine-scale positioning arrays require receivers to have overlapping detection ranges, from which high-resolution continuous (or near continuous) data can be used to infer fine-scale habitat use (Riley et al. 2014), behavioural interactions (Armansin et al. 2016), unique behavioural modes (Ivanova et al. 2018) and drivers of movement behaviour (Bacheler et al. 2019). The VEMCO positioning system (hereafter "VPS") is one of the most widely used commercial underwater fine-scale positioning systems. A VPS comprises autonomous underwater acoustic hydrophones (compatible with VEMCO VR2W, VR2Tx, VR2AR or high residency "HR2" and "HR3" receivers) with integrated or paired synchronisation (hereafter referred to as "sync") transmitters ("tags") used to account for clock drift between receivers. A sentinel receiver is selected and surrounding receivers are calibrated to this selected receiver. Sync tags can also be used to identify periods with non-ideal system performance, for example, due to environmental variation (Espinoza et al. 2011) or extreme weather events (Payne et al. 2010, Dahl & Patterson 2020, Rasmuson et al. 2021). In addition, reference tags can be used to provide a known, often fixed-reference point for comparing positioning error and detection performance among different areas of the receiver array and as control tags for interpreting observed movements (Payne et al. 2010, Smith 2013). Reference tags are typically the same size and power (dB) as the animal transmitters used within a study to provide comparable error and positioning performance results. Derived tag detections are positioned using a hyperbolic Time Difference of Arrival (TDOA) algorithm, which requires a simultaneous detection of an individual animal on three or more receivers. TDOA measures the differences in the transmission detection time at pairs of receivers, which is then converted into a distance difference using the estimated signal propagation speed based on water temperature, salinity, and depth (Smith, 2013). This results in three equations for a set of three receivers, which can then be solved to determine the position and time of a detected transmitter, and thereafter be used to reconstruct a continuous time series of locations for an individual. To enable positioning receivers must be deployed with overlapping detection ranges (distance at which a transmitter is reliably detected by a receiver, see Kessel et al. 2014) to maximise the likelihood that a detection is simultaneously recorded on at least three receivers (Smith 2013).

Applied methodological studies using discontinuous arrays of acoustic receivers to infer the presence-absence of animals (within 50 to 2000 m depending on the detection range of the listening receiver; see Table 3.1 for definition) across a range of aquatic systems and habitats have revealed a plethora of factors which can reduce how reliably an animal is detected (Heupel et al. 2006, Kessel et al. 2014, Ellis et al. 2018, Brownscombe et al. 2019). Moreover, these studies have detailed key considerations that study design should consider to maximise data acquisition relative to the study question and focal species. Factors that limit detection success are essentially linked to how effectively sound is transmitted and received by a receiver, related to metrics including tag signal intensity (or strength) in the context of the study environment and ambient noise. Signal intensity at the receiver is impacted by distance, signal spreading, attenuation, absorption losses, and distortion. For example, the acoustic energy emitted through the tag's transducer decays at increasing distances due to the above factors, reducing the chance of signal reception (Singh et al. 2009). These factors are influenced by the properties of the water body itself, including temperature, salinity, entrapped particles and substrate type (Medwin & Clay 1998, see summary in Kessel et al. 2014). Ambient noise is deleterious when it occurs over the same frequency band as the listening receiver and is introduced by biophony (biological sound), geophony (geophysical sound) and anthropophony (anthropogenic derived sound). How these factors influence data acquisition and introduce error in location estimates in fine-scale systems has yet to be synthesized. In addition to considering how the signal intensity and ambient noise may shape VPS array design, key decisions are required including, but not limited to, receiver spacing, orientation and depth.

Table 3.1 Glossary of acoustic telemetry terminology

Terminology	Definition
Absorption	The loss of acoustic energy due to conversion to other forms, e.g., loss as heat. Transmission frequency and conductivity of the medium, e.g., freshwater or saltwater, are key factors influencing absorption loss
Ambient noise	An instantaneous measurement of acoustic background noise that occurs over the same frequency band as a listening receiver, this value can be set to record at specific intervals using VRTx, VR2AR and HR generation receivers
Attenuation	Loss in acoustic energy which occurs due to the process of absorption, typically defined as a process with a rate and level, e.g., a 69 kHz signal attenuates at a rate of 2 dB km^{-1}
Close Proximity Detection Inference (CDPI)	Low detection likelihood near and far from a receiver and highest at an intermediate distance. Often tied with transmitter power output, reflective surfaces and ambient sound levels; see Kessel et al. (2015)
Detection efficiency	A measure of performance that is typically given as a proportion for a given distance, e.g. 50% detection efficiency at 100m which equates to a 50% likelihood of a detection received and stored by a listening receiver that is 100 m away from an active tag
Detection range	Defined by Kessel et al. (2014) as “the relationship between detection probability and the distance between the receiver and tag”
Diffusion	The spreading of an acoustic signal, which in turn reduces signal strength at the receiver
Maximum detection range	The furthest a pinging transmitter and a listening receiver can be apart, and the transmission recorded
Array coverage	Also commonly referred to as “detection coverage”. Describes the cumulative detection area of the deployed receivers within an array

Table 3.1 Glossary of acoustic telemetry terminology

Terminology	Definition
Refraction	Bending of a sound wave owing to changes in its speed, e.g., as depth increases, water temperature may decrease, which leads to downward refraction of a soundwave that originates just below the water's surface. This refraction causes an acoustic "shadow zone" where the strength of an acoustic signal is reduced due to the divergence of sound signals (see Kuai et al. 2021)
Signal strength (dB)	Describes the strength of the received detection, also referred to as "signal intensity".
Signal to noise ratio (SNR)	The difference between the background noise level and the received signal level (signal strength), whereby a larger SNR means a receiver can easily hear the sent transmission (signal) over the background noise, and a low SNR means the receiver is limited in its ability to decode the signal

To bridge this knowledge gap for fine-scale tracking studies, the specific objectives of the current study were to (i) conduct a review of published applications of the VPS to identify the factors limiting data acquisition, and that introduce positioning error, (ii) develop a framework to guide new and existing users in designing and conducting a VPS study encompassing pre, in-situ and post-study assessment tools to evaluate and assess system performance related to data yield, spatiotemporal variation in detection performance, and identify potential sources of positioning error, and; (iii) detail an applied case study to explore the interaction of complex environmental, ecological, and technological factors that can limit VPS when operating within a challenging nearshore environment to highlight the useability of the proposed framework.

3.2 Methods

To synthesise existing peer-reviewed VPS literature, a global search of peer-reviewed literature was conducted in ISI Web of Science using the keywords "VPS" OR "VEMCO Positioning System" OR ("acoustic telemetry" AND "fine-scale"). Due to the use of this acronym across other fields, the search output was filtered to categories which included “Environmental Sciences”, “Environmental Studies”, “Zoology”, “Evolutionary Biology”, “Marine Freshwater Biology”, “Fisheries”, “Ecology”, “Biology”, and “Oceanography”. Duplicate searches were conducted using SCOPUS and Google Scholar. In addition, literature cited within these studies that were not identified directly by the search were also reviewed. Abstracts were screened for relevance, with only studies explicitly using or testing VPS included. All studies identified before November 3, 2021, were included. Data on explicitly stated factors that reduced data acquisition, detection range, positioning performance (number of positions yielded) or introduced error were extracted. In addition, the species tagged, study location, water type (freshwater, saltwater or brackish), habitat and bathymetric depth of the study area, the quantity, model, transmission rate of tags used in the study (animal, sync and reference tags), the number of animals detected and positioned, positioning performance for animal, sync and reference tags (% positioned versus detected), quantity, model, spacing, and coverage (area) of receivers in the deployed VPS array and the number of additional receivers (non-VPS e.g. additional discontinuous strings of receivers) were extracted.

To demonstrate the application of the proposed framework, we provide a VPS case study conducted in the coastal waters of Ascension Island (7.9467°S, 14.3559°W). Ascension Island is a remote volcanic island in the South Atlantic Ocean, 1,660 km from Africa and 2,250 km from South America. The nearshore substrate is primarily comprised of volcanic rock reefs and sand. We conducted a 60-day study to estimate activity rates of two mesopredators abundant in Ascension’s nearshore environment, namely the rock hind grouper (*Epinephelus adscensionis*) and spotted moray (*Gymnothorax moringa*). In 2019, a grid of VEMCO VR2W acoustic receivers (*n* = 18; Innovasea Ltd., Canada) with 55-80 m spacing (spacing determined through fixed and drift range testing, see Supplementary

Material S3.1) was deployed northwest of Ascension Island across rock and sand habitats at depths of 9-32 m, with receivers positioned between 5 – 11 m below the water's surface. Co-located V16-6x sync tags were inter dispersed within the array (*n* = 12; 69 kHz, 540-660 s transmission rate, 162 dB power) attached 1-2 m below the acoustic receiver to facilitate time synchronisation and to refine VPS positioning. Three reference tags (VEMCO V16-TP, 69 kHz, transmission rate = 540 – 660s, nominal transmission rate = 600 s, 162 dB power) were also spaced within the array and attached 1-2 m below the acoustic receiver. Rock hind (*n* = 5) and spotted moray (*n* = 5) were captured at depths of <15 m (to reduce the risk of barotrauma) and tagged with VEMCO V16-TP acoustic transmitters, each tag transmitting a unique identification code and temperature and pressure (depth) data every 25 to 45 seconds at 158 dB power output. Fish were tagged and released at several locations within the VPS array. Using the proposed fine-scale telemetry framework, we applied pre-during and post-assessment criteria to identify aspects of this study that may have influenced data acquisition and could have been addressed to improve data quality.

3.3 Results

Using Web of Science, 189 articles were identified, of which 27 were deemed relevant i.e. studies deployed a Vemco Positioning System and use data from acoustically tagged animals and/or fixed static tags. A duplicate search using SCOPUS identified 169 articles; 28 unique articles remained following abstract screening. A duplicate search using Google scholar yielded 2278 articles, from which 68 unique articles were directly relevant. An additional four articles were identified from in-text citations. Combined searches yielded 127 peer-reviewed articles that analyzed data from 119 unique species datasets and included 10 methodological papers that did not tag any animals. All peer-reviewed publications published before November 3, 2021, were included in this review (complete list of articles in Supplementary Material S3.1 and S3.2).

3.3.1 Key considerations: factors that can reduce or compromise system performance

Identifying key considerations and associated factors that potentially influence the performance of VPS is a proactive step to ensure data yield is sufficient to meet the study objectives, which in turn governs data analysis choices. These factors include the characteristics of the system studied, including water type (freshwater, saltwater and brackish), habitat type (Guzzo et al. 2018, Becker et al. 2020, Swadling et al. 2020), depth (Brownscombe et al. 2017, Taylor et al. 2017), bathymetric complexity (Andrews et al. 2011) and in-water structures (Bašić et al. 2019, Barilotti et al. 2020, van der Knaap et al. 2021). Secondly, the ecology of the animal studied and their associated behavioural strategies (e.g. refuge seeking behaviours described in Coates et al. 2013, Skerritt et al. 2015, Dahl & Patterson 2020, Fahlman et al. 2020), species interactions (Williams-Grove & Szedlmayer 2017) and movement capabilities (Coates et al. 2013, Logan & Lowe 2019). These factors can influence signal reception (strength) and ambient noise, which drives detection success and the volume of data available for subsequent positioning. It should be noted that these factors may act synergistically, and disentangling the relative contribution of each is challenging (Binder et al. 2016); however, their consideration is essential in ensuring the optimisation of a VPS deployment. It is also important to consider that a VPS study may not be suitable under certain conditions, and suitability can be assessed prior to installation.

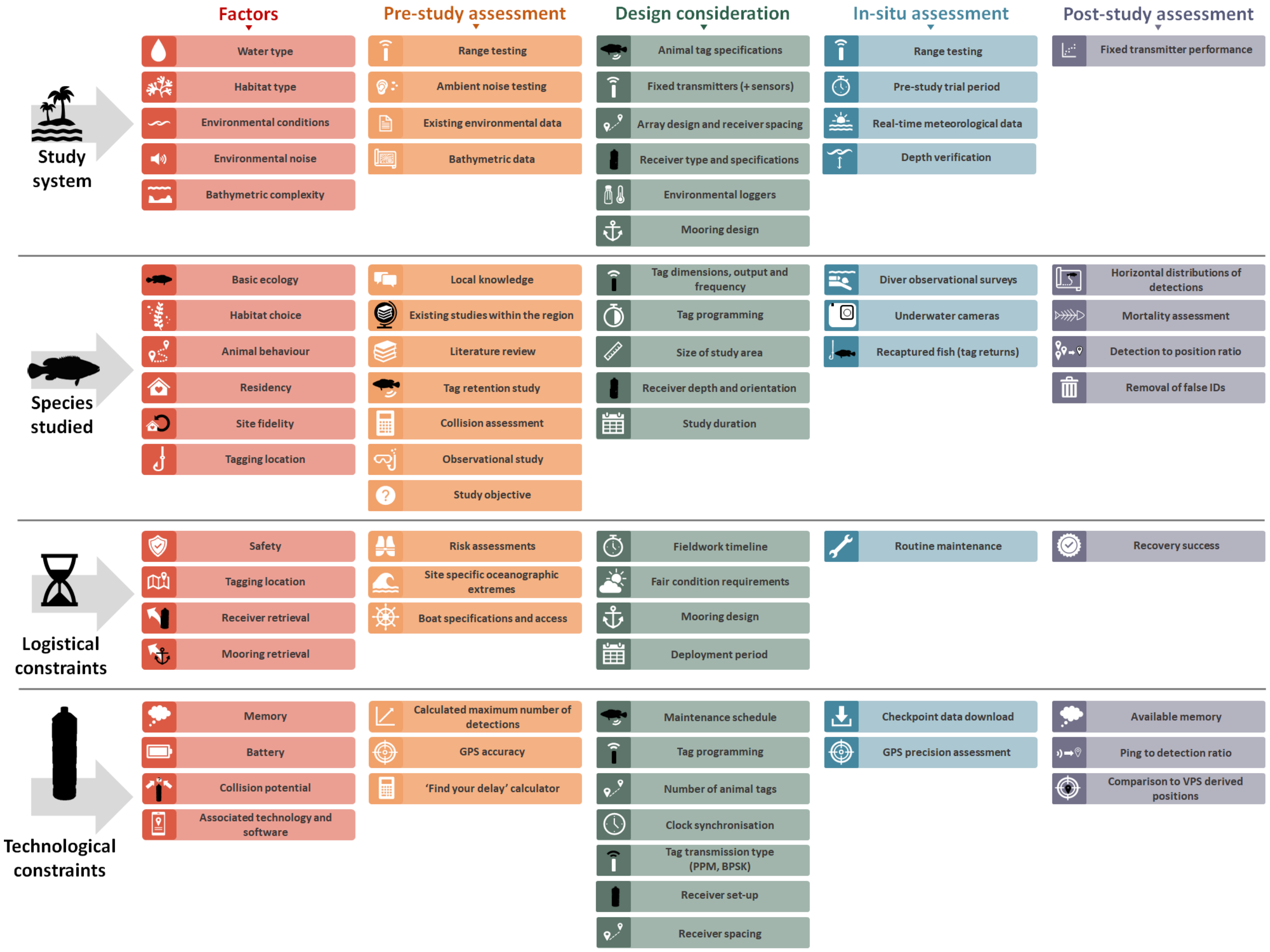


Figure 3.1 A framework to guide new and existing users in selecting appropriate pre-during-post study assessment techniques to maximise the potential for VPS data acquisition.

3.3.1.2 Study system

Water type

Absorption of sound depends on temperature, salinity, and conductivity (Tucker & Gazey 1966), which naturally varies between fresh, saltwater and brackish systems (a 69 kHz signal attenuates at a rate of 2 dB km^{-1} in freshwater, compared to 30 dB km^{-1} within saltwater, Tucker & Gazey 1966). As a result, the typical detection range of an acoustic telemetry system deployed within a freshwater system is higher than in marine environments (e.g. 7 km detection range under calm conditions in freshwater reported by Jellyman & Unwin 2019). However, this is not always true as detection range is frequently more variable in freshwater, primarily due to dynamic water quality, with strong seasonality commonplace (Klinard et al. 2019). This consideration, in turn, influences the chosen spacing between receivers as a VPS system requires at least three receivers with overlapping detection ranges for positioning.

An underlying assumption of VPS data processing is that signal propagation is optimal and follows the Coppens equation (Coppens, 1981), which calculates the speed of sound in water based on temperatures between 0 and 35°C, salinities of 0-45 parts per thousand (PPT), and depths of 0-4000 m (Smith 2013). Accurately measuring these parameters to inform data processing is vital, as sound propagation speed in water varies under differing conditions. For example, a 1°C increase in temperature leads to an increase of 4.5 m s^{-1} in propagation speed, and a 1 PPT change in salinity a 1.3 m s^{-1} increase in speed (Duxbury et al. 2018). Current TDOA processing temperature and salinity inputs can accommodate user-generated values at any resolution or assumed values (in the absence of user data) using best judgement. It is recommended that these variables be measured, particularly within VPS arrays deployed in highly dynamic and seasonal environments, to reduce positioning error. For example, seasonal thermoclines were observed during a VPS study in an arctic lake (Guzzo et al. 2016), with recorded temperatures of -20°C in surface waters (0-5 m) and 5°C at 20 m depth. While some of these sources of error may be difficult to correct without investing in fixed environmental sensors (i.e. temperature and salinity) and, or the use of sensor tags (to record animal depth), acknowledging uncontrollable sources of error is critical. For example, when determining thresholds for social interactions in sociality experiments (Armansin et al. 2016).

Study system depth

VPS studies report a reduced detection range in shallow environments (Moulton et al. 2017, Westrelin et al. 2018). However, testing the limits of this technology in deep water environments (>200 m) has yet to be undertaken. The deepest deployments of VPS arrays to date include installations at 181 m in freshwater (Marsden et al. 2016, Buchinger et al. 2017), 115 m in marine (Cote et al. 2019) and 58 m in brackish waters (Furey et al. 2013). In general, a 100 m increase in depth equates to a 1.7 m s^{-1} increase in the speed of sound transmission (Duxbury 2021). Consequently, deep water VPS arrays should theoretically have improved detection ranges, allowing larger distances between receiver placements within an array (Loher 2017). Therefore, study depth is a crucial factor for potential receiver placement-spacing when considering both data yield and the coverage area for monitoring tagged animals.

Habitat type

Transmission loss (via attenuation) and a subsequent reduction in detection range have been linked to the presence of certain habitat features, including macrophytic fauna such as dense kelp forests (Logan & Lowe 2019), lake- and seagrasses (Selby et al. 2016, Guzzo et al. 2018). Signal attenuation lowers the signal to noise ratio (SNR) at the receiver, leading to less accurate TDOA and increased error in positioning. Few methodological VPS studies have assessed the role of habitat on system performance to date, and its impact is challenging to quantify. However, it is important to consider seasonal changes in habitat from the period the study was initiated (for example, in seasonally higher macrophyte biomass, or coastal areas exposed to strong seasonal upwelling events) when assessing potential receiver spacing and evaluating system performance.

Environmental conditions and noise

Oceanographic conditions may reduce temporal VPS performance due to changes in the chemical and physical properties of water; the change may be abrupt and discontinuous or persistent and continuous (Medwin & Clay 1998). Cyclonic conditions are an example of an abrupt, discontinuous change that can reduce data acquisition due to turbulent waters, storm surges, and equipment loss (Thums et al. 2013, Dahl & Patterson 2020, Rasmuson et al. 2021). Persistent, continuous changes in oceanographic conditions are typically seasonal and include the presence of thermoclines which may be more common in static bodies of freshwater (Westrelin et al. 2018) and haloclines present in brackish and marine environments (Tucker & Gazey 1966). Additionally, heightened discharge in impounded systems due to snowmelt and/or heightened surface runoff can lead to increased turbidity (Wyman et al. 2018).

Underwater noise can directly influence whether a listening receiver detects the complete series of pings that constitute a PPM acoustic transmission due to signal masking (Steel et al. 2014). Abiotic noise becomes potentially deleterious when the noise spectra overlap on the same frequency band as the transmitter frequency, either 69, 180 or 307 kHz for standard VEMCO acoustic tags (operating on pulse per modulation, PPM), or 170 kHz for the digital transmission of a high residency tag (HR2 and HR3 transmitters). In addition, the maximum detection range of a transmitter can be significantly reduced by high background noise levels (while there is no VPS-specific study to date, see acoustic telemetry example in Stocks et al. 2014). The threshold at which noise dramatically reduces detection yield (% of detections received versus sent) has not been defined across different system types but is likely highly variable. In an impounded freshwater system, high noise for HR2 VPS technology was defined as >21 dB (Leander et al. 2019), while average ambient noise in reef environments is likely much higher due to high levels of biological activity (Radford et al. 2010, Steel et al. 2014). Sound absorption increases an order of magnitude between 69 – 300 kHz (Burdic 1984, Baggeroer 1984), equating to a reduced detection range between tag and listening receiver. Due to more advanced receiver circuitry, newer HR2 generation receivers have more sophisticated noise filtering (compared to older model VR2Ws). Measuring ambient sound within a VPS array can provide a baseline to determine noise impacts on transmission reception. Newer models of VEMCO receivers, including the VR2Tx, VR2AR and HR2 generation, can be set to record ambient environmental noise at fixed intervals throughout a deployment period. However, spatiotemporal trends in noise and how ambient noise values are integrated into the modelling of positioning error for underwater positioning remain unexplored and require focused attention.

Sources of underwater noise can include biological sound (biophony), geophysical sound (geophony, e.g. wind, waves, rain, water flow, ice cracking and movement), and anthropogenic derived sound (anthropophony, e.g. hydropower, seismic testing and resource extraction) (Mooney et al. 2020). To date, key sources of biophony reported in acoustic telemetry systems include nocturnally active crustaceans (e.g. shrimp and zooplankton, see a non-VPS acoustic study by Payne et al. 2010), and triggerfish and urchins (Cagua et al. 2013; *n* VPS articles listing biophony as reducing performance = 0). In shallow coastal environments, geophony is generated by waves washing to shore (Thums et al. 2013, Brownscombe et al. 2017), while increased geophony in impounded rivers and reservoirs is associated with heightened water discharge during hydropower generation (Wyman et al. 2018). These conditions reduce detection range through signal scatter associated with increased bubble entrapment in the water column (Medwin & Clay 1998) and proliferation of debris and suspended material (Richards & Leighton 2000). Anthropony in underwater soundscapes can include continuous underlying noise, for example, power stations operating at low-frequency bands (Taylor et al. 2017) or discontinuous noise sources such as boat engines (Brownscombe et al. 2019). When positioning receivers, researchers should be mindful of the source and frequency of the noise. For example, to improve detection performance and reduce the influence of geophony, a receiver may be deployed in a wider part of a river where water velocity is lower (reduced geophony) or in a deeper area further away from surface noise (waves). In tidally influenced areas, noise and detection performance may vary with the tidal cycle.

3.3.1.3 Bathymetric complexity and underwater structures

The topography of underwater landscapes and the presence of structural irregularities such as canyons and ridges, large boulders, and high rugosity reefs create a physical barrier to “line of sight” between acoustic receivers (Andrews et al. 2011, Selby et al. 2016, Stieglitz & Dujon 2017, Schlaff et al. 2020, Espinoza et al. 2020, Dahl & Patterson 2020, Fahlman et al. 2020, Mucientes et al. 2021, Rasmuson et al. 2021) which is a crucial consideration for mooring location, receiver height in the water column, and overall array design. Physical barriers can lead to a loss of signal or the detection of reflections where the primary path is blocked or signal distorted; consequently, data yield may be higher across homogeneous (sand) habitats versus heterogeneous (rocky) habitats. Reference tags enable a user to identify the influence of barriers on VPS positioning power. Reference tags can be deployed around these structures to distinguish their role in signal transmission and subsequent positioning. Reference tag nominal transmission rates are typically ~5 minutes (mean = 317 s; range = 50 – 700 s, *n* animal tracking studies that mention reference tags = 38; 46%; *n* that detail nominal tag delay = 11, 13%). Note tag programming is study-specific, and transmission rates are typically matched to those selected for animal tags to enable comparisons of positioning error.

To ensure overlapping detection ranges for positioning, users should consider receiver arrangements that maintain the line of sight between receivers to maximise the probability of simultaneous detection and accommodate structural irregularities. Grids that form squares or equilateral triangles are recommended, as this creates smaller areas of error sensitivity, reducing the propensity for extreme positioning error values (Smith 2013). Human-made structures, including concrete walls at hydropower facilities, are also associated with signal reflection (Bašić et al. 2019), which can also occur in calm environments when surface waters are flat (see Kessel et al. 2015). Signal reflection can cause a partial loss in the series of 8 or 10 pings that make up a PPM signal transmission. Without reception of the full ping ‘train’ (sequence), which takes 3.5 to 5 s to transit, an acoustic receiver cannot decode the signal and match it to a tagged animal (Kessel et al. 2015). In reflective systems, transmission echoes can lead to ‘Close Proximity Detection Interference’ (CDPI), which leads to a low detection range close to a receiver with a peak at an intermediate distance (see Kessel et al. 2015). CDPI is particularly problematic when using high power tags in low ambient noise environments or where reflective surfaces are present (calm surface waters or underwater structures). Studies that aim to quantify the role of underwater structures on animal behaviour, including recreational piers (Barilotti et al. 2020) and wind farms (van der Knaap et al. 2021), should consider that the ability to position animals is likely reduced closer to these complex structures, which could directly influence biological inference, e.g. habitat selection indices. This issue highlights that standardized spacing between receivers within a VPS array is not always appropriate depending on the system topography and composition.

3.3.1.4 Animal ecology

Ideal study species for VPS include animals easily detected in the mid-water column, with slow movement rates and restricted activity space (Teleosti, Logan & Lowe 2019; Chrondrichthyes, Armansin et al. 2016). A single VPS is designed typically to track species where the investigator has a priori knowledge of limited space use during a given study time frame or life stage. For example, tracking animals moving through closed linear freshwater systems (Wyman et al. 2018, Carpenter-Bundhoo et al. 2019, Balazik et al. 2020) and during spawning events (Marsden et al. 2016). Additionally, animals that show an association with reefs or underwater structures/features (Herbig & Szedlmayer 2016, Williams-Grove & Szedlmayer 2017), have restricted core activity space (typically tied with body size; Lindstedt et al. 1986) or to capture interactions with other species with high site fidelity (e.g. cleaning interactions; Armstrong 2021).

Major sources of data loss

For shelter-dwelling species or those occupying heterogeneous substrates or structures which may prevent line-of-sight between listening receivers, it is critical to identify periods of refuge-seeking behaviour and distinguish an associated reduction in detections from the animal exiting the study area. Sync tag data can be used to determine periods of inactivity of focal species. For example, Skerritt et al. (2015) identified when tagged European lobster (*Homarus gammarus*) were in shelters (i.e. limited detectability) from a lack of detections relative to a benchmark of >80% sync tag detection rate. In an ideal scenario, a “moving tag” that simulates an animal’s trajectory is moved through the study area to assess how performance varies within different areas of an array. It should be noted that reference tags may be best suited to this purpose as they are typically set to the same power output and transmission rate as animal tags, whereas sync tags are often set to a slower transmission rate given their primary use for clock synchronisation and system calibration.

Deployment of additional single receivers or “gates” (lines of receivers) can provide useful information that can later inform animal fate, particularly for fast-moving species or animal tags using slow transmission rates or species that travel within areas of poor positioning efficiency, e.g., along high-velocity riverbanks. Additional gates can also be used to confirm that tagged animals have left a system (Heupel et al. 2006), for example, by successfully migrating downstream (Baker et al. 2020) or showing affinity to structures along a coastline (Barilotti et al. 2020). Less than half of published VPS animal tracking studies use additional receivers (35%). Integrating VPS into existing acoustic arrays or networks has become more attainable with improved connectivity between acoustic telemetry users, but must consider the tag frequency used. For example, the European Tracking Network (ETN) and Ocean Tracking Network (OTN) now assimilate data from the private, public, and academic sectors and can provide updates on whether tagged fish have been detected on arrays maintained by other users.

Selecting the appropriate tagging protocol relies on knowledge of the animal’s physiology, the environment it inhabits and tag retention (Runde et al. 2022). Tag retention studies are recommended when studying species where knowledge of best practices for anaesthetic dosage and tag attachment procedures is limited (*n* VPS studies = 2; Bridger & Booth 2003). For example, Miyoshi et al. (2018) conducted rearing experiments to design a tag attachment method for Northern pacific sea stars (*Asterias amurensis*) and confirmed that tag attachment did not affect growth rates. External tag retention may vary due to temperature extremes for ectotherms; the common sea star (*Asterias rubens*) retained external acoustic transmitters for 200 hours in 10°C water and only 3 hours in 16°C water (Olsen et al. 2015). To date, most VPS studies have opted for internal tagging (*n* unique VPS datasets = 87; 74%). For cryptic or “shelter dwelling” species, tag attachment must consider tag entrapment in crevices, burrowing, or loss during moult (Coates et al. 2013, Miyoshi et al. 2018, Itakura et al. 2018). External placement of acoustic tags has been used to track large mobile animals (Armstrong 2021), animals with venomous spines (Dahl & Patterson 2020), arthropods (*n* = 4; 100%), molluscs (*n* = 4; 100%), echinoderms (*n* = 1; 100%) and chordates (15%). Suggested reasons for external tagging include improvements in transmitter detectability (Dance et al. 2016), reduced handling times and, in the case of in-water tagging (at depth), a reduced likelihood of barotrauma (Dahl & Patterson 2020). Efforts to reduce tagging-associated mortality include pre-attachment steps such as considering tag burden using size to body-weight ratios (Stieglitz & Dujon 2017, Wilson et al. 2018, Bašić et al. 2019), and the collection of target animals using SCUBA diving (Nanami et al. 2018). Post-attachment mortality reduction measures include returning tagged animals using predator protection cages on reefs (Williams-Grove & Szedlmayer 2016), recompression cages, and open-bottom sea pens post-tagging so that animals can descend of their own free will (Rasmuson et al. 2021).

Major sources of positioning error

VPS utilizes hyperbolic equations that calculate a 3-dimensional (*x, y, z*) position for transmitters without integrated pressure sensors by utilizing a user-provided depth value for the species being studied or geometry based on detections recorded simultaneously on four receivers. In the first scenario, the animal's position is calculated at the same depth (specified by the user; typically an average or estimate of depth commonly occupied) regardless of the vertical movements of the animal. In some instances, this can result in significant positioning error. For benthic animals, the error is typically minimal. However, for animals that continuously move throughout the water column and where the available depth is a significant percentage of the horizontal distance between receivers, the calculated position may be quite different from the actual position of the tagged animal. In the absence of a known tag depth, depth can also be estimated using geometry if a transmission has been recorded simultaneously on a minimum of four receivers. However, the error associated with geometric estimates will vary depending on where the animal is within the array's geometry. To reduce positioning error associated with depth, VPS analysts recommend using tags with integrated pressure sensors where the actual depth of the tag is incorporated in the equation to provide a true *x*, *y*, *z* estimate.

Optimising data yield

Selecting the appropriate tag transmission rate depends on the study question, and the swim speed of the animal studied. While the average transmission rate used within a VPS study is 2 minutes (123 s), which, in theory, can generate upward of 500 positions a day, the range of rates chosen varies significantly. For example, Wilson et al. (2018) selected a 7.5 s nominal transmission rate (range = 5 – 10 s) to track neonate sea turtles on their first foray into the ocean to examine the role of artificial light on turtle dispersal. It could be assumed that this rate was chosen given the estimated time each individual spent within the array (<90 minutes), the speed at which neonate green turtles complete this transition (mean speed = 0.50 m s^{-1}, Wilson et al. 2018), the constrained study area (e. 0.04 km^2), and the study objectives which required the calculation of turn angles and animal speed. In contrast, Cote et al. (2020) chose a 1200 s nominal transmission rate (range = 960 – 1440 s) to estimate the seasonal and diel activity of brook trout (*Salvelinus fontinalis*, *n* = 22) within a small, shallow lake over 17 months. This slow transmission rate reduced the probability of signal collisions within the confined study area and the chance of receiver memory saturation while still providing the required resolution and yield of data.

3.3.1.5 Technological constraints

Over time both transmitters and receivers have experienced improvements in hardware and software capabilities. For example, while older generation VEMCO VR2 receivers have a memory capacity of >32 MB (3 million detections), newer VEMCO HR2 receivers have 2

GB of integrated memory which can store 170 million detections (dependent on the frequency that diagnostic data is recorded). With a move towards longer duration VPS studies, the potential volume of data a study could generate needs to be considered (i.e., expected received transmission rate per day *x* proposed study duration *x* number of tagged fish to ensure all data can be recorded). Improved memory capabilities enable more animals to be tagged and studied within a single VPS, typically resulting in more generalisable population-level study results. In addition, newer models (VR2AR, HR2 and HR3) can also record ambient noise, temperature, and tilt (a coarse measure of current), contextualising findings.

While listening receivers are considered omnidirectional, this is not the case in reality. VEMCO receivers use a top-mounted transducer design whereby sensitivity is highest around the transducer, with reduced sensitivity at the top and bottom of the receiver body (due to the receiver casing). For this reason, receiver orientation can influence detection rates depending on the animal's position (e.g. demersal versus surface swimming), water depth and benthic topography (Huveneers et al. 2016). Orientation and receiver depth also depends on the study question, e.g., if the aim is to detect prey capture events and the study species feeds primarily on demersal prey, then the receiver orientation may be best deployed facing downwards and lower in the water column. However, receiver depth may be constrained by available recovery techniques and associated equipment.

The average area a VPS array covers is typically relatively small, i.e., <2 km^2 (*n* VPS articles = 68, 63%; *n* VPS articles where array scale not described = 15; 15%; min. array coverage = 0.0075 km^2, max. array coverage = 18.9 km^2). The constrained spatial scale of VPS arrays is due to the need for overlapping receiver ranges required for tag positioning and is commonly limited by the number of available receivers, associated costs, and expected animal movement range. Accuracy of positioning animals that occupy or occur at the edge of a VPS array, where the likelihood of 3+ overlapping receiver detection ranges is low, is a vital consideration for system deployment design (Andrews et al. 2011, Becker et al. 2020). The relative error associated with an animal position depends on where the location is recorded within a group of listening receivers due to the nature of geometry and hyperbolic estimates (see Smith 2013). Therefore, to reduce the propensity of edge effects, care should be taken to place the array with study species centred in the design (based on prior knowledge). The investigator, however, must consider the number of tagged animals released in a given area of an array due to potential tag signal collisions. Existing literature on the effects of VPS shadow regions (which describes areas of poor positioning accuracy due to geometry, Smith 2013) on the accuracy of positions remains limited. However, this concept is similar to the dilution of precision observed in GPS or the Loran C radio navigation system (see Enge 1994).

One of the most important data elements in VPS calculations is the precise measure of receiver location (latitude and longitude) (Andrews et al. 2011). A handheld GPS costs upwards of $150 USD and typically has an accuracy of around 3 m. In contrast, Differential GPS (DGPS) is an enhanced version of a GPS that costs upwards of $1200 USD and improves location accuracy through the use of differential correction estimated using a fixed base station with a known position (Parkinson & Spilker 1996), giving an accuracy of 1 – 3 m. Given the high spatial accuracy desired from VPS, procuring accurate GPS for deployed receivers is key to limiting the propagation of technological error. Lower GPS error is ideal, however, with adequate data yield the true location of the receivers can be solved during positioning.

3.3.1.6 Logistical constraints

Given the impact of surface waters on receiver listening range and considering the study question at hand, the depth at which at receiver sits within the water column can be critical to

VPS data acquisition. For this reason, receivers are typically deployed >10 m below the water's surface to minimise the influence of surface water movement and interactions with other water users, for example, boat propeller entanglement on receiver lines. As with all fieldwork, safety governs all operations and stages of study design. Prior to recent innovations in receiver design and associated technology, an autonomous receiver's deployment depth was largely constrained by recreational dive limits and ease of recovery. Innovations that have improved data acquisition include using acoustic release mechanisms to recover deployed receivers (integrated or externally attached), data download via autonomous underwater vehicles (wave gliders; Cote et al. 2019) and the development of paired technologies. For example, an onboard VR100-200 communications unit and a transponding hydrophone can be used to communicate with a VR2AR to generate a simple data summary. In addition, an underwater modem can communicate with a deployed VR4-UVM to acquire a complete data download without needing receiver recovery. Improved ease of data acquisition is vital for monitoring deep water species, hard-to-reach environments and geographic locations or given the presence of other hazardous or sensitive flora and fauna. For example, Cote et al. (2019) used acoustic releases and ocean gliders to retrieve data generated by tagged snow crab (*Chionoecetes opilio*) occupying depths of >116 m in the Cabot Strait, Canada. Improved accessibility can also facilitate higher transmission rates due to improved access to equipment for regular downloads at a reduced incidence of memory saturation and easier data quality checks during the first stage of the study (i.e. to assess collision rate and data acquisition). It should be noted that newer recovery technologies (receivers and releases) come at an increased cost. Therefore, traditional recovery methods, including SCUBA-assisted retrieval and extraction using grapples and winches, may be preferable.

Considering the cost of equipment is pivotal in defining the scope of a VPS study. The most commonly used acoustic receiver within VPS arrays is the VR2W, likely related to its widespread use in acoustic telemetry and affordability. While VR2AR and HR2 receivers are 41% and 42% more expensive, respectively (Table 3.2), there are several benefits associated with this technology. Firstly, retrieving receivers using an acoustic release mechanism (incorporated into a VR2AR receiver) offers greater flexibility and useability (see above). In addition, newer models have integrated sync tags and are capable of recording ambient noise (VR2AR and HR2) and have the potential to collect extremely high-resolution movement data (HR) (Table 2). At the time of this review, there was no published and peer-reviewed study using HR3 technology. However, HR3 technology can incorporate 307 kHz V3 tags akin to the Lotek JSATS AMT series (V4 180 kHz are the smallest compatible HR2 generation tag). When considering VPS data processing, users can conduct their own positioning analysis for standard VR2W/VR2AR VPS arrays following in-house training and the purchase of proprietary software ($2400 USD). However, this does not currently support HR systems, and a higher cost is associated with processing 3D versus 2D data. Given that the average cost of tracking equipment required for a PPM VPS study equates to ~$73k, and the average BPSK (HR) VPS study equates to ~$139 k (Table 2), the factors which can impact data yield, system performance and induce error are acknowledged to optimise system performance and resultant research output.

Table 3.2 The most commonly used VEMCO positioning system (VPS) array configurations used for VR2 (VR2W, VR2AR) and HR2 generation technology. Note that newer acoustic receivers (VR2AR and HR2) have integrated synchronisation ("sync") tags and therefore do not require the purchase of additional sync tags. Range test tag and communications equipment not included. 2021 prices given.

Equipment	VR2 generation			HR2 generation		
	Model	No	Total cost ($USD)	Model	No	Total cost ($USD)
Acoustic receiver	VR2W	23	37,935	HR2	13	50,447
	VR2AR	23	92,223			
Sync tag	V16-4x	20	14,188			
Reference tag	V16-4x	4	1,577	V9-1x	1	312
Animal tag	V9-1x	61	18,918	V9-1x	41	18,918

3.3.2 Pre-study, in situ and post-study assessment to maximize VPS performance and data acquisition

3.3.2.1 Pre-study assessment

Pre-study assessment tools to determine whether a TDOA positioning system is appropriate to address the study question for a given geographic location include investigating environmental conditions which may influence detection range and consequent array deployment considerations (Fig. 3.1). For example, conducting pre-study detection range trials, actively measuring ambient noise, and compiling existing data on environmental conditions, habitat type and bathymetry and variation in dynamic parameters over time within the proposed study area is recommended. Prior to the study, sources of information on the focal species ecology could include incorporating traditional knowledge, identification of existing studies within the region by the public, private or Government stakeholders (e.g., environmental assessments) and conducting a systematic literature review (to assess animal mobility, space use and home range if applicable even if at other localities or for related species). In addition, short-term observational surveys using SCUBA/snorkelling, drones or non-baited underwater cameras (RUVs) can provide basic information on site-specific fidelity of species, species interactions and underwater topography/habitat composition at the study site. A short-term standard mark-recapture study, if possible, could prove helpful in assessing recapture potential (or recapture observation either through direct observation or using RUVs) and population abundance. A mark-recapture study could also be used to test appropriate capture techniques for little-studied species. Practical pre-study assessment techniques depend on the site accessibility, often linked to site-specific oceanographic extremes (e.g. variability in daily/seasonal weather conditions) and logistics (e.g. boat access, availability, and associated costs). The ease of accessibility to a study site will dictate the receiver maintenance schedule (frequency of receiver downloads), which may influence transmitter programming (alongside data requirements for the proposed study question). Technological capability (memory, battery and receiver specific collision potential, e.g. reduced collision rate using HR2 technology versus VR2) and available funding is also a factor in the pre-assessment of technological choices (e.g. tag type and frequency).

Essential pre-assessment tools include using range testing to determine receiver spacing and thus achievable array size and total detection area coverage. Range testing can also identify potential areas of poor positioning, e.g. due to underwater barriers and topographic features and be used to select appropriate transmitter programming (size and power) relative to range and study question. Ambient noise tests can also provide insight into required transmitter power output to ensure higher signal to noise ratios at listening receivers and/or to reduce CDPI (see definition in Table 3.1). In addition, pre-study estimates of the expected number of transmissions can be made using basic calculations of maximum data yield (based on nominal transmission rate per hour) and collision propensity (accounting for the number of tags in the system, tag burst rates and the desired nominal transmission delay).

Range testing

Range testing allows the evaluation of receivers' acoustic “detection range” within an array and is a crucial step for VPS considering the requirement for overlapping detection ranges of groups of receivers for positioning. Aiming for close to 100% detection probabilities is recommended to maximise the chance of successful positioning. There are several different range test types, including but not limited to; boat/vessel-based testing, using a single tag at fixed intervals from a receiver, or several fixed sentinel tags at set distances from a receiver (see Kessel et al. 2014 for further details). We recommend range testing using transmitters with a similar size, frequency, and power output as those proposed for the study animal to yield representative range results.

During the synthesis of VPS literature, six unique reporting styles for range test data were identified, with poorly defined statistical parameters and unclear language commonplace (Supplementary Material S3.2; Supplementary Table 3.1; Supplementary Table 3.2). A large proportion of VPS studies excluded crucial contextual parameters when reporting range test methods, including range test location, test type, and duration. Inconsistent reporting of detection range within the VPS literature limited detection range summaries and comparisons among studies and different system types (freshwater, saltwater, brackish), further highlighting the need for standardized reporting (Kessel et al. 2014). Essential information required when reporting range test results includes; the type of test (drift, roaming or static), at what stage the test was conducted (pre-during-post study), and the test duration and tag specifications (size, nominal transmission rate, fixed delay interval, frequency, output). The detection range should be reported with a clearly defined distance and proportion of detections recorded. Given that VPS requires overlapping detection ranges we recommend reporting the maximum distance at which 100% and 50% of detections are reliably recorded with a visualization of the logistic regression curve (see Kessel et al. 2014 for an example).

Ambient noise recordings

High levels of ambient environment noise are deleterious to signal reception and subsequent positioning capabilities (see section 3.1.1. *Environmental conditions and noise*). Pre-study deployment of a single receiver capable of recording ambient noise levels (VR2Tx, VR2AR, HR generation receivers) can help inform subsequent array design/tag transmission rate in systems that experience potentially deleterious noise. Deleterious or “challenging” (high noise) levels” have been described as 650-950 mV, wherein it can be expected that very few (if any) detections are received (Document-5680-01 previously available from Vemco Ltd. website). How this measurement is comparable to the decibel noise measurements recorded by acoustic receivers and whether uncalibrated noise measurements are comparable between studies or receivers is not clearly defined. A 24-hour deployment of a single receiver recording ambient noise can provide informative data on noise levels over a tidal cycle or identify areas of heightened noise that should be avoided. In-situ noise assessments can also be generated while receivers are deployed (VR2Tx, VR2AR, HR2) using a VR100-200 surface unit and a transponding VHTx hydrophone. Adjustments can then be made to the receiver’s location, e.g., to avoid seasonal noise sources such as increased boat traffic in travel corridors during an open fishing season (see Zemeckis et al. 2014).

Currently, there is no uniformly accepted or utilized technique used to account for ambient noise when modelling fine-scale positioning data. However, basic visualizations of ambient noise levels recorded by VEMCO VR2 and HR generation receivers can be insightful in identifying periods of suboptimal system performance during post-study assessment. For example, Swadling et al. (2020) identified how environmental conditions, including environmental noise, changed throughout the day and used generalised additive mixed models (GAMMs) to assess their relative role in the detection probability of fixed tags. Best practice is currently identifying periods of high ambient noise, poor sync tag performance, and excluding these data during data filtering, or at the very least reporting when these conditions occur. Evidence of extreme weather events such as hurricanes and storm surges can also provide insight into ambient noise recordings outside the normal range of observed values. It is important to note that the absence of or lower position rates during periods of very high noise does not mean that the animal(s) is absent; it likely means that the receivers cannot detect the tags.

Estimating transmission collision potential

A signal collision occurs when a single acoustic frequency is selected (e.g. 69 or 180 kHz) and transmission ping-trains overlap, impeding a receiver's ability to decode individual transmitters (Kessel et al. 2015). Sync tags within VPS systems can also contribute to collision potential (Espinoza et al. 2011). However, this risk is typically low as sync tags are often set to transmit at a slow rate, e.g., once every ten minutes. Collision propensity typically increases with an increase in the average transmission rate of a PPM transmitter (i.e., a lower nominal delay), higher power transmissions, and an increase in the number of tagged fish in a system (compounded by the number of tagged fish already in a system). Collision rates can also increase when numerous individuals are present within the same region within the VPS array. Clustering of tagged individuals can be related to intraspecific (schooling) and interspecific interactions (e.g., predation, mutualism), dispersal capability from the release site, and size of the tagged cohort released at a given location, and the presence of geographic bottlenecks, e.g. dams and levees. Clustering of tagged individuals is often an issue within constrained systems such as rivers and lakes as the potential occupied area is reduced versus open-water systems. However, clustering can still occur in open-water systems where tagged individuals aggregate at habitat features associated with feeding, mating or within a constrained home range. Single erroneous detections that occur due to signal collision (Pincock 2012) are eliminated during positioning, therefore, pose less of an issue in TDOA systems. Fortunately, newer generation acoustic tags using BPSK encoding transmit information in a single transmission (ID, time of detection and sensor data); consequently, the chance of collision is reduced as data transfer occurs within a few milliseconds.

To reduce the potential for collision; during the initial VPS planning stages, Innovasea Ltd. (VEMCO product vendor) offer advice on selecting an appropriate transmission rate considering factors including receiver detection range and the area covered by the VPS system, seasonal differences in detection range, water quality, the desired number of tags and the study question at hand (D. Webber, October 13 2021, *pers. comm.*). This advice is based on an in-depth knowledge of the technology and details on the study system, the ecology of the target species and a basic calculation to estimate the minimum attainable transmission rate (which would not lead to deleterious collision rates). This calculation requires the user to input the number of tags in a system, the average burst rate (the time it takes for the acoustic signal to send), and the transmission delay. It can also be used to estimate the collision rate of adding tags to a system where acoustic tags are already present (worked example in Supplementary Material S3.3; Supplementary Table 3.3).

3.3.2.2 In-situ assessment tools

During a study, routine or “checkpoint” data download is critical to ensure the system design is optimal, for example, to assess whether the receiver spacing is adequate to facilitate simultaneous detections on groups of receivers and, ultimately, whether the study will succeed. At this time, downloading range test data conducted in-situ can also provide helpful insight into system performance and detection efficiency. Confirmation of post-release behaviour and fate through the use of observational SCUBA surveys and underwater video (Bohaboy et al. 2019) can also be used to inform later data filtering choices. Additional in-water sampling techniques can also be used to confirm theorised behavioural states, e.g. diver deployed egg bags to confirm spawning (Binder et al. 2016) and in-water surveys using SCUBA (Armstrong 2021).

Monitoring meteorological data and conditions can inform receiver anchoring choices to minimise the possibility of equipment loss during extreme weather events, such as during storms or periods of high wave action. These data can also be used during post-processing to help identify or reason for periods of poor signal reception or low signal to noise ratios. Identifying which meteorological data streams are available can also guide which data are ideally measured in situ.

3.3.2.3 Post-study assessment tools

Data filtering and positioning error evaluation are crucial to ensure that the data analyzed reflects the animal's behaviour and is not related to animal handling, mortality, tag loss, or poor array geometry. The required filtering depends on the species' sensitivity, the selected analytical technique, and the study question. Filtering steps can include; the removal of (i) detections recorded during post-tagging recovery periods, which depend on perceived animal sensitivity to capture and handling, e.g. those at high risk of barotrauma (Dean et al. 2014) and nocturnal animals (Itakura et al. 2018), and (ii) continuous static detections suggestive of direct mortality (see Bohaboy et al. 2019, Everett et al. 2020, Bacheler et al. 2021 for recommendations) or unrealistic swim speeds indicative of a predation event (Barilotti et al. 2020, Schlaff et al. 2020), (iii) identifying and isolating periods of poor system performance due to reduced detection efficiency, and; (iv) consideration of horizontal positioning error (HPE). Critical data evaluation and sensible data filtering and error assessment ensure that resultant findings are ecologically meaningful and not an artefact of study design and implementation or environmental-habitat conditions.

Using synchronisation tags to assess detection efficiency

During the study, detection efficiency will likely fluctuate across a range of temporal scales, such as over diel periods (day/night) and seasons. Assessing sync tag detection data can provide insight into spatiotemporal variation in detection efficiency across a deployed array. Given that VPS requires either active internal sync tags or external tags for clock synchronisation, this step comes at no extra cost. Sync tags are typically programmed with higher power than the animal, and reference tags. However, high power tags can also result in signal collisions and needs to be carefully considered. Clock synchronisation is key for system calibration and vital for identifying poor positioning periods and signal reflection. On average, sync transmitters are set to a ~7.5 minute nominal transmission rate (mean = 453 s; range = 30 – 700 s; *n* animal tracking studies that mention sync tags = 65; 78%; *n* that detail nominal tag delay = 27; 33%; range = 50 – 700 s). The VEMCO VPS post-processing report currently summarises sync tag data during the study period. The VPS user can conduct higher resolution summarises to investigate spatiotemporal variation in detection efficiency and isolate periods of poor signal reception.

Sync tag detection variability is often not reported in VPS studies to date. Summarising periods of poor detectability (diel periods, seasons, weather events) promotes transparency and confidence in interpreting study findings. Identifying sync tag variability is particularly relevant for VPS as this knowledge can be used to identify why certain studies fail to gather or collect limited data (e.g., due to receiver spacing or other factors, which could be rectified using an in-situ assessment). These data may also indicate why a study could produce unexpected results, e.g., calculated activity rates, emigration rates or space use estimates. For this reason, we recommend that users include basic visualizations of sync tag detections across the array for the study period and across diurnal and seasonal periods if relevant.

Using reference tags to assess positioning error

Horizontal positioning error (HPE) is commonly used to identify and filter positions with high associated uncertainty. Post-processing of VPS detections provides time-corrected positions and a dimensionless horizontal positioning error (HPE) value for all calculated positions, i.e. for each successful position derived for each synchronisation ("sync") and animal tag (Smith et al. 2013). HPE is the radius of estimated circular error around each position and can be used to describe the relative precision (consistent positioning within a given area) (Espinoza et al. 2011). HPE is derived from where on the hyperbolic plane the animal's position intersects, which influences its accuracy (Smith 2013), and is not generalisable across systems or studies. Only 64% of VPS studies tracking animals reported HPE (*n* = 74). HPE is typically translated into HPEm by assessing the relationship between the recorded position of fixed tags (sync and reference tags) and the position calculated using TDOA analysis (Coates et al. 2013). This relationship is then generalised to animal tags and their associated HPE calculated during position processing, but this is often not reported (*n* studies = 53 of VPS, 47% mention the relationship between dimensionless HPE error and HPEm). Determining HPE thresholds often involves investigating the median, 90th and 95th percentiles of binned HPE positions and establishing the appropriate threshold of error, which will retain sufficient reliable data for subsequent analysis while ensuring the scale of error does not exceed the scale of measurement (Meckley et al. 2014, C. H. Fleming et al. preprint; https://doi.org/10.1101/2020.06.12.130195). While HPE filtering is commonplace (*n* = 53; 46%), selecting a HPEm cutoff is often poorly defined and seemingly arbitrary. Few VPS studies have evaluated the use of HPEm filters and their subsequent effect on analysis (Meckley et al. 2014). We suggest that if accurate positioning is required for estimating fine-scale movement characteristics, including turning angles, acceleration, and short-distance swim velocity measurements, then more sophisticated filtering techniques will be required beyond the arbitrary removal of HPE values over a given threshold.

Ping to detection and detection to position ratios to quantify collision rates

While it is difficult to disentangle the role of any given factor, including collision, on data integrity and yield (VPS positions), it is possible to assess a relative proxy of data loss using ping to detection ratios (i) and for poor positioning, detection to position ratios (ii). Namely, by calculating the ratio of the number of hourly (i) pings or (ii) hourly detections relative to the expected number of hourly (i) detections or (ii) positions. The latest firmware of VR2W receivers reports pings every hour, as do all newer generations of receivers. While it may be easiest to assess ping to detection and detection to position ratios following completion of the study, we recommend assessing these ratios during initial testing, i.e. at the first-week checkpoint as recommended above (see section 3.2.2). In study systems where other acoustic tags are already present or where animals are likely to aggregate within some areas of the acoustic array, it may be beneficial to start the study by releasing only a portion of the total tagged animals to assess these ratios prior to addition of more animals. Essentially a ping conversion ratio can be calculated by multiplying the number of observed detections in 24-hours by the number of pings per detection (e.g. for 9006-code space animal tags, this equates to 10 pings per detection) and dividing the sum of these components by the number of observed pings in 24 hours.Case study: Ascension Island

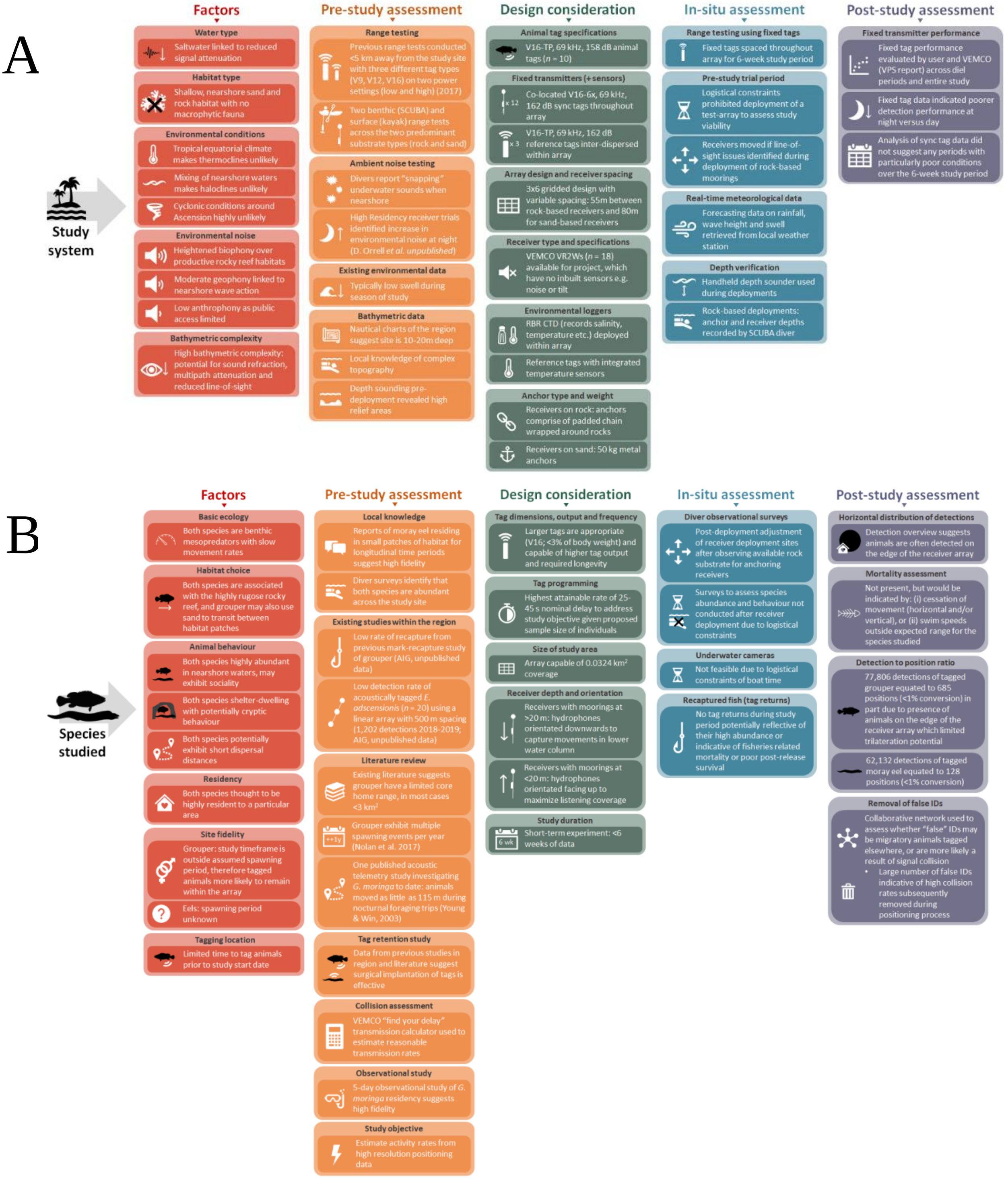
3.3.3.1 Results Part II: Applying the fine-scale framework

Following VEMCO in-house processing using TDOA analysis and applying a 12 h post-tagging recovery period, 685 rock hind grouper (*N* unique individuals positioned = 5; *N* unique positions per individual = 14 - 453) and 128 spotted moray eel positions (*N* unique individuals positioned = 2; range = 37 - 91 positions per individual) were calculated (Table

3.3, Fig. 3.7). Given the limited number of animal positions, it was not possible to address the study’s aim (animal activity estimates).

Table 3.3 Summary of adult rock hind grouper (*E. adscensionis*) and spotted moray eel (*G. moringa*) tagged with V16-TP (detections and positions are the cumulative sum of pressure and temperature transmissions) acoustic tags off the northwest coast of Ascension Island. The study dataset spanned 09:30 June 10 2019 (first fish tagged plus 12 h recovery window) – 10:00 July 27 2019 (first receiver removed). Animal weights (Wt.) were recorded with a scale accuracy ± 100 g and total length (TL) to the nearest cm.

Species	Animal ID	TL (cm)	Wt. (g)	Detection period (yyyy-mm-dd hh:mm:ss)		Number of recorded detections		Number of triangulated positions	
				First	Last	Day	Night	Day	Night
Rock hind grouper	RH02	51	1800	2019-06-10 09:35:46	2019-07-27 09:59:51	15,380	3,100	452	1
	RH03	46	1800	2019-06-10 10:19:39	2019-07-27 09:58:56	13,889	3,265	34	10
	RH04	45	1800	2019-06-09 23:05:24	2019-07-27 09:56:55	14,202	2,451	82	0
	RH05	45	1800	2019-06-10 11:08:10	2019-07-27 09:53:48	14,171	2,439	91	1
	RH06	47	1800	2019-06-10 12:04:55	2019-07-27 09:49:14	6,228	2,681	14	0
	Total					**63,870**	**13,936**	**673**	**12**
Spotted moray eel	SM03	74	1100	2019-06-20 18:05:37	2019-07-26 18:45:35	5,028	72	0	0
	SM04	85	1600	2019-06-18 03:10:22	2019-07-27 09:58:06	18,778	13,717	89	2
	SM05	120	3600	2019-06-19 07:52:48	2019-07-27 09:58:48	12,927	510	0	0
	SM06	91	1900	2019-06-23 09:18:25	2019-07-18 15:21:52	248	2	0	0
	SM07	84	1500	2019-06-19 05:59:44	2019-07-27 09:59:12	10,366	484	37	0
	Total					**47,347**	**14,785**	**126**	**2**



Water type
Saltwater linked to reduced signal attenuation

Habitat type
Shallow, nearshore sand and rock habitat with no macrophytic fauna

Environmental conditions
Tropical equatorial climate makes thermoclines unlikely
Mixing of nearshore waters makes haloclines unlikely
Cyclonic conditions around Ascension highly unlikely

Environmental noise
Heightened biophony over productive rocky reef habitats
Moderate geophony linked to nearshore wave action
Low anthrophony as public access limited

Bathymetric complexity
High bathymetric complexity: potential for sound refraction, multipath attenuation and reduced line-of-sight

Range testing
Previous range tests conducted <5 km away from the study site with three different tag types (V9, V12, V16) on two power settings (low and high) (2017)
Two benthic (SCUBA) and surface (kayak) range tests across the two predominant substrate types (rock and sand)

Ambient noise testing
Divers report "snapping" underwater sounds when nearshore
High Residency receiver trials identified increase in environmental noise at night (D. Orrell *et al. unpublished*)

Existing environmental data
Typically low swell during season of study

Bathymetric data
Nautical charts of the region suggest site is 10-20m deep
Local knowledge of complex topography
Depth sounding pre-deployment revealed high relief areas

Animal tag specifications
V16-TP, 69 kHz, 158 dB animal tags ($n = 10$)

Fixed transmitters (+ sensors)
Co-located V16-6x, 69 kHz, 162 dB sync tags throughout array
V16-TP, 69 kHz, 162 dB reference tags inter-dispersed within array

Array design and receiver spacing
3x6 gridded design with variable spacing: 55m between rock-based receivers and 80m for sand-based receivers

Receiver type and specifications
VEMCO VR2Ws ($n = 18$) available for project, which have no inbuilt sensors e.g. noise or tilt

Environmental loggers
RBR CTD (records salinity, temperature etc.) deployed within array
Reference tags with integrated temperature sensors

Anchor type and weight
Receivers on rock: anchors comprise of padded chain wrapped around rocks
Receivers on sand: 50 kg metal anchors

Range testing using fixed tags
Fixed tags spaced throughout array for 6-week study period

Pre-study trial period
Logistical constraints prohibited deployment of a test-array to assess study viability
Receivers moved if line-of-sight issues identified during deployment of rock-based moorings

Real-time meteorological data
Forecasting data on rainfall, wave height and swell retrieved from local weather station

Depth verification
Handheld depth sounder used during deployments
Rock-based deployments: anchor and receiver depths recorded by SCUBA diver

Fixed transmitter performance
Fixed tag performance evaluated by user and VEMCO (VPS report) across diel periods and entire study
Fixed tag data indicated poorer detection performance at night versus day
Analysis of sync tag data did not suggest any periods with particularly poor conditions over the 6-week study period

Basic ecology
Both species are benthic mesopredators with slow movement rates

Habitat choice
Both species are associated with the highly rugose rocky reef, and grouper may also use sand to transit between habitat patches

Animal behaviour
Both species highly abundant in nearshore waters, may exhibit sociality
Both species shelter-dwelling with potentially cryptic behaviour
Both species potentially exhibit short dispersal distances

Residency
Both species thought to be highly resident to a particular area

Site fidelity
Grouper: study timeframe is outside assumed spawning period, therefore tagged animals more likely to remain within the array
Eels: spawning period unknown

Tagging location
Limited time to tag animals prior to study start date

Local knowledge
Reports of moray eel residing in small patches of habitat for longitudinal time periods suggest high fidelity
Diver surveys identify that both species are abundant across the study site

Existing studies within the region
Low rate of recapture from previous mark-recapture study of grouper (AIG, unpublished data)
Low detection rate of acoustically tagged *E. adscensionis* ($n = 20$) using a linear array with 500 m spacing (1,202 detections 2018-2019; AIG, unpublished data)

Literature review
Existing literature suggests grouper have a limited core home range, in most cases <3 km^2
Grouper exhibit multiple spawning events per year (Nolan et al. 2017)
One published acoustic telemetry study investigating *G. moringa* to date: animals moved as little as 115 m during nocturnal foraging trips (Young & Win, 2003)

Tag retention study
Data from previous studies in region and literature suggest surgical implantation of tags is effective

Collision assessment
VEMCO "find your delay" transmission calculator used to estimate reasonable transmission rates

Observational study
5-day observational study of *G. moringa* residency suggests high fidelity

Study objective
Estimate activity rates from high resolution positioning data

Tag dimensions, output and frequency
Larger tags are appropriate (V16; <3% of body weight) and capable of higher tag output and required longevity

Tag programming
Highest attainable rate of 25-45 s nominal delay to address study objective given proposed sample size of individuals

Size of study area
Array capable of 0.0324 km^2 coverage

Receiver depth and orientation
Receivers with moorings at >20 m: hydrophones orientated downwards to capture movements in lower water column
Receivers with moorings at <20 m: hydrophones orientated facing up to maximize listening coverage

Study duration
Short-term experiment: <6 weeks of data

Diver observational surveys
Post-deployment adjustment of receiver deployment sites after observing available rock substrate for anchoring receivers
Surveys to assess species abundance and behaviour not conducted after receiver deployment due to logistical constraints

Underwater cameras
Not feasible due to logistical constraints of boat time

Recaptured fish (tag returns)
No tag returns during study period potentially reflective of their high abundance or indicative of fisheries related mortality or poor post-release survival

Horizontal distribution of detections
Detection overview suggests animals are often detected on the edge of the receiver array

Mortality assessment
Not present, but would be indicated by: (i) cessation of movement (horizontal and/or vertical), or (ii) swim speeds outside expected range for the species studied

Detection to position ratio
77,806 detections of tagged grouper equated to 685 positions (<1% conversion) in part due to presence of animals on the edge of the receiver array which limited trilateration potential
62,132 detections of tagged moray eel equated to 128 positions (<1% conversion)

Removal of false IDs
Collaborative network used to assess whether "false" IDs may be migratory animals tagged elsewhere, or are more likely a result of signal collision
- Large number of false IDs indicative of high collision rates subsequently removed during positioning process

Figure 3.2 Applying the VPS considerations framework to the Ascension Island six-week study. Considerations fall under four key themes relating to **A**. the study system, **B**. the species studies, **C**. logistical constraints and **D**. technological constraints. The framework incorporates factors (red boxes) linked to the four key themes, with associated pre-study assessment criteria (orange box) that will drive design considerations. In turn in-situ and post-study assessment tools are detailed which can be used to pinpoint the underlying causes of poor data yield.

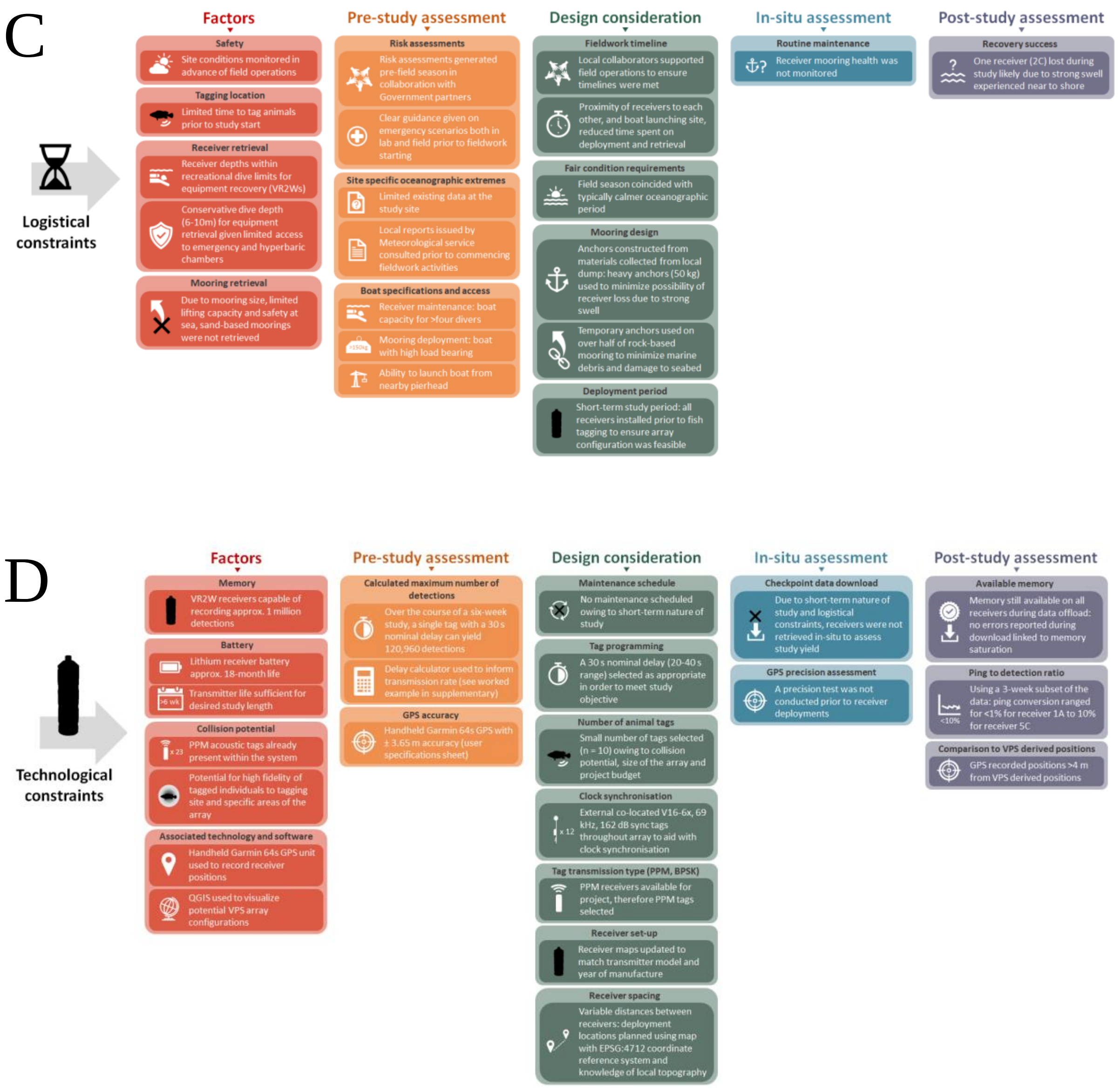


Figure 3.2. Applying the VPS considerations framework to the Ascension Island six-week study. Considerations fall under four key themes relating to **A**. the study system, **B**. the species studies, **C**. logistical constraints and **D**. technological constraints. The framework incorporates factors (red boxes) linked to the four key themes, with associated pre-study assessment criteria (orange box) that will drove design considerations. In turn in-situ and post-study assessment tools are detailed which can be used to pinpoint the causes of poor data yield.

3.3.3.2 Application of the fine-scale positioning consideration framework

By fitting our study in the fine-scale positioning considerations framework (Fig. 3.1) and undertaking the post-study assessments techniques, we identified three elements of this study that likely explain low data yield (see Fig. 3.2 for a full breakdown of pre- in-situ and post-study assessment steps). These elements fell into categories linked to; (i) the *study system*, including high environmental noise and limited detection range, which likely limited positioning and caused signal masking, (ii) the *species studied* whereby tagged individuals spent a large proportion of time in refuge and likely out of line-of-sight of receivers, and (iii) *logistical* and *technological constraints* caused by the small distance between receivers, limited detection area coverage of the array, programmed high transmission rates and clustering of animals at the edges of the array leading to high rates of signal collision. In addition, logistical constraints meant that it was not possible to obtain data from a small window prior to the study e.g. the first week, to confirm the design was optimal.

Study system

Preliminary range testing using fixed-interval (0-500 m; 50 m increments), short-term (<24 hours) benthic (SCUBA) and surface (kayak) range testing (methods detailed in Supplementary Material S3.1) conducted in May 2019 identified lower detection efficiency across rock habitats (*N* range tests = 2; Fig. 3.4B) than sand (*N* range tests = 2) (Fig. 3.4A). These findings were similar to those generated from range tests conducted within the area in 2017 (Supplementary Material S3.1), wherein larger VEMCO V16 tags were identified as the best performing tag type. The detection range was estimated as 90% at 50 m using VEMCO V9, V13 and V16 tags (Fig. 3.4A), with the V16 tag having the highest detection efficiency compared to other tags at greater distances from the listening receiver, as would be expected (70% at 100 m versus 30% at 100m for the V9 tag). We opted for non-uniform spacing between VPS receivers; 55 m between those deployed in rock habitats versus 80 m spacing across sand habitats to accommodate the disparity between detection range and substrate type (Fig. 3.5). Due to *logistical limitations,* including limited boat access and time constraints, we could not assess the system's performance using a short-term pilot study or an early checkpoint data download.

It is unlikely that seasonality caused detection variation owing to the six-week study period and low tidal fluctuation due to proximity to the equator. However, post-study performance assessments of data yield using fixed tags within the array (sync and reference tags) identified fewer detections recorded at night versus the day (Fig. 3.4B); the array recorded 311,696 sync (range = 19,022 – 38,183) and 56,933 (range = 8,564 – 28,198) reference tag detections (Table 3.4). This equated to 38,719 sync and 6,306 reference positions. Diurnal differences in system performance were evident across the array, regardless of the substrate (Table 3.4). During 24-hour ambient noise testing using VEMCO High Residency (HR2) receivers (180 kHz; 60 s sampling interval) conducted in 2019 and 2021 within the area (>0.5 km away), we identified that ambient environmental noise levels were significantly higher on rock versus sand (*unpublished data*) which likely caused signal masking in areas where we anticipated tagged animals were residing. Tied with this Ascension's sea state can be unpredictable, with limited existing data available. During the study, one of the acoustic receivers deployed inshore (between 1C and 3C; Fig. 3.3) with a collocated sync tag was lost, likely as a result of deterioration of the volcanic rock under pressure; all rock-based receivers were moored using a 2 mm steel chain insulated in 64 mm firehose wrapped around large arches of volcanic rock. Dynamic oceanographic conditions in the coastal region, e.g. high wave action across the array owing to its proximity to shore, likely led to high levels of geophony during the study.

The identified diurnal differences in system performance and suspected high ambient environmental noise limited the behavioural inferences that could be made from these data due to the introduced bias in detection ratios (night versus day). In addition, given that one of the study species (*G. moringa*) is primarily nocturnal, it is unclear whether a lack of detections was due to its cryptic behaviour and inactivity or the system's performance during nighttime hours.

Table 3.4 Summary of detections and positions for fixed transmitters (reference and sync) deployed alongside (sync) or within (reference) the VPS array. The study dataset spanned from when the array was completed on June 7 2019 (all receivers in-water), to the first receiver removal on July 26 2019.

Tag type	No. tags	No. recorded detections			No. triangulated positions		
		Day	Night	**Total**	Day	Night	**Total**
Reference	3	39,700	16,713	**56,413**	5,798	508	**6,306**
Sync	11	213,984	91,527	**305,511**	31,189	7,530	**38,719**
Total	**14**	**253,684**	**107,240**	**361,924**	**36,987**	**8,038**	**45,025**

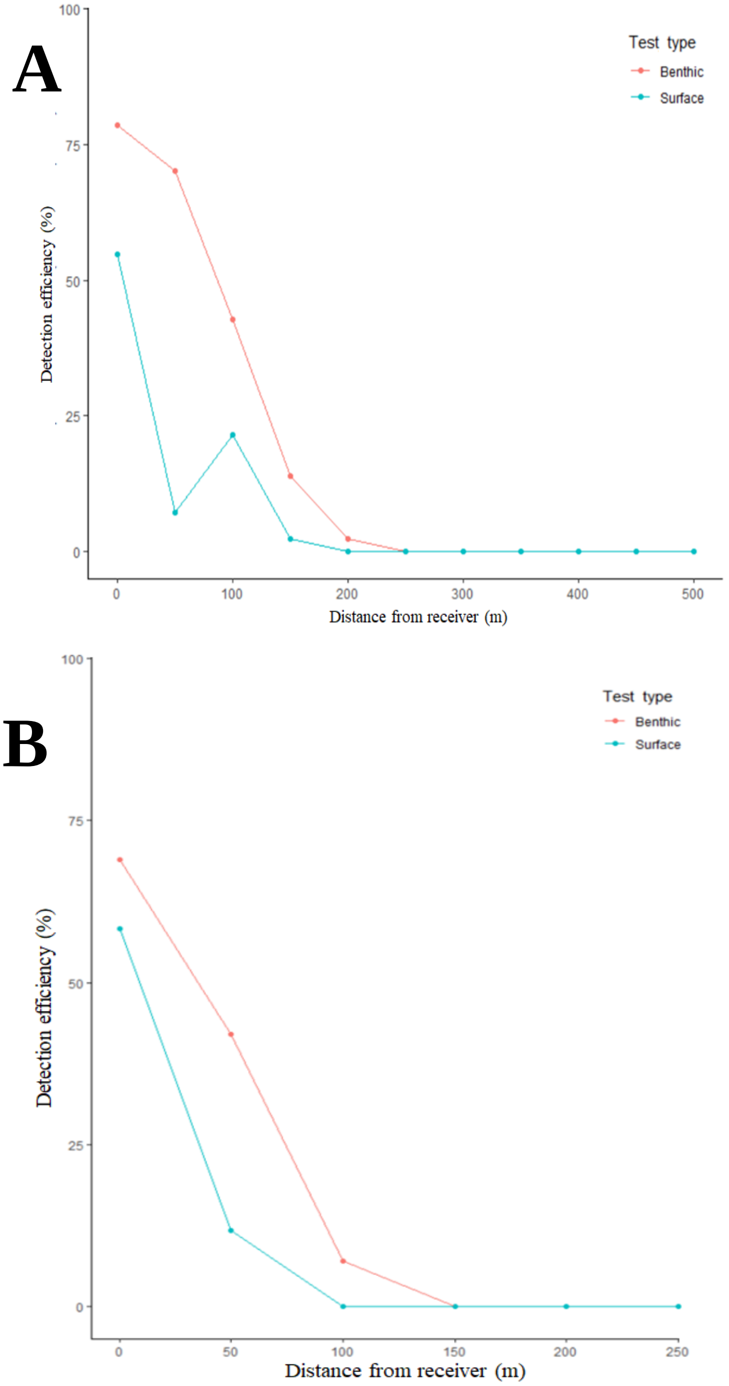


Figure 3.3 Range tests conducted in English Bay, northwest of Ascension Island. Surface tests (blue line) were conducted from a kayak, and benthic tests using SCUBA (red line; full methodology in Supplementary Material S3.1) using a VEMCO V16 range test tag (7 s nominal transmission rate, 158 dB) power. A) Trials conducted across sand environments, with the range test tag held at fixed distances of 0 – 250 m during benthic trials, and 0 – 500 m during surface trials. B) Trials conducted across rock environments, with the tag held at distances of 0 – 250 m for both surface and benthic trials.

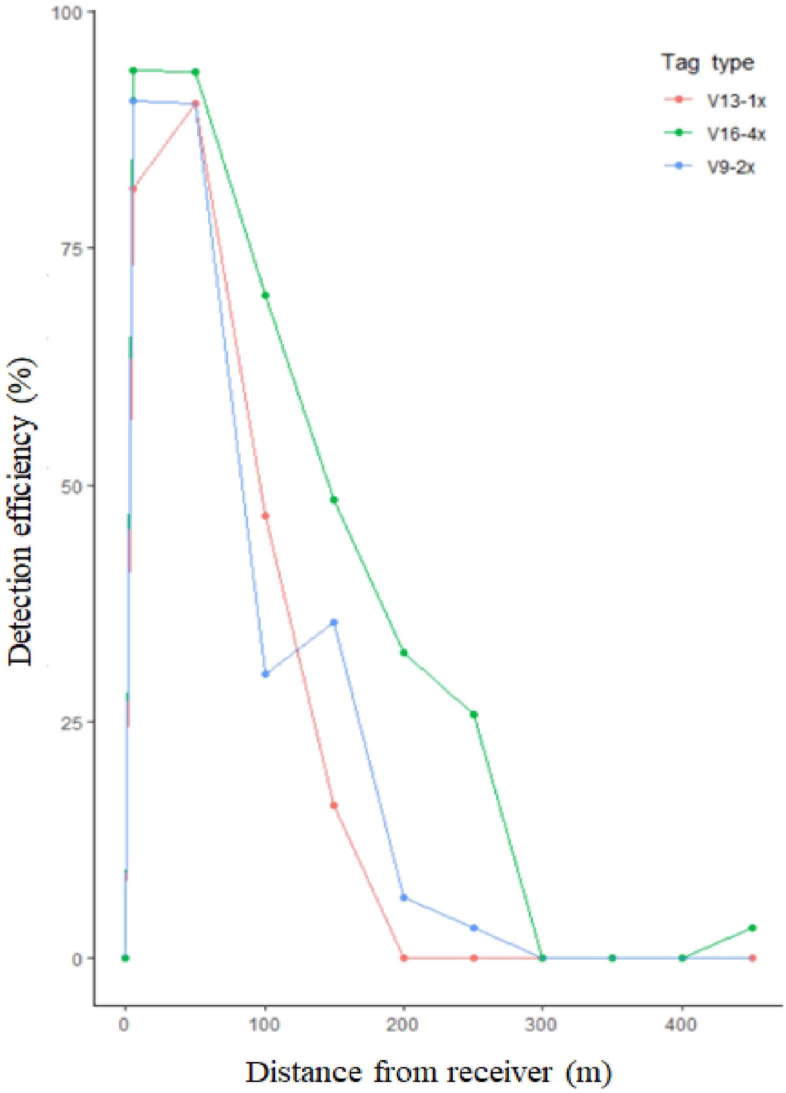


Figure 3.4 Range test output for tests conducted in English Bay, northwest of Ascension Island in March 2017 using three tag types (red = V13-1; green = V16-4x; blue = V9-2x) using fixed-distance surface tests from a kayak (0 - 450 m at 50 m intervals)

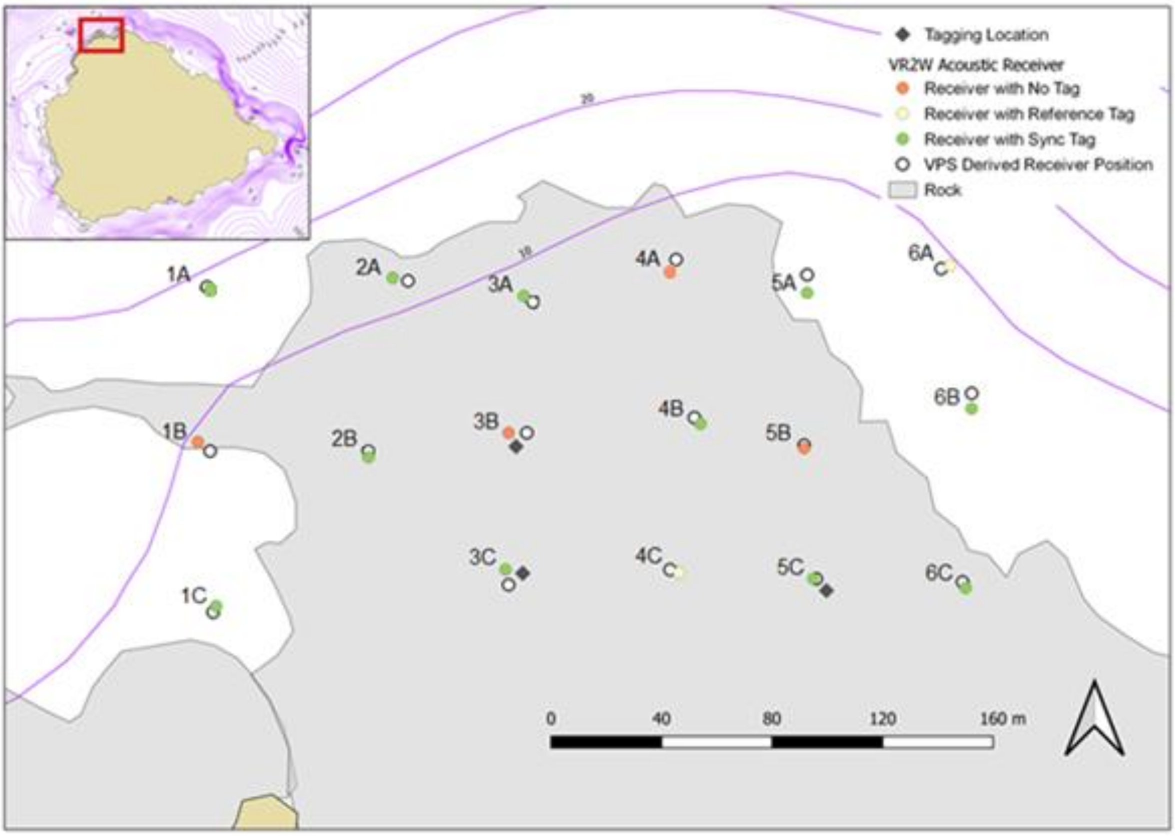


Figure 3.5 VPS array comprised of acoustic receivers (VR2W, *n* = 17; 69 kHz), situated northwest of Ascension Island (inset: top left) in the South Atlantic Ocean (7°56'S 14°25'W). Receivers without attached sensor tags are shown by the filled orange circles (*n* = 3), receivers with a reference tag attached to the line are shown by the filled yellow circles (V16-6x; 540-600 s transmission delay, 158 dB; *n* = 2), and receivers with a synchronisation ("sync" tag) tag attached to the receiver line are shown by the filled green circles (V16-6x, 540–660 s transmission delay, 158 dB, *n* = 12). The triangulated location (filled white circle) of the receivers differed to that recorded by the handheld GPS (Garmin eTrex 20x) by > 7 m. Animals were tagged at station 3B (*n Epinephelus adscensionis* = 5), 3C (*n Gymnothorax moringa* = 3), and 5C (*G. moringa* = 2), these locations are indicated by the gray filled diamond.

Species studied

Local knowledge and published literature (tracking species within the same families) suggested that rock hind grouper and spotted morays exhibit high site fidelity and a small home range. For example, Young & Winn (2003) recorded that *G. moringa* moved as little as 115 m during nocturnal foraging trips using observational surveys, and Hutchinson & Rhodes (2010) reported a home range for coral trout (*Plectropomus areolatus*) of 0.004 km^2 using active tracking. We also confirmed the fidelity of our focal species using a week-long observational diver survey of *G. moringa* conducted prior to the VPS (using methods adapted from Abrams et al. 1973). We found that both species showed high fidelity to complex volcanic habitats and burrows during this time.

Due to time constraints and data limitations, bathymetric data for VPS planning was interpolated from existing admiralty charts to guide the array design. Depth surveys of the proposed array site were conducted using a handheld depth sounder (HawkEye DT1H) to ensure the deployed receivers sat c. 6 m below the water's surface to (i) facilitate recovery on SCUBA, (ii) limit line of sight issues and (iii) to reduce the impact of surface water noise on signal reception. Post-study assessment of the array bathymetry using datapoints opportunistically collected during additional fieldwork revealed the heterogeneous landscape of Ascension’s nearshore environment (Fig. 3.6). It is highly likely that the cryptic nature of the focal species within the highly rugose volcanic substrate limited simultaneous detection on three or more receivers due to line of sight issues between tagged animals and listening receivers.

Logistical constraints and technological limitations

During pre-study planning, we used the VEMCO calculator (Supplementary Material S3.3) to estimate the fastest transmission rate achievable to address the study objectives while minimizing signal collision due to identified factors (see section above) and tagged animals already present in the system. Given the limited detection range identified through pre-study range testing, receivers were conservatively placed 55 m (rock) and 80 m apart (sand), which amounted to a VPS coverage of c. 0.11 km^2. Due to logistical constraints, including opportune weather window and available boat time, fish (N = 10 for both species combined) were tagged at three locations within the array (Fig. 3.3). Given the close proximity of receivers and the high power of associated sync tags across this array, this likely compounded the collision probability. In addition, as noted above, a pre-study trial or checkpoint was not logistically possible, preventing an in-situ assessment of collision that ultimately compromised this study. Post-study assessment using visualizations of the tagged animal detections and (limited) positions suggested grouper (Fig. 3.8A) and eel (Fig. 3.8B) clustered towards the edges of the array, limiting interpretation of space use, e.g. whether the true home range was captured. In addition, calculated ping to detection and detection to position ratios for these edge receivers revealed extremely high collision rates (Table 3.5) (<1% transmissions received by an acoustic receiver versus the number transmitted at 1A). High collision rates were likely due to a combination of factors linked to animal behaviour (clustering of individuals in regions of the array), the study system's topography (signal reflection from the rocky substrate, multipath signal attenuation), and study design choices (close receiver spacing, high tag transmission rates, high power settings of animal and fixed tags). Signal collisions were also evident from the number of false IDs (*n* = 67) generated during the 6-week study period.

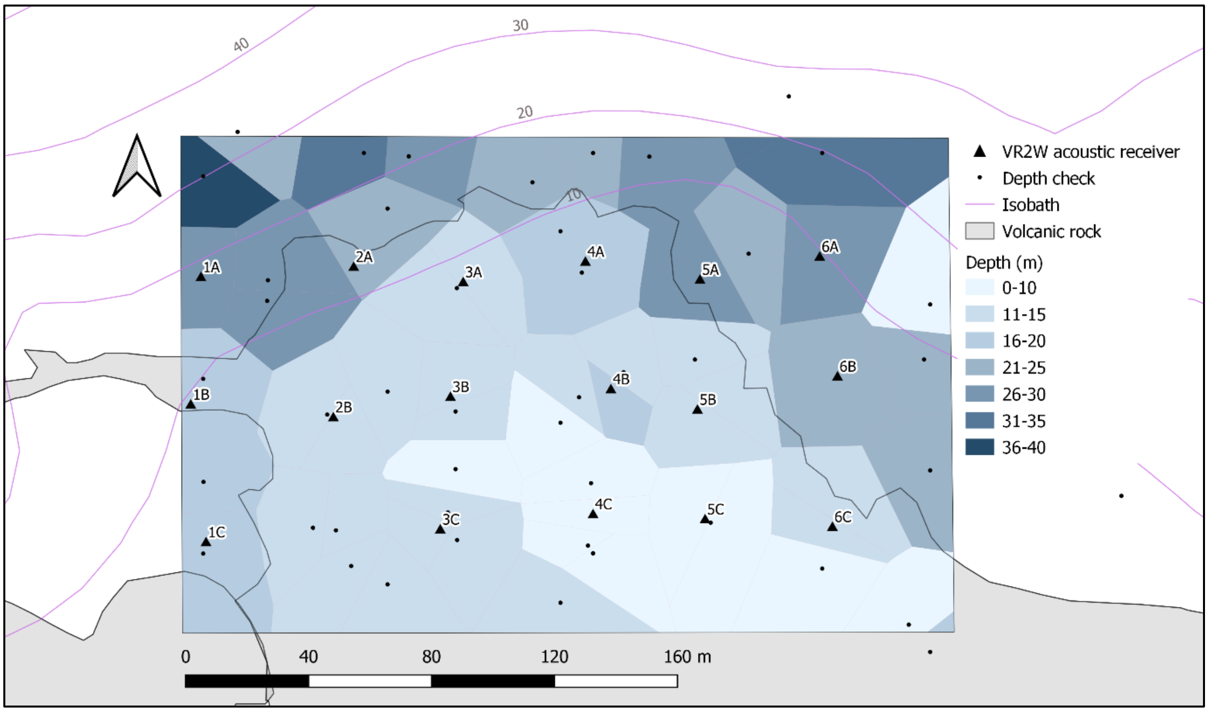


Figure 3.6 Bathymetric complexity across the study site where the array was deployed off northwest Ascension Island. A comparison of the inferred bathymetry from the 1691 British Admiralty Nautical Chart to Voronoi polygons (5% buffer) generated from opportunistic depth point data (*n* = 78) collected using a handheld GPS (Garmin eTrex 30x) during the study period.

Table 3.5 The total number of detections and pings recorded by VEMCO VR2W acoustic receivers (*N* = 17) deployed northwest of Ascension Island from June 6 2019 to July 27 2019. The ping conversion (PCR) was calculated as: (No. recorded detections in 24 hours * the number of pings per detection) / No. observed pings in 24 hours) * 100. The PCR was rounded to 2 d.p.

Station	Total detections	Total pings	PCR (%)
1A	16,870	1,794,700	0.94
1B	49,758	614,865	8.09
1C	34,897	322,615	10.82
2A	54,587	1,796,069	3.04
2B	20,838	1,338,882	1.56
3A	29,414	1,660,953	1.77
3B	43,848	804,293	5.45
3C	20,574	1,163,630	1.77
4A	46,606	920,355	5.06
4B	17,509	587,183	2.98
4C	43,905	450,316	9.75
5A	19,311	698,545	2.76
5B	42,305	1,003,989	4.21
5C	37,083	364,453	10.17
6A	41,076	795,802	5.16
6B	36,354	748,598	4.86
6C	26,215	314,510	8.34

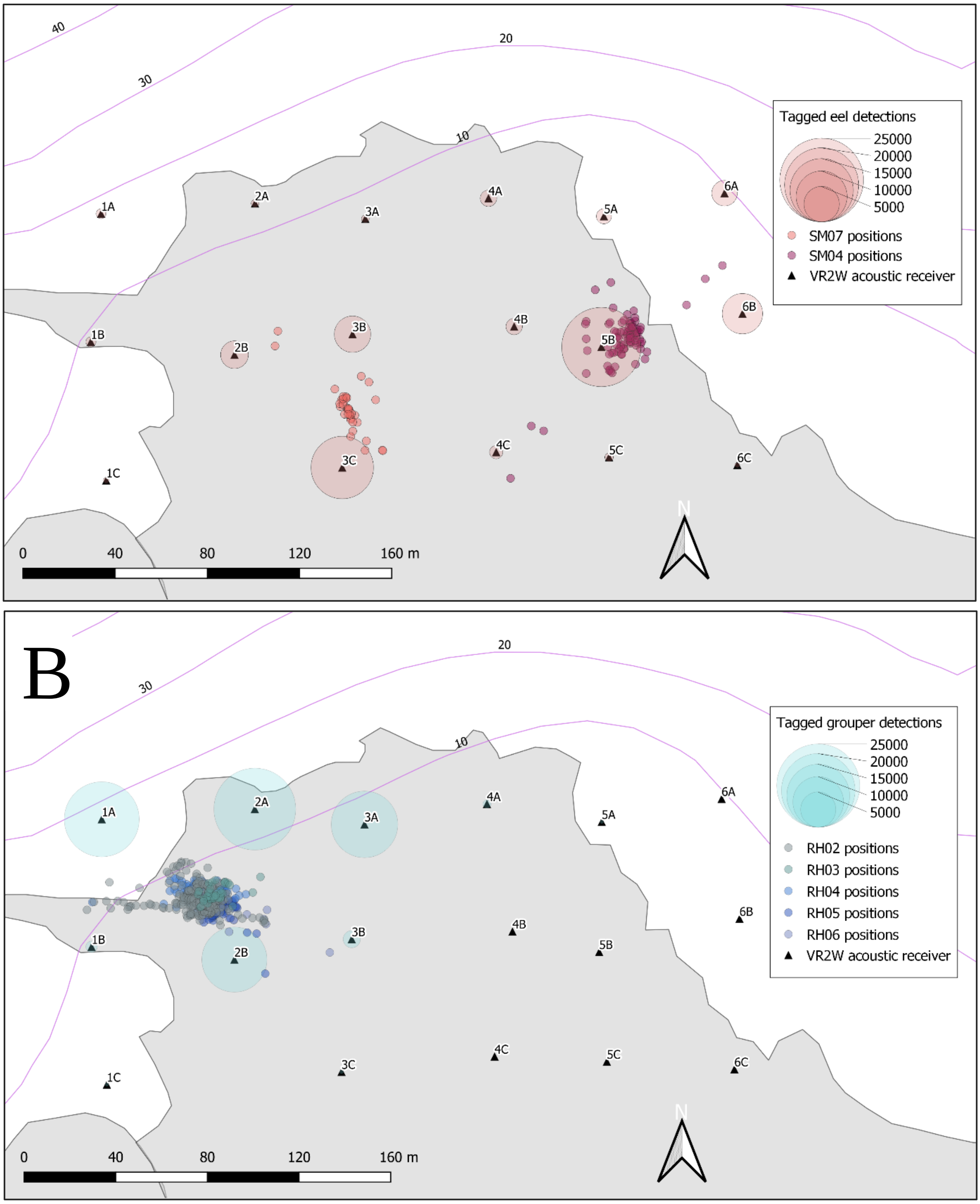


Figure 3.7 Raw acoustic detections of tagged fish (proportional circle) and estimated positions from VPS processed data (different colours indicating different individuals). A) Tagged spotted moray (*G. moringa*, *n* = 5) detections and locations with only two individuals positioned, B) Tagged rock hind (*E. adscensionis*, *n* = 5).

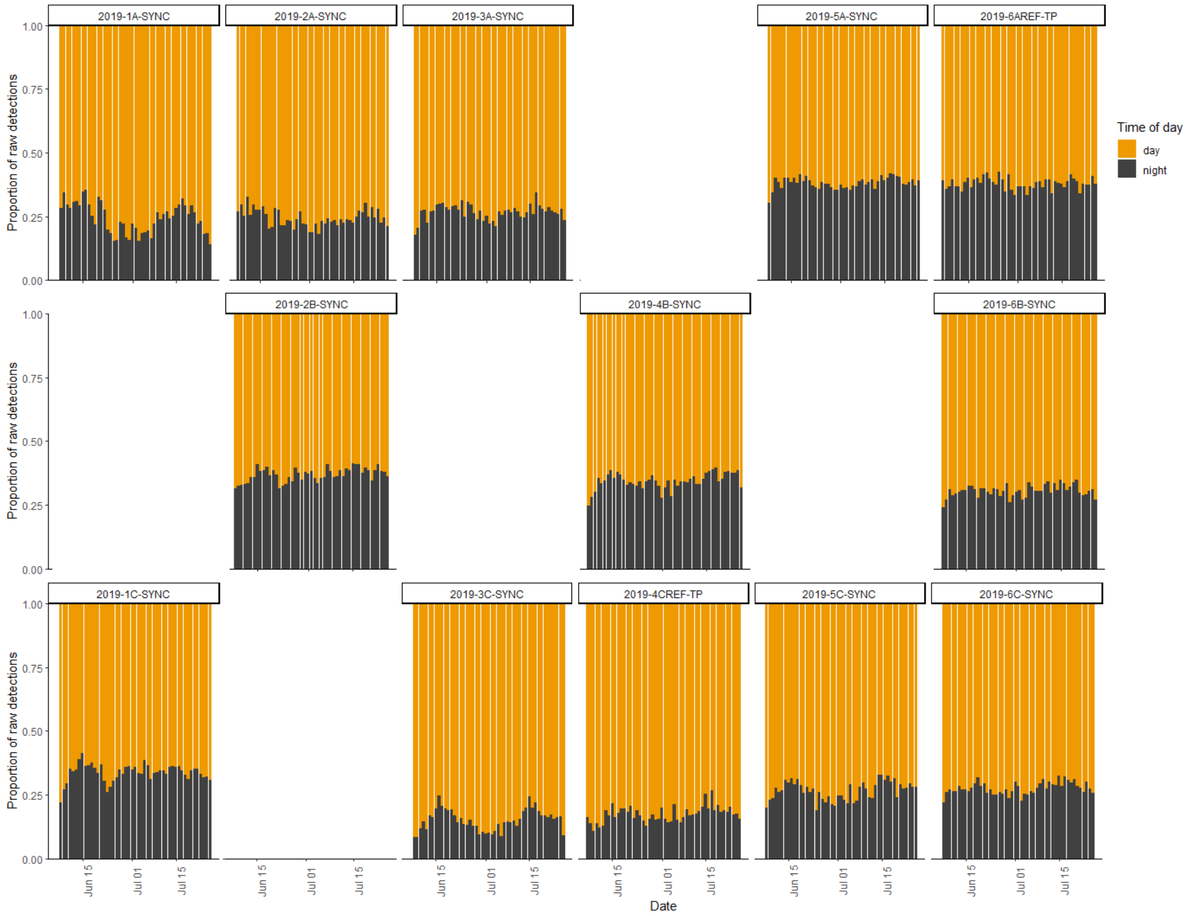


Figure 3.8 Sync tag performance within the Ascension Island acoustic array: number of detections of fixed co-located acoustic synchronisation (“sync”, *n* = 12) and reference (“REF-TP, *n* = 2) tags (VEMCO V16-H, 152 dB, 240-300 s delay; deployed during the six-week study period. Total detections are expressed as a proportion of diurnal detections (day, orange; night, black). Graph grid arrangement matches position (and presence) of fixed tags within 6x3 Vemco Positioning System array of VEMCO VR2W acoustic receivers (see Fig. 3.5).

3.4 Conclusions

This review highlights key considerations for designing a fine-scale acoustic positioning study and provides a framework to identify pre-study, in-situ, and post-study assessment criteria that new or experienced users can follow to maximise data acquisition and accuracy. We highlight the importance of reporting the technical specifications of VPS study design (applied pre-during-post study assessment criteria) in published papers or supplementary material files to promote transparency and allow a robust assessment of the ecological findings. We note that the framework presented here, while based on VPS, is largely applicable to other fine-scale tracking systems. Given the recommendations highlighted in this framework (including factoring in the additional boat time for initial checkpoints, collection of initial bathymetry data, and pre-study examination of species movements), we highly suggest that pre-study tools are incorporated into budgets when writing project proposals. This step could become standard and accepted practice and would maximise data output from fine-scale tracking studies. A clear description of the technical specifications of the study is of particular importance, given that fine-scale positioning data is central to our understanding of animal behaviour and ecophysiology and is often used to inform management. With the continued exploration of the factors which affect VPS performance (and other similar fine-scale tracking systems) and the adoption of this standardized framework, these systems have tremendous potential to redefine our understanding of fine-scale movement behaviours of fully aquatic animals.

3.5 References

Abrams RW, Abrams MD, Schein MW (1973) Diurnal Observations on the Behavioral Ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean Coral Reef. Coral Reefs 1:185–192.

Andrews KS, Tolimieri N, Williams GD, Samhouri JF, Harvey CJ, Levin PS (2011) Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. Mar Biol 158:2377–2387.

Armansin NC, Lee KA, Huveneers C, Harcourt RG (2016) Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark. Anim Behav 115:245–258.

Armstrong AO (2021) Mutualism promotes site selection in a large marine planktivore. Ecol Evol 11:5606-5623.

Bacheler NM, Shertzer KW, Cheshire RT, MacMahan JH (2019) Tropical storms influence the movement behavior of a demersal oceanic fish species. Sci Rep 9:1481.

Bacheler NM, Shertzer KW, Runde BJ, Rudershausen PJ, Buckel JA (2021) Environmental conditions, diel period, and fish size influence the horizontal and vertical movements of red snapper. Sci Rep 11:9580.

Baggeroer A (1984) Acoustic telemetry - An overview. IEEE Journal of Oceanic Engineering 9:229–235.

Baker NJ, Boubée J, Lokman PM, Bolland JD (2020) Evaluating the impact of hydropower on downstream migrating anguillid eels: Catchment-wide and fine-scale approaches to identify cost-effective solutions. Sci Total Environ 748:141111.

Balazik M, Barber M, Altman S, Reine K, Katzenmeyer A, Bunch A, Garman G (2020) Dredging activity and associated sound have negligible effects on adult Atlantic sturgeon migration to spawning habitat in a large coastal river. PLoS ONE 15:e0230029.

Barilotti AA, White CF, Lowe CG (2020) Are fishes attracted to piers? Movements and association of marine fishes to a public fishing pier within a commercial harbor. Bulletin, Southern California Academy of Sciences 119:18.

Bašić T, Aislabie L, Ives M, Fronkova L, Piper A, Walker A (2019) Spatial and temporal behavioural patterns of the European eel *Anguilla anguilla* in a lacustrine environment. Aquat Sci 81:73.

Becker SL, Finn JT, Novak AJ, Danylchuk AJ, Pollock CG, Hillis-Starr Z, Lundgren I, Jordaan A (2020) Coarse- and fine-scale acoustic telemetry elucidates movement patterns and temporal variability in individual territories for a key coastal mesopredator. Environ Biol Fishes 103:13-29.

Binder TR, Holbrook CM, Hayden TA, Krueger CC (2016) Spatial and temporal variation in positioning probability of acoustic telemetry arrays: fine-scale variability and complex interactions. Animal Biotelemetry 4:1–15.

Bohaboy E, Guttridge TL, Hammerschlag N, Van Zinnicq Bergman MPM, Patterson W F (2020) Application of three-dimensional acoustic telemetry to assess the effects of rapid recompression on reef fish discard mortality. ICES J Mar Sci 77:83–96.

Bridger CJ, Booth RK (2003) The Effects of Biotelemetry Transmitter Presence and Attachment Procedures on Fish Physiology and Behavior. Rev Fish Sci 11:13–34.

Brownscombe JW, Cooke SJ, Danylchuk AJ (2017) Spatiotemporal drivers of energy expenditure in a coastal marine fish. Oecologia 183:689–699.

Brownscombe JW, Lédée EJI, Raby GD, Struthers DP and others (2019) Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. Rev Fish Biol Fish 29:369–400.

Buchinger TJ, Marsden JE, Binder TR, Huertas M, Bussy U, Li K, Hanson JE, Krueger CC, Li W, Johnson NS (2017) Temporal constraints on the potential role of fry odors as cues of past reproductive success for spawning lake trout. Ecol Evol 7:10196–10206.

Burdic WS (1984) Underwater acoustic system analysis. Prentice-Hill, Englewood Cliffs, New Jersey, USA.

Cagua EF, Berumen ML, Tyler EHM (2013) Topography and biological noise determine acoustic detectability on coral reefs. Coral Reefs 32:1123–1134.

Carpenter-Bundhoo L, Butler GL, Espinoza T, Bond NR, Bunn SE, Kennard MJ (2019) Reservoir to river: Quantifying fine-scale fish movements after translocation. Ecol Freshw Fish 29:89–102.

Coates J, Hovel K, Butler J, Klimley A, Morgan S (2013) Movement and home range of pink abalone Haliotis corrugata: implications for restoration and population recovery. Mar Ecol Prog Ser 486:189–201.

Coppens, A.B. (1981) Simple equations for the speed of sound in Neptunian waters J. Acoust. Soc. Am. 69(3), 862-863.

Cote D, Nicolas J-M, Whoriskey F, Cook AdamM, Broome J, Regular PM, Baker D (2019) Characterizing snow crab (*Chionoecetes opilio*) movements in the Sydney Bight (Nova Scotia, Canada): A collaborative approach using multiscale acoustic telemetry. Can J Fish Aquat Sci 76:334–346.

Cote D, Tibble B, Curry RA, Peake S, Adams BK, Clarke KD, Perry R (2020) Seasonal and diel patterns in activity and habitat use by brook trout (*Salvelinus fontinalis*) in a small Newfoundland lake. Environ Biol Fishes 103:31–47.

Dahl KA, Patterson WF (2020) Movement, home range, and depredation of invasive lionfish revealed by fine-scale acoustic telemetry in the northern Gulf of Mexico. Mar Biol 167:111.

Dance MA, Moulton DL, Furey NB, Rooker JR (2016) Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research? Fish Res 183:80–85.

Dean MJ, Hoffman WS, Zemickis DR, Armstrong MP (2014) Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine. ICES J Mar Sci 71:1474–1489.

Duxbury A C (2021) Chemical and physical properties of sewater: Acoustic properties. Britannica.

Duxbury AC, Mackenzie FT, Bryne HB (2018) Seawater. https://www.britannica.com/science/seawater

Ellis RD, Flaherty-Walia KE, Collins AB, Bickford JW, Boucek R, Walters Burnsed SL, Lowerre-Barbieri SK (2018) Acoustic telemetry array evolution: From species- and project-specific designs to large-scale, multispecies, cooperative networks. Fish Res 209:186–195.

Enge PK (1994) The Global Positioning System: Signals, measurements, and performance. Int J Wireless Inf Networks 1:83–105.

Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res 108:364–371.

Espinoza T, Burke C, Carpenter-Bundhoo L, Marshall S, Roberts D, Kennard M (2020) Fine-scale acoustic telemetry in a riverine environment: movement and habitat use of the endangered Mary River cod *Maccullochella mariensis*. Endang Species Res 42:125–131.

Everett A, Szedlmayer S, Gallaway B (2020) Movement patterns of red snapper *Lutjanus campechanus* based on acoustic telemetry around oil and gas platforms in the northern Gulf of Mexico. Mar Ecol Prog Ser 649:155–173.

Fahlman J, Hellström G, Jonsson M, Veenstra A, Klaminder J (2020) Six common behavioral trials and their relevance for perch performance in natural lakes. Sci Total Environ 732:139101.

Furey NB, Dance MA, Rooker JR (2013) Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape. J Fish Biol 82:1469–1483.

Guzzo MM, Blanchfield PJ, Chapelsky AJ, Cott PA (2016) Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. J Great Lakes Res 42:276–285.

Guzzo MM, Van Leeuwen TE, Hollins J, Koeck B, Newton M, Webber DM, Smith FI, Bailey DM, Killen SS (2018) Field testing a novel high residence positioning system for monitoring the fine-scale movements of aquatic organisms. Methods Ecol Evol 9:1478–1488.

Herbig JL, Szedlmayer ST (2016) Movement patterns of gray triggerfish, *Balistes capriscus*, around artificial reefs in the northern Gulf of Mexico. Fish Manag Ecol 23:418–427.

Heupel MR, Semmens JM, Hobday AJ, Arendt MD and others (2006) Automated Acoustic Tracking of Aquatic Animals: Scales, Design and Deployment of Listening Station Arrays. Mar Freshw Res 57:1.

Hutchinson N, Rhodes KL (2010) Home range estimates for squaretail coralgrouper, *Plectropomus areolatus* (Rüppell 1830). Coral Reefs 29:511–519.

Huveneers C, Simpfendorfer CA, Kim S, Semmens JM, Hobday AJ, Pederson H, Stieglitz TC, Vallee R, Webber D, Heupel MR, Peddemors V, Harcourt RG (2016) The influence of environmental parameters on the performance and detection range of acoustic receivers. Methods Ecol Evol 7:825–835.

Itakura H, Miyake Y, Kitagawa T, Kimura S (2018) Site fidelity, diel and seasonal activities of yellow-phase Japanese eels (*Anguilla japonica*) in a freshwater habitat as inferred from acoustic telemetry. Ecology of Freshwater Fish 27:737–751.

Ivanova SV, Kessel ST, Landry J, O’Neill C, McLean MF, Espinoza M, Vagle S, Hussey NE, Fisk AT (2018) Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. Can J Fish Aquat Sci 75:2390–2400.

Jellyman DJ, Unwin MJ (2019) Fine-scale swimming movement and behaviour of female silver eels, *Anguilla dieffenbachii*, within a lake affected by hydro-power generation. Fish Manag Ecol 26:57–69.

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218.

Kessel ST, Hussey NE, Webber DM, Gruber SH, Young JM, Smale MJ, Fisk AT (2015) Close proximity detection interference with acoustic telemetry: The importance of considering tag power output in low ambient noise environments. Anim Biotelemetry 3:5.

Klinard NV, Halfyard EA, Matley JK, Fisk AT, Johnson TB (2019) The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. Anim Biotelemetry 7:1–17.

van der Knaap I, Slabbekoorn H, Winter HV, Moens T, Reubens J (2021) Evaluating receiver contributions to acoustic positional telemetry: A case study on Atlantic cod around wind turbines in the North Sea. Anim Biotelemetry 9:14.

Kuai Y, Klinard NV, Fisk AT, Johnson TB, Halfyard EA, Webber DM, Smedbol SJ, Wells MG (2021) Strong thermal stratification reduces detection efficiency and range of acoustic telemetry in a large freshwater lake. Anim Biotelemetry 9:46.

Leander J, Brodin T, Leonardsson K (2019) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. Can J Fish Aquat Sci.

Lindstedt SL, Miller BJ, Buskirk SW (1986) Home Range, Time, and Body Size in Mammals. Ecology 67:413–418.

Logan RK, Lowe CG (2019) Space use and inferred spawning activity of three exploited gamefish species on a large artificial reef. Fish Manag Ecol 26:558–569.

Loher T (2017) A test of the detection range of acoustic transmitters and receivers deployed in deep waters of Southeast Alaska, USA. Animal Biotelemetry 5:22.

Marsden JE, Binder TR, Johnson J, He J, Dingledine N, Adams J, Johnson NS, Buchinger TJ, Krueger CC (2016) Five-year evaluation of habitat remediation in Thunder Bay, Lake Huron: Comparison of constructed reef characteristics that attract spawning lake trout. Fish Res 183:275–286.

Meckley TD, Holbrook CM, Wagner C, Binder TR (2014) An approach for filtering hyperbolically positioned underwater acoustic telemetry data with position precision estimates. Anim Biotelem 2:7.

Medwin H, Clay CS (1998) Fundamentals of acoustical oceanography. Academic Press, Boston.

Miyoshi K, Kuwahara Y, Miyashita K (2018) Tracking the Northern Pacific sea star *Asterias amurensis* with acoustic transmitters in the scallop mariculture field of Hokkaido, Japan. Fish Sci 84:349–355.

Mooney TA, Di Iorio L, Lammers M, Lin T-H, Nedelec SL, Parsons M, Radford C, Urban E, Stanley J (2020) Listening forward: approaching marine biodiversity assessments using acoustic methods. R Soc open sci 7:201287.

Moulton DL, Dance MA, Williams JA, Sluis MZ, Stunz GW, Rooker JR (2017) Habitat partitioning and seasonal movement of red drum and spotted seatrout. Estuar Coasts 40:905–916.

Mucientes G, Leeb K, Straßer F-E, Villegas-Ríos D, Alonso-Fernández A (2021) Short-term survival, space use and diel patterns of coastal fish species revealed from 'solo datasets.' Mar Freshwat Behav Physiol 54:87–95.

Nanami A, Mitamura H, Sato T, Yamaguchi T, Yamamoto K, Kawabe R, Soyano K, Arai N, Kawabata Y (2018) Diel variation in home range size and precise returning ability after spawning migration of coral reef grouper *Epinephelus ongus*: Implications for effective marine protected area design. Mar Ecol Prog Ser 606:119–132.

Olsen TB, Christensen FEG, Lundgreen K, Dunn PH, Levitis DA (2015) Coelomic transport and clearance of durable foreign bodies by starfish (*Asterias rubens*). The Biological Bulletin 228:156–162.

Orrell DL, Hussey NE (2022) Using the VEMCO Positioning System (VPS) to explore fine-scale movements of aquatic species: applications, analytical approaches and future directions. Mar Ecol Prog Ser 687:195–216.

Özgül A, Lök A, Tansel Tanrıkul T, Alós J (2019) Home range and residency of S*corpaena porcus* and *Scorpaena scrofa* in artificial reefs revealed by fine-scale acoustic tracking. Fish Res 210:22–30.

Parkinson BW, Spilker JJ (1996) Progress In Astronautics and Aeronautics: Global Positioning System: Theory and Applications. AIAA.

Payne N, Gillanders B, Webber D, Semmens J (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. Mar Ecol Prog Ser 419:295–301.

Pincock DG (2012) False detections: What they are and how to remove them from detection data. Amirix Document DOC-004691 Version 03: Available: http://vemco.com/wp-content/uploads/201.

Piraino MN, Szedlmayer ST (2014) Fine-Scale Movements and Home Ranges of Red Snapper around Artificial Reefs in the Northern Gulf of Mexico. Trans Am Fish Soc 143:988–998.

Radford C, Stanley J, Tindle C, Montgomery J, Jeffs A (2010) Localised coastal habitats have distinct underwater sound signatures. Mar Ecol Prog Ser 401:21–29.

Rasmuson LK, Blume MTO, Rankin PS (2021) Habitat use and activity patterns of female Deacon Rockfish (*Sebastes diaconus*) at seasonal scales and in response to episodic hypoxia. Environ Biol Fishes 104:535–553.

Richards SD, Leighton TG (2000) Sonar performance in turbid and bubbly environments. Journal of the Acoustical Society of America 108:2562.

Riley SC, Binder TR, Wattrus NJ, Faust MD, Janssen J, Menzies J, Marsden JE, Ebener MP, Bronte CR, He JX, Tucker TR, Hansen MJ, Thompson HT, Muir AM, Krueger CC (2014) Lake trout in northern Lake Huron spawn on submerged drumlins. J Great Lakes Res 40:415–420.

Runde BJ, Buckel JA, Bacheler NM, Tharp RM, Rudershausen PJ, Harms CA, Ben-Horin T (2022) Evaluation of six methods for external attachment of electronic tags to fish: assessment of tag retention, growth, and fish welfare. J Fish Biol.

Schlaff A, Menéndez P, Hall M, Heupel M, Armstrong T, Motti C (2020) Acoustic tracking of a large predatory marine gastropod, *Charonia tritonis*, on the Great Barrier Reef. Mar Ecol Prog Ser 642:147–161.

Selby TH, Hart KM, Fujisaki I, Smith BJ, Pollock CJ, Hillis-Starr Z, Lundgren I, Oli MK (2016) Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. Ecol Evol 6:4823–4835.

Singh L, Downey NJ, Roberts MJ, Webber DM, Smale MJ, van den Berg MA, Harding RT, Engelbrecht DC, Blows BM (2009) Design and calibration of an acoustic telemetry system subject to upwelling events. Afr J Mar Sci 31:355–364.

Skerritt D, Robertson P, Mill A, Polunin N, Fitzsimmons C (2015) Fine-scale movement, activity patterns and home-ranges of European lobster *Homarus gammarus*. Mar Ecol Prog Ser 536:203–219.

Smith F (2013) Understanding HPE in the VEMCO Positioning System (VPS). VEMCO DOC-005457-01. Available from: http://www.oceans-research.com/wp-content/uploads/2016/09/understanding-hpe-vps.pdf

Steel AE, Coates JH, Hearn AR, Klimley AP (2014) Performance of an ultrasonic telemetry positioning system under varied environmental conditions. Anim Biotelem 2:15.

Stieglitz TC, Dujon AM (2017) A groundwater-fed coastal inlet as habitat for the Caribbean queen conch *Lobatus gigas*-an acoustic telemetry and space use analysis. Mar Ecol Prog Ser 571:139–152.

Stocks JR, Gray CA, Taylor MD (2014) Testing the effects of near-shore environmental variables on acoustic detections: Implications on telemetry array design and data interpretation. Mar Technol Soc J 48:28–35.

Swadling DS, Knott NA, Rees MJ, Pederson H, Adams KR, Taylor MD, Davis AR (2020) Seagrass canopies and the performance of acoustic telemetry: implications for the interpretation of fish movements. Anim Biotelemetry 8:8.

Taylor MD, Payne NL, Becker A, Lowry MB (2017) Feels like home: Homing of mature large-bodied fish following translocation from a power-station canal. ICES J Mar Sci 74:301–310.

Thums M, Whiting SD, Reisser JW, Pendoley KL, Pattiaratchi CB, Harcourt RG, McMahon CR, Meekan MG (2013) Tracking sea turtle hatchlings — A pilot study using acoustic telemetry. J Exp Mar Biol Ecol 440:156–163.

Tucker DG, Gazey BK (1966) Applied underwater acoustics. Elsevier Science & Technology.

Veilleux MAN, Midwood JD, Boston CM, Lapointe NWR, Portiss R, Wells M, Doka SE, Cooke SJ (2018) Assessing occupancy of freshwater fishes in urban boat slips of Toronto Harbour. Aquatic Ecosystem Health & Management 21:331–341.

Vemco Ltd. (no date) Receiver Noise Measurements.

Westrelin S, Roy R, Tissot-Rey L, Bergès L, Argillier C (2018) Habitat use and preference of adult perch (*Perca fluviatilis* L.) in a deep reservoir: variations with seasons, water levels and individuals. Hydrobiologia 809:121–139.

Williams-Grove L, Szedlmayer S (2016) Acoustic positioning and movement patterns of red snapper, *Lutjanus campechanus*, around artificial reefs in the northern Gulf of Mexico. Mar Ecol Prog Ser 553:233–251.

Williams-Grove LJ, Szedlmayer ST (2017) Depth preferences and three-dimensional movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. Fish Res 190:61–70.

Wilson P, Thums M, Pattiaratchi C, Meekan M, Pendoley K, Fisher R, Whiting S (2018) Artificial light disrupts the nearshore dispersal of neonate flatback turtles *Natator depressus*. Mar Ecol Prog Ser 600:179–192.

Wolfe BW (2013) Movements of the white croaker (*Genyonemus lineatus*) on the Palos Verdes Shelf, Los Angeles, California. California State University, Long Beach.

Wyman MT, Thomas MJ, McDonald RR, Hearn AR, Battleson RD, Chapman ED, Kinzel P, Minear JT, Mora EA, Nelson JM, Pagel MD, Klimley AP (2018) Fine-scale habitat selection of green sturgeon (*Acipenser medirostris*) within three spawning locations in the Sacramento River, California. Can J Fish Aquat Sci 75:779–791.

Young RF, Winn HE (2003) Activity Patterns, Diet, and Shelter Site Use for Two Species of Moray Eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. American Society of Ichthyologists and Herpetologists 2003:44–55.

Zemeckis DR, Hoffman WS, Dean MJ, Armstrong MP, Cadrin SX (2014) Spawning site fidelity by Atlantic cod (*Gadus morhua*) in the Gulf of Maine: implications for population structure and rebuilding. ICES J Mari Sci 71:1356–1365.

Supplementary Materials for Chapter 3

S3.1 Ascension Island case study

Preliminary assessment: estimating detection range using range tests

To evaluate detection efficiency across the two predominant substrate types, range tests were conducted across rock and sand habitats. A single acoustic receiver (VEMCO VR2W) was affixed to a 14 mm polypropylene line attached 3 m below an 8” trawl float (850 g lift) terminating in a 30 kg anchor. An inflatable surface marker buoy was attached to the float to enable quick visual assessments of the receiver’s position. All range tests were conducted using a range test tag (VEMCO V16-6x, fixed 7 s transmission rate, 158 dB) >500 m from English Bay. The detection range of the range test tag was assessed at distances of 0 – 250 m (using benthic SCUBA trials) and 0 – 500 m (using surface kayak trials replicating the 2017 methodology described above, 250 m max during rock range testing) at 50 m intervals. During benthic testing the range test tag was affixed to a 14 mm polypropylene line which terminated in an 8” trawl float (850 g lift) which was held to one side by a SCUBA diver for 4 - 5 minutes at each fixed distance. During surface testing, the range test tag was affixed to 4 mm nylon kernmantle rope which terminated in a 2 kg dive weight and lowered 3 m from the base of a two-person kayak. The position of the boat was marked using a handheld GPS (Garmin eTrex 30x) to ensure the boats position was maintained. Both sand range tests were conducted on the 15th of May 2019, and rock range test were conducted on the 17th of May 2019. Observed conditions were markedly similar (e. swell 0.5 – 1 m, sunny and clear skies). Across both substrates benthic range testing outperformed surface range test results, we theorise this is due to winds impacting surface water stability and increasing ambient noise (thus reducing signal reception). Detection range was slightly higher for sand habitat versus rock which is likely due to signal scatter.

In March 2017, range tests were conducted off the northwest coast of Ascension Island in English Bay by the Ascension Island Government Conservation and Fisheries Directorate (*unpublished data*). Three trials were conducted to test the detection range of three acoustic transmitter types (VEMCO V13-1x, V16-4x, V9-2x) to identify which would be best suited for tracking studies conducted in the nearshore environment. During each trial a single tag was suspended off the back of a kayak, several metres below the water’s surface, at 50 m intervals (0 - 450 m) from a listening VR2W acoustic receiver. Detection efficiency was calculated by dividing the number of observed detections (number recorded during the 5-minute waiting interval at each fixed distance from the receiver) by the number of expected detections (burst rate * transmission rate). Detection range was calculated as c. 90% for all tag types at 50 m from the listening receiver, however, dropped to 30-70% at 100 m (Fig. 3.4).

S3.2 Range test reporting

To date, over a third of unique VPS tracking studies have not mentioned range testing (*n* = 31, 37%). Of the 52 studies that mentioned range testing, 19 (37%) did not conduct their study-specific range testing and often referenced studies conducted <100 km from the study site and/or over a different time frame. Of the 33 studies that utilized unique range test data, six (18%) did not report their results, and the remaining 26 studies explained their results using six unique reporting styles with poorly defined statistical parameters and language commonplace (Table S3a). The period of range testing (pre-during-post) and duration (short or long term) has also been poorly defined by VPS studies to date (Table S3b), with few studies reporting factors which may reduce performance (*n* = 7). This lack of consistent reporting echoes the call of Kessel et al. (2014) for non-VPS acoustic telemetry, that as a community consistent reporting is essential for robust hypothesis testing.

Supplementary Table 3.1 Summary of in-test reporting style for the 33 (of 52) unique VPS tracking studies which mention range testing. Of these 33 studies, 16 studies did not provide any information. Asterisk (*) indicates that one study reported results in a format that matches both D and G and is included in both rows.

Rule category	In-text reporting style	Defining characteristics	No. studies
A	"Estimated minimum"	Minimum % or distance given	1
B	“100% at..”	Maximum distance with 100% assumed	2
C	“<99% at a specified distance”	User defines %, between 1-99%	12*
D	Range of values for a given percentage, "350-900m at 85%"	Range of values given	6
E	Two values for DE given at two distances: “>80% @ 330m; >50% @ 600m”	Two proportions given	2
F	“400m **detection range**” OR “**effective detection range** extends up to… “ “400m detection **radius**” OR “detection **efficiency** higher at Xm” “**Average** receiver range" “Range was **optimal**…” “**optimal** spacing at..” “**range extended** up to…” “**operating range** of …”	Unclear language, or poorly defined statistical relationship	14*

Supplementary Table 3.2 Summary of range test duration for the 33 (of 52) unique VPS tracking studies which mention range testing. Range test durations include short-term testing (<24 hours) and long-term testing (>24 hours).

Information type	Duration	No. unique tracking studies
Range testing period	Pre-study	19
	During study	1
	Post-study	1
	Not described	12
Range test duration	Short term	5
	Long term	8
	Not described	20

S3.3 Using the VEMCO Calculator

In this worked example (Table S4), the user aims to determine the delay programming for 69 kHz pulse per modulation (PPM) tags they plan to add to a study system which will enable >50% detection probability (ideal for Vemco Positioning System). This simple calculator is used to indicate the worst-case scenario, e.g., many tagged animals are detected on a small section of the array. In this scenario, a 3x3 array is initially deployed (therefore 9 sync tags are present to enable time synchronisation, one on each deployed receiver).

Note this is an approximate estimate given the average transmission rate of an 8-ping tag (e.g. 1601/1602 code space tags) is 3.3s but in reality ranges from 2.34 - 4.26 s (Colleen Burliuk, *pers. comm*), in addition a 10-ping tag (sensor tags, 9002-generation etc.) takes an average of 5 s to transmit but ranges from 3.72 - 6.28 s.

Supplementary Table 3.3 Worked example using the VEMCO collision calculator. Decimals rounded to 3 d.p.

	Existing tags		New tags
	Sync tags	Animal and/or reference tags	Animal and/or reference tags
No. Tags	6	2	5
Burst rate (s)	3.3	5	5
Delay (s)	600	120	65
	0.033	0.080	0.387[†]

[†] Users should not aim to reach high saturation rates (negative values) given the delay associated with tag transmissions, reaching negative values will likely result in data loss due to ping saturation which can lead to signal collisions. Experimental work is required to resolve at what saturation rate is likely deleterious.

The following steps were taken to calculate the above example (Supplementary Table 3.3):

1. The estimated ping-time saturation (time taken up by existing tag pings in the system) of the existing sync tags in the system (purple highlight) is calculated as:

Equation 1.

$$\frac{(\text{Number existing sync tags in the system} * \text{Burst rate of the existing sync tags})}{(\mathit{Burst\ rate\ of\ the\ existing\ sync\ tags} + \mathit{Existing\ sync\ tag\ delay})}$$

2. Equation 1 is also used to solve the ping-time saturation of animal and/or reference tags in the system (gray highlight). The sum of two components equates to the total ping saturation.
3. The estimated time available to fill with pings (yellow highlight) is calculated with a desired detection probability of 50% (0.5) using the following:

Equation 2.

$$(1 - 0.5) - \mathit{Ping\ time\ saturation\ of\ existing\ sync\ tags} \\ - \mathit{Ping\ time\ saturation\ of\ existing\ animal\ and\ reference\ tags}$$

4. The minimum advisable nominal delay (blue highlight) for the new tag types is calculated as:

Equation 3.

$$((Number\ of\ new\ animal\ pinger\ tags\ added * Burst\ rate\ of\ pinger\ tag) + (Number\ of\ new\ animal\ sensor\ tags\ added *\ Burst\ rate\ of sensor\ tag)) / Output\ of\ Equation$$

Chapter 4. Demystifying Time Difference of Arrival Positioning: from user tools to deriving positions

4.0 Chapter summary

Acoustic positioning solvers offer data resolution on aquatic animal movements which can far exceed the precision obtained from popularised discrete acoustic telemetry arrays (receivers deployed with non-overlapping detection ranges), allowing estimation of an animal's location within metres of its true position. Increased data resolution has the potential to allow the identification of fine-scale movement behaviour, which could significantly improve our understanding of critical areas in movement ecology and animal behaviour, including, social and predatory intra- and interspecies interactions, bioenergetics, behavioural traits and personality, and responses to fishing activity. However, key consideration of factors that can limit data yield and introduce error is integral to defining the capabilities of fine-scale receiver arrays. We provide herein a basic toolbelt of user tools and techniques to assess data quality prior to positioning, including identifying assessing receiver tilt, signal to noise ratios, the presence of signal reflections, simultaneous detections and available time synchronisation data. We then exemplify the application of these tools and techniques using an applied case study conducted in a nearshore marine environment. In addition, we detail the three steps undertaken by data analysts prior to deriving positions using the Time Difference of Arrival processing offered by Innovasea, which includes: estimating the speed of sound through water, correcting for inaccurate receiver locations by calibrating the array, and determining a precise time of arrival using clock synchronisation. We hope that by providing a user toolbelt, and listing the steps undertaken during processing, this will improve the transparency of these large datasets.

4.1 Introduction

Advances in biotelemetry technology have greatly improved our ability to track aquatic animals in the wild (Hussey et al. 2015). Innovation in paired technologies and positioning solvers offer the potential to redefine our understanding of fine-scale movement and its drivers (Baktoft et al. 2017, Nathan et al. 2022). Acoustic telemetry can be used to determine the presence/absence of a fish around a listening receiver (depending on the detection range, typically a few hundred metres), whereby a fish is equipped with an acoustic transmitter that emits a unique ID and when in the detection range of an acoustic receiver the tag is detected and the time of detection logged (Thorstad et al. 2013). Gridded arrays of acoustic receivers with overlapping detection ranges can be used to generate simultaneous detections, from which positioning algorithms can derive animal locations with potential sub-metre precision. The VEMCO Positioning System (VPS, commercial vendor Innovasea Ltd.) is a type of fine scale acoustic array that uses commercial TDOA processing to estimate continuous animal positions. Pulse per modulation (PPM) VEMCO tags are usually paired with the VPS to derive animal positions, i.e., every 30 s. The newest iteration of tags and receivers that can be paired with VPS is VEMCO High Residence technology. HR tags use binary phase-shift keying (BPSK) encoding and can transmit an order of magnitude faster and with shorter transmission intervals (i.e. a transmission every 2-3 s). These features reduce the probability of signal collision (signal collision occurs when part of a tag transmission is lost; therefore, the unique ID cannot be decoded, see Kessel et al. 2015). Using BPSK encoding, a listening receiver can determine precise arrival times of transmissions based on signal phase shifts (millisecond data), which, when combined with high-resolution receiver clocks, can generate sub-metre precision (Leander et al. 2019). Sub-metre continuous positions can be used to generate more precise and accurate foundational movement metrics (such as turning angles, rate of movement, and direction of travel) and can be inputted into complex models to explore fine-scale movement behaviour. Fine-scale movements, including burst swimming to seek prey or escape predators and courtship and spawning behaviour, contribute to energetic budgets (Wilson et al. 2011, Silva et al. 2015, Brownscombe et al. 2017a); these fine scale movements have not been possible to capture previously using slower PPM transmission rates.

Both PPM and HR VPS rely on the same foundational steps. To estimate the signal travel speed from a tag (i.e. sync tag or animal tag), a speed of sound model is generated (namely using the Coppens equation; Coppens 1981). Acoustic receivers must be deployed with overlapping detection ranges (evidenced by prior range testing, see Kessel et al. 2014 for information on range tests) to maximize the likelihood of simultaneous detections of tags. Owing to clock drift on autonomous listening receivers, time synchronisation using fixed integrated or paired synchronisation tags which are at a known location, is essential to estimating a precise time of detection. After system calibration, tag positions can be derived based on where along intersecting hyperbola a tag is located. Deriving tag positions can use 3 to 6 receivers (if simultaneous detections are recorded), equating to up to 20 possible receiver combinations (triads are used for positioning).

The process for deriving positions is the same for PPM and HR tags. HR generates a larger volume of data given the increased transmission rates. To generate positions from detection data, a user can either pay for training and access to proprietary software (training covers 2D VR2Tx and VR2AR datasets) or pay for specialist ‘in-house’ analysts to process the positioning data (all PPM and HR datasets). Commercial position processing offers researchers flexibility and may be preferable over user-led positioning techniques when time is a fundamental project constraint. Currently, the steps involved in evaluating and analyzing VPS datasets by analysts are poorly understood by researchers leading to a black box of analysis. Given the complexities of TDOA analysis, users must understand the environmental factors that shape detection data yield, how data is integrated into the TDOA analysis framework, and what ultimately shapes the success of using a TDOA positioning system.

To bridge the knowledge gap between pre-and in-situ processing steps when using fine scale acoustic telemetry data, the objectives of this study were to (i) identify and exemplify step-wise procedures users can conduct to assess data quality and limiting factors to data yield, and (ii) detail the steps undertaken during TDOA positioning by analysts, and the system design features necessary for successful data acquisition. While we detail an HR-VPS case study, the steps translate between VPS systems and can be applied to PPM and HR datasets.

4.2 Methods

4.2.1 Case study: Ascension Island nearshore HR-receiver array

Ascension Island is a remote volcanic island situated in the South Atlantic Ocean. A volcanic rocky reef fringes the island, which is punctuated by pockets of sand and Rhodolith. Owing to its equatorial location, nearshore water temperatures are relatively stable ranging from 23 to 29°C (Orrell, *unpublished data*).

High Residency 2 (180 kHz) acoustic receivers were deployed in a 2x2 grid northwest of One-hook, northwest of Ascension Island (Fig. 4.1). Receiver sync tags were set to very high (HR transmission rate = 25-35 s, PPM transmission rate = 270-330 s; 147 dB) with tilt and ambient noise sensors (receiver tilt, accuracy = ±5°, resolution = 1°; ambient noise) logging every 60s. Adjacent receiver moorings were deployed on average 53 m apart (range = 39 – 73 m; Fig. 4.1) with overlapping detection ranges (as determined from benthic and surface range test trials, Supplementary Material S4.1; Supplementary Figure 4.1) on either a low-relief rhodolith bed (HR1) or sand habitat (HR2, HR3 and HR4). Each receiver mooring line comprised of a single HR2 receiver affixed to a 14 mm polypropylene rope terminating in a float (either a large surface marker buoy or an 8” travel float), which sat at the water’s surface so the equipment could be easily retrieved (further details in Supplementary Table 4.1). To examine the potential effect of tag depth on data acquisition, independent fixed moorings were deployed with two tags, with an “upper” tag (e. 15 m above anchor) to simulate a pelagic fish and a “lower” tag (e. 10 m above the anchor) to simulate a benthopelagic fish. Each tag mooring line was comprised of two HR tags (V9P-2x; “high power”, HR transmission rate = 1.8-2.2 s, 180 kHz, PPM delay = 25-35 s) affixed to 8 mm polypropylene rope using 3 mm kernmantle rope (secured through a loop on the tags terminal end) which was moored using a 15 kg anchor and terminated in a two 3” trawl floats (buffered between with material to prevent noise, 1600 g lift per line). To assess whether the spacing and geometry of the array was suitable to generate simultaneous detections and subsequently derive positions, HR tag lines were deployed at three fixed positions inside- and three fixed positions outside the receiver array. Each static tag line was deployed for <10 minutes, with “in” (inside the array) and “outside” (outside the array) tag lines dropped at the same time.

Trial data were first trimmed to the study period during which there was no boat activity (deployment vessel moored, engines off, i.e., data for the trial drop periods when the boat was active within the array were excluded) (Table S4.1). Positioning data was processed using the VEMCO hyperbolic positioning algorithm, which uses the time difference of arrival

(TDOA) of an acoustic signal at 3 or more receivers to calculate a single position and its associated error by averaging all intermediate positions from receiver pairs (Smith, 2013).

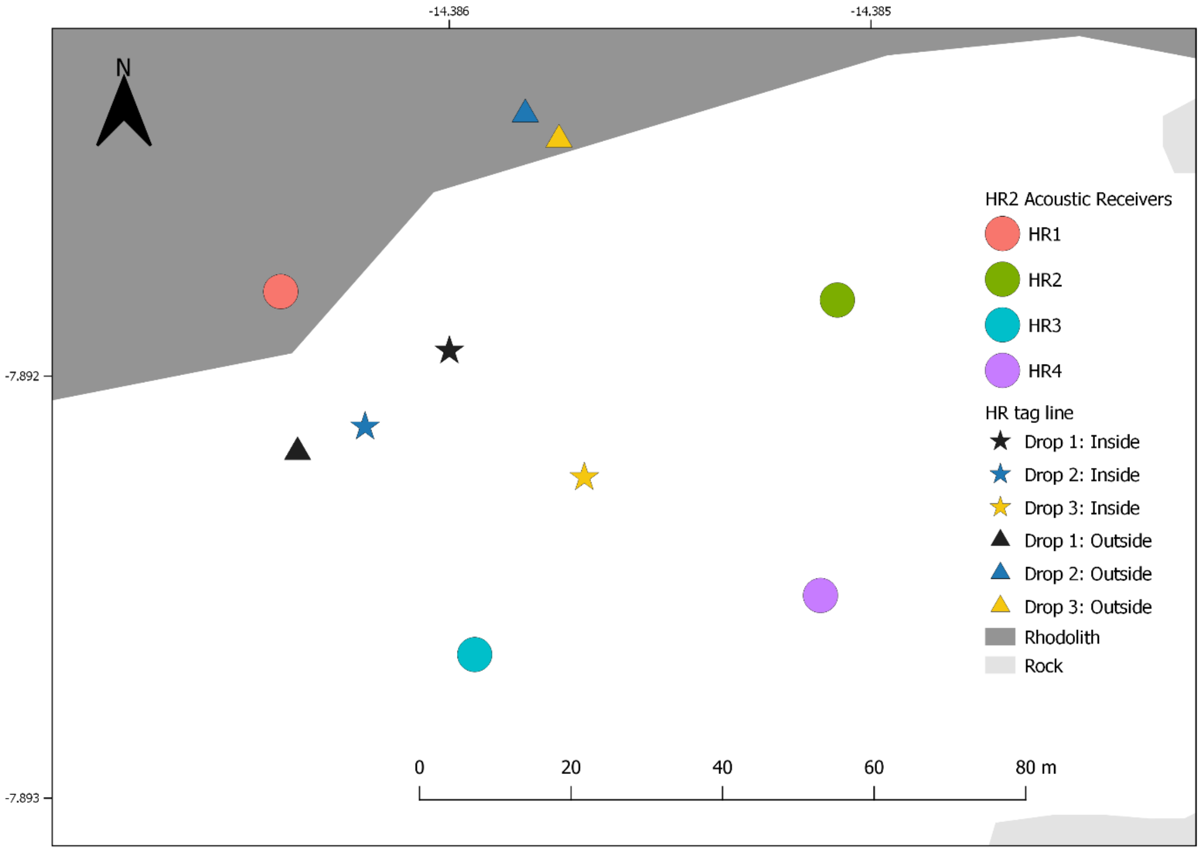


Figure 4.1 Fine-scale acoustic array of four VEMCO HR2 180 kHz acoustic receivers deployed northwest of Ascension Island (7.9467°S, 14.3559°W). High Residency (HR) tag lines were dropped in pairs (highlighted by matched colours), with three independent deployments conducted within a 1-hour study period (tags inside the array denoted by star symbols, tags outside by triangles).

4.3 Results and discussion

4.3.1 A user toolbox: initial checks to assess raw data acquisition

There are several steps a user can take to assess and understand the potential data yield of their own dataset, prior to TDOA positioning. These preliminary steps can also increase confidence in data interpretation, namely by assessing the receiver tilt, the prevalence of signal reflections, ambient noise levels across the array and signal strength of recorded transmissions. While we demonstrate these steps for a HR VPS system, this description is also transferrable across PPM VPS systems.

4.3.1.1 Assessing receiver tilt

Newer models of VEMCO receivers (e.g., VR2AR and HR receivers sold by the vendor Innovasea Ltd.) are capable of self-recording tilt values at fixed intervals (e.g., 60 s) which can provide essential context to array performance. High levels of tilt on receiver mooring lines can affect the detection probability due to the angle created between an incoming sound wave and hydrophone (which can lead to signal loss) and potential shadowing by the receiver body (Bergé et al. 2012, Reubens et al. 2019). Users should aim for <25° of tilt to ensure this does not affect data acquisition and subsequent positioning. Mooring design and buoyancy can have direct implications on receiver tilt. For example, less buoyancy may lead to slack lines, and increased surface areas of surface floats can lead to increased drag. Moorings close to or on the water surface may also experience wave action, changes to tidal height and prevailing currents, all of which can introduce mooring line tilt and therefore receiver tilt.

In the example four-receiver array, two of the moorings (HR1, HR3) were buoyed using a diving surface marker buoy (e. surface area = 1.08 m^2; equated to 15 kg and 18 kg lift). While the other two receiver mooring lines used trawl floats (e. surface area = 0.13 m^2; 8 kg and 19 kg lift respectively) (Fig. 4.2). The higher surface area of the surface marker buoy (HR1, HR3) likely led to higher observed tilt values, which often exceeded the recommended 25° causing data loss and affecting data quality, making subsequent calibration and positioning difficult or with error (inbuilt sensor recordings above 25°: HR1 = 40 [51% of total observations], HR2 = 2 [2%], HR3 = 38 [49%], HR4 = 0 [0%]; Fig. 4.2).

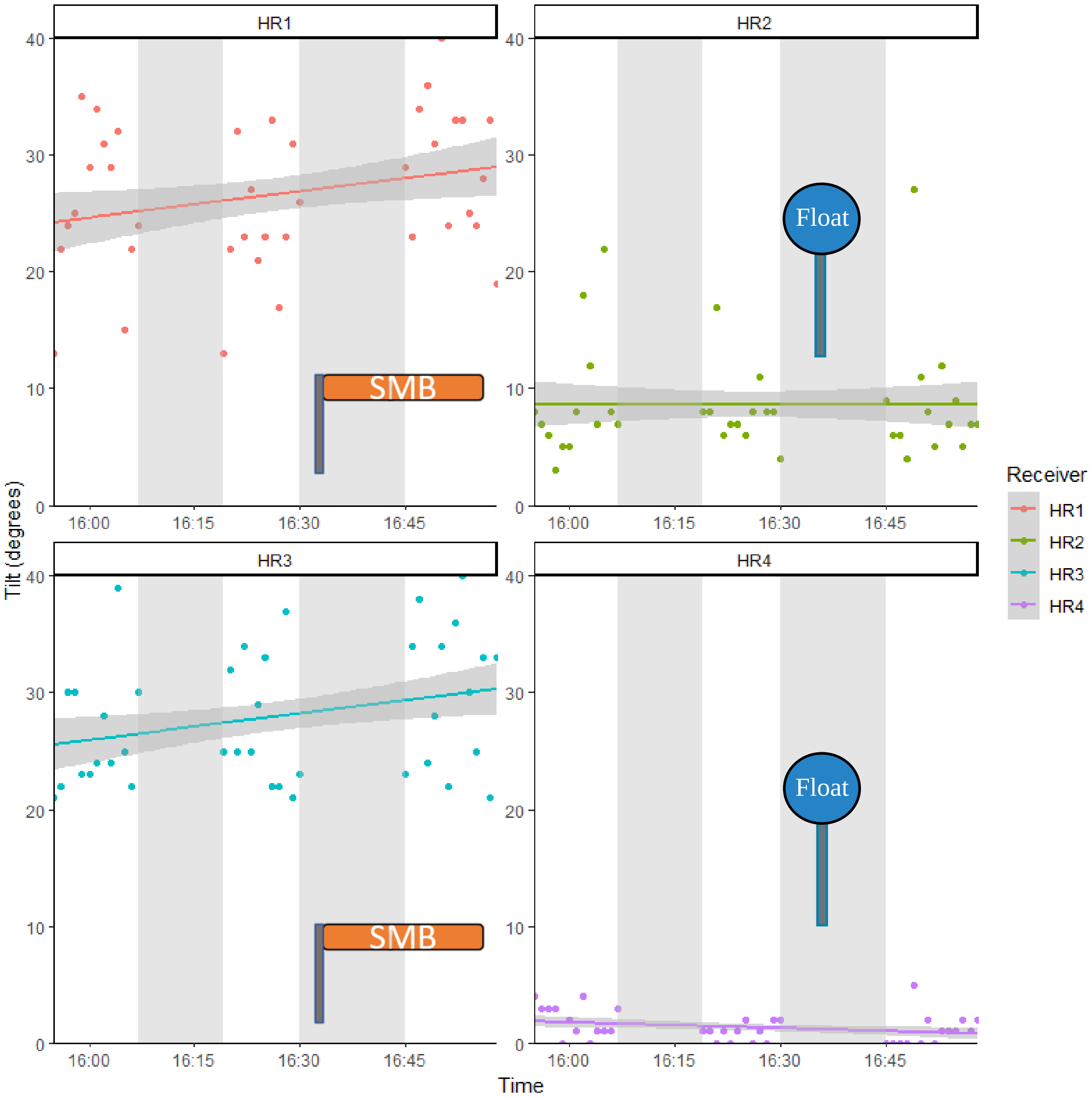


Figure 4.2 Receiver tilt was programmed to record every 60 s across the fine-scale positioning array (resulting in 78 data points per receiver). Each mooring consisted of an HR2 receiver affixed to a line which terminated in a diving surface marker buoy (SMB, e. 15-18 kg lift) or a trawl float (e. 8-19 kg lift). Grey shaded panels indicate periods where the boat was present, and observations recorded during this period were removed.

4.3.1.2 Ambient noise and identifying signal reflections

Patterns in ambient noise levels can indicate signal reflections, and when combined with signal strength, subsequent signal-to-noise ratios can identify periods with poor tag signal reception. Ambient noise can be introduced by biological, geophysical, and anthropogenic-derived sources and becomes deleterious when it occurs over the same frequency band as the listening receiver. Certain environments are associated with elevated noise, for example, nearshore habitats which experience persistent wave action (Brownscombe et al. 2017b). Ambient noise levels recorded in decibels (dB) are visualized on a logarithmic scale; therefore, a 20 dB noise is 10 times louder than a 10 dB, and a 30 dB noise is 100 times louder than a 10 dB noise. Newer models of acoustic receivers can record ambient noise at fixed intervals (recorded in dB for HR2 receivers and mV for VR2Tx and VR2AR receivers; InnovaSea Systems Inc. 2018) and ambient noise at the time of signal detection (HR and PPM detections on HR2 receivers only). PPM and HR noise are not comparable owing to the differences in how the signal is processed; while PPM noise is calculated in the frequency domain, HR is calculated via the time domain. Therefore, generating a signal to noise ratio (section 4.3.1.3) is often more informative in determining periods when noise levels are deleterious.

Research into the prevalence of signal reflections in VPS data is limited. A key assumption of TDOA analysis is that acoustic transmissions follow a linear path. Signal reflections and multipath signal attenuation, however, can violate linearity and can lead to increased positioning error (Vergeynst et al. 2020). Potential signal reflections can be identified according to their source. Using the case study example, by visualizing data from source 1 (the static tags deployed inside and outside the array), a pattern of detections with low ambient noise is apparent (Fig. 4.3). Signal reflection is unlikely to be linked to the position of the tag relative to the array (inside or outside the array) but due to complex topography, physical structures in the water column, and surface waters (Kessel et al. 2015). In the case of HR signal reflections, a receiver may decode its' internal sync tag (source 2) as an external tag rather than a “self” detection (resultant output visualized in Fig. 4.4). In the case study example, HR4 decoded several of its internal sync tag transmissions as from an external source due to the signal reflecting off the water's surface.

Every recorded detection on a listening receiver includes a noise value which essentially describes the ambient noise level around a receiver. As previously described, receivers can also be set to record ambient noise at fixed intervals, i.e. every 60 s. Visualizing noise levels at different receivers over time can be used as a basic indicator of ambient noise. Using the case study example: detections and associated ambient noise values were recorded on listening receivers generated by three mechanisms, (1) tags dropped inside/outside the array, (2) receiver sync tag detections or (3) noise recorded by the receiver sensor every 60 s. Note that during periods of high noise, receivers may fail to decode detections leading to fewer detections overall and a biased profile, i.e., skewing observations towards detections with low noise values (see Fig. 4.3A, receiver HR4; Vemco Ltd., DOC-5680-01).

In addition, summarising unique transmitters detected within an array at the start of data interrogation and comparing these to known tags within the system can identify signal collisions and false tag IDs (Table 4.1), which commonly occur when using PPM signals and deploying a large quantity of tags with high transmission rates (Kraus et al. 2018, Vergeynst et al. 2020).

4.3.1.3 Signal strength and calculating signal to noise ratios

Signal strength describes the signal intensity of a detection received by a receiver. For a transmission to be decoded by a listening receiver, the signal strength of a transmission must exceed the background noise (Vemco Ltd. DOC-5680-01). Factors that may affect the time of arrival of a signal at a listening receiver include reflection, refraction, attenuation, and signal diffusion (spreading) (Singh et al. 2009), which will impact the signal strength of a given detection. These factors are intrinsically linked to water properties, including temperature, salinity, entrapped particles, substrate type, water turbidity and habitat type through multipath signal propagation (reviewed in Kessel et al. 2014). In addition, greater distances between a tag and a receiver will reduce signal strength due to signal attenuation (Reubens et al. 2019). Using the experimental case study, visualizing the distance between the static HR tags and each acoustic receiver highlights that signal strength decreases with increasing distance (Fig. 4.5). Receiver spacing is central to having adequate signal strength of sync tag detections which is key for clock synchronisation and system calibration. The difference between the ambient noise level and signal level (signal strength minus noise) is referred to as the signal-to-noise ratio (SNR; Vemco Ltd. DOC-5680-01; Fig. 4.6). Low SNR ratios have been linked to an increase in positioning error (Smith et al. 1998, Ehrenberg & Steig 2003).

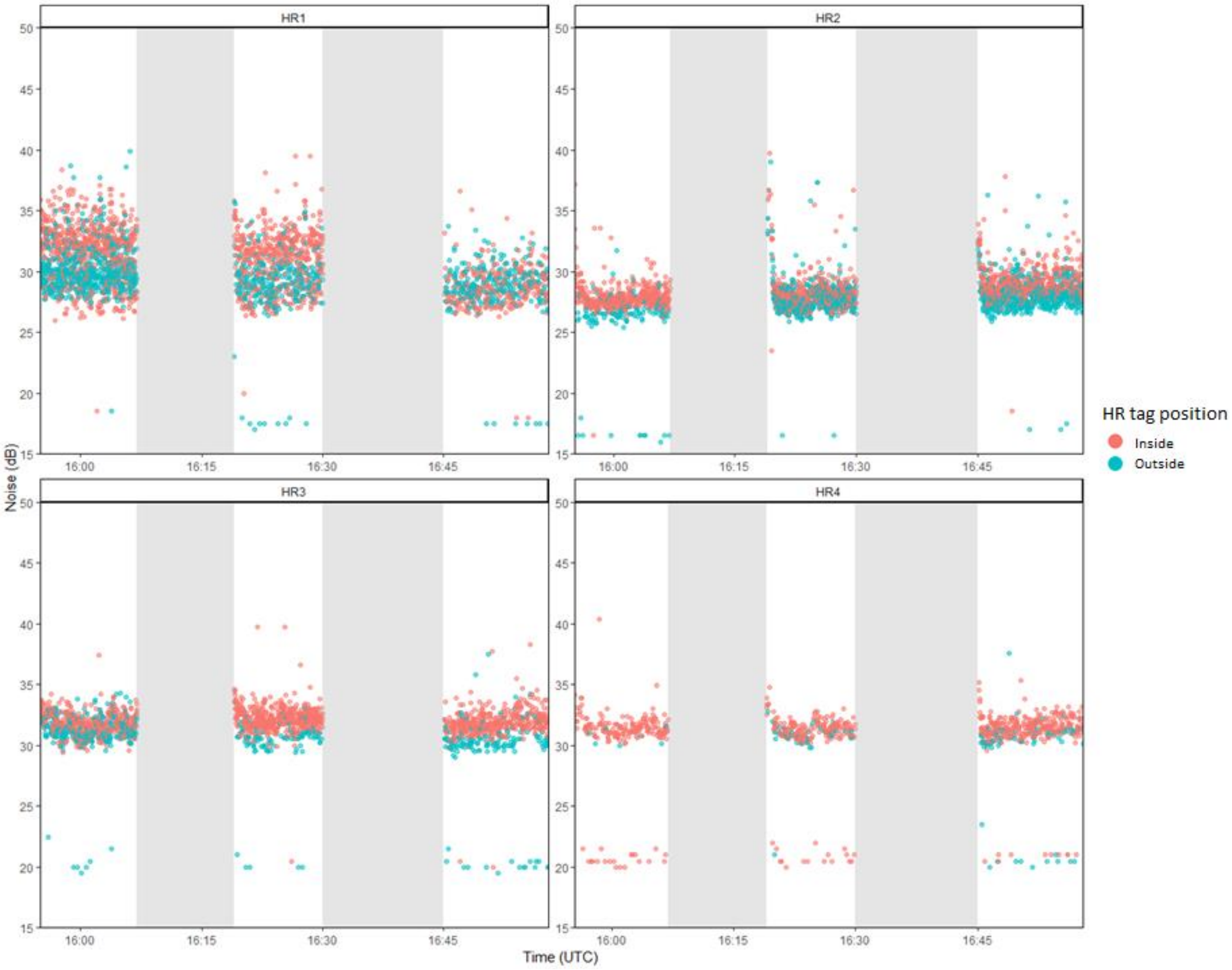


Figure 4.3 An overview of ambient noise levels (dB at 170 kHz and 180 kHz) recorded alongside PPM and HR tag detections. Static tag lines were positioned inside or outside a 2x2 grid of VEMCO HR2 180 kHz acoustic receivers. Data were trimmed to periods where the boat was absent (the boat's presence is indicated by gray panel shading). Signal reflections can be identified by ambient noise values far below the typical noise level (i.e. 10-20 dB detections in the example above). Identifying certain time periods or areas of the array prone to signal reflections can help direct system calibration choices when deriving positions.

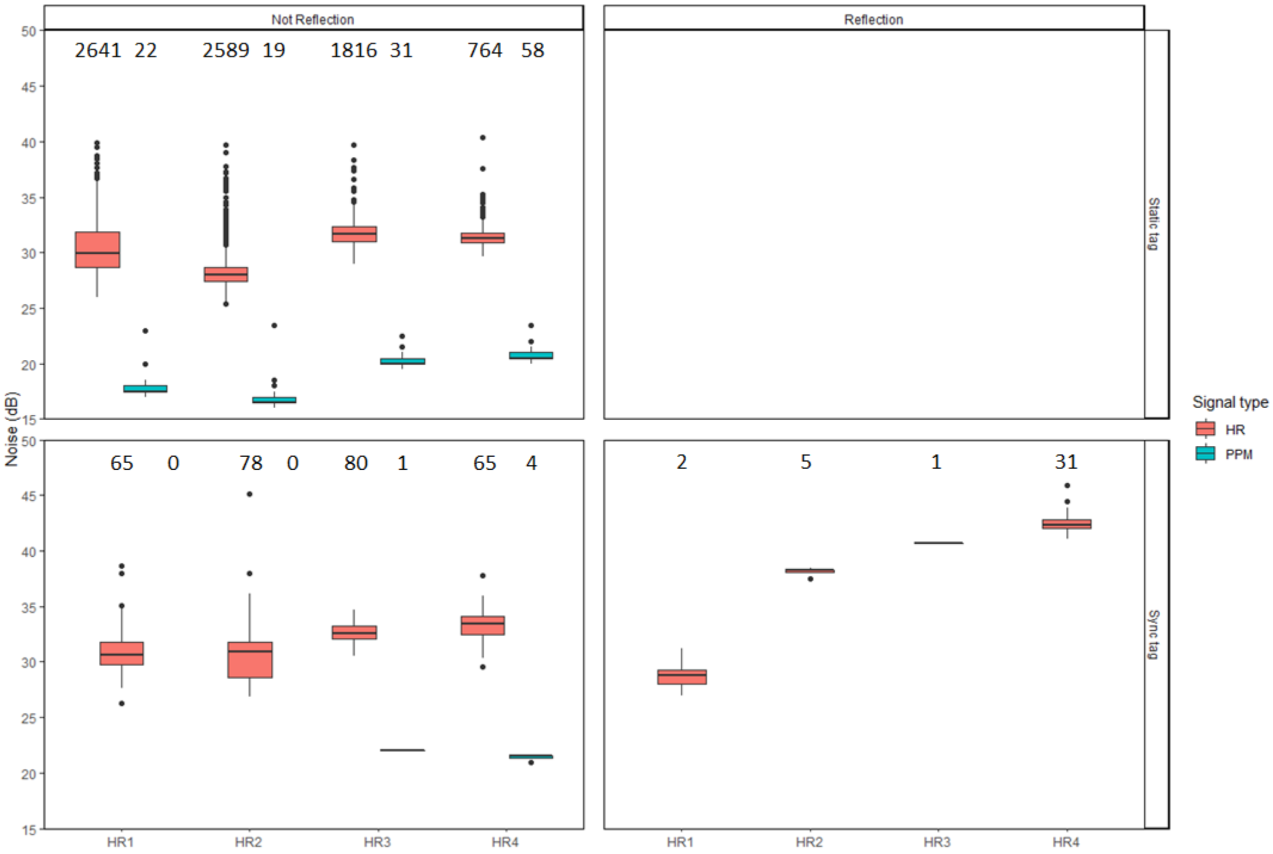


Figure 4.4 An overview of ambient noise recordings (dB at 170 kHz and 180 kHz) associated with detections recorded on the four deployed HR2 180 kHz receivers, with data from two sources: (1) static tags dropped inside or outside the receiver array, and (2) internal receiver sync tag. Colour indicates the signal type of the recorded detection, either pulse per modulation (PPM) or high residency (HR). Where applicable, the number of detections is given above the corresponding bar plot. Note that given the difference in how PPM and HR noise is filtered by an HR2 receiver, comparing these values is not recommended. Signal types are shown here to illustrate reflections and not for comparisons between PPM and HR noise.

Table 4.1 An example summary for a given receiver within a listening array, shown here for receiver HR1 in the northwest corner of the 4-receiver High Residency 2 acoustic receiver array. Transmission origins include static HR V9P-2x tags (high power, HR transmission rate = 1.8-2.2 s, PPM transmission rate = 25-35 s), unknown IDs (typically result from signal collision), the internal sensor recording, the receiver's own internal sync transmissions (successful detections are "HR_SELF" or "PPM_SELF", reflections are decoded as "HR" and not self), and detections of the surrounding receiver's internal sync tags (HR2_SYNC, HR3_SYNC, HR4_SYNC).

		Number of detections by transmission type				
		HR	PPM	HR_SELF	PPM_SELF	SENSOR
Transmission origin	V9P tags	2641	116			
	Unknown IDs	1	0			
	HR1 sensor					78
	Own sync	2	0	72	8	
	HR2_SYNC	14	4			
	HR3_SYNC	36	4			
	HR4_SYNC	15	3			

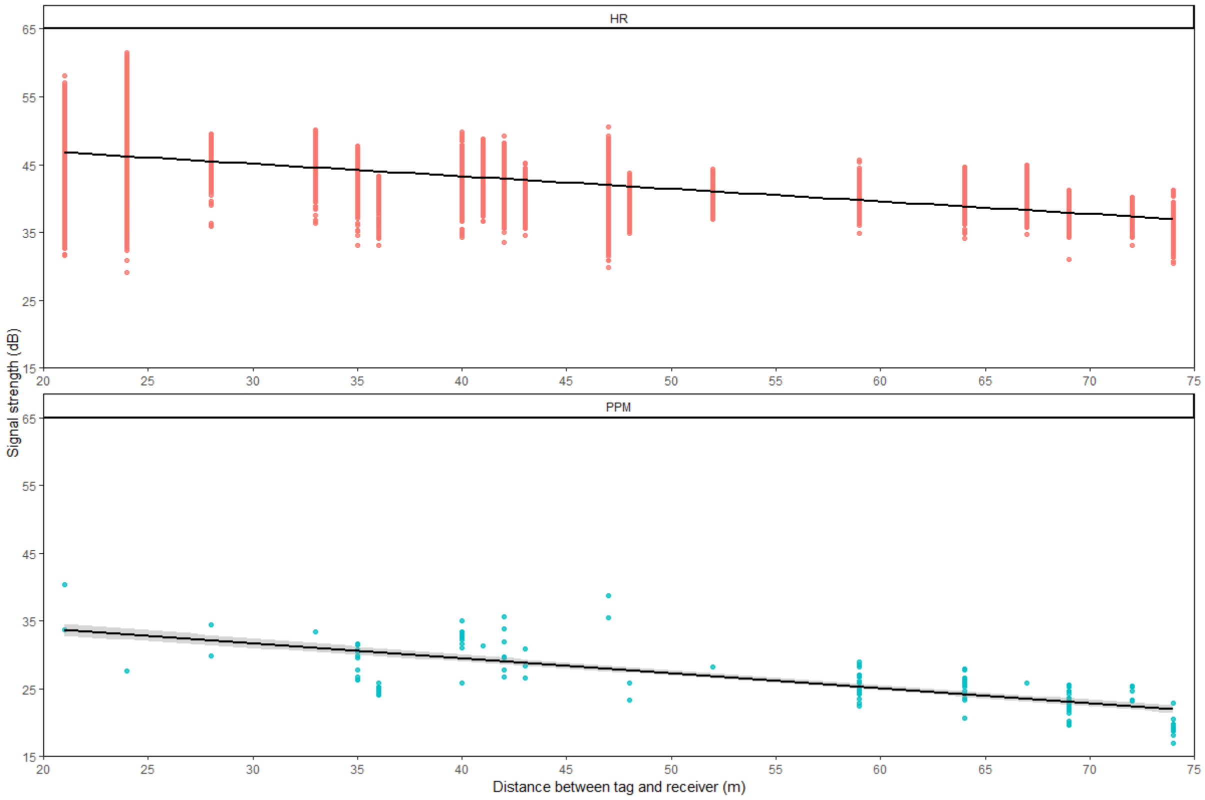


Figure 4.5 Distance between a static HR tag (V9P-2x; high power, High residency [HR] transmission rate = 1.8-2.2 s, 180 kHz, pulse per modulation [PPM] delay = 25-35 s) and a listening HR2 acoustic receiver. Upper graph shows HR detections, and lower panel shows PPM detections. A linear trendline with a shaded 95% confidence interval is fit to each signal type

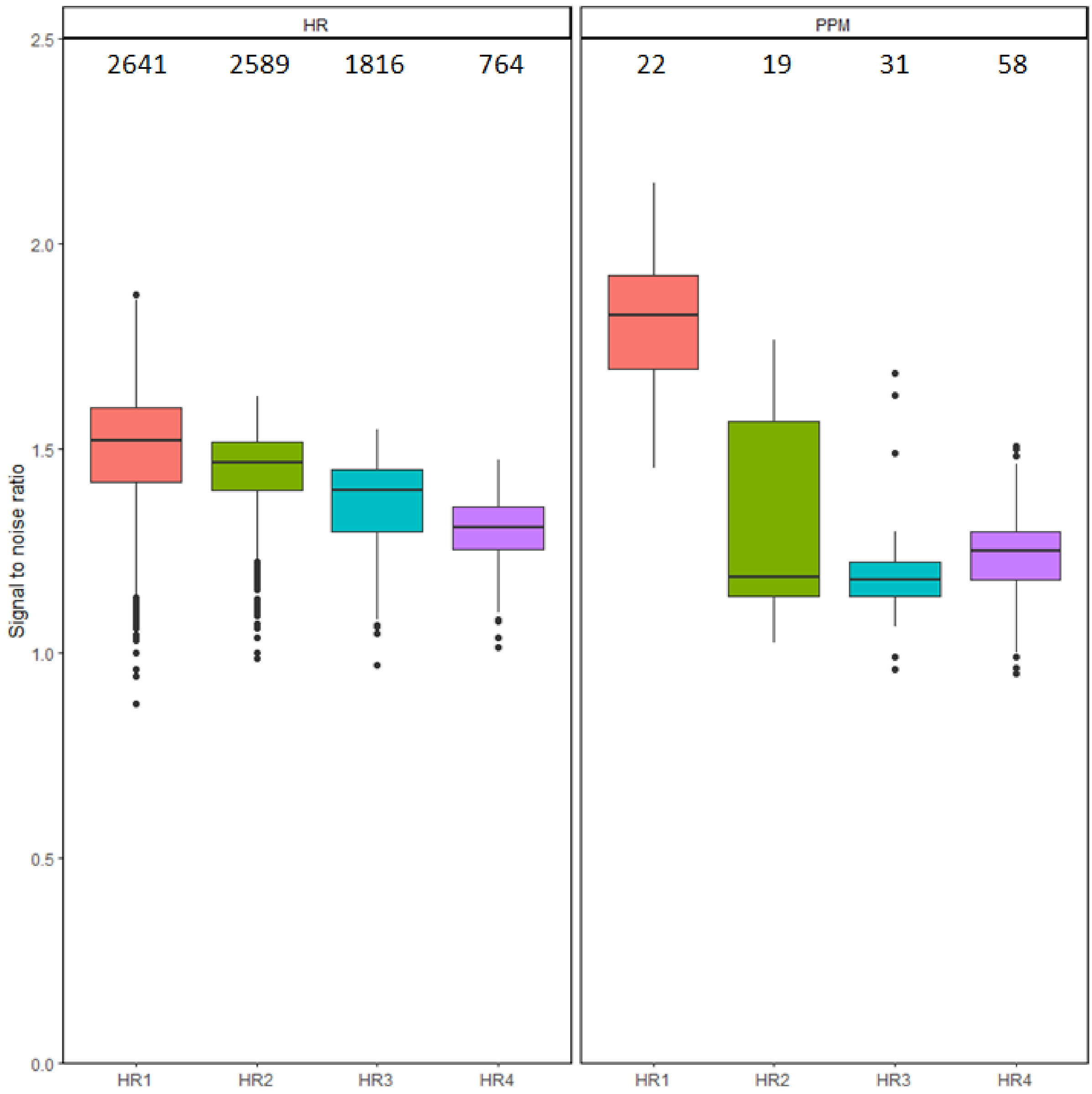


Figure 4.6 Signal to noise ratios of High Residency (HR) and pulse per modulation (PPM) transmissions of tags (V9P-2x; high power, High residency [HR] transmission rate = 1.8-2.2 s, 180 kHz, pulse per modulation [PPM] delay = 25-35 s) dropped at three locations with a four-receiver VEMCO HR2 180 kHz acoustic receiver array. Data includes 7,810 HR detections and 130 PPM detections cumulatively, the number of detections provided above the corresponding receiver.

4.3.1.4 Assessing position yield and system synchronisation using simultaneous tag detections

Synchronisation tags

It is recommended that range tests are undertaken to select the appropriate distances between receivers to maximize reception of sync tag detections (see Kessel et al. 2014 for range test information). A test array deployment prior to the start of a study is useful to ensure spacing facilitates appropriate clock synchronisation and the geometry of the array is appropriate to derive accurate positions. A transmission from a sync tag must be simultaneously detected on three or more receivers for positioning using the Time Difference of Arrival algorithm. Simultaneous sync tag detections are required for clock synchronisation, without which subsequent derived positions will be less precise (further detail in section 4.3.5). Sync tags may be either internal (VR2AR, HR2 receivers) or external (co-located on a receiver mooring line, i.e., VR2W receivers). It is recommended that a VPS array with active sync tags is deployed for atleast 1 h (ideally 24 h) prior to deploying animal tags so to generate data to aid later clock synchronisation choices. Sync tags can either transmit PPM or PPM and HR transmissions, the selection of which will dictate the rate of sync tag transmission (given HR can have higher transmission rates), i.e., a PPM sync tag with a 10-minute transmission delay (would result in max. 6 detections per hour). It should be noted that sync tags present within the system can contribute to collision potential in PPM VPS arrays (Espinoza et al. 2011), particularly at high power settings. A basic visualization of the number of simultaneous sync tag detections over time can be used to estimate whether there is adequate data available for system calibration and potential difficulties in signal reception between receivers which may be linked to incorrect spacing between receivers or system topography reducing line-of-sight between receiver pairs.

In the case study example, the cumulative number of detections of internal sync tags recorded across the array indicates reception issues between receivers and sync tags. For example, receiver HR2 and HR4 did not record many of HR1's sync transmissions (Fig. 4.7). This may be due to the distance between receivers exceeding the receiver's range e.g., HR2 and HR1 were 73 m apart, and H4 and HR1 were 82 m apart. This is supported by range test results (Supplementary Figure 4.1) which indicate a 35 to 45 % detection probability at 75 m, therefore distance between receivers likely reduced the number of sync tag detections. It is highly recommended that a test dataset using an array with active sync syncs is reviewed prior to conducting a VPS study so to assess whether simultaneous sync tag detections are attainable for later clock synchronisation. This test dataset can either be provisionally assessed using the steps outlined above or shared with an analyst to assess data yield.

Animal tags

Before positioning, users or analysts can assess whether there are enough simultaneous detections for hyperbolic positioning. Visualizing detections for a given tag across the receiver array over time can be useful in identifying whether transmissions were simultaneously recorded (Fig. 4.8). Additionally, for a short-term trial (like the 1-hour experimental case study detailed) this can be estimated by calculating a cumulative total number of detections on each receiver within an array, comparing this to the total number expected for the time period and to each surrounding receiver. For example, in the case study example there is not enough raw detections (without even considering simultaneous detections) for positioning (Fig. 4.9). During Trial 1 tag drops outside the array the expected yield from this 10-minute trial was 260 detections on each receiver, this value is exceeded on HR1 which is indicative of signal reflections. Additionally, HR2 and HR4 record <60 detections which suggests the likelihood of deriving continuous positions is low. By comparing "deep" (tags closer to benthos) and "shallow" (tags closer to the water's surface) static tags (Fig. 4.9), it is possible to assess whether tag position in this environment affects signal reception. A provisional assessment on the ability for shallow or deep-water static tag transmissions to be detected, i.e., simulating pelagic versus benthic animals, may be beneficial in selecting appropriate tag types (size and power). In the case study example, there was no clear relationship in the detectability of shallow or deep HR static tags. For example, in some cases shallower tags yielded a greater number of detections than deeper tags (and vice versa). In habitats with complex topography and underwater structures, tags closer to the benthos can result in lower detection yield due to reduced line-of-sight (the transmission path is blocked due to a structure) and multipath signal attenuation (the transmission reflects or scatters making it not possible to detect).

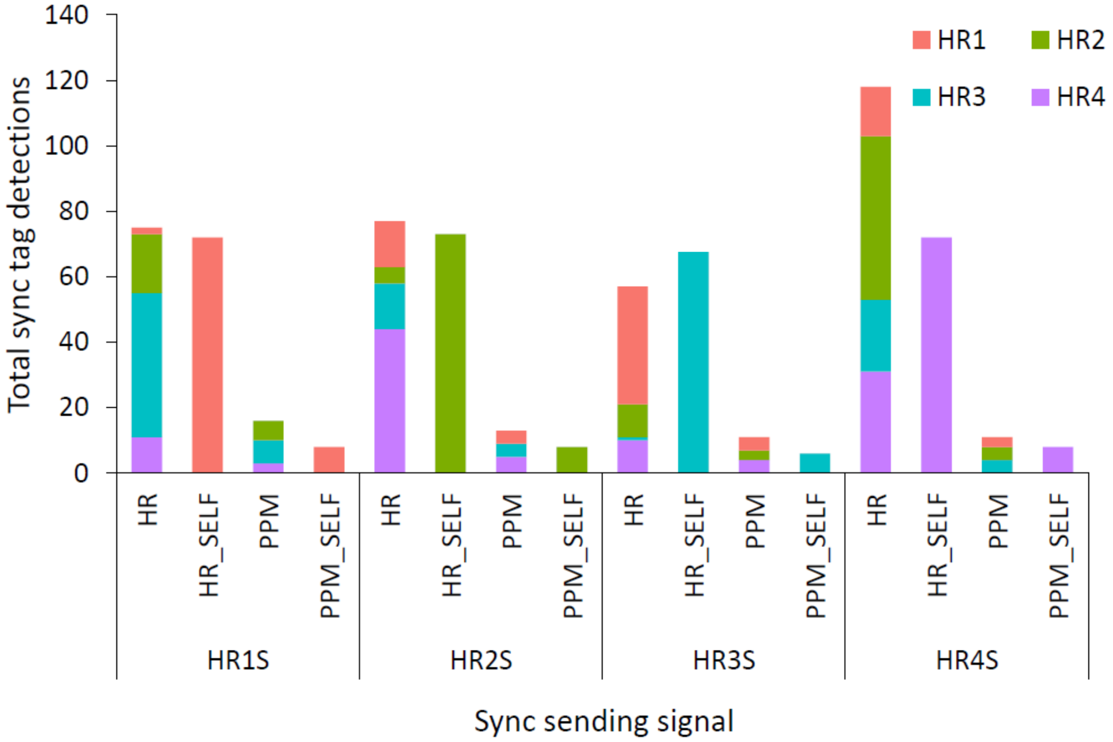


Figure 4.7 Total number of detections of internal sync tags (HR transmission rate = 25-45 s, PPM transmission rate = 270-330 s; 147 dB) aggregated across the 36 min study period. Number of detections displayed as a stacked bar for each signal type. Detections of surrounding sync tags are logged as either "HR" or "PPM" detections, and detections of internal sync tags are logged as either "HR_SELF" or "PPM_SELF". Reflections are included in this visualization and are identified according to listening receiver (e.g., HR4) decoding its own sync tag (e.g., HR4S) as a "HR" rather than "HR_SELF" detection. Expected number of sync detections: 7 (range 6 - 8) PPM detections per sync tag, and 61 (range 48 - 86) HR PPM detections per sync tag.

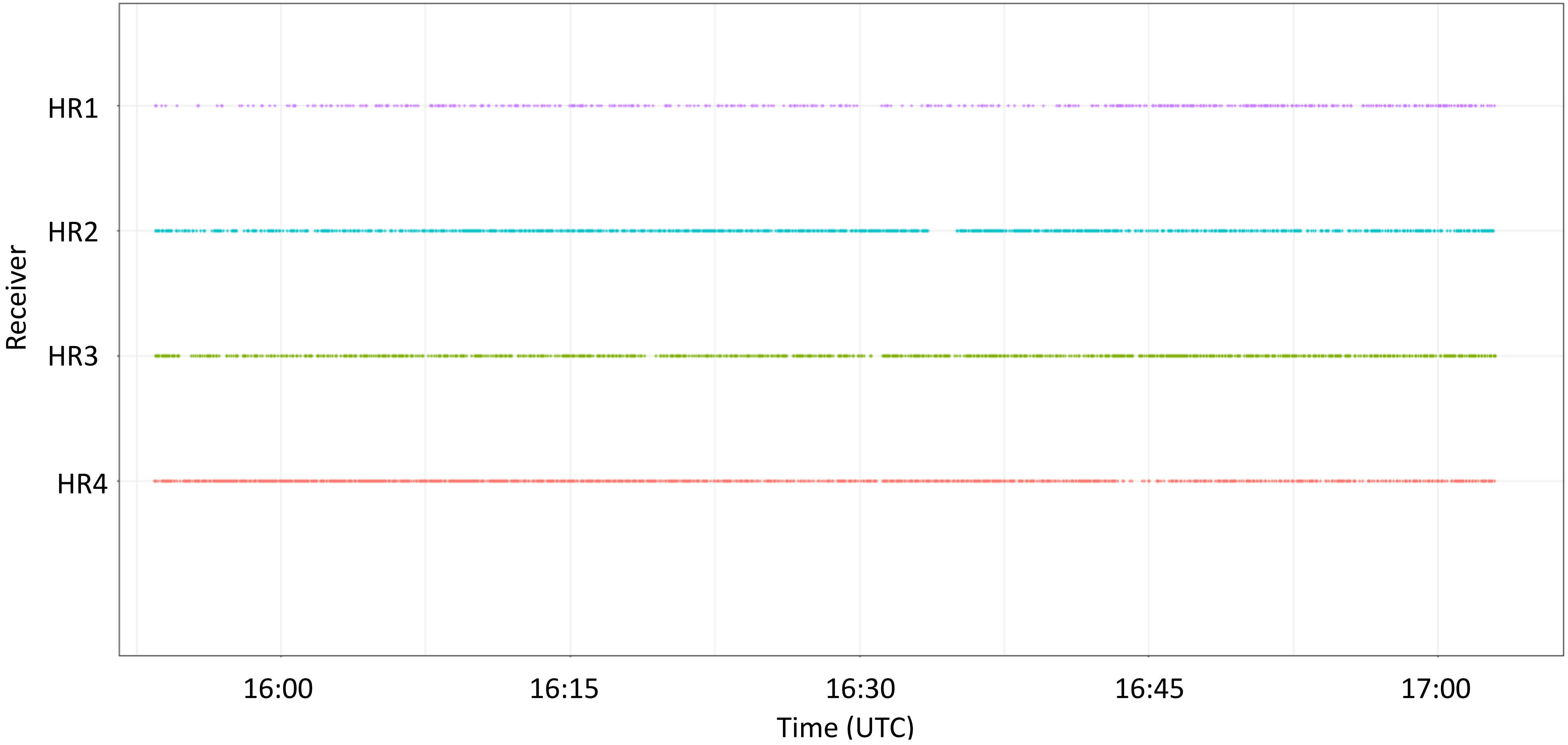


Figure 4.8 Viewing detections of a V9-HR tag (1.5 s mean transmission rate, 1-2 s range, 180 kHz, high power across the receiver array over time to assess the potential yield of simultaneous detections. Note, that during time synchronisation small differences may arise in the timing of these detections, but initial visualizations can be useful in identifying clear issues in system performance. Detections are denoted by a filled circle which is coloured according to the listening receivers storing the detection, includes HR1 (red), HR2 (green), HR3 (blue) and HR4 (purple). Ideally all four lines would be filled which would suggest continuous detections of the tag on the four receivers. Interruptions in detections of the tag on HR4 suggests poor detectability.

.

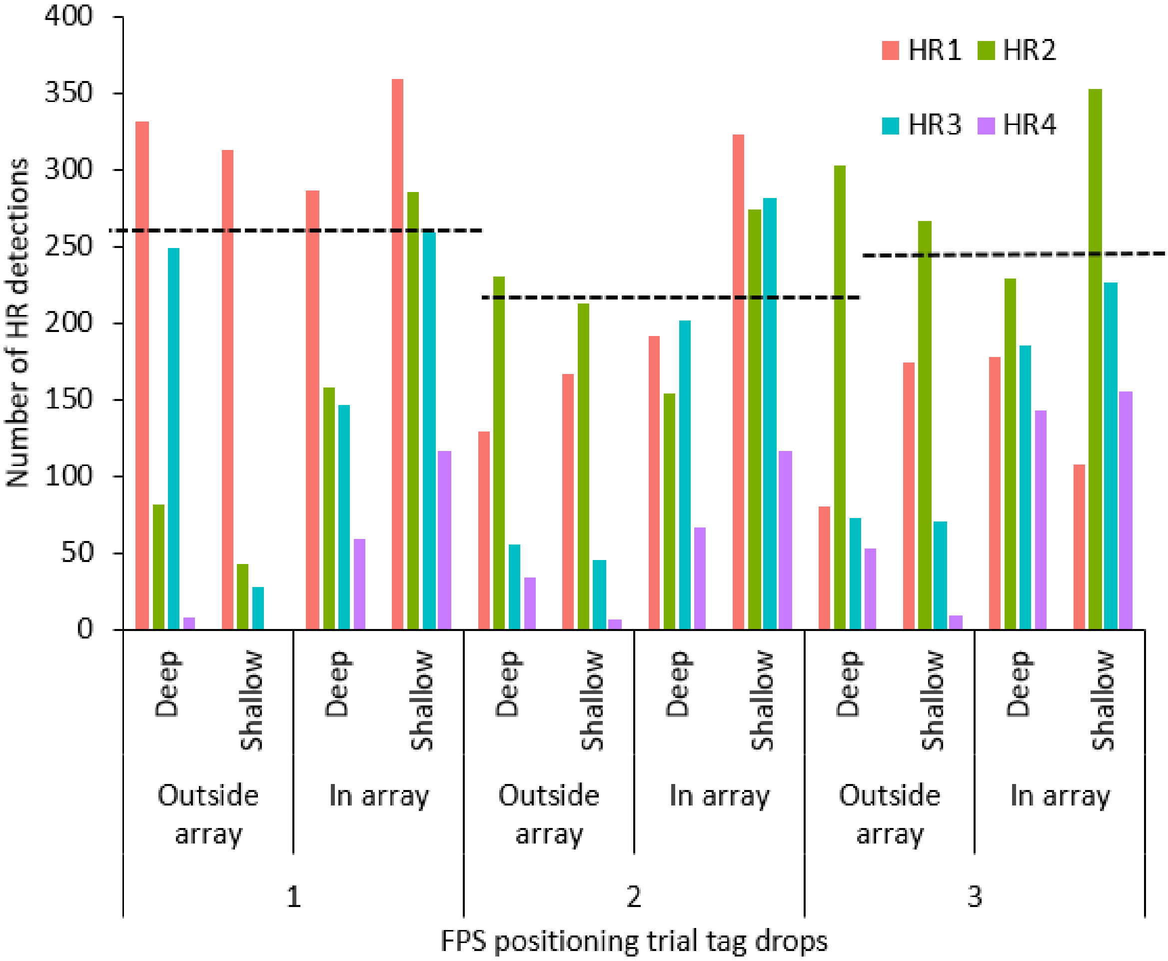


Figure 4.9 Number of HR detections of static tag drops per trial period (1-3). Each tag line deployed inside or outside the array comprised of two V9-HR range test tags (1.5 s mean transmission rate, 1-2 s range, 180 kHz, high power). The expected number of tag detections (dividing the trial duration by the sum of the nominal transmission rate plus the burst rate) is given above the corresponding trial as a dashed line.

4.3.2 Demystifying the black box

In VPS, the TDOA algorithm is used to derive animal positions. Given the direction of a transmission is unknown as an acoustic receiver is omnidirectional, TDOA uses hyperbolic positioning (geometry) to solve where the tag is located. In the simplest terms, by detecting a tag on at least three listening receivers, the intersection of these hyperbola defines the location of the tag. Prior to hyperbolic positioning, the VPS TDOA algorithm requires 1) a speed of sound model, 2) selection of good correlations to be used for array calibration and time synchronisation, and (3) the transmissions of a tag to be detected on 3 or more receivers.

1) Speed of sound model

To estimate the speed of sound in water, VPS uses the Coppens Equation (Coppens 1981). This equation calculates the speed of sound in water based on temperatures between 0 and 35°C, salinities of 0-45 parts per thousand (PPT), and depths of 0-4000 m (Smith 2013). For example, a 1°C increase in temperature leads to an increase of 4.5 m s^{-1} in sound propagation speed, and a 1 PPT change in salinity a 1.3 m s^{-1} increase in speed (Duxbury et al. 2018).

Generating a continuous speed of sound model

Temperature data can be provided by the user at any resolution e.g. every second or minute. Using these data, a spline function is applied to generate a continuous input for the speed of sound model. The speed of sound model is applied uniformly across the array. For example, if the study site has an area within the array which is 5°C cooler than the rest of the area, the same model is used which can exacerbate positional errors of animal tags across the temperature gradient.

2) System calibration

Owing to GPS error and the unexpected movement of receivers, the true location of the receivers is corrected using “good correlations”. A good correlation describes a simultaneous detection of a sync tag on a pair of receivers. Acoustic receivers and paired sync tags remain at fixed distances, therefore the range difference is calculated between these two fixed reference points which translates to the distance between receiver pairs and hence the location of each receiver (Fig. 4.10). Through this calculation, signal reflections can also be identified i.e. detections that arrive earlier than expected based on the tag power and the speed of sound model. Owing to the nature of a PPM signal (8 to 10 ping train translates to a single detection), PPM detections form a broad band which makes determining the precise time of arrival difficult (Fig. 4.11). In contrast, a HR transmission is a single pulse, and therefore facilitates more accurate range estimates. Multiple receiver pairs are used to correct the position of each receiver in the array (typically 2-4 pairs per receiver). The same receiver pairs can be used for later time synchronisation.

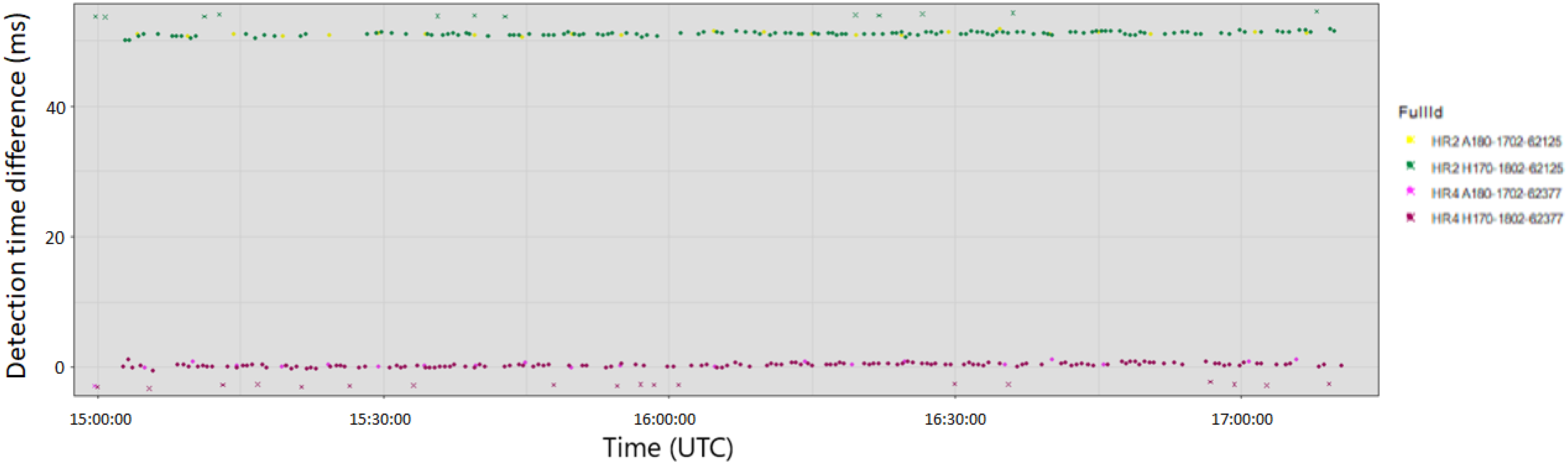


Figure 4.10 Vizualizing range differences between a pair of receivers (HR2, green points and HR4, maroon points). Given the receivers typically remain static, these differences should form an upper band (HR2) and a lower band (HR4) with the difference between points showing the detection time difference between the sync transmission sent and subsequently received by a listening receiver. The cross symbol indicates detections which do not meet two criteria, (1) the sync transmissions is received too early (exceeding the range difference) likely a result of signal reflections, and (2) a sync transmission is only recorded on one receiver. Filled circles depict good correlations, which describes a sync detection simultaneously recorded on both receivers.

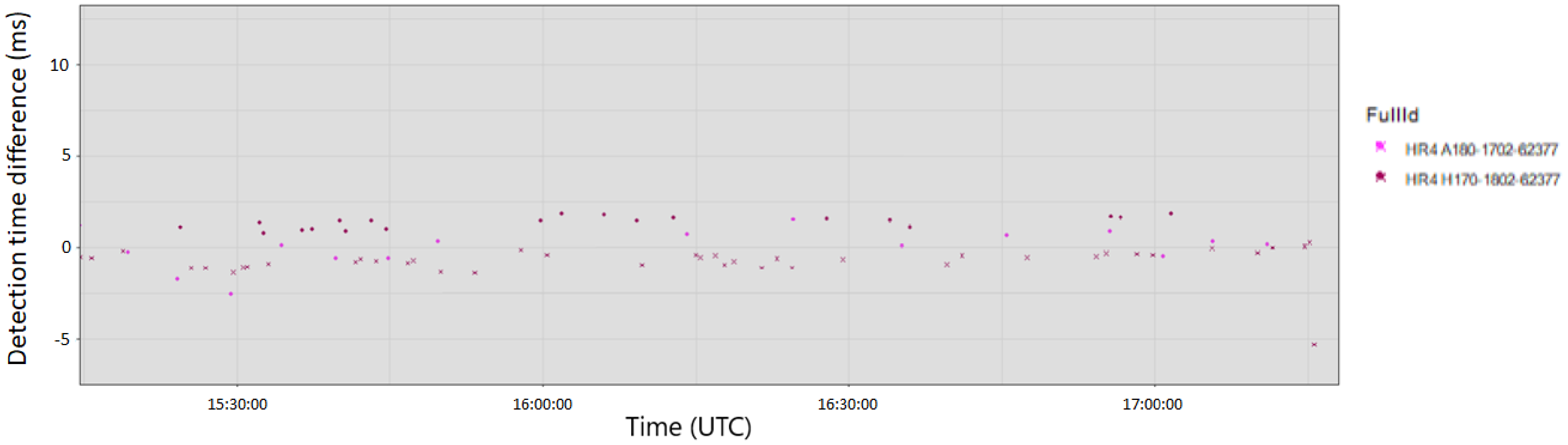


Figure 4.11 . A close up of the range difference of sync tag detections on a single receiver (HR4), showing how the band (width) of range differences for HR transmissions (maroon) is smaller than for PPM transmissions (pink).

3) Time synchronisation

Receiver clocks require correction in order to derive accurate detection times. This is due to clock drift in autonomous (non-cabled) receivers and subsequent inaccuracies in the detection time recorded by a listening receiver,

What is clock drift?

Each listening receiver contains an inbuilt clock which is controlled by a crystal oscillator. Clock drift is either constant or temperature related and arises due to manufactured differences in the crystal oscillator (constant drift, ±1.728 s d^{-1}; Smith et al. 2013) and can be variable due to temperature fluctuations (which follows a non-linear relationship with clock drift). Clock drift essentially describes the rate of change in skew, whereby a positive or negative value equates to a receiver clock that is faster or slower than another receiver clock. For a precise arrival time to be calculated, receiver clocks must be corrected across an array.

How do you estimate clock drift?

Using sync tags, it is possible to estimate clock drift between a pair of receivers by subtracting the signal propagation time difference (the amount of time taken for a signal to be received by a listening receiver after transmission) from the detection time difference.

Selecting a receiver base for time synchronisation

A receiver is selected that will act as the system base for time synchronisation. The base station receiver is ideally: (1) deployed for the entire length of the study, (2) is located towards the centre of the array, and (3) reliably detects nearby sync tags. Time synchronisation paths are then selected for neighbouring receivers. All receiver clocks are then time corrected according to the system base so to account for clock drift using a skew model. Peripheral receivers may need to “jump” connect to neighbouring receivers if it cannot communicate with the selected base (i.e., base is too far away to detect sync tag transmissions or there are topographic features obstructing line of sight). These data can be selected from the same receiver pairs used for system calibration.

How does sync tag data yield influence positioning error?

Clock synchronisation using fixed sync tags is central to generating accurate animal positions. Poor clock synchronisation i.e., due to a lack of sync tag detections between receivers will lead to inaccurate position estimates (higher associated horizontal positioning error, “HPE” or high root-mean-squared error “RMSE”). Additionally, insufficient sync tag data hinders system calibration (step 2). In cases when only a reflected signal is recorded it is not possible to correct the location of receivers which also reduces the accuracy of subsequent animal tag positions.

4.4 Conclusion

This study demonstrates user tools which can be used to assess potential data yield prior to embarking on estimating animal positions and associated error. While these steps are proposed for the HR-VPS, a commercial Time Difference of Arrival positioning system, they are transferable across both PPM and HR systems. This technology has the potential to redefine our understanding of fine-scale animal movements and spatial niche through the generation of animal positions with sub-metre precision. Empowering users by providing simple tools to identify factors that can limit data yield and therefore positioning yield is central to optimizing study design. Additionally, detailing the steps involved in VPS TDOA analysis highlights why several key features of an array must be carefully considering including receiver spacing and geometry, and sync tag transmission rates to ensure precise positions can be derived during subsequent positioning.

4.5 References

Baktoft H, Gjelland KØ, Økland F, Thygesen UH (2017) Positioning of aquatic animals based on time-of-arrival and random walk models using YAPS (Yet Another Positioning Solver). Sci Rep 7:14294.

Bergé J, Capra H, Pella H, Steig T, Ovidio M, Bultel E, Lamouroux N (2012) Probability of detection and positioning error of a hydro acoustic telemetry system in a fast-flowing river: Intrinsic and environmental determinants. Fish Res 125–126:1–13.

Brownscombe J, Cooke S, Algera D, Hanson K, Eliason E, Burnett N, Danylchuk A, Hinch S, Farrell A (2017a) Ecology of exercise in wild fish: Integrating concepts of individual physiological capacity, behavior, and fitness through diverse case studies. Integr Comp Biol 57:281–292.

Brownscombe JW, Cooke SJ, Danylchuk AJ (2017b) Spatiotemporal drivers of energy expenditure in a coastal marine fish. Oecologia 183:689–699.

Coppens AB (1981) Simple equations for the speed of sound in Neptunian waters. J Acoust Soc Am 69:862–863.

Ehrenberg JE, Steig T (2003) A method for estimating the ‘position accuracy’ of acoustic tags. ICES J Mar Sci 59:140–149.

Espinoza M, Farrugia TJ, Webber DM, Smith F, Lowe CG (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fish Res 108:364–371.

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Flemming JEM, Whoriskey FG (2015) Aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1255642.

InnovaSea Systems Inc. (2018) HR2 receiver and software user guide (5726-06).

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218.

Kessel ST, Hussey NE, Webber DM, Gruber SH, Young JM, Smale MJ, Fisk AT (2015) Close proximity detection interference with acoustic telemetry: the importance of considering tag power output in low ambient noise environments. Anim Biotelemetry 3:5.

Kraus RT, Holbrook CM, Vandergoot CS, Stewart TR, Faust MD, Watkinson DA, Charles C, Pegg M, Enders EC, Krueger CC (2018) Evaluation of acoustic telemetry grids for determining aquatic animal movement and survival. Methods Ecol Evol 9:1489–1502.

Leander J, Brodin T, Leonardsson K (2019) The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. Can J Fish Aquat Sci.

Nathan R *et al.* (2022) Big-data approaches lead to an increased understanding of the ecology of animal movement. Science 375:eabg1780.

Reubens J, Verhelst P, van der Knaap I, Deneudt K, Moens T, Hernandez F (2019) Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup. Hydrobiologia 845:81–94.

Silva AT, Hatry C, Thiem JD, Gutowsky LFG, Hatin D, Zhu DZ, W. Dawson J, Katopodis C, J. Cooke S (2015) Behaviour and Locomotor Activity of a Migratory Catostomid during Fishway Passage. PLoS One 10:e0123051.

Singh L, Downey NJ, Roberts MJ, Webber DM, Smale MJ, van den Berg MA, Harding RT, Engelbrecht DC, Blows BM (2009) Design and calibration of an acoustic telemetry system subject to upwelling events. Afr J Mar Sci 31:355–364.

Smith F (2013) Understanding HPE in the VEMCO Positioning System (VPS). Available rom https://www.oceans-research.com.

Smith GW, Urquhart GG, MacLennan DN, Sarno B (1998) A comparison of theoretical estimates of the errors associated with ultrasonic tracking using a fixed hydrophone array and field measurements. Hydrobiologia 371:9–17.

Thorstad EB, Rikardsen AH, Alp A, Økland F (2013) The use of electronic tags in fish research – An overview of fish telemetry methods. Turkish J Fish Aquat Sci 13:881–896.

Vergeynst J, Baktoft H, Mouton A, De Mulder T, Nopens I, Pauwels I (2020) The influence of system settings on positioning accuracy in acoustic telemetry, using the YAPS algorithm. Anim Biotelemetry 8:25.

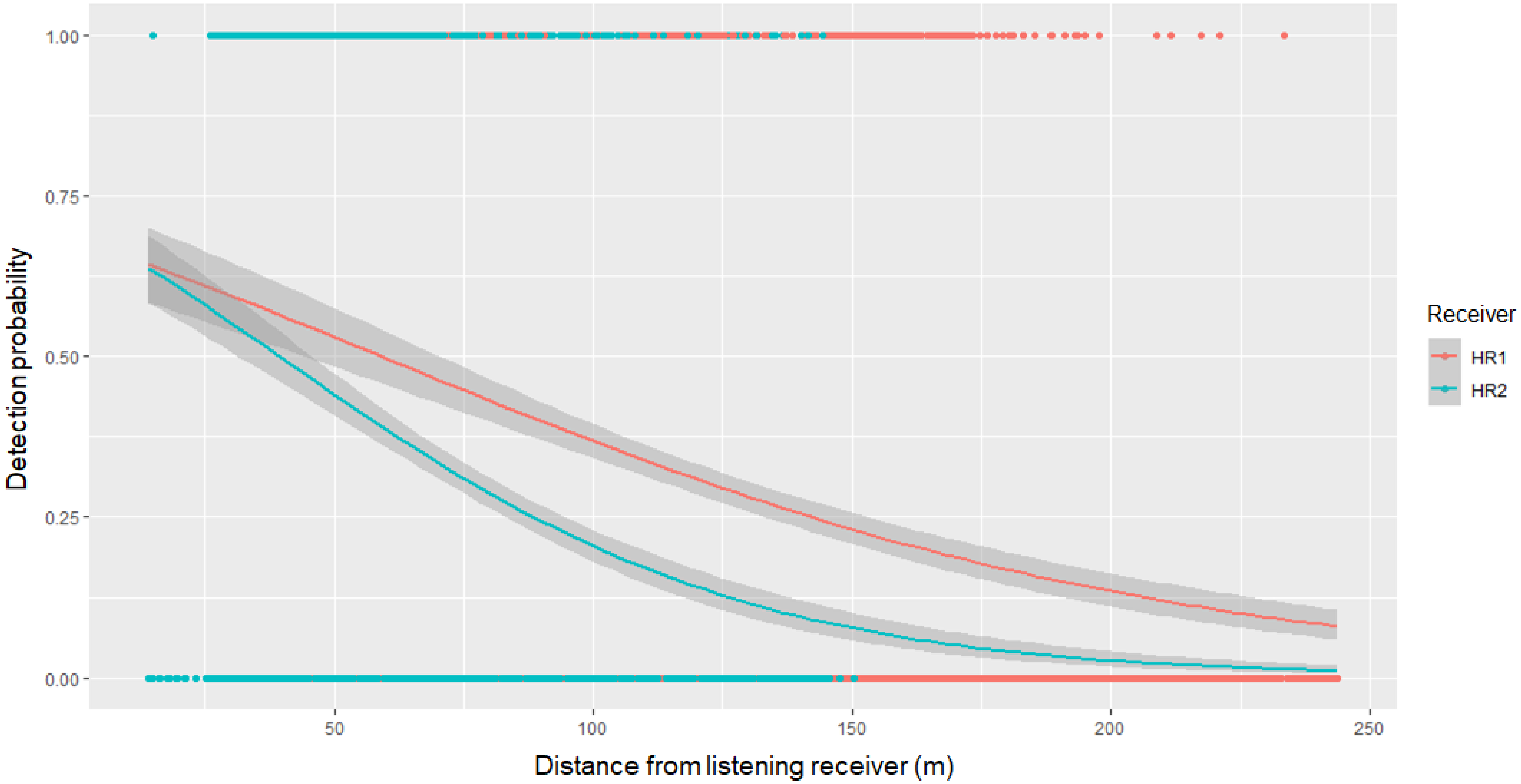
Wilson R, Wilson RP, Quintana F, Hobson VJ (2011) Construction of energy landscapes can clarify the movement and distribution. Proc R Soc B. 279: 975-980. doi:10.1098/rspb.2011.1544.

Supplementary material for Chapter 4

S4.1 Range tests

Range tests were conducted northwest of Ascension Island. Two HR2 receivers were deployed 130 m apart, each HR2 mooring line comprised of a 14 mm polypropylene line which terminated in two 3” travel floats (buffered in-between to prevent noise) which sat at the water’s surface so the equipment could be easily retrieved. A single HR2 receiver (180 kHz) was attached pointing upwards on each mooring line, and mooring lines were anchored using a 30 kg weight. A single V9-HR range test tag (1.5 s mean transmission rate, 1-2 s range, 180 kHz, high power) was affixed onto a 3 m monofilament line which terminated in a 1 kg dive weight, the line was held approx. 2 m beneath the water’s surface from onboard a 3 m rigid inflatable boat with the engines off. The boats position during drift trials was recorded using a handheld GPS (Garmin GPSMAP 64x) set to a 2 s automatic sampling interval. Each test lasted 6 to 11 mins. Data were rounded to the nearest second and a binary value assigned depending on whether the transmission was detected (1) or not detected (0) on the listening receiver for each metre travelled, in each respective trial.

Data were then aggregated, and at each metre increment the expected number of detections (time to travel 1 m/tag transmission rate x burst rate) was calculated relative to the number of observed detections (time to travel 1 m/number of transmissions received in that time interval) (following Kessel et al. 2014).



Supplementary Figure 4.1 Detection efficiency of a V9-HR range test tag at increasing distance from two HR2 acoustic receivers (180 kHz) deployed in a sand (HR1) and rock (HR2) environment (130 m apart). Filled points represent a binary probability of detection (1 = detected, 0 = not detected) for each metre travelled, with a logistic regression used to generate an average detection probability (1 = 100%, 0 = 0%) for each unit of distance

Supplementary Table 4.1 Tag positioning trial metadata. “In” and “outside” describes tag line location relative to the 4-receiver HR2 FPS. Note time start here is with a buffer added (e.g., the drop was at 15:53, the time period where the boat was nearby to reduce the impact of boat noise on signal reception/positioning power was removed making it 15:55).

Drop position	Drop no.	Time start	Time end	Tag mooring depth (m)	Tag ID	Mean tag depth (m)
In	1	15:55:00	16:07:00	23.7	3824 3825	10.0 14.2
	2	16:19:00	16:30:00	22.7	3824 3825	9.9 14.2
	3	16:45:00	16:58:00	23.7	3824 3825	9.77 14.0
Out	1	15:55:00	16:07:00	22.5	3822 3823	13.1 17.8
	2	16:19:00	16:30:00	23.2	3822 3823	10.8 17.0
	3	16:45:00	16:58:00	24.3	3822 3823	10.8 16.9

Chapter 5. Exploring coexistence of two abundant aquatic mesopredators in a complex equatorial system

5.0 Chapter summary

Rock hind (*Epinephelus adscensionis*) and spotted moray (*Gymnothorax moringa*) are ubiquitous mesopredators that co-occur in the nearshore waters of Ascension Island in the South Atlantic Ocean. This isolated volcanic system is home to high biomass and low species diversity, which poses the question, how can two mesopredators that perform similar ecological roles coexist? Here, we combined acoustic telemetry, stomach content analysis, and stable isotope analysis to explore space use and diet choices, respectively, within and between these two species. While *E. adscensionis* had high residency and small calculated home ranges (0.0001 – 0.0920 km^2), *G. moringa* exhibited short periods of residency (<3 months) prior to emigration. A hierarchical generalized additive model using 12 h averaged depth data identified grouper were lower in the water column than moray eel, and both species occupy depths 1.6% deeper at night versus day. Vertical space use differed significantly across the 20-month study duration, and moray eel depth was significantly predicted by lunar illumination. Individuals of both species showed individual differences in vertical space use. Additionally, visualizations of individual detection profiles indicate a potential synchronized spawning event by grouper in September 2019. Aggregating samples by species and tissue type, Bayesian ecological niche modelling showed a 53.14 to 54.15% probability of niche overlap from fin clips and 78.02 to 97.08% chance from white muscle. Stable isotope values from fin clip and white muscle found a high degree of overlap in isotopic niche, however, variability in niche breadth between years suggest these species utilise a range of prey items over time. These findings suggest that generalist diets enable individuals to utilise all available prey within exceedingly small home ranges, in conjunction

individual variation in horizontal and vertical space use, these behaviours likely facilitate the coexistence of these two highly abundant mesopredators.

5.1 Introduction

The term “niche” describes how animals partition resources in time and space, shaped by behavioural choices and environmental conditions (Hutchinson 1957, Leibold 1995). External forcing (e.g., competition, food availability, environmental conditions) drives how the fundamental niche of an organism (where it could exist) translates into realized niche (where it actually exists) (Hutchinson 1957, Johnston et al. 2019). Species coexistence is central to the maintenance of biodiversity (Chesson 2000), therefore understanding the mechanisms which facilitate coexistence is pivotal to conservation. The competitive exclusion principle suggests that two species occupying the same niche cannot coexist (Hardin 1960). To explain how coexistence can occur in nature, Macarthur & Levins (1967) proposed that species can coexist within a certain threshold of similarity. Namely how resource partitioning, and differences in how species with two similar trophic roles differ over space, time or the resources utilized, will facilitate coexistence (Bolnick et al. 2011). In aquatic systems, resource partitioning often occurs via dietary segregation whereby individuals will consume different dietary items, or size spectra of prey to alleviate competition for resources (St-John 1999, Meyer & Dierking 2011, Higgins & Mehta 2018). Behavioural strategies such as dietary generalism which describes an ability to consume a wide variety of available resources can also enable species to exploit seasonal prey pulses (Gkenas et al. 2012, Ward et al. 2018). Generalism is often facilitated by a range of ecophysiological and morphological adaptations which enable a species to utilize available resources, for example, flexible diel activity rhythms enable a species to make use of fluxes in available prey (Piet & Guruge 1997, Fox & Bellwood 2011, Sánchez-Hernández et al. 2020). Dietary generalism facilitates the maintenance of small home ranges, whereby individuals can acquire resources and minimize energy spending transiting to forage (in line with Optimal Foraging Theory, MacArthur & Pianka 1966). Understanding the mechanisms which support coexistence is pivotal to exploring the mechanisms which maintain biodiversity, particularly where functional redundancy (the role of one species is fulfiled by another) occurs (Walker 1992).

Medium- and large-bodied mesopredator fishes which inhabit nearshore habitats play a vital role in food web functioning and maintaining stability, for example, through transferring energy between herbivores and predators (Polovina 1984). Grouper (family Serranidae) and moray eels (Gymnothorax) are two commonly co-occuring mesopredators found in shallow-water reef systems (Sanchez Henao et al. 2020). Their high abundance and occupation and similar trophic roles raises a key question: how do these species coexist? These species have been seen to exhibit contrasting feeding strategies owing to their diverse morphologies. Grouper are diurnal semi-benthic piscivores, which typically hunt in open water (Bshary et al. 2006), while the anguilliform body morphology of moray eels enables them to maneuver through crevices and ambush prey (Randall & Golani 1995, Bshary et al. 2006). Grouper feed opportunistically on available prey to reduce competition with conspecifics, but are limited by gape size and therefore prey size (St-John 1999, Meyer & Dierking 2011). Moray eels are also scavengers which use a range of prey manipulation behaviours to consume larger prey, including knotting, shaking, rotational feeding and ramming to improve gripping capability, with a second set of jaws nested in its throat that can pull prey towards its mouth (Mehta & Wainwright 2007). The mechanisms that facilitate their coexistence, particularly in high biomass systems, are poorly described.

The development of acoustic telemetry has enabled the tracking of multiple species across a plethora of habitats and environmental gradients and informed ecosystem-based approaches to fisheries management (Hussey et al. 2017, Lennox et al. 2019). Discontinuous lines and gates of acoustic receivers can provide information on the presence/absence of species, which can be used to derive estimates of residency, activity space and home range (Heupel et al. 2006). Combining this technology with measures of dietary niche, including stomach content and stable isotope analysis, can contextualize spatial data and identify differences in dietary choice over a range of temporal scales (Harmelin-Vivien et al. 1989, Guzzo et al. 2016, Chan et al. 2022).

Visualization of bulk nitrogen and carbon stable isotopes in delta space are akin to initial descriptions of Hutchinson's *n*-dimensional niche hypervolume (*n* equates to the number of isotopes) (Shipley & Matich 2020). These established tools have been used to study coexistence and resource partitioning in a range of aquatic environments, including arctic lakes (Guzzo et al. 2016), fjords (Kristensen et al. 2010) and estuaries (Matich et al. 2017). The heavy-to-light isotopic rates of carbon (denoted as $\delta^{13}C$) are underpinned by basal primary production pathways and are considered an important proxy for habitat-use variation e.g., whether animals use pelagic or coastal areas, owing to minimal isotopic fractionation of 0-2‰ between consumer and prey (Fry 2006, Matich et al 2017, Shipley & Matich 2020). Heavy-to-light ratios of nitrogen ($\delta^{15}N$) are used to define an animal's trophic position within a food web, owing to a predictable stepwise enrichment of ^{15}N of 3-4‰ of a consumer relative to its diet (Peterson & Fry 1987). After a shift in diet, different tissues react at different rates according to macromolecular synthesis and catabolism leading to differing isotopic signatures depending on the tissue analyzed (Martinez & Wolf 2005, Carleton et al. 2008). By using multiple tissues with differing turnover rates, trophic interactions can be compared across a range of temporal scales (Bearhop et al. 2004). For example, using a controlled-diet stable isotope feeding trial Matley et al. (2016) identified that adult leopard coral grouper (*Plectropomus leopardus*) tissue turnover rates were estimated as 37 d for fin, and 126 d for white muscle. Isotopic signatures of fishes can be derived from lethal and non-lethal sources, including small (>2 g) muscle samples and fin clips (Post 2002, Cunjak et al 2005, Church et al 2009).

To investigate the mechanisms supporting coexistence of two mesopredators found in a remote nearshore aquatic system, we collected acoustic telemetry data over a range of spatial scales using different array designs to assess horizontal and vertical distributions of *E. adscensionis* and *G. moringa*. These spatial data were contextualized by stomach content analysis and stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) derived from fin clips and white muscle to quantify isotopic niche size and dietary overlap over a range of timescales. Based off of existing literature and local knowledge, we hypothesized that both species would exhibit significant overlap in their observed spatial niche and exhibit high residency and site fidelity to the study area. Both species would alleviate intra- and interspecific competition via resource partition namely through temporal differences in the space use, which will facilitate their coexistence. Additionally, due to high levels of resource competition among these predators, individuals will consume a wide variety of prey items, resulting in generalist diets and a broad trophic niche. Overlap in the dietary niche of these two mesopredator species will indicate a degree of functional redundancy. The current research addresses critical regional knowledge gaps and will inform practical marine management objectives.

5.2 Methodology

5.2.1 Study Area and the Acoustic Receiver Deployments

Ascension Island (7.9467°S, 14.3559°W) is a young volcanic island situated in the South Atlantic Ocean, 1,500 km from Africa and 2,300 km from South America (Wirtz et al. 2017) (Fig. 5.1). Unlike other tropical islands, Ascension's nearshore environment lacks coral reefs, mangroves and seagrass beds. Instead, the nearshore environment is a fringing volcanic reef punctuated by pockets of sand and rhodolith. This study incorporates data from three separate receiver array deployments (see overview in Fig. 5.2), which includes: a single line of receivers positioned along the coastline in a line ("NW array", 2018-2019), a grid of receivers with overlapping detection ranges situated in the northwest of the island in English Bay

("EBAY array", 2019 – 2021; moored at 11 – 33 m depth, -14.39°S -7.89148°W), and a grid of receivers at Bates Point ("BP array", 2020 – 2021; 1 km west of the English Bay site, moored at 13 - 71 m depth; -14.40154°S -7.89615°W).

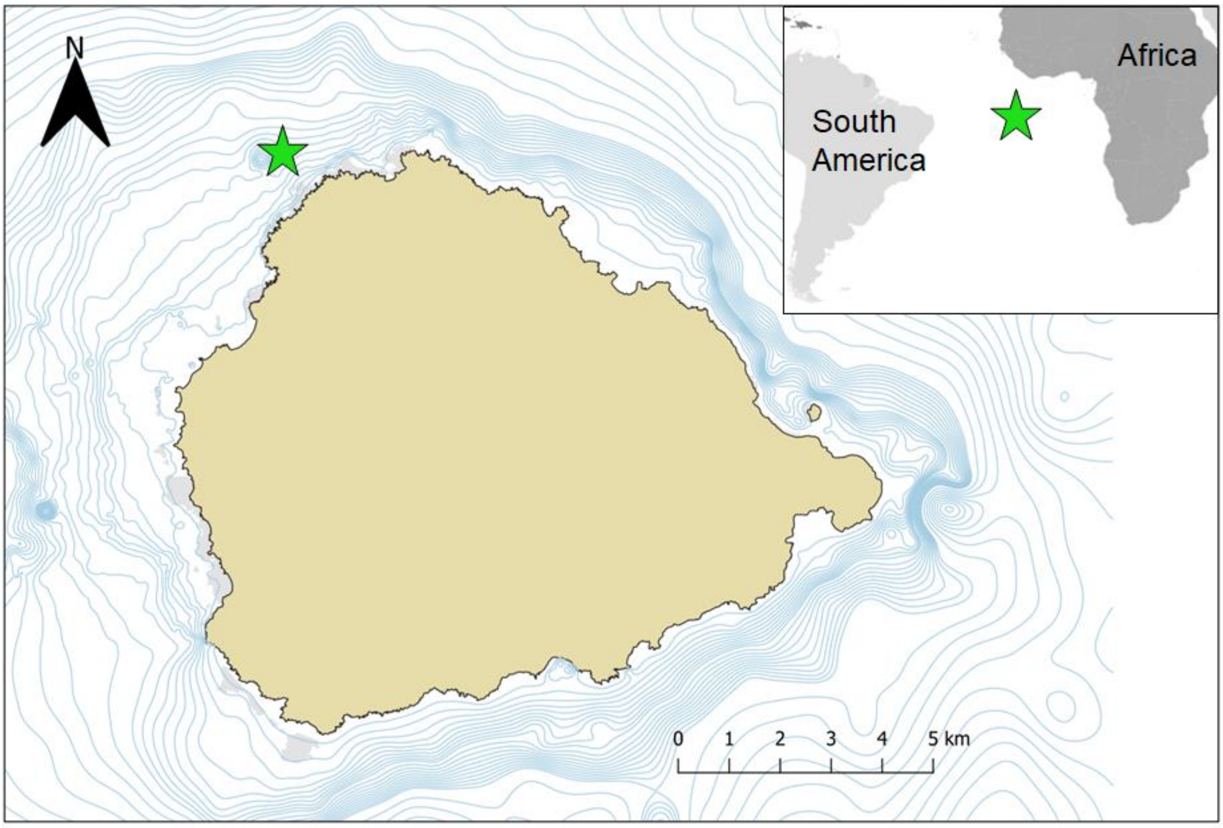


Figure 5.1 Ascension Island in the South Atlantic Ocean (7.9467°S, 14.3559°W). Green star indicates the region of the tracking study.

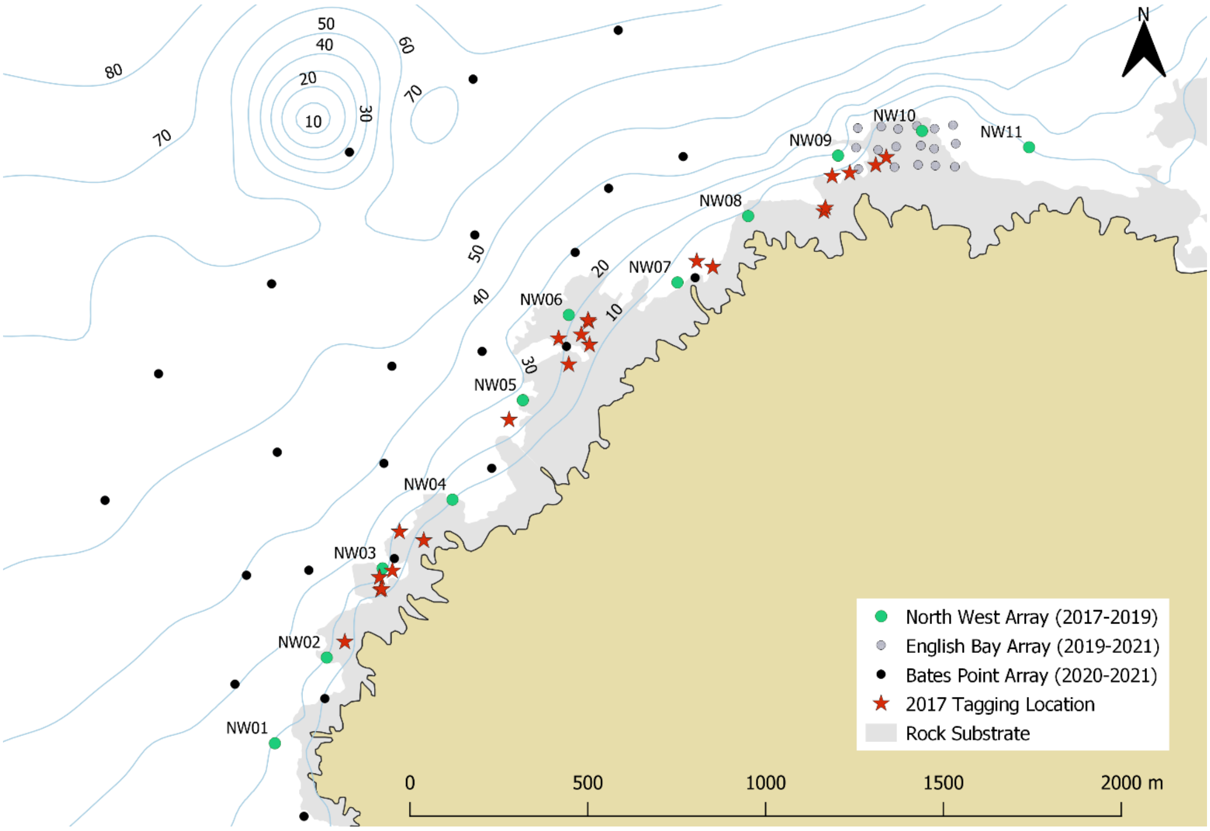


Figure 5.2 Ascension Island with the three acoustic arrays deployed between 2017-2021, includes: the North West linear array (“NW”, *n* VR2W acoustic receivers = 11; 2017-2019 deployment, green circle), English Bay Vemco Positioning System (*n* acoustic receivers = 9-22, 2019-2021, the gray circle with crosshatch fill), Bates Point array (*n* acoustic receivers = 23, 2020-2021, black circle). Fish were tagged in 2017 for the North West array (*n* rock hind grouper = 20, indicated by red stars), 2019 within the English Bay array (*n* rock hind grouper = 10; *n* moray eels = 10), and 2021 within the Bates Point array (*n* rock hind grouper = 16; *n* moray eels = 5). The gray-filled polygon indicates rock substrate.

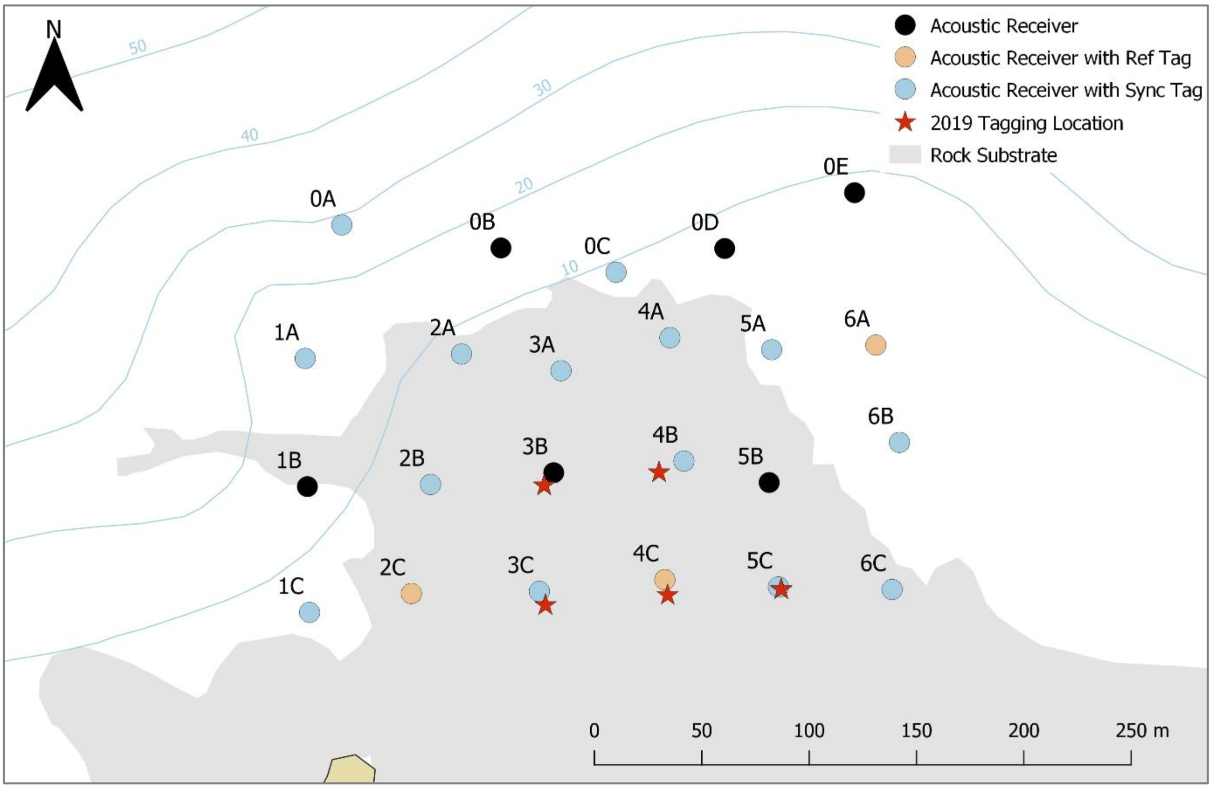


Figure 5.3 The English Bay Vemco Positioning System (VPS) deployed northwest of Ascension Island from 27th July 2019 – 14th January 2020 comprised of VR2W acoustic receivers (*n* total = 23) with co-located synchronisation tags (*n* = 14, black circle) or reference tags (*n* = 3, orange circle). Animals tagged in 2019 include rock hind grouper (*n* = 10) and moray eel (*n* = 10); red stars denote tagging locations. The majority of the array remained in place from 17th January 2020 – 15th June 2020, excluding receivers 2C and 6C. From 15th June 2020 – 15th April 2021, receivers 1A – 6A and 4B - 6B remained.

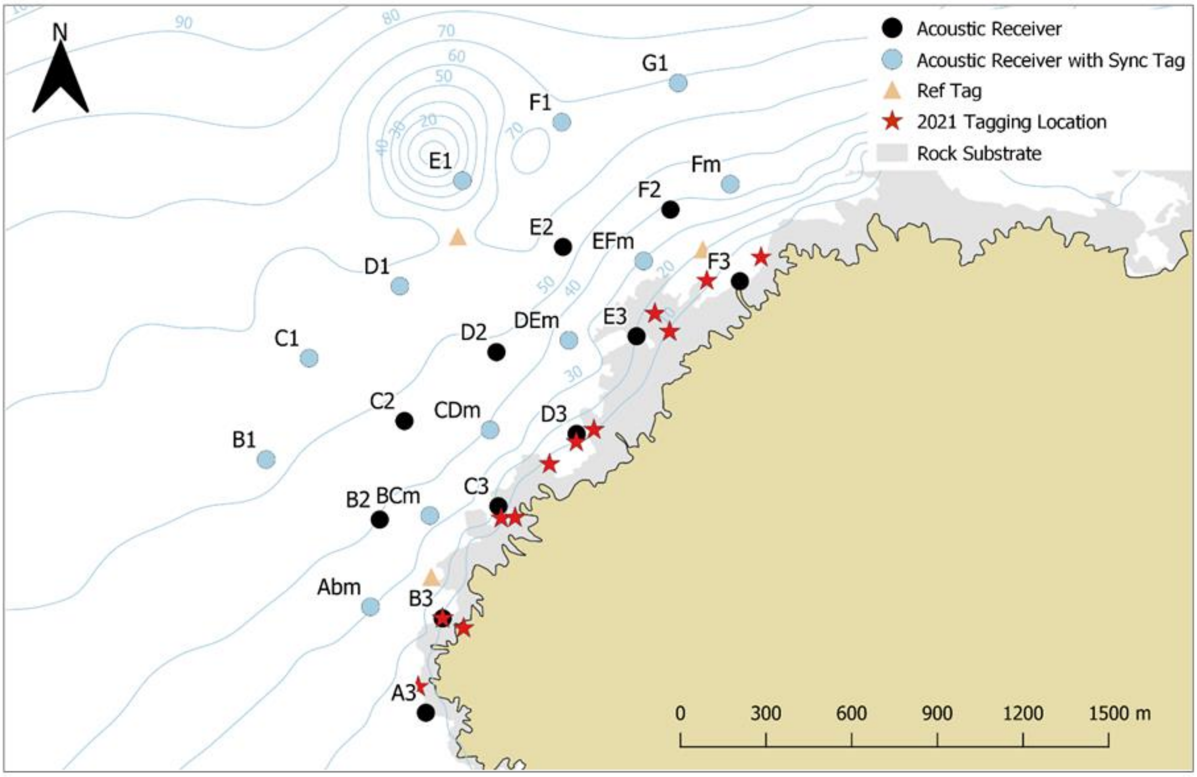


Figure 5.4 The Bates Point array (*n* acoustic receivers = 23, *n* acoustic receivers with co-located synchronisation "Sync" tags = 12) deployed from 21st December 2020 to May 2021 northwest of Ascension Island. Orange triangles indicate position of reference tags (*n* V16-6x = 3; transmission rate = 540 – 660 s, 69 kHz, 158 dB). Bates Point 2021 tagging locations (*n* rock hind = 16, *n* spotted moray = 5) denoted by red stars.

In 2017, a line of VEMCO VR2W acoustic receivers (*n* = 11, 180 kHz, Innovasea Systems Inc., Nova Scotia, Canada) was deployed with an average spacing of 291 m (range = 241 – 336 m; hereafter referred to as the "NW array") (Fig. 5.2). Receiver lines comprised of an 8" trawl float (800 g lift) spliced onto a 14 mm polypropylene line terminating in a 30 kg anchor. Data from this array was trimmed, and the resultant dataset spanned from 3rd August 2018 – 14th April 2019.

In 2019, VEMCO VR2W acoustic receivers (*n* = 23; 69 kHz) were deployed with a conservative spacing of 55 m to 80 m to form a Vemco Positioning System (Fig. 5.3). Receiver lines comprised of two 8" trawl floats (1700 g combined lift) spliced onto a 14 mm polypropylene line which terminated in a 35 kg anchor (for receivers deployed on sand) or a 4 mm chain insulated in fireman's hose (64 mm thickness) which was shackled around underwater structures to limit damage to the seabed (for receivers deployed on rock). The acoustic receivers were affixed to receiver lines so to sit >4 m below the water's surface to limit the influence of surface turbulence (noise) on signal reception, with all receivers positioned at depths of >20 m with hydrophones facing downwards and those <20 m facing upwards to improve the likelihood of animal detection (typically demersal). External synchronisation (hereafter, "sync" tags, *n* = 14, VEMCO V16-6x, transmission rate = 540 - 660 s, nominal transmission rate = 600 s, 69 kHz, 154 dB) were attached 1 or 2 m below the majority of acoustic receivers to aid with clock synchronisation. In addition, three reference tags (VEMCO V16TP-6x, transmission rate = 540 – 660 s, nominal transmission rate = 600 s, 69 kHz, 152 dB) were co-located within the array. The number of deployed receivers fluctuated between years, ranging from 23 acoustic receivers deployed on 27th July 2019 – 14th January 2020 (1 lost during deployment, 2C) to 20 receivers on 17th January 2020 – 15th June 2020 (no 2C or 6C), and 9 receivers deployed 15th June 2020 – 15th April 2021. Data from the array was trimmed to 3rd August 2019 – 14th April 2021, where the array was fully installed and utilized. Calculated Time Difference of Arrival (TDOA) positions generated from this data was limited due to various factors (see chapter 3). Therefore, raw detections were used in subsequent visualizations and analyzes.

Between the 14th to 21st of December 2020, at Bates Point a total of 23 VEMCO acoustic receivers (VEMCO VR2W, *n* = 11; VEMCO VR2AR, *n* = 12; 69 kHz) with either active internal synchronisation (hereafter, "sync" tags; *n* = 12, 154 dB) or external sync tags (VEMCO V16, *n* = 1, 158 dB, 69 kHz; Innovasea Systems Inc., Nova Scotia, Canada) were affixed to receiver lines 1 m below receivers (transmission rate = 540 – 660s, nominal transmission rate = 600 s, 69 kHz, high power). The VR2AR receivers were also set to record ambient noise levels every 60 s. All receiver lines comprised of one 11" trawl float (8400 g lift) spliced onto a 14 mm polypropylene line terminating in a 55 kg chain anchor. Three reference tags (VEMCO V16-6x, transmission rate = 540 – 660 s, nominal transmission rate

= 600 s, 69 kHz, 158 dB) were also deployed throughout the array (at depths of 28.5 m, 36.9 m and 46.4 m, respectively). Data from this array was trimmed to 7th January 2021 – 15th April 2021.

Before receiver deployment, range test results were critically assessed, including data from fixed-distance range tests conducted in 2017 used to identify detection range and guide appropriate tag selection (*n* surface range tests from a kayak = 3, Ascension Island Government). The second set of range tests were conducted in 2019, to identify the role of substrate type on detection range (for each substrate type: *n* surface range tests from a kayak = 1, *n* benthic range tests on SCUBA = 1; see Chapter 3 Fig 3). Sync tag data generated between 1st September 2019 to 1st October 2019 within the English Bay array (Supplementary Figure 5.1) were also used to determine detection range and select appropriate receiver spacing (the distance that an emitting tag and listening receiver can be apart and the tag reliably detected, see Simpfendorfer et al. 2008 for more details) for the Bates point array. A 400 m spacing between receivers was used within a grid design (Fig. 5.4). An interstitial gate of receivers was then deployed between the two shallowest receiver lines to enable the generation of fine-scale positions (namely by forming a VEMCO positioning system). Due to insufficient simultaneous detections required for deriving positions (likely due to limited detection ranges across the volcanic substrate), raw detections were used for visualizations and analysis.

5.2.2 Tag attachment

Adult *E. adscensionis* (*n* 2017 = 20; *n* 2019 = 10; *n* 2021 = 16) were captured using a conventional medium rig fishing rods or handlines with size 10/0 barbless circle hooks. Adult *G. moringa* (total *n* 2019 = 10; total *n* 2021 = 5) were collected using both rod and handline with 8/0 barbless circle hooks (*n* 2019 = 10; *n* 2021 = 2) and from the shore using a soaked pelagic carcass (*Acanthocybium solandri*, *n* 2021 = 3). For biological information of tagged fish, see Table 5.1. To reduce the risk of barotrauma and to ease capture due to an observed shift to shallow depths in the pursuit of seasonal prey pulses (e.g. green turtle *Chelonia mydas* hatchlings in 2020), all individuals were caught at depths of <20 m. Upon capture, animals were transferred to a 25 L saltwater tote containing 300 PPM of clove oil to reduce stress before handling. After anaesthesia was induced, fish were measured, and total length and weight were recorded. A small non-lethal tissue sample was then taken from the front dorsal fin (posterior region, tip; 600 - 800 mg; only fish tagged in 2019 and 2020), and two bicolour t-bar tags (FD-94 Floy tag, Floy Inc., USA) inserted into the body midway along the dorsal fin to aid with future identification (sex was not determined). A V16 VEMCO acoustic transmitter was surgically implanted into the intraperitoneal cavity (see Table 5.2 for tag specifications and programming), and the incision was closed with two independent sterile sutures (Ethicon 2-0 non-absorbable suture used on grouper; Ethicon 3-0 absorbable suture used on eels; Ethicon Inc., New Jersey, USA). All fish were aspirated with a combination of clove oil (300 PPM) and seawater throughout the procedure. All tagged fish were held for <30 minutes until a strong swim response was observed prior to release at their original capture site to aid recovery and reduce the risk of predation.

To identify potential differences in space use and diet due to animal size, we first assessed whether grouper and eel total length (a proxy for fish size) differed between tagging years. Due to unequal tagging cohort sizes (*n* tagged grouper 2017 = 20; *n* 2019 = 10, *n* 2021 = 16), and unequal sample variances (2017 = 42.1, 2019 = 9.752, 2021 = 10.86), a Welch's ANOVA was used to compare mean total length of tagged grouper across the three tagging years (2017, 2019 and 2021). A Games Howell post-hoc test was then used to identify significant differences between years. Data for tagged eels were not normally distributed. However, variances were almost equal between the two tagging years (2019 = 215.389, 2021 = 252.908). Therefore a non-parametric Mann-Whitney U test was used to test for differences in median tagging size between the two years.

Table 5.1 Biological information for VEMCO acoustic-tagged rock hind (“RH”; *Epinephelus adscensionis*, *n* = 36) and spotted moray (“SM”; *Gymnothorax moringa*, *n* = 15). Lengths were recorded to an accuracy of 1 cm for all species, with corresponding weights recorded to an accuracy of 500 g for *E. adscensionis* and 100 g to >1 g of accuracy for *G. moringa*. **Bold** text indicates that in 2017 animal weight was only recorded for 9 individuals; therefore, summary statistics were generated from the available data. Tag burden was calculated using the available data and amounted to <3.6% for *G. moringa* and <2.4% for *E. adscensionis* across all years. x̄ = mean, M = median. Calculated values (mean and median) were rounded to the nearest whole number.

Year	Species	Total tength (cm)				Weight (g)				Transmitter type			
Tagged		x̄	M	Min.	Max.	x̄	M	Min.	Max.	V13	V16	V16P	V16TP
2017	RH	44	45	33	51	**1357**	**1457**	**650**	**3480**	10	10	0	0
2019		47	46	45	55	1950	1800	1500	3250	0	0	0	10
2021		52	51	46	56	2069	2000	1500	3000	0	10	6	0
2019	SM	94	88	84	120	2345	1750	1100	3750	0	0	0	10
2021		95	88	82	122	2108	1540	1000	4670	0	1	4	0

Table 5.2 Transmitter information for the VEMCO acoustic tags deployed in 2017, 2019 and 2020. Asterisk (*) used to distinguish V16 tags used in 2017

Tag type	Number	Transmission rate (s)			Power (db)	Battery life (days)
		Nominal	Min.	Max.		
V13	10	210	240	180	152	904
V16	10*	210	240	180	158	3393
	11	220	170	270	152	1825
V16P	6	220	170	270	158	3650
V16TP	5	60	40	80	158	1236
	5	60	40	80	152	1271

5.2.3 Fish fate and residency

All statistical analyses were completed using the R statistical computing package (v. 3.6.2; RStudio Team 2021). For fish tagged in 2019 and 2021, fish fate was determined using location and depth data. Fate classifications included: resident, resident^E, emigrant, or predated (following Bacheler et al. 2021). Residents were defined by persistent detections within the study area, and residents on the edge (terminal line or "edge" of the receiver grid) of the array (resident^E) were classed as consistent detections across receivers at the edge of the array (applies to "stage 1" with full English Bay receiver array only). Emigration was assumed if the transmitter was detected at the edge of the array and was not re-detected. Predation (e.g. by Galapagos sharks *Carcharhinus galapagensis*) was inferred from two potential data patterns: the transmitter rapidly moved horizontally or vertically and/or at a swim speed that far exceeded plausible limits for the focal species. Both predation scenarios were likely linked to the later cessation of tag movement (continuous detection on a single receiver with depth variation less than 1.3 m (± 0.5 m quoted tag accuracy, InnovaSea Systems Inc. 2021; plus 0.8 m average tidal range, Ascension Island Government 2015). For fish tagged in English Bay, due to variable array size and related difficulties inferring fate across the entire study period, fish fate was classified within two distinct periods; stage 1, which encapsulated fate during a 20-23 receiver array (August 2019 – May 2020), and stage 2 which covered the period the 9-receiver array remained (May 2020 – April 2021). For each individual, detection data were trimmed to the point at which emigration or predation occurred. Harvest events were not considered due to the close relationship established with the few active local fishers and the absence of recapture reports. For fish tagged within the receiver deployment periods (2021 grouper and eel only), detections were filtered to incorporate a 12 h recovery period to ensure the data generated was reflective of animal behaviour and not due to handling effects.

Fish residence time was estimated using residency days (number of days detected in the receiver array, RD) and residency indices (RI). Residency indices were used to summarise the amount of time a tagged animal was detected within the array (number of days detected as a proportion of the total study period) and were calculated using base R (Collins et al. 2007). The resultant decimal (0-1) was converted to a percentage ranging from 0 (no residency) to 100% (absolute residency). The linear arrangement of the northwest receiver line (e. 2.9 km between furthest west and east receivers) and limited coverage of the English Bay (cumulative listening area = 0.0984 km^2) array prevented the calculation of additional spatial statistics.

5.2.4 Horizontal space use

At Bates Point, space use was investigated using Center of Activity analysis. Center of Activity analysis was used to estimate the fine-scale space use of acoustic-tagged animals across a 60-minute period; the algorithm estimates an average position within the specified period based on the proportion of detections at each receiver location (see Simpfendorfer et al. 2002). Center of Activity positions were calculated using the Animal Tracking Toolbox (*ATT* package; Udyawer et al. 2018). This approach disaggregates detection data from receiver location, reducing the propensity for autocorrelation by subsampling data into specified time steps (in this case, 60-minutes) (Matley et al. 2017). COA analysis was only conducted for fish with >100 detections (*n* rock hind = 4, *n* spotted moray = 0). These sequential average positions were then used to estimate fish home range (95% utilization distribution) using an autocorrelated kernel density estimator (*akde* function) in the *ctmm* package (Fleming & Calabrese 2021). AKDE was selected as it accounts for temporal autocorrelation in telemetry data and has been found to outperform traditional home range estimators across species and sample sizes (Noonan et al. 2019).

5.2.5 Modelling vertical space use

Hierarchical General Additive Models (hGAMs) were used to assess grouper and eel vertical space use. A hierarchical GAM is an extension of a GAM which allows a smooth functional relationship between predictor and a response to vary between groups (Pedersen et al. 2019). This approach was selected to identify differences between species (grouper and eel) and to account for cyclic patterns in environmental covariates, e.g., lunar illumination. hGAMs were fit using the *bam* function in the *mgcv* package (Wood 2011). This function requires less computational power and memory than the *mgcv* package's *gam* and *gamm* functions.

Raw depth sensor values were converted so that the animal's depth was relative to the listening receiver's mooring depth, i.e. 2 m in a 10 m water column translated to a value of 0.2. This conversion accounts for how small depth changes may have different ecological impacts depending on the total depth of the water column. For example, a 2 m change in depth at 6 m equates to a 33% change in depth relative to the water column, whereas a 2 m change at 36 m equates to 6%. The conditions a fish is exposed to, including currents and tidal changes, are more likely to be buffered at depth. Due to Ascension’s topographic complexity, 35% (of the 702,573 fish pressure detections) had a water column depth exceeding 1 and were forced to 0.99 (reoccurring). Relative depth values were then aggregated over diel periods (day or night) to generate a mean position in the water column for each diel period and date. In addition to improving ecological validity, aggregating data reduces the influence of autocorrelation, and given that most model covariates were measured on a coarse resolution (i.e. daily scales), no explanatory information was lost.

Models were fit using a restricted maximum likelihood specification (Wood 2011), with a beta regression distribution family given that converted depths ranged between 0 and 1. Sunrise and sunset times were extracted using the package *suncalc* in R (Thieurmel & Elmarhraoui 2019), and detections were assigned to either “day” or “night”. Lunar illumination values were retrieved using the *lunar* package (Emmanuel 2014) and were converted into a percentage (%) for each day of the year. Data were trimmed to include only the 23-receiver array (>18th April 2020; 286 days) to ensure array design would not influence the observed variance.

Fish depth in the water column was predicted to vary as a function of animal total length (converted to a *z*-score for each species to enable comparison), lunar illumination (0-100), and day of the year (0 - 286). Species was incorporated as a fixed effect to test for differences in grouper and moray eel depth. Diel period (day or night) was included as a fixed effect. All smooth terms were fitted with interaction terms by species so as to account for differences in animal ecology. Fish ID was considered a random effect in the model and fitted with the smooth term “re”. The most complex model included the following terms (for definitions, see Table 5.3):

$D\sim$ Species + s(DP, by=species) + s(TL, by=species) + $s(f_{i,DOY}(i,t), \text{by} = \text{species})$ + s(DOY, by = species) + s(FishID, by=species)

Table 5.3 Hierarchical General Additive Model terms used to explore drivers of rock hind *Epinephelus adscensionis* and spotted moray *Gymnothorax moringa* depth between 3rd August 2019 and 14th April 2021.

Model term	**Definition**
D	Animal depth relative to water column ranges from 0 (surface) to 1 (maximum depth of benthos)
DP	Diel period (day or night)
TL	Animal total length, converted into a *z*-score to account for differences between species
$f_{i,\,month}(i, t)$	Tensor product of a cubic spline function of lunar illumination *i* and a cyclic cubic spline function with a monthly cycle of *t*
DOY	Day of year
FishID	Unique fish ID code

hGAMs require a user to input a smoothness parameter *k*. A starting value of k = 5 was selected for simple smooths such as fish total length. A higher *k* was selected for day of year given the range of values (0-285), with a starting value of *k* = 20 selected (which accounts for depth differences every 14 days). Tensor products require two values for *k* (see ?te in *mgcv* documentation in R) and was set to c(10, 5) to explain the interaction between lunar illumination and month across the 10 months of the study. The *gam.check* function in *mgcv* was used to evaluate whether an optimal value for *k* was selected. After model inspection, the *k* value for total length was set to 6, and the *k* value for day of year was set to 30. Random effects were assigned a *k* value equal to the number of levels (as recommended in Pedersen et al. 2019; therefore, fish ID *k* was set to 19. The full model with all terms, as well as candidate subset models were evaluated using Akaike Information Criterion (AIC) values. Models with ΔAIC scores within 10 units of the best model were deemed as informative and have reasonable support (Burham & Anderson 2004).

5.2.6 Dietary niche

Stomach content sampling and stable isotope analysis (of fin clips and white muscle) were used to examine the dietary niche of both *E. adscensionis* and *G. moringa*. Lethal and opportunistic fisher sampling was used to collect stomach content data, with contents weighed (to the nearest 0.01g) and identified to family level. Digested material which could not be identified was removed from subsequent analysis. Prior to stable isotope analysis, tissues were dried at 80°C to enable transport and thereafter freeze dried and ground into a fine powder. Lipid extraction of all samples was undertaken by agitating the dried tissue sample in a 2:1 chloroform-methanol solution for 24 h (following Hussey et al. 2011). The excess solvent was then removed, and the sample was left to dry for 48 h in a fume cupboard to evaporate off any remaining solvent. All samples were lipid extracted. Between 400 – 600 µg of lipid extracted tissue was then weighed into a tin capsule and analyzed using a continuous-flow isotope ratio mass spectrometer (IMRS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA) equipped with an elemental analyzer (Costech, Valenica, CA, USA).

Stable isotope abundances are expressed in delta (δ) values as the deviation from standards in parts per thousand (‰) using the following equation:

$$\delta\mathrm{X} = \left[\left(R_{sample} \ / \ R_{standard}\right) - 1\right] \times 1000$$

Where X is ^{13}C or ^{15}N and R is the ratio of ^{13}C/^{12}C or ^{15}N/^{14}N. Isotope ratios are expressed per mille (‰) relative to a secondary standard which includes Pee Dee Belemnite carbonate for δ^{13}C and atmospheric nitrogen for δ^{15}N.

Samples with percent carbon to nitrogen ratios of > 4 were removed prior to analysis as lipids were likely still present within the sample (3 rock hind grouper white muscle tissue samples). Isotopic ellipses were then fit for each species, for both tissue types (fin and muscle) and for each of the three sample years using the *stat_ellipse* function in *ggplot2*

(Wickham 2016). This *stat_ellipse* function assumes a multivariate t-distribution and fits an ellipse to the data with a 95% confidence level (Wickham 2016). The range of $\delta^{13}C$ (CR) and $\delta^{15}N$ (CN) (Layman et al. 2007) was calculated for each isotope and tissue type to examine isotopic variation between species. Hypervolume isotopic niche area and overlap between the two study species were calculated for white muscle and fin using the package *nicheROVER* (Lysy et al. 2014), with the number of Monte Carlo draws set to 10,000 and α to 0.95 (95% overlap). The overlap metric is directional, representing the probability that species A is found in the niche of species B and vice versa (see Swanson et al. 2015 for detailed methodology). By incorporating a Bayesian inference framework and simulating multiple iterations of each ellipse (10,000), all measures incorporate a measure of uncertainty (Lysy et al. 2014).

5.3 Results

5.3.1 Tagged animal total length and tag burden

In total, 46 rock hind ranging from 33 to 58 cm TL (mean ± SE = 47.1 ± 0.853) and 15 spotted morays ranging from 74 to 122 cm TL (mean ± SD = 94.2 ± 3.749) were tagged with acoustic tags and released into the three respective arrays (see biological information in Table 5.1). A Welch's ANOVA found there was a statistically significant difference in grouper TL between the tagging years ($F_{2, 25.189} = 10.217$, $p = <0.001$). Grouper tagged in 2021 had a significantly larger mean total length than total than those tagged in 2017 (Games Howell post-hoc test; $P = <0.001$, 95% C.I. = 7.160, 11.300) and 2019 (Games Howell post-hoc test; $P = 0.024$, 95% C.I. = 3.700, 0.443). However, no statistical difference was found in the median total length of the moray eels tagged in 2019 and 2021 (Mann-Whitney U test; $W = 23$; $p = 0.854$). Tag burden (weight of tag in the air in relation to animal mass) was calculated as >2.4% for tagged grouper (note 11 grouper weights were not recorded in 2017 and were therefore not included) and >3.6% for tagged moray eels.

5.3.2 Fish fate and residency

Residency and horizontal movements of rock hind grouper tagged in 2017

Of the *E. adscensionis* tagged in 2017 ($n = 20$), 12 (60%) were detected on the North West array (2018-2019), 3 (15% of those tagged) were detected across the English Bay array (2019-2021; equates to 60% of those tagged <200 m from the edge of the array), and 4 (20%) across the Bates Point array (2020-2021) (Fig. 5.5). Calculated residency indices ranged from 0 – 15% (RH11) (Table 5.4). Of those tagged, 7 were recorded over 1-year post-tagging near to their original tagging location. For example, 3,549 detections were recorded for RH01 across 2018-2020 (Fig. 5.6A), with the majority of detections within <50 m of the original tagging location (Fig. 5.6B).

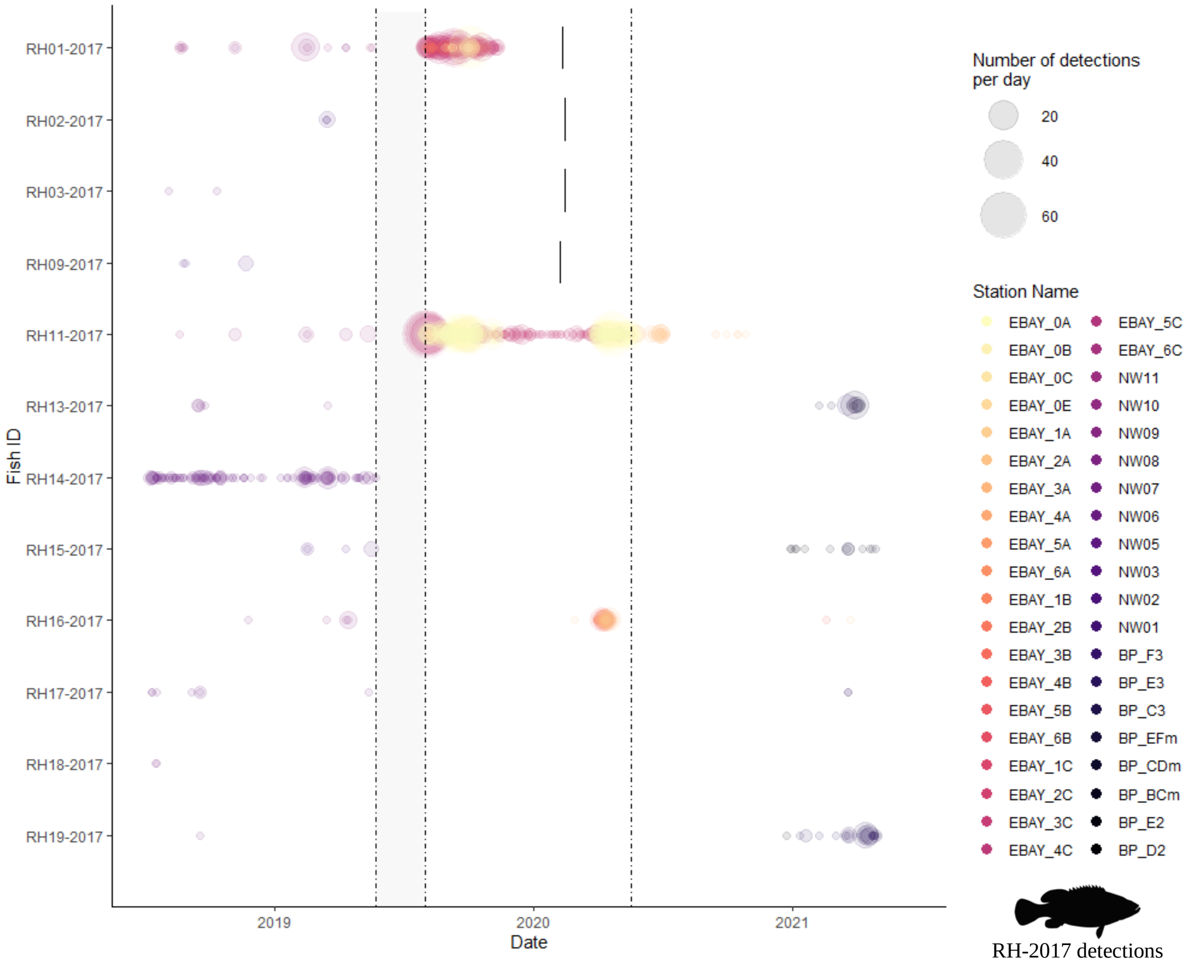


Figure 5.5 Horizontal movements of rock hind grouper (*Epinephelus adscensionis*) acoustically tagged in 2017 across the three array configurations: the northwest line of receivers (“NW array”, 2018-2019 installation), the English Bay array (“EBAY”, 2019-2021), and Bates Point array (“BP”, 2020-2021) from 3rd August 2018 – 24th May 2021. Dashed lines indicate maintenance periods, with the grey rectangle showing the time when no receivers were installed. Proportional circles indicate the total number of detections of a given fish on a specific receiver on a given day. Straight lines indicate the end of tag battery life (relevant for 4 individuals).

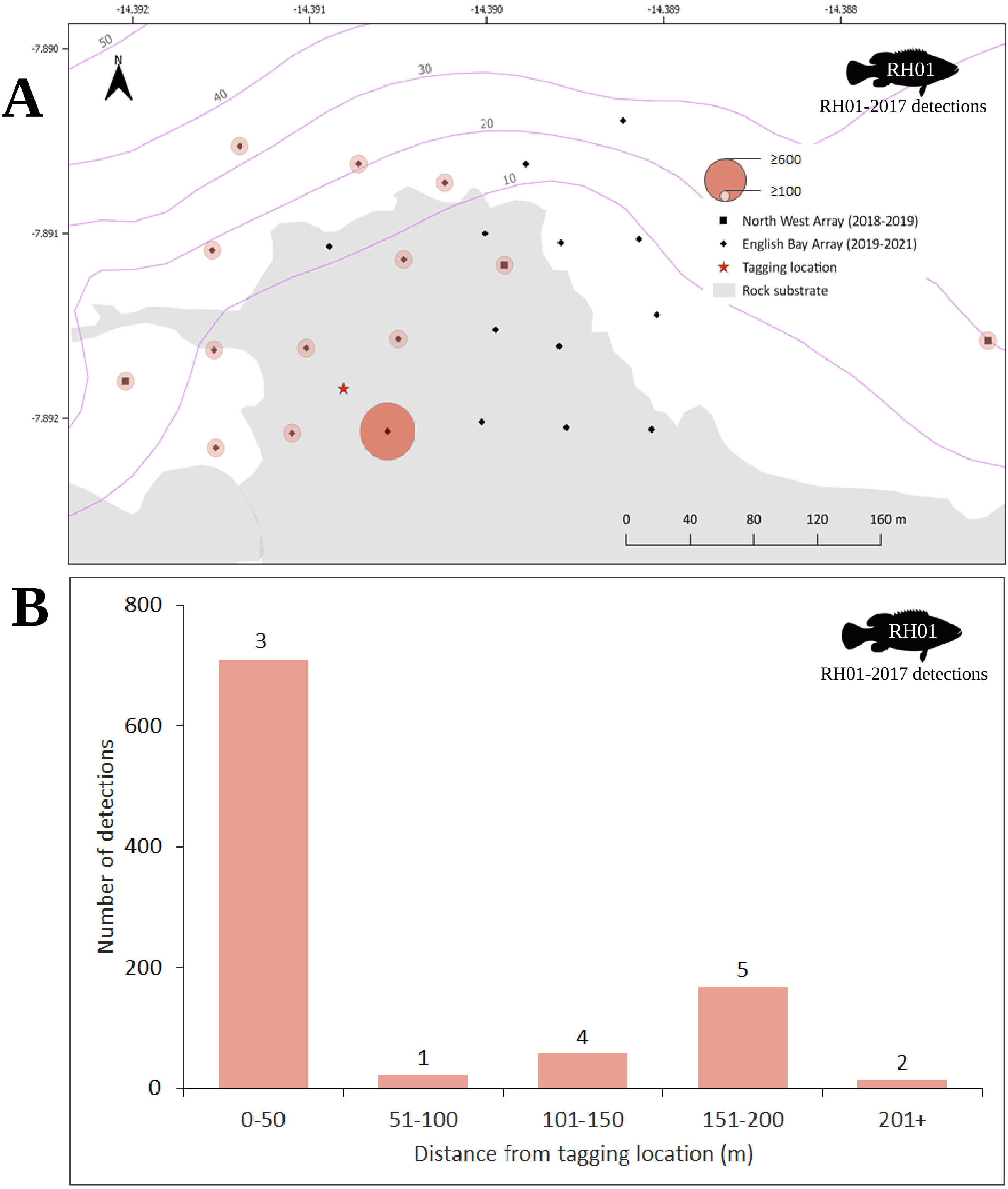


Figure 5.6 Detections of a rock hind grouper tagged in 2017 within English Bay (northwest of Ascension Island (fish ID, "RH01"). A) Proportional circles represent the cumulative number of detections across the two discrete arrays. Grouper tagging location indicated by red star. B) Cumulative number of detections grouped by distance from the original 2017 tagging location (number of unique stations expressed above the respective bar).

5.3.3 Residency, horizontal and vertical movements of grouper and eel tagged in 2019

Between the 7th August 2019 and 13th April 2021 a total of 2,211,588 detections of animals acoustically tagged in 2019 (*n* grouper = 10; *n* moray eel = 9) were recorded across the English Bay receiver array (Fig. 5.7).

Horizontal movements

Of the 10 tagged grouper, 90% (*n* = 9) remained within the monitored region for at least 50% of the study duration and 60% (n = 6) for at least 75% of the study period. On average, tagged grouper remained in the array for a total period of 474 ± 132 (3 s.f.) days, which corresponded to residency indices of between 27 and 100% (mean ± SD = 78.2 ± 22.05) (Table 5.5). Of the 10 tagged moray eels, 9 (90%) were detected with 1 moray eel predated 38 days after tagging. In total, 8 (89% of those detected) remained within English Bay for >25% of the study period, and 2 (22%) were detected for >75% of the study period. Residency ranged from 0 (SM06) to 605 days (SM04) which equated to residency indices ranging from 0 to 100% (Table 5.5).

Vertical movements

Grouper occupied a mean depth of 17.2 m ± 4.83 m SD (1 d.p.), with depths ranging from the water's surface to the seafloor (max recorded depth = 38.1 m) (Fig. 5.8A). Individuals showed variability in their vertical position over time (Fig. 5.8A; Fig. 5.9A), with 70% (*n* = 7) traversing beyond their most commonly occupied depth range between September 25th and October 4th 2019 (see examples: Fig 5.10, 5.11 and 5.12). The mean depth of detected morays was 15.2 ± 10.9 m SD (1 d.p.) (Fig. 5.8B); however, animal depth ranged from 2.4 – 38.1 m. Moray eels also showed individual variability in their vertical position over time (Fig. 5.9B), with some individuals showing frequent short-duration movements to depth (e.g. SM04, Fig 5.13) while other individuals undertook a directional shift to deeper habitats (e.g. SM 10, Fig. 5.14; SM13, Fig. 5.15).

The hGAM including all terms except animal total length was chosen ($R^2 = 0.69$, deviance explained = 87.2%), given that the additional term (TL) did not improve the model fit (most complex model AIC = -24,525; model excluding TL AIC = -24,525). The intercept was log-transformed to convert to relative depth (because the log link function was used in the beta regression family) and was 12.5% for grouper, which was significantly different from the intercept for eel at 8.2% depth of the water column ($t = -3.21$, $P = <0.001$). Time of day (day or night) had a significant effect for both species ($t = 9.00$, $P = <0.001$), indicating diel vertical activity, with a preference for a 1.6% deeper position in the water column at night. The interactive effect of month on lunar illumination found that depth of moray eels within the water column was significantly different across the lunar cycle ($F = 0.73$, $P = <0.001$); however, no effect was observed for grouper ($F = 0.12$, $P = 0.08$). Day of year was a significant predictor of depth for both grouper ($F = 1.65$, $P = <0.05$) and moray eels ($F = 20.17$, $P = <0.001$). There was a significant random effect of individual fish ID on relative fish depth in the water column ($F = 844.82$, $P = <0.001$). Smoothers visualized in Supplementary Figure 5.2.

Temperature data

Tagged fish (*n* detected *E. adscensionis* = 10, *n* detected *G. moringa* = 9) generated 803,048 and 303,227 temperature detections over the study period, with recorded values ranging from 21.99 – 29.52°C (Fig. 5.16). These profiles matched the measured sea temperature recorded independently at English Bay, which ranged from 23.61°C – 29.20°C (7th August 2019 – 13th April 2021, mean ± SD = 26.15 ± 1.48; Fig. 5.17). Some individual *E. adscensionis* (RH02) and *G. moringa* (SM03, SM10) showed variability in temperature occupied and these fish predominantly occupied deeper moored receiver stations, e.g. A-line receivers and 0-line receivers moored at >20 m.

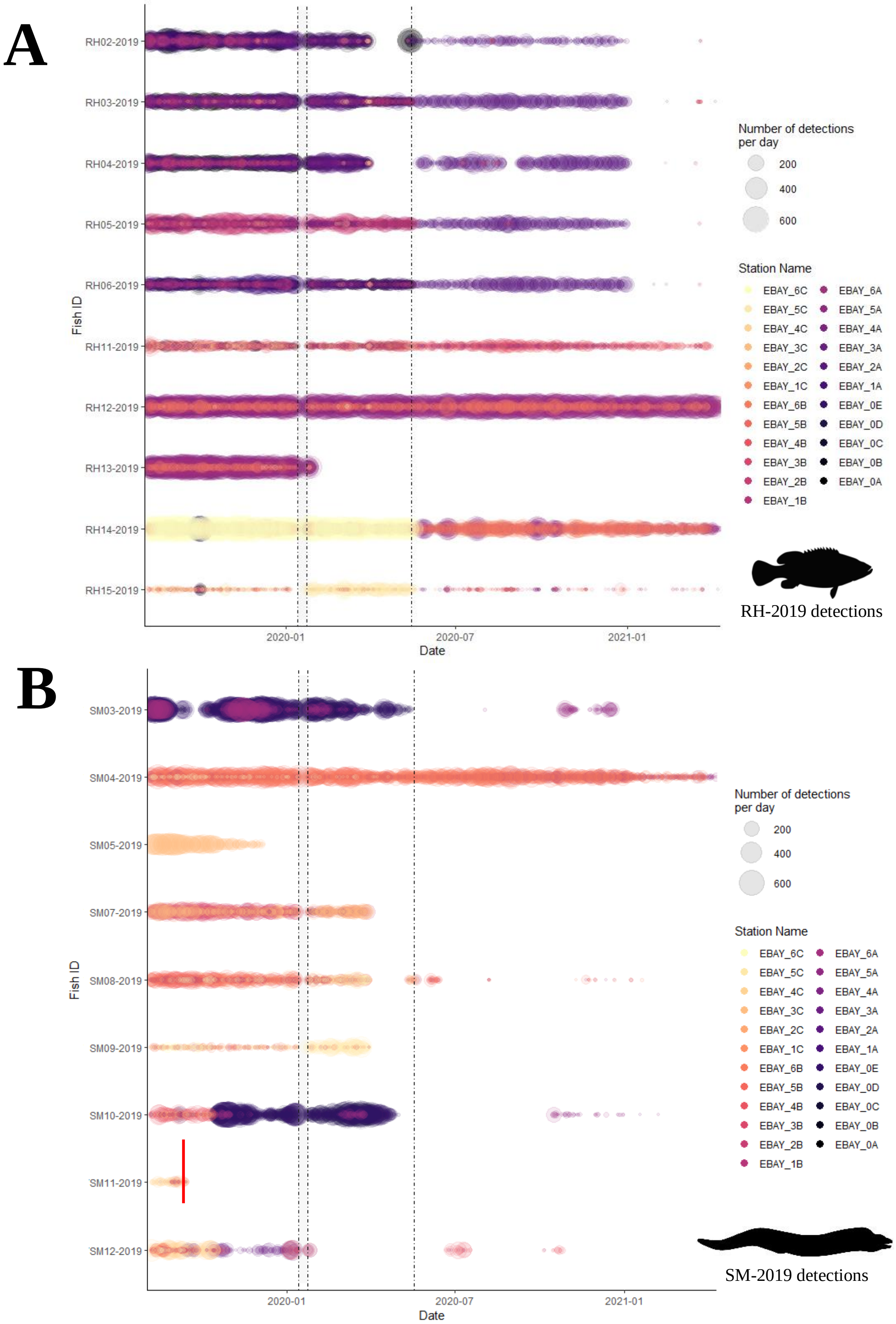


Figure 5.7 Horizontal movements of individual fish acoustically tagged in 2019 across the English Bay array ("EBAY") between 7th August 2019 and 13th April 2021. Dashed lines indicate maintenance periods where receivers were out of the water for battery replacements, with the grey rectangle showing when no receivers were installed. Proportional circles indicate the total number of detections of a fish on a specific receiver on a given day. Includes two species, A) rock hind (*Epinephelus adscensionis*) and B) spotted moray (*Gymnothorax moringa*). A solid red line indicates a mortality event.

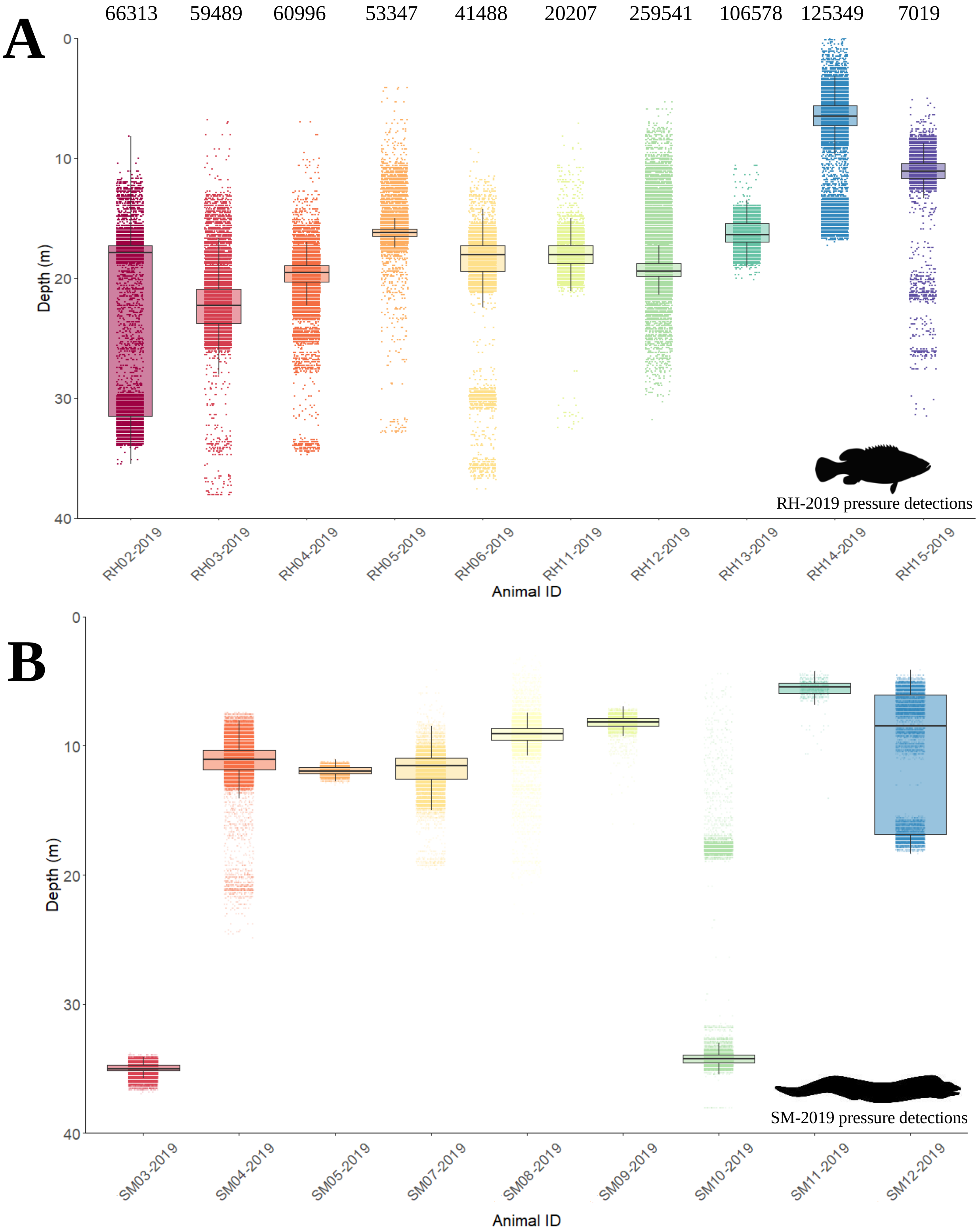


Figure 5.8 Summary of all pressure sensor detections of animals acoustically tagged in 2019 across the English Bay array between 7th August 2019 and 13th April 2021. Excludes detections post-predation (indicated by an asterisk *) and any detections during the 10-day maintenance period (14th January 2020 – 24th January 2020). The total number of pressure detections per tagged individual is given above the corresponding boxplot, with data presented indicating the mean ± 1 SD. Includes the two focal species, A) rock hind (*Epinephelus adscensionis*) and B) spotted moray (*Gymnothorax moringa*).

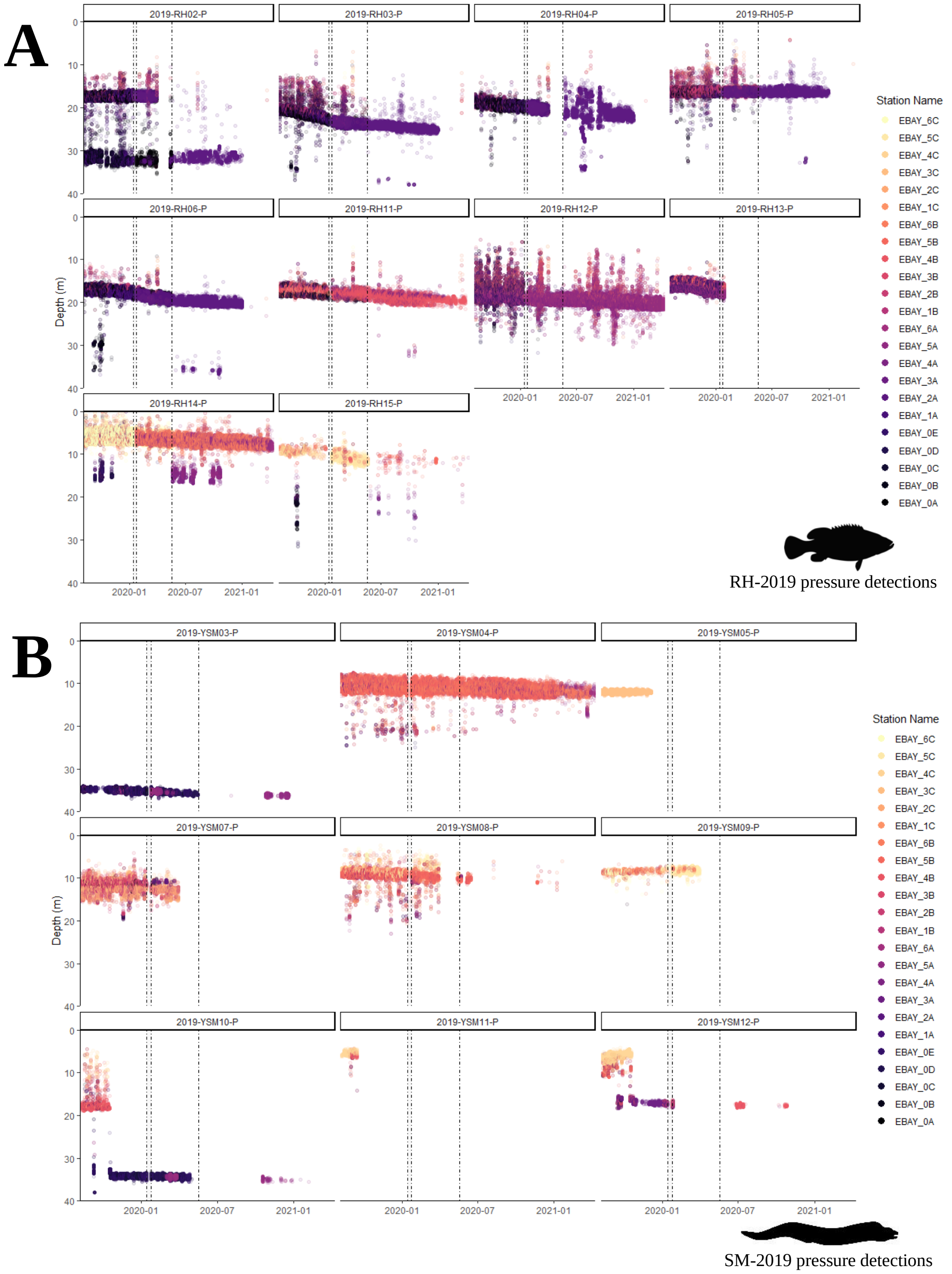


Figure 5.9 Vertical movements of individual fish acoustically tagged in 2019 across the English Bay array between 7th August 2019, and 13th April 2021. Excludes detections post-predation (indicated by an asterisk *) and any detections during the 10-day maintenance period (grey rectangle, 14th January 2020 – 24th January 2020). Dashed lines indicate changes in receiver configuration, e.g., maintenance period (January 2020) or reduction in array size (reduced from 23 to 9 receivers on 13th May 2020. Includes two species, A) rock hind (*Epinephelus adscensionis*) and B) spotted moray (*Gymnothorax moringa*).

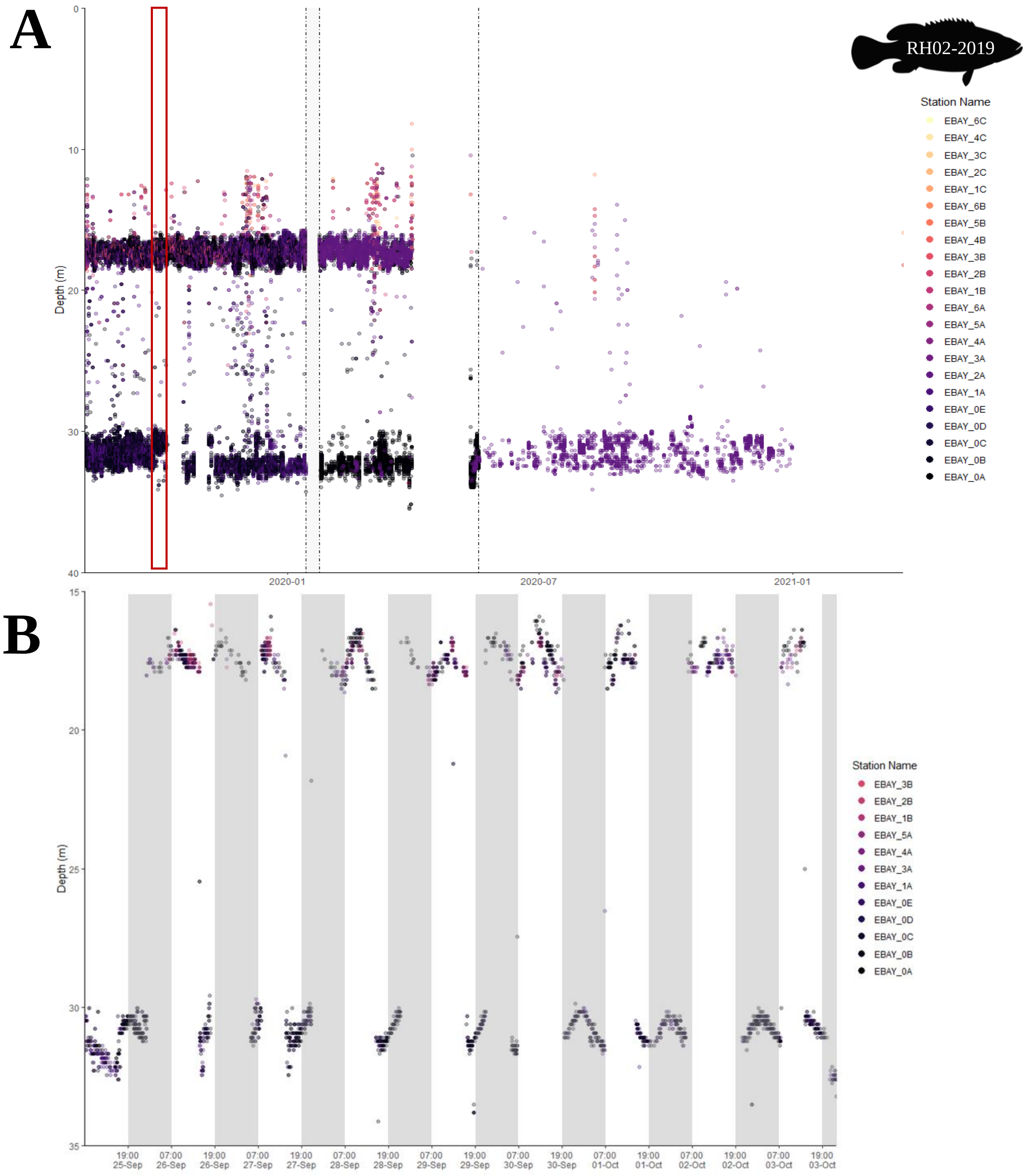


Figure 5.10 Example vertical movements of a rock hind (fish ID, “RH02”) tagged in 2019 within English Bay array (“EBAY”). A) Detections recorded between August 7th 2019, and April 13th 2021. Dashed lines indicate changes in receiver configuration, e.g., maintenance period (January 14th – 24th 2020, grey fill rectangle) or reduction in array size (reduced from 23 to 9 receivers on 13th May 2020. Hollow red rectangle highlights time-period visualised in panel B. B) Vertical movements of RH02 between 07:00 25th September – 00:00 4th October 2019, within the English Bay array (*n* detections = 3.640). The shaded rectangles indicate night (after sunset at 19:00 and before sunrise at 07:00).

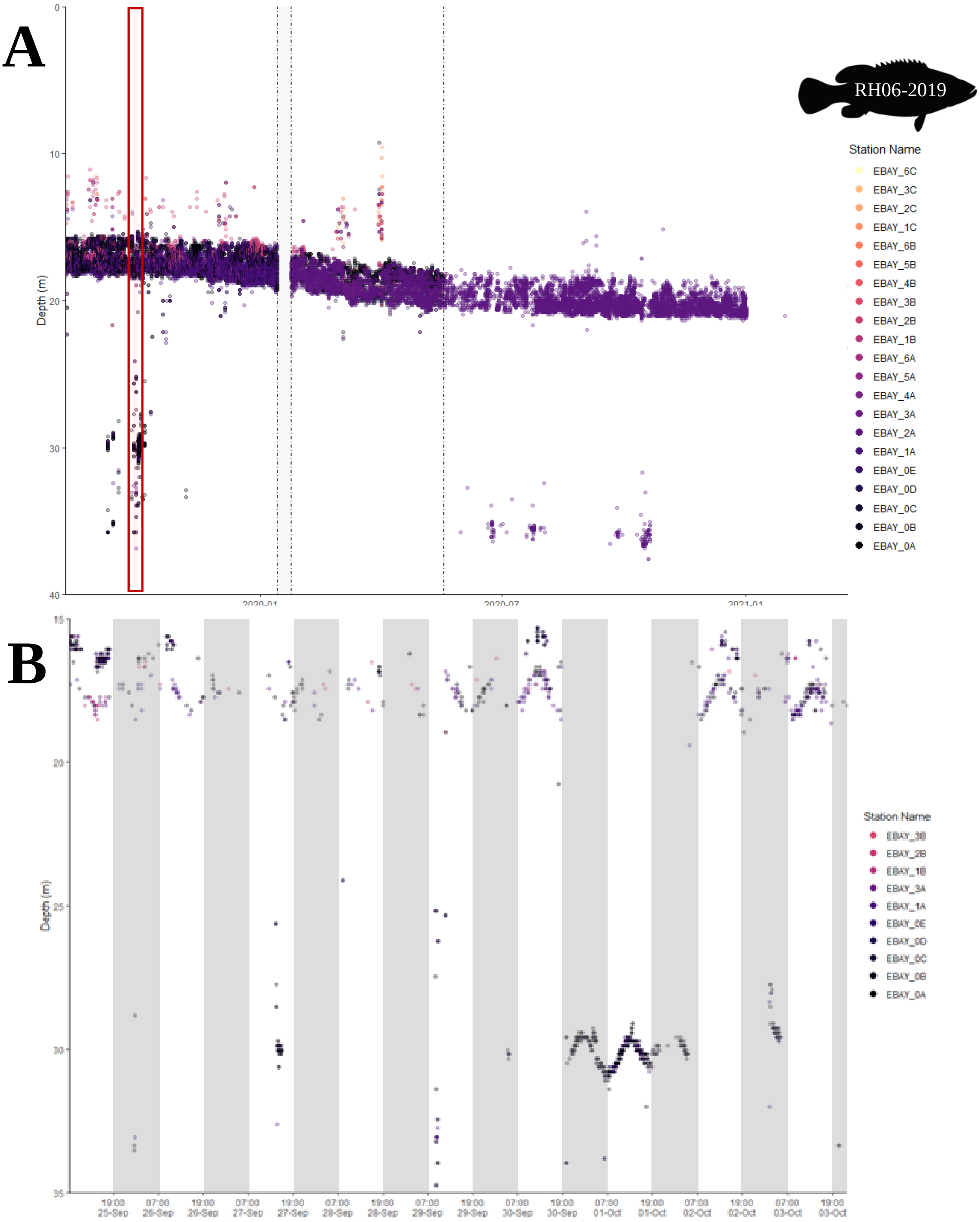


Figure 5.11 Vertical movements of a rock hind (fish ID, "RH02") tagged in 2019 within English Bay array ("EBAY"). A) Detections recorded between 7th August 2019 and 13th April 2021. Dashed lines indicate changes in receiver configuration, e.g., maintenance period (14th – 24th January 2020, grey filled rectangle), or a reduction in array size (reduced from 23 to 9 receivers on 13th May 2020. The hollow red rectangle highlights the time-period visualised in panel B. B) Vertical movements of an acoustically tagged rock hind grouper (fish ID, "RH15") between 07:00 25th September – 00:00 4th October 2019, within the English Bay array (*n* detections = 360). The shaded rectangles indicate night (after sunset at 19:00 and before sunrise at 07:00).

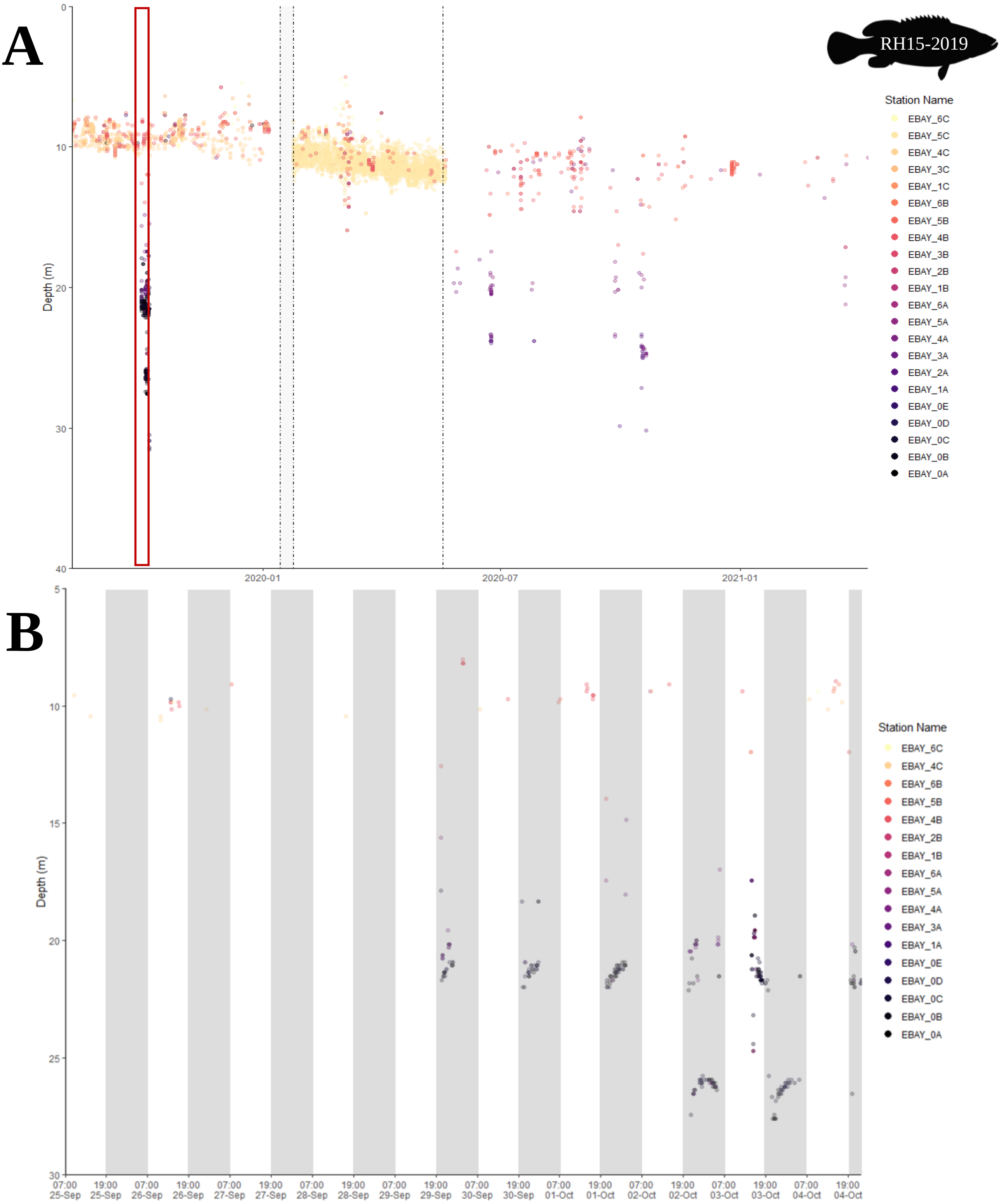


Figure 5.12 Vertical movements of a rock hind (fish ID, "RH15") tagged in 2019 within English Bay array ("EBAY"). A) Detections recorded between 7th August 2019, and 13th April 2021. Dashed lines indicate changes in receiver configuration, e.g., maintenance period (14th– 24th January 2020, grey fill rectangle) or reduction in array size (reduced from 23 to 9 receivers on 13th May 2020. Hollow red rectangle highlights time-period visualised in panel B. B) Vertical movements of RH15 between 07:00 25th September – 00:00 4th October 2019, within the English Bay array (*n* detections = 360). The shaded rectangles indicate night (after sunset at 19:00 and before sunrise at 07:00).

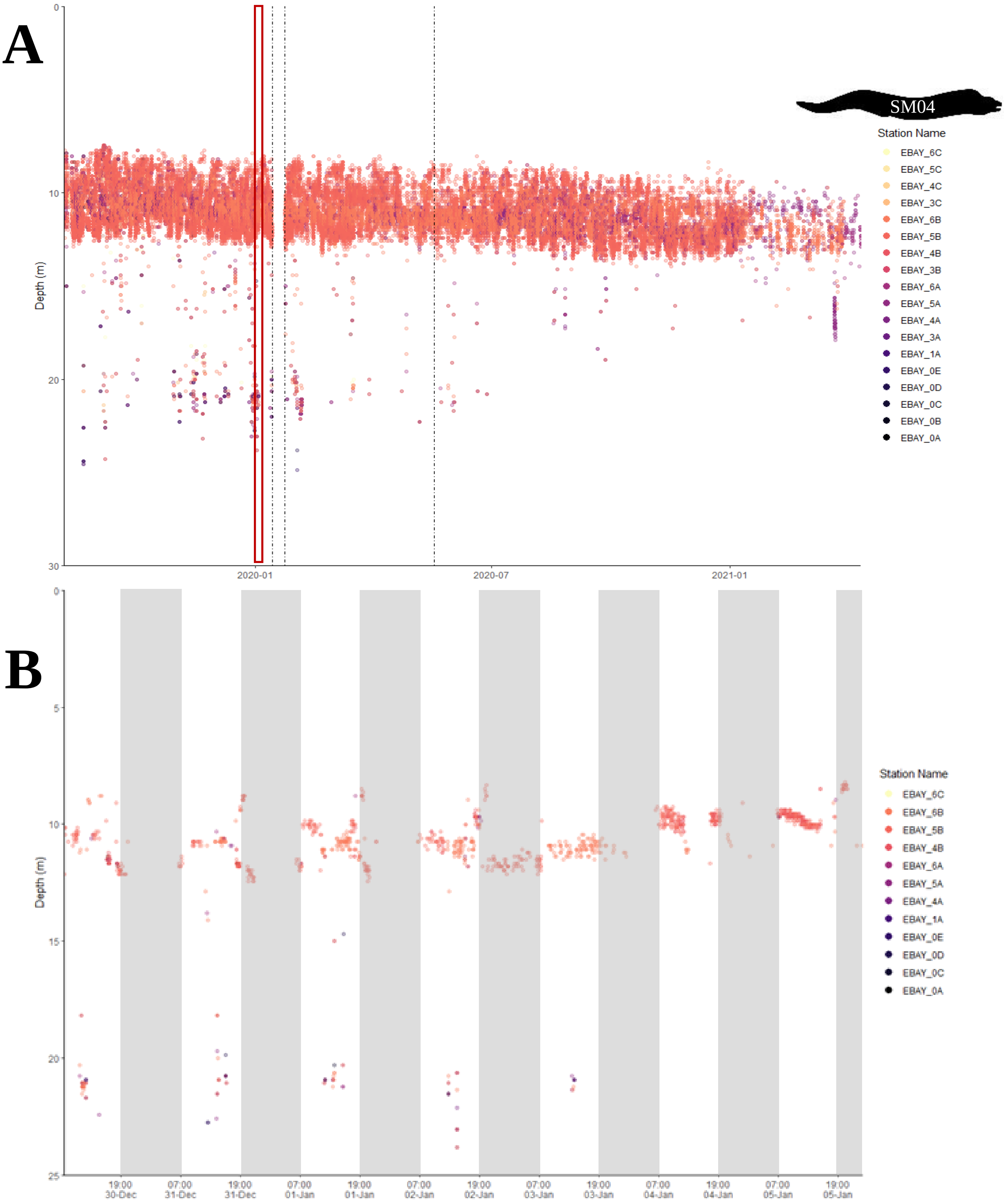


Figure 5.13 Example vertical movements of a spotted moray (fish ID, "SM03") tagged in 2019 within English Bay array ("EBAY"). A) Detections recorded between 7th August 2019, and 13th April 2021. Dashed lines indicate changes in receiver configuration, e.g. maintenance period (14th – 24th January 2020, grey fill rectangle) or reduction in array size (reduced from 23 to 9 receivers on 13th May 2020. Hollow red rectangle highlights the time-period visualised in panel B. B) Vertical movements of SM03 between 07:00 30th December – 00:00 5th January 2019, within the English Bay array (*n* detections = 1125). The shaded rectangles indicate night (after sunset at 19:00 and before sunrise at 07:00).

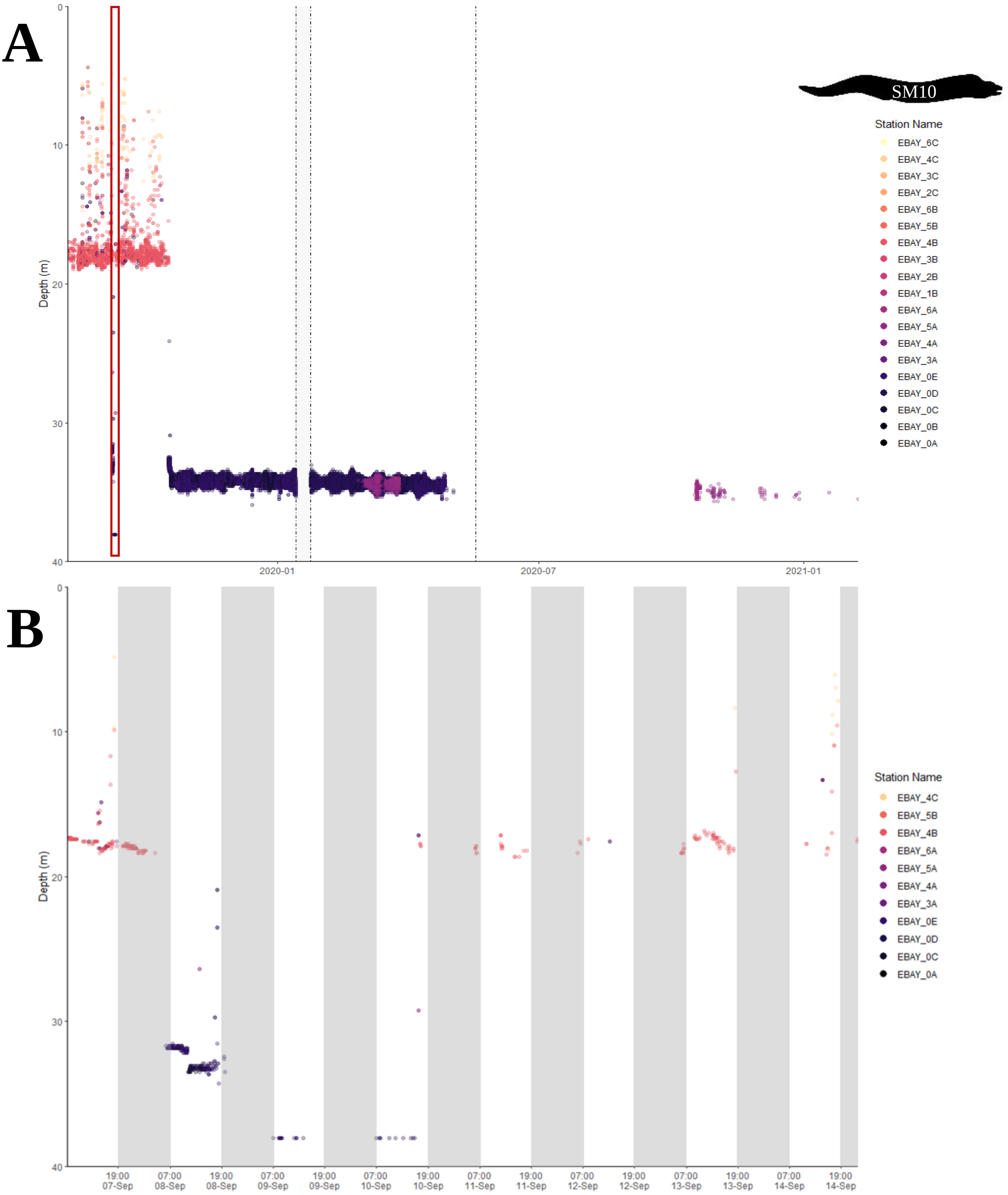


Figure 5.14 Example vertical movements of a spotted moray (fish ID, "SM10") tagged in 2019 within English Bay array ("EBAY"). A) Detections recorded between 7th August 2019 and 13th April 2021. Dashed lines indicate changes in receiver configuration, e.g. maintenance period (14th – 24th January 2020, grey fill rectangle) or reduction in array size (reduced from 23 to 9 receivers on 13th May 2020. Hollow red rectangle highlights time-period visualised in panel B. B) Vertical movements of SM10 between 07:00 7th September – 00:00 14th September 2019, within the English Bay array (*n* detections = 601). The shaded rectangles indicate night (after sunset at 19:00 and before sunrise at 07:00).

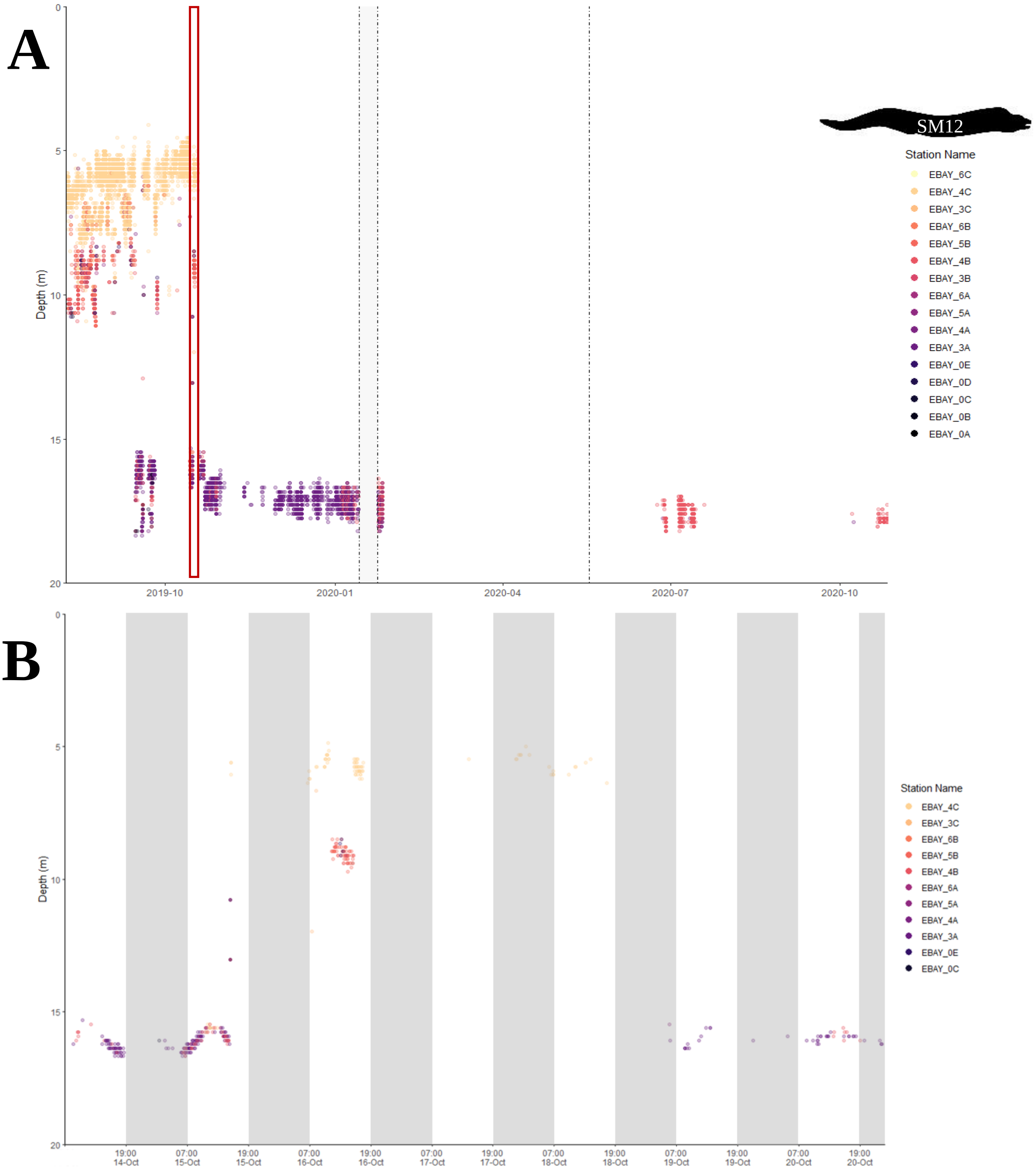


Figure 5.15 Example vertical movements of a spotted moray (“SM12”) tagged in 2019 within English Bay array (“EBAY”). A) Detections recorded 7th August 2019 – 26th October 2020. Dashed lines indicate changes in receiver configuration, e.g., maintenance period (14th – 24th January 2020, grey fill rectangle) or reduction in array size (reduced from 23 to 9 receivers. Hollow red rectangle highlights time-period visualised in panel B. B) Vertical movements of SM12 between 07:00 14th October – 00:00 21st October 2019, within the English Bay array (*n* detections = 529). The shaded rectangle indicate night (after sunset at 19:00 and before sunrise at 07:00).

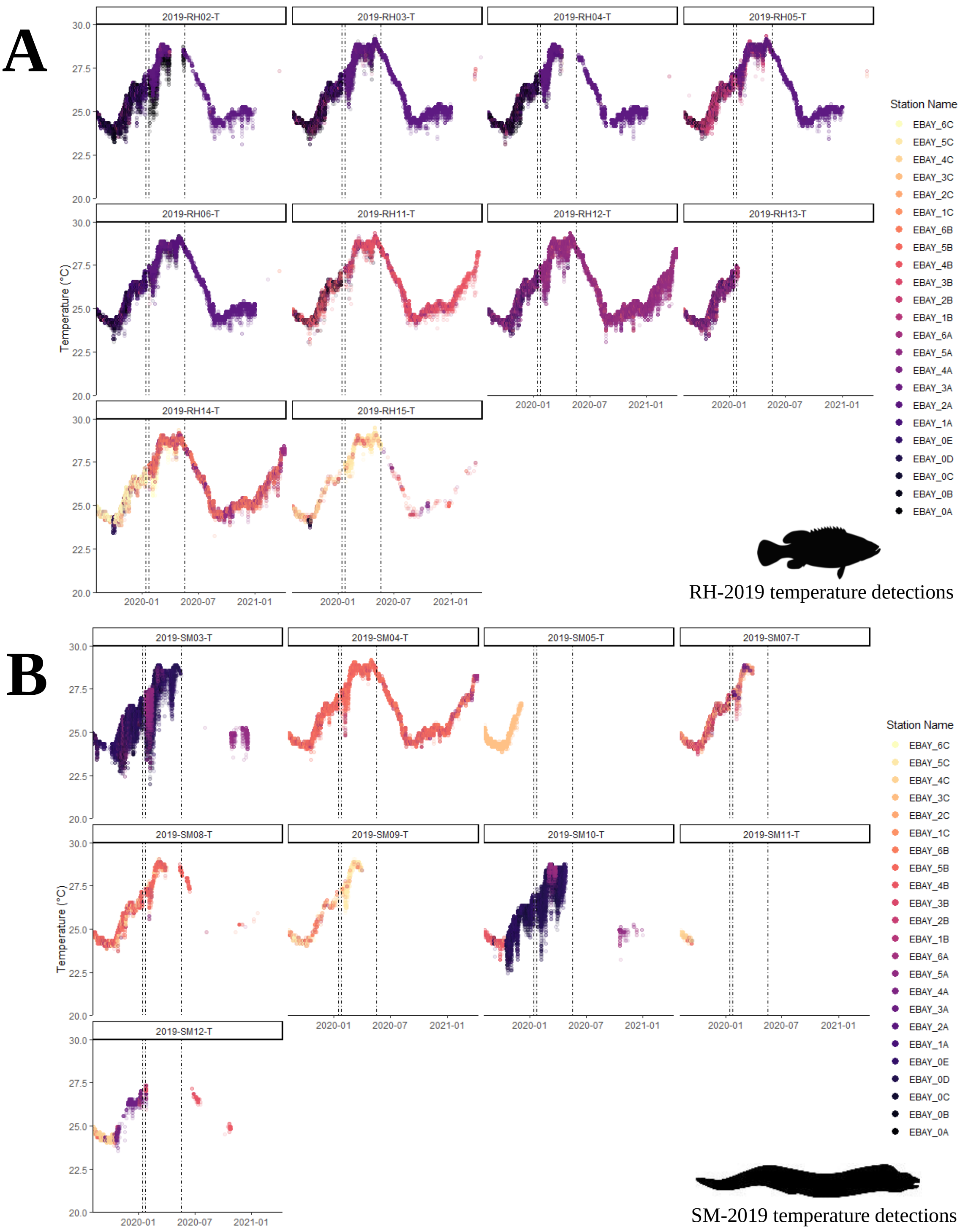


Figure 5.16 The internal body temperature of fish tagged in 2019 recorded between 7th August 2019 and 13th April 2021 across the English Bay receiver array (“EBAY”). Dashed lines indicate changes in receiver configuration, e.g. maintenance period (14th – 24th January 2020, grey fill rectangle) or reduction in array size (reduced from 23 to 9 receivers on 13th May 2020. A) Acoustically tagged rock hind (*Epinephelus adscensionis*) internal temperature and, B) acoustically tagged spotted moray (*Gymnothorax moringa*) internal temperature.

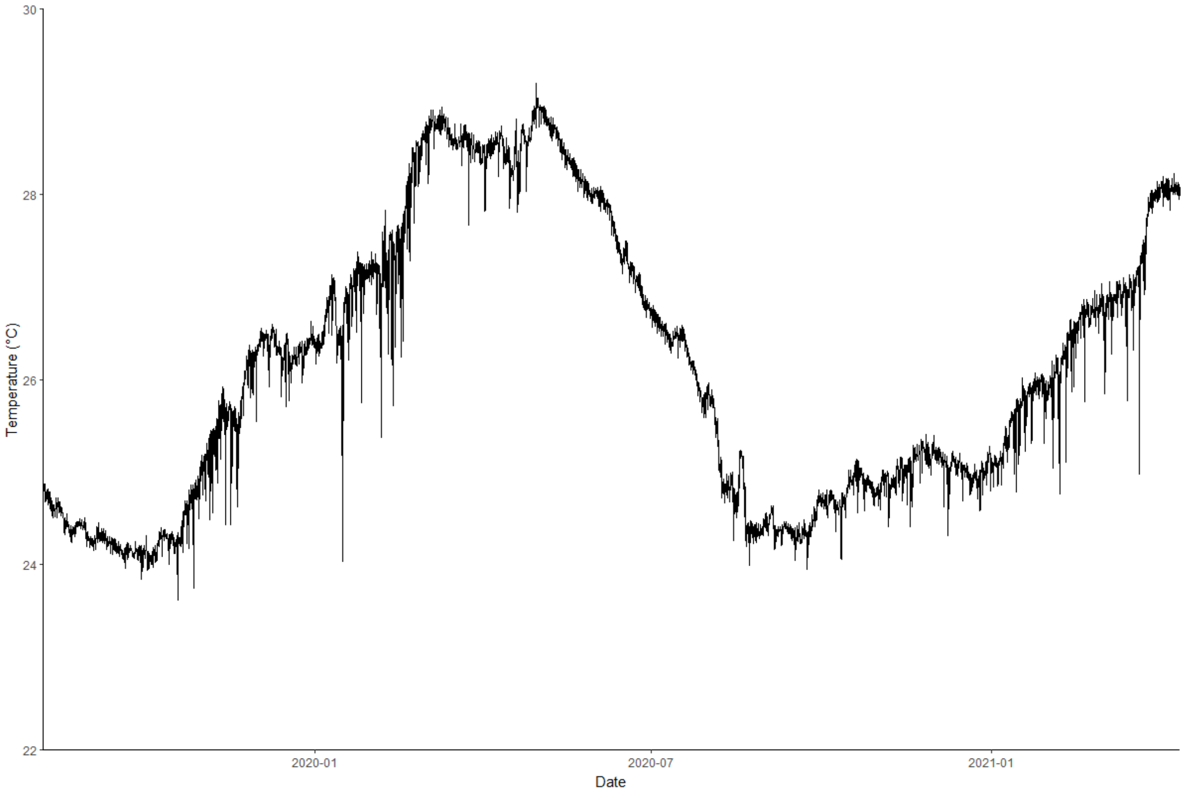


Figure 5.17 Sea temperature recordings logged between 7th August 2019, and 13th April 2021 by an RBR Concerto[3] environmental logger deployed within the English Bay acoustic array (depth = 6 m, accuracy = ± 0.002°C; 10 min recording interval; RBR Ltd. 2021).

5.3.4 Residency, horizontal and vertical movements of grouper and eel tagged in 2021

Of the *E. adscensionis* tagged in 2021 (*n* = 16), 14 (87%) were detected within the Bates Point array (Fig. 5.18) across the <98-day study period. Of the 2021 tagged grouper, 3 (19%) were detected for the full study duration (100% residency) and 8 (50% tagged) remained in the array for >25% of the study (Table 5.6). *E. adscensionis* home ranges (95% AKDE) estimates ranged from 0.0003 km^2 to 0.3114 km^2 (*n* individuals = 4; mean ± SE = 0.1013 ± 0.07; Fig. 5.19). Grouper depth ranged from 7.57 – 33.66 m (mean ± SE = 17.28 ± 0.54; Fig. 5.20).

Of the 5 moray eels tagged in 2021, only 2 (20%) were detected across the 3-month study period with a total of 3 and 12 detections each. Corresponding residency indices were low and ranged from 1% (SM20) to 7% (SM22) (Table 5.6).

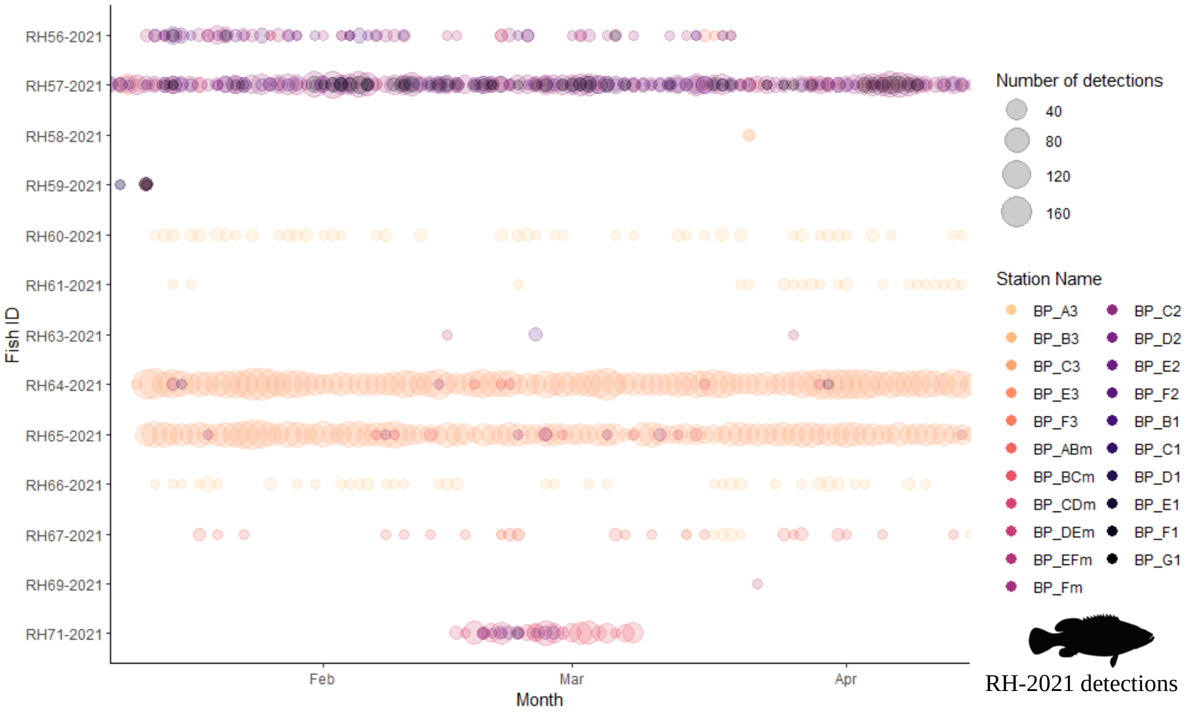


Figure 5.18 Horizontal movements of rock hind (*Epinephelus adscensionis*) acoustically tagged in 2021 across Bates Point array ("BP") array between 7th January 2021 – 15th April 2021.

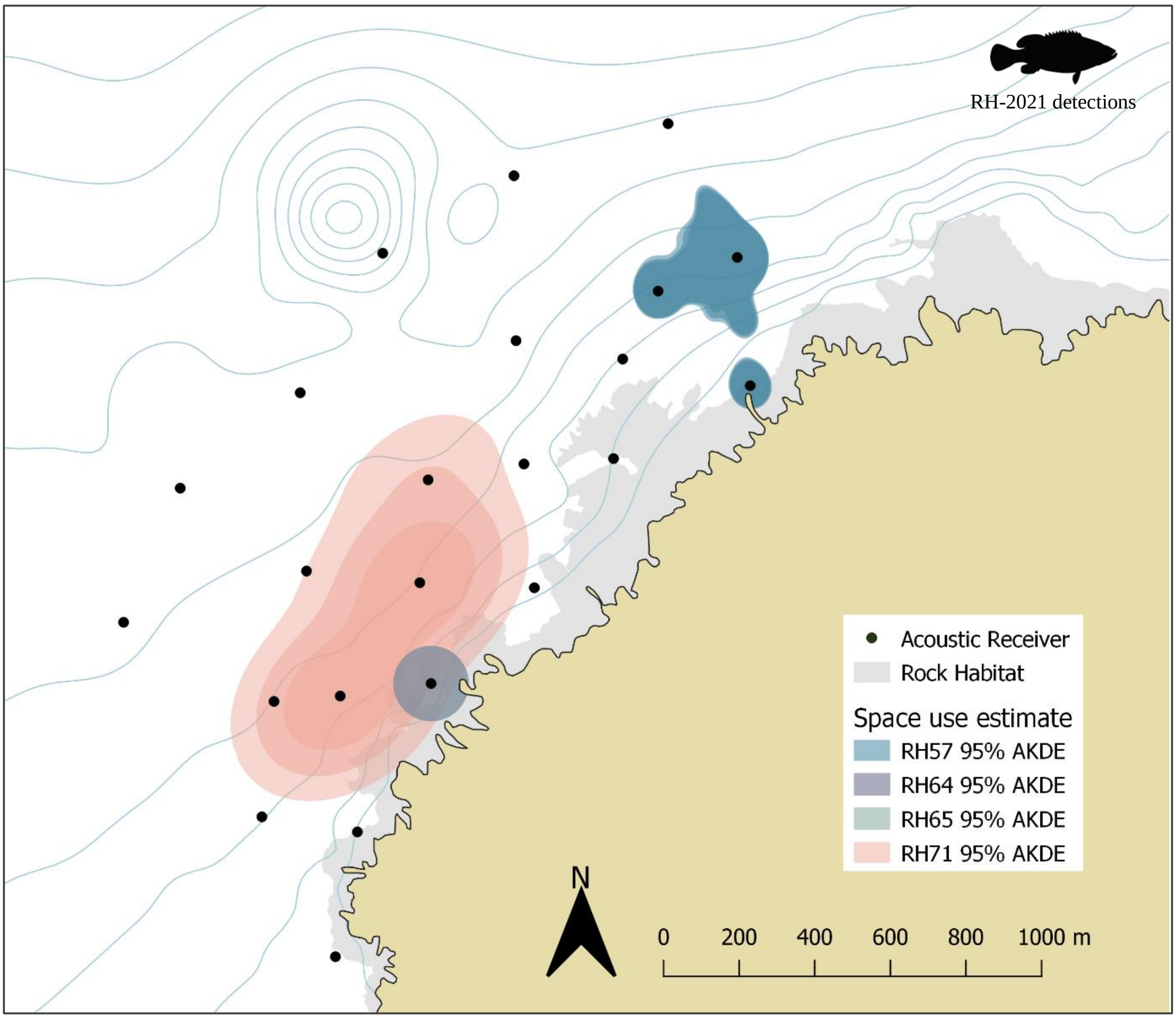


Figure 5.19 Space use estimates (95% autocorrelated kernel density estimate, "AKDE") of rock hind, *Epinephelus adscensionis* (*n* = 4) tagged in 2021 off of Bates Point, northwest of Ascension Island (RH57, RH71). Two fish (RH64 and RH65) 95% AKDE estimates overlap and appear as a single circle. The middle AKDE contour represents the maximum likelihood area where the animal spends 95% of its time, and the inner and outer contours correspond to confidence intervals on the magnitude of the calculated area.

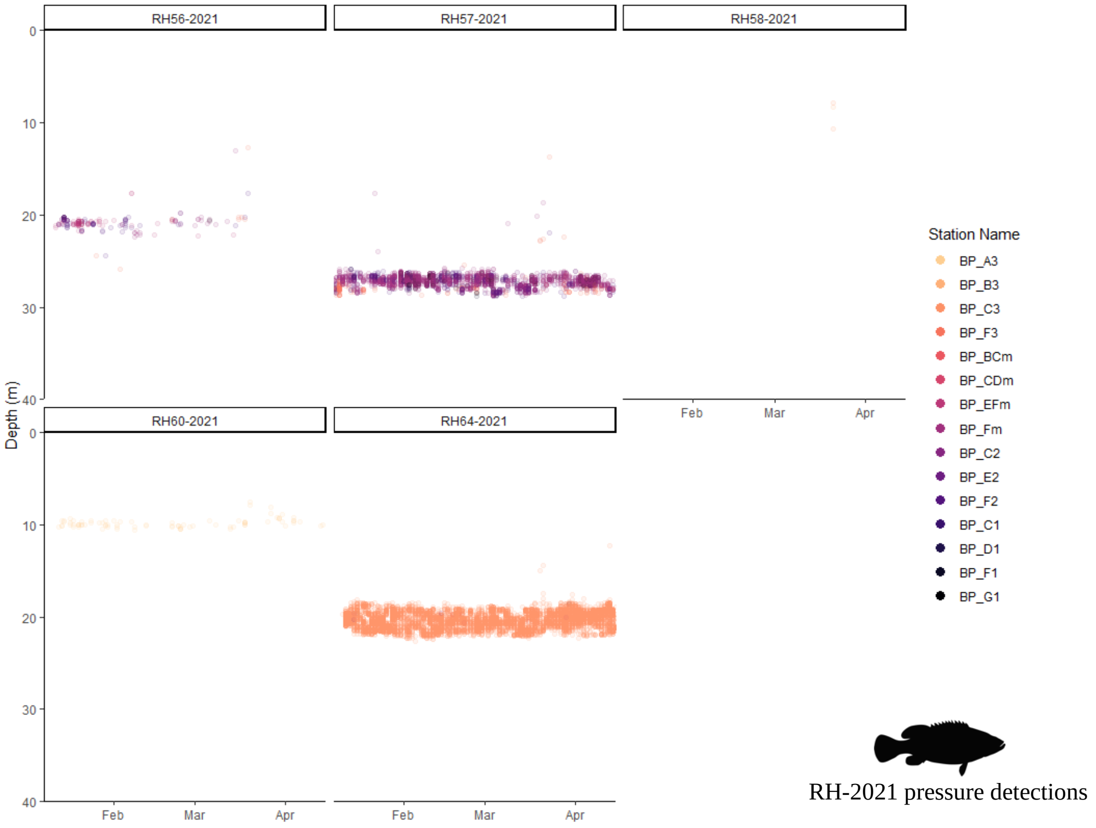


Figure 5.20 Vertical movements of rock hind grouper (*Epinephelus adscensionis*) acoustically tagged in 2021 across Bates Point array ("BP") array between 7th January 2021 – 15th April 2021.

Table 5.4 Summary data for *E. adscensionis* tagged in 2017 tracked from 3rd August 2018 – 14th April 2021. Includes acoustic tag type, capture date, date of first and last detection, study duration (date tagged to either end of tag life, or >14th April 2021), total number of detections, fish fate (resident, resident^{E}, unknown, predated), Rd (residency days), residency index (%), number of center of activity (COA) estimates, and calculated core activity area (50% KUD, km^2) and home range (95% KUD, km^2).

Species	Animal ID	Tag type	Capture date	Tracking data			Study duration (days)	No. detections	Fate	Rd	RI (%)
				Tracking start date	First detection	Last detection					
E. adscensionis	RH01-2017	V13-1x	22 Aug. 2017	3 Aug. 2018	20 Aug. 2018	13 Nov. 2019	904	923	R	111	12
	RH02-2017		25 Aug. 2017		1 Mar. 2019	16 Mar. 2019	904	6	R	2	0
	RH03-2017		22 Aug. 2017		3 Aug. 2018	12 Oct. 2018	904	2	R	2	0
	RH04-2017		22 Aug. 2017					0	UK	0	0
	RH05-2017		22 Aug. 2017					0	UK	0	0
	RH06-2017		22 Aug. 2017					0	UK	0	0
	RH07-2017		17 Aug. 2017					0	UK	0	0
	RH08-2017		17 Aug. 2017					0	UK	0	0
	RH09-2017		17 Aug. 2017		25 Aug. 2018	21 Nov. 2018	904	5	R	3	0
	RH10-2017		22. Aug. 2017					0	UK	0	0
	RH11-2017	V16-4x	22 Aug. 2017	3 Aug. 2018	19 Aug. 2018	27 Oct. 2020	1330	2162	R	192	14
	RH12-2017		22 Aug. 2017					0	UK	0	0
	RH13-2017		22 Aug. 2017		14 Sep. 2018	4 Apr. 2021	1330	53	R	15	1
	RH14-2017		22 Aug. 2017		9 Jul. 2019	24 May 2019	1330	163	R	103	8
	RH15-2017		25 Aug. 2017		15 Feb. 2019	29 Apr. 2021	1335	22	R	16	1
	RH16-2017		17 Aug. 2017		25 Nov. 2018	23 Mar. 2021	1327	140	R	20	2
	RH17-2017		22 Aug. 2017		11 Jul. 2018	21 Mar. 2021	1330	10	R	9	1
	RH18-2017		22 Aug. 2017		17 Jul. 2018	18 Jul. 2018	1330	2	R	2	0
	RH19-2017		17 Aug. 2017		17 Sep. 2018	30 Apr. 2021	1327	61	R	22	2
	RH20-2017		25 Aug. 2017					0	UK	0	0

Table 5.5 Summary data for *E. adscensionis* and *G. moringa* tagged in 2019 tracked from >7th August 2019 – 14th April 2021. Excludes maintenance days during receiver recovery and redeployment from 14th Jan. 2020 to >24th Jan. 2020 (10 days). Fish tagged within the study period were given a 12h recovery window, e.g. SM11 and SM12. Summary data includes associated tag type, capture date, tracking start date, date of first and last detection, study duration, and the total number of detections (excludes 12h recovery period after tagging, and if relevant until predation event occurred with detections post predation given in brackets). Includes fish fate during the 23-receiver array (S1) and 9-receiver array (S2) [resident (R), resident^{E} (R^{E}), unknown (UK), and predated (P) states], Rd (residency days), and residency index (%).

Species	Animal ID	Tag type	Capture date	Tracking start date	Tracking data		Study duration (days)	No. detections	Fate		Rd	RI (%)
					First detection	Last detection			S1	S2		
E. adscensionis	RH02-2019	V16TP	9 Jun. 2019	7 Aug. 2019	7 Aug. 2019	21 Mar. 2021	605	131 253	R	R	436	72
	RH03-2019		9 Jun. 2019		7 Aug. 2019	7 Apr. 2021	605	119 217	R	R	509	84
	RH04-2019		9 Jun. 2019		7 Aug. 2019	15 Mar. 2021	605	121 775	R	R	430	71
	RH05-2019		9 Jun. 2019		7 Aug. 2019	20 Mar. 2021	605	107 338	R	R	505	83
	RH06-2019		9 Jun. 2019		7 Aug. 2019	20 Mar. 2021	605	82 450	R	R	507	84
	RH11-2019		6 Aug. 2019		7 Aug. 2019	2 Apr. 2021	605	40 644	R	R	592	98
	RH12-2019		6 Aug. 2019		7 Aug. 2019	14 Apr. 2021	605	521 502	R	R	605	100
	RH13-2019		6 Aug. 2019		7 Aug. 2019	29 Jan. 2021	605	213 341	E	UK	166	27
	RH14-2019		6 Aug. 2019		7 Aug. 2019	14 Apr. 2021	605	251 529	R	R	604	100
	RH15-2019		6 Aug. 2019		7 Aug. 2019	9 Apr. 2021	605	14 326	R	R	382	63
G. moringa	SM03-2019	V16TP	17 Jun. 2019	7 Aug. 2019	7 Aug. 2019	21 Dec. 2021	605	190 937	R	E	284	47
	SM04-2019		17 Jun. 2019		7 Aug. 2019	12 Apr. 2021	605	150 407	R	R	605	100
	SM05-2019		18 Jun. 2019		7 Aug. 2019	6 Dec. 2019	605	23 144	R^{E}	R	122	20
	SM06-2019		18 Jun. 2019				605	0	UK	UK	0	0
	SM07-2019		18 Jun. 2019		7 Aug. 2019	29 Mar. 2020	605	58 909	R	E	226	37
	SM08-2019		6 Aug. 2019		7 Aug. 2019	20 Jan. 2021	605	45 855	R	R	262	43
	SM09-2019		6 Aug. 2019		7 Aug. 2019	31 Mar. 2020	605	10 390	R^{E}	E	216	36
	SM10-2019		7 Aug. 2019		8 Aug. 2019	7 Feb. 2021	604	104 680	R	R	283	47
	SM11-2019		7 Aug. 2019	8 Aug. 2019	8 Aug. 2019	15 Sep. 2019	38 (235)	1 750 (15 576)	P		38	100
	SM12-2019		7 Aug. 2019		8 Aug. 2019	26 Oct. 2020	604	22 273	R	R	169	28

Table 5.6 Summary table for rock hind grouper, *Epinephelus adscensionis* and spotted moray, *Gymnothorax moringa* acoustically tagged in 2021. Tracking start date excludes a 12h recovery period where relevant. Summary data includes associated tag type, capture date, date of first and last detection, study duration, and the total number of detections (excludes 12h recovery period after tagging, and if relevant until predation event occurred with detections post predation given in brackets). Includes fish fate (resident R, resident^E R^E, unknown UK, and predated P), Rd (residency days), residency index (%), number of center of activity (COA) estimates, and home range estimates.

Species	Animal ID	Tag type	Tracking start date	Tracking data		Study duration (days)	No. detections	Fate	Rd	RI (%)	No. COA estimates	Home range (95% KUD, km^2)
				First detection	Last detection							
E. adscensionis	RH56-2021	V16P	8 Jan. 2021	12 Jan. 2021	12 Mar. 2021	60 (82)	181 (192)	P	41	68		
	RH57-2021	V16P	8 Jan. 2021	8 Jan. 2021	15 Apr. 2021	98	3150	R	98	100	815	0.0920
	RH58-2021	V16P	8 Jan. 2021	21 Mar. 2021	21 Mar. 2021	98	3	E	1	1		
	RH59-2021	V16	8 Jan. 2021	9 Jan. 2021	12 Jan. 2021	98	21	E	2	2		
	RH60-2021	V16P	9 Jan. 2021	13 Jan. 2021	14 Apr. 2021	97	83	R^E	42	42		
	RH61-2021	V16	9 Jan. 2021	15 Jan. 2021	14 Apr. 2021	97	25	E	20	20		
	RH62-2021	V16P	11 Jan. 2021			95	0	UK	0	0		
	RH63-2021	V16	11 Jan. 2021	15 Feb. 2021	26 Mar. 2021	95	6	E	3	3		
	RH64-2021	V16P	11 Jan. 2021	11 Jan. 2021	15 Apr. 2021	95	8055	R	95	100	1799	0.0003
	RH65-2021	V16	11 Jan. 2021	11 Jan. 2021	15 Apr. 2021	95	4973	R	95	100	1328	0.0001
	RH66-2021	V16	12 Jan. 2021	13 Jan. 2021	10 Apr. 2021	94	66	R^E	36	38		
	RH67-2021	V16	12 Jan. 2021	18 Jan. 2021	15 Apr. 2021	94	43	R^E	27	28		
	RH68-2021	V16	13 Jan. 2021			0 (57)	0 (834)	P				
	RH69-2021	V16	13 Jan. 2021	22 Mar. 2021	22 Mar. 2021	93	1	E	1	1		
	RH70-2021	V16	16 Jan. 2021			90	0	UK	0	0		
	RH71-2020	V16	16 Jan. 2021	16 Feb. 2021	8 Mar. 2021	90	592	E	21	21	166	0.3114
G. moringa	SM18-2021	V16P	9 Jan. 2021			97	0	UK	0	0		
	SM19-2021	V16P	15 Jan. 2021			91	0	UK	0	0		
	SM20-2021	V16P	21 Jan. 2021	25 Mar. 2021	25 Mar. 2021	85	3	UK	1	1		
	SM21-2021	V16P	21 Jan. 2021			85	0	UK	0	0		
	SM22-2021	V16	21 Jan. 2021	24 Jan. 2021	30 Jan. 2021	85	12	E	6	7		

5.3.5 Dietary niche

Stomach content data

The majority of sampled *E. adscensionis* (*n* = 46, 87%) and *G. moringa* (*n* = 14, 70%) had empty stomachs upon collection (Table 5.7). Of the *E. adscensionis* sampled (*n* = 53), only individuals caught in 2020 (*n* = 22) had identifiable stomach contents (*n* = 7, 13% of all sampled grouper) (Figure 5.21A). Individuals with identifiable stomach content were caught at 08:45 (*n* unique days = 1, *n* individuals = 1), 15:30 (*n* unique days = 1, *n* individuals = 4), and 17:00 (*n* unique days = 1, *n* individuals = 1) (1 sample with unspecified "morning" capture time). Of identifiable grouper stomach contents, teleost fish were the most commonly consumed (%F = 54.55) and contributed the most to mass (%W = 97.09) with prey including rock hind grouper *E. adscensionis* (*n* = 1), black triggerfish *Melichthys niger* (*n* = 1) and unidentifiable teleosts (*n* = 4, in *n* stomachs = 4). Decapoda and Crustacea were the second most frequently identified diet item (%F of both items = 18.18). Predated crustaceans included mole crab *Emerita* sp. (%N = 7.69, %W = 1.01) and sallylight foot crab *Grapsus adscensionis* (%N = 23.08, %W = 0.14), and decapods included unidentifiable shrimp (%N = 15.38, %W = 1.76). One miscellaneous item was identified, a single leaf (%N = 1, %F = 1, %W = not recorded).

Sampled *G. moringa* (*n* = 20) with identifiable stomach contents (*n* = 6) were collected in 2019 (*n* = 2) and 2021 (*n* = 4) (Table 5.7B) (Figure 5.21B). Individuals with identifiable contents were caught during daylight hours (08:45-19:30), with teleost fish the most common prey items in both 2019 (%F = 50) and 2021 (%F = 97.67) which also accounted for the largest proportion of prey mass (2019 %W = 98.42; 2021 %W = 98.39) and number (2019 %N = 86.67, 2021 %N = 97.67). In 2019 and 2021, long jaw squirrelfish *Holocentrus adscensionis* were the common teleost prey items (2019: %F of all 2019 samples = 50, %N = 80, %W = 83.47; 2021: %F = 88.37, %N = 88.37, %W = 92.67) accepting the small sample size. Unidentifiable teleosts comprised of 25% (%F) and 2.33% (%F) of prey items in 2019 and 2021 respectively. In 2021, other teleost species included surgeonfish *Acanthurus* sp. (%F = 4.65, %N = 4.65, %W = 0.73) and *G. moringa* (%F = 2.33, %N = 2.33, %W = 4.69; likely fishing bait). In both years, a fishing hook (*n* = 1, 2019) or lure (*n* = 1, 2021) were found in the sampled stomachs (which were not a result of targetted sampling events described here). One sampled stomach contained a single unidentifiable crustacean (2021: %N = 6.67, %W = 0.5).

Table 5.7 Stomach content analysis data. A) Stomach content of rock hind (*Epinephelus adscensionis*) by year of study, includes 2019 (July - August), 2020 (November - December) and 2021 (January - April). Time of capture (TOC, note only includes times where fish were captured, and not all fishing events regardless of success), animal total length (TL, mean ± SD, and size range given in brackets), number of samples (total N, N empty, N with content) and dietary items present as a proportion of identifiable stomach content (weighed with 0.01 g accuracy).

Species	Year	TOC	TL (cm)	Total N	N empty (N with digested material present)	N with content	Dietary item			
							Teleost	Crustacea	Decapoda	Misc.
E. adscensionis	2019	09:00-19:00	43.62 ± 11.14 (14.6-61.1) * 1 unknown TL	17	17(1)	0	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00
	2020	08:45-17:00	39.59 ± 10.29 (20.7-56.0) * 1 unknown TL	22	15(4)	7	%W: 97.09 %N: 46.15 %F: 54.55	%W: 0.70 %N: 30.77 %F: 18.18	%W: 1.76 %N: 15.38 %F: 18.18	%W: 0.00* %N: 7.69 %F: 9.09
	2021	09:00-13:00	46.48 ± 7.51 (32.0-58.0)	14	14(8)	0	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00

Table 5.7 Stomach content analysis data B) spotted moray (*Gymnothorax moringa*) stomach content by year of study, includes samples collected in 2019 (July-August), 2020 (November-December) and 2021 (January-April). Time of capture (TOC, note only includes times where fish were captured, and not all fishing events regardless of success), animal total length (TL, mean ± SD, with size range given in brackets), number of samples (total N, N empty, N with content) and dietary items present as a proportion of identifiable stomach content (weighed with 0.01 g accuracy).

Species	Year	TOC	TL (cm)	Total N	N empty (N with digested material present)	N with content	Dietary item			
							Teleost	Crustacea	Decapoda	Misc.
G. moringa	2019	>08:45 - <19:30	87.1 ± 6.3 (80.0-92.1) *1 TL unknown	4	2(0)	2	%W: 98.42 %N: 86.67 %F: 50.00	%W: 0.50 %N: 6.67 %F: 25.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 1.08 %N: 6.67 %F: 25.00
	2020	08:45-13:00	80.8 ± 4.5 (76.0-85.0)	3	3(1)	0	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00
	2021	09:00 – 19:30	90.2 ± 18.7 (51.7-120.1) *1 TL unknown	13	9(3)	4	%W: 98.39 %N: 97.67 %F: 97.67	%W: 0.00 %N: 0.00 %F: 0.00	%W: 0.00 %N: 0.00 %F: 0.00	%W: 1.62 %N: 2.33 %F: 2.33

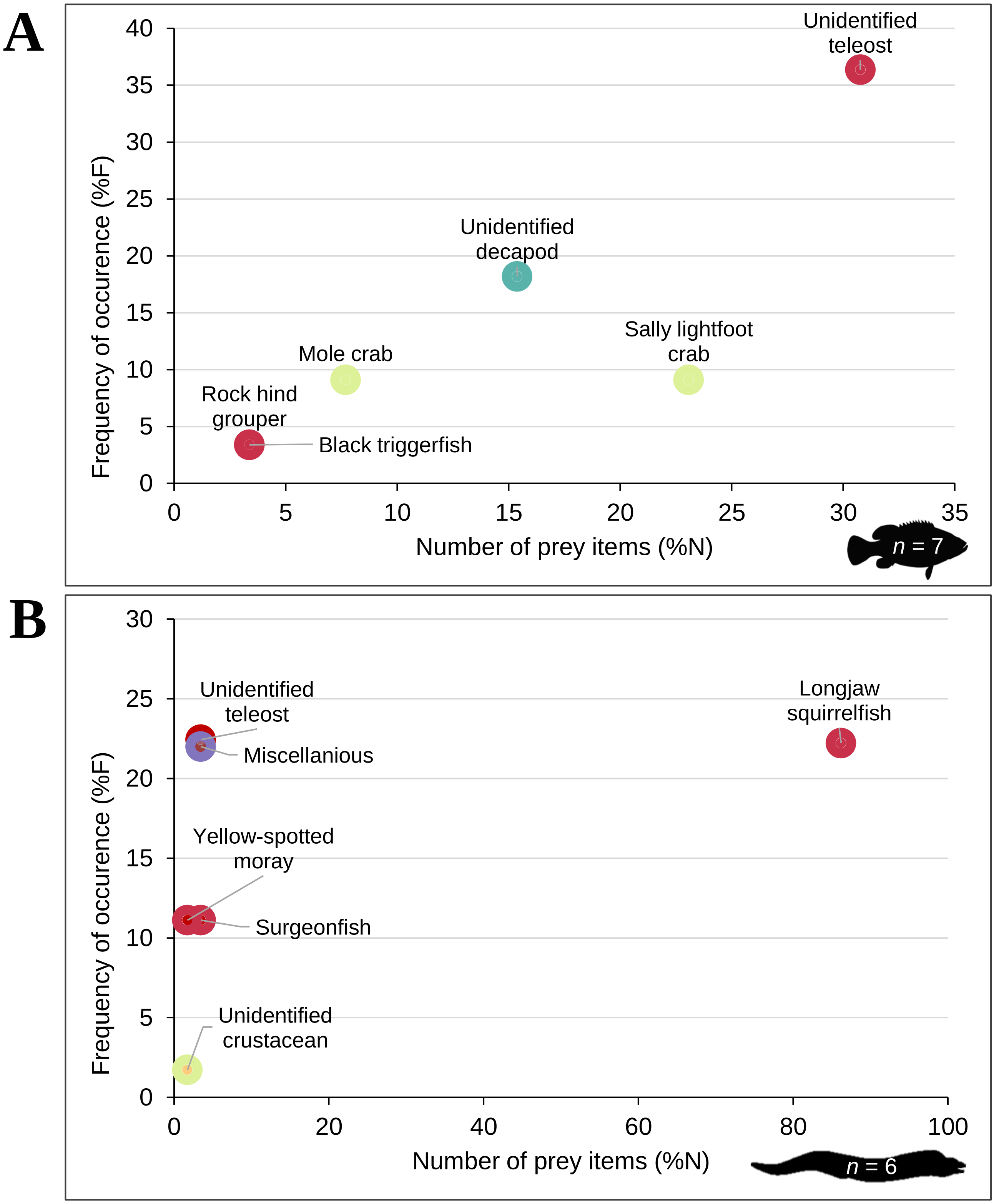


Figure 5.21 Stomach content analysis of cadavers collected in 2019 (July-August), 2020 (November-December) and 2021 (January-April). Only individuals were identifiable prey items included (sample size provided in species silhouette). A) Rock hind (*Epinephelus adscensionis*) includes 53 individuals comprised of *n* sampled in 2019 = 17, *n* 2020 = 22, and *n* 2021 = 14; included 33 empty stomachs. B) Spotted moray (*Gymnothorax moringa*) totalled 20 individuals with *n* sampled in 2019 = 4, *n* 2020 = 3, *n* 2021 = 13.; included 11 empty stomachs. Points coloured by species class.

Stable isotopes

For the two mesopredators, $\delta^{13}C$ values of muscle tissue and fin clip ranged from -15.7‰ to -13.8‰ and -18.3‰ to -13.6‰, respectively (Table 5.8) (Fig. 5.22). Ecological niche modelling indicated overlap in isotopic niches of *E. adscensionis* and *G. moringa* for both fin clips and white muscle (Fig. 5.22). For fin clips, the 95% mean posterior probability that an individual *E. adscensionis* would be present in the niche of *G. moringa* was estimated as 53.1%. Conversely, the mean probability that an individual *G. moringa* would be found in the niche of *E. adscensionis* was 54.2%. The 95% mean posterior overlap probability was higher for white muscle tissue. An individual *E. adscensionis* was estimated to be present in the niche space of *G. moringa* 97.08%, while there was a 78.02% that *G. moringa* would be found in the niche space of *E. adscensionis*. The niche size of *E. adscensionis* was estimated as 3.3 ± 0.5 and *G. moringa* as 2.5 ± 0.5 based on fin clips. White muscle tissue niche size estimates were larger at 5.7 ± 0.7 (*E. adscensionis*) and 9.6 ± 1.8 (*G. moringa*).

When isotope data were visualized by year, variation in fin tissue isotopic values between the two species were observed over the three study years (2019, 2020, 2021), while white muscle showed consistent overlap (Fig. 5.23, Fig. 5.24). Fin clips suggest that *G. moringa* utilizes a broader range of $\delta^{13}C$ basal sources. However, this interpretation is made with caution due to small sample sizes.

Table 5.8 Number of samples (*N*) by tissue type (FC = fin clip, WM = white muscle), total length (cm; note not all tissue samples were associated with a known animal length as opportunistic samples were also collected from fishers). Data also includes stable isotope values (‰) and elemental ratios of tissues (carbon to nitrogen provided as C:N ratio) from rock hind (*Epinephelus adscensionis*) and spotted moray eel (*Gymnothorax moringa*). Data are provided as a mean ± 1 SD, with the range of values given in brackets.

Species	Tissue	*n*	TL	$\delta^{13}C$	$\delta^{15}N$	C:N
Epinephelus adscensionis	FC	48	45.4 ± 9.5 (*n* = 44) 14.6-56.0	-14.3 ± 0.7 (-14.9 to -13.8)	13.0 ± 0.7 (11.6-14.2)	2.9 ± 0.1 (2.7-3.1)
	WM	76	43.8 ± 10.1 (*n* = 70) 14.6-62.0	-16.44 ± 0.6 (-18.3 to -15.0)	13.2 ± 0.6 (11.3-14.6)	3.2 ± 0.1 (3.0-4.0)
Gymnothorax moringa	FC	28	90.9 ± 14.7 (*n* = 26) 67.8-122.0	-14.8 ± 0.5 (-15.7 to -14.1)	12.8 ± 0.5 (12.1-13.9)	2.8 ± 0.1 (2.6-3.0)
	WM	28	92.4 ± 17.1 (*n* = 22) 51.7-121.0	-16.2 ± 0.7 (-17.8 to -13.6)	13.2 ± 0.7 (12.1-15.0)	3.1 ± 0.2 (2.7-3.8)

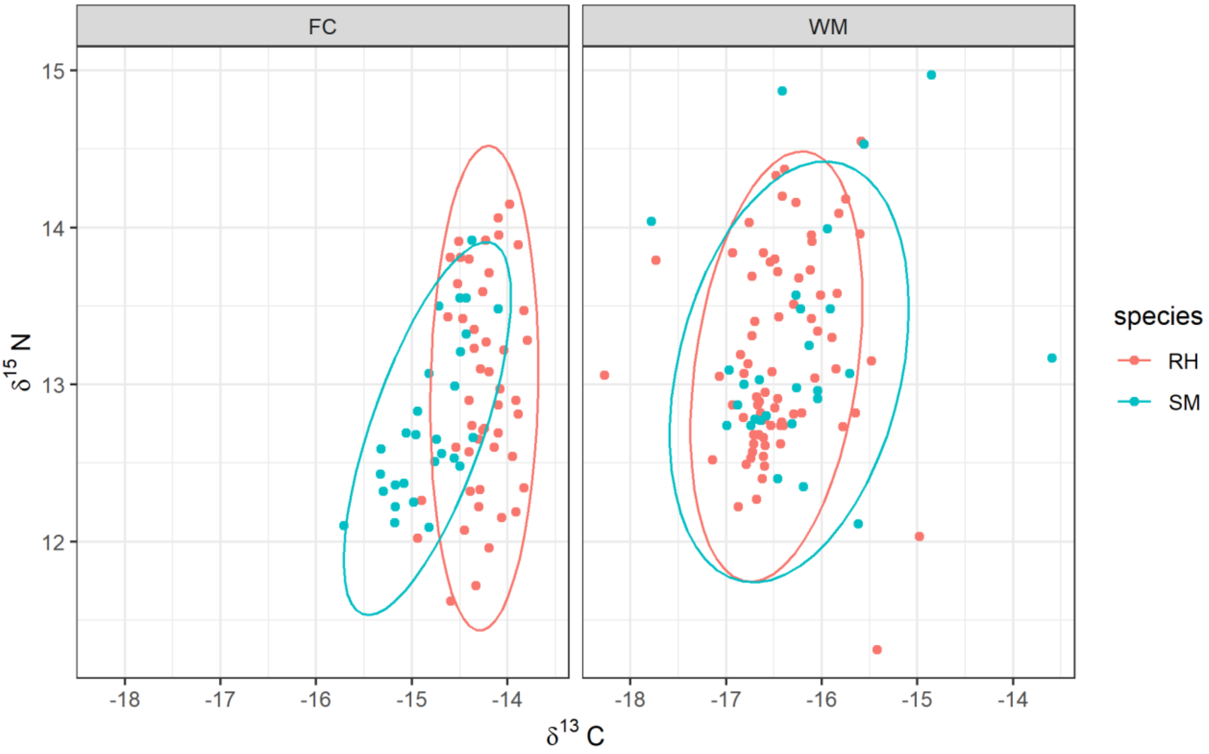


Figure 5.22 Fin clip (FC, left) and white muscle (WM, right) isotopic compositions (δ^{13}C, top: δ^{15}N, bottom) of rock hind (*Epinephelus adscensionis*, red points; *n FCs* samples = 38, *n* WM samples = 76) and spotted moray (*Gymnothorax moringa*, blue points; *n* FC samples = 28, *n* WM samples = 28). Points represent values for individual fish, and ellipses represent the species' isotopic niche.

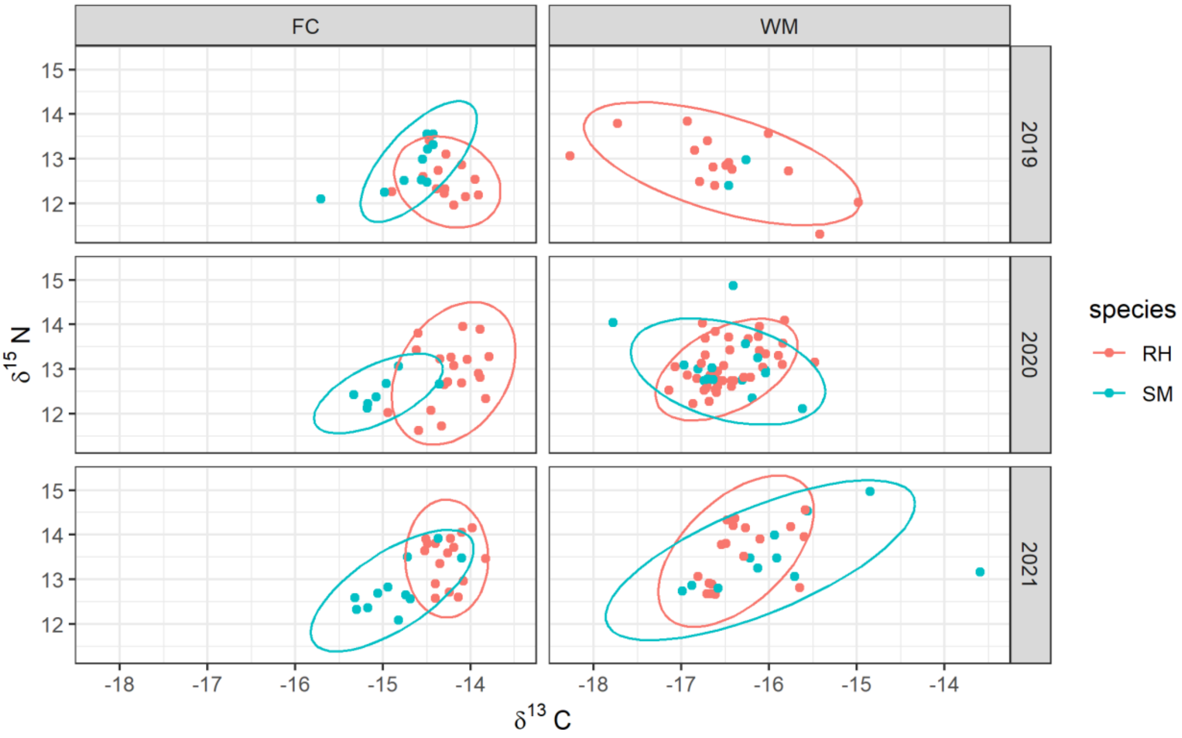


Figure 5.23 Fin clip (FC, left) and white muscle (WM, right) isotopic compositions (δ^{13}C, top: δ^{15}N, bottom) of rock hind (RH, *Epinephelus adscensionis*, red points) and spotted moray (SM, *Gymnothorax moringa*, blue points). Points represent values for individual fish and ellipses represent the species' isotopic niche, in an absence of enough data, ellipses were not generated. Data spans April – August 2019 (RH FC samples = 13, SM FC =10, RH WM = 16, SM WM = 2), November – December 2020 (RH FC samples = 19, SM FC = 7, RH WM = 41, SM WM = 15) and January – April 2021 (RH FC samples = 16, SM FC = 11, RH WM = 19, SM WM = 11).

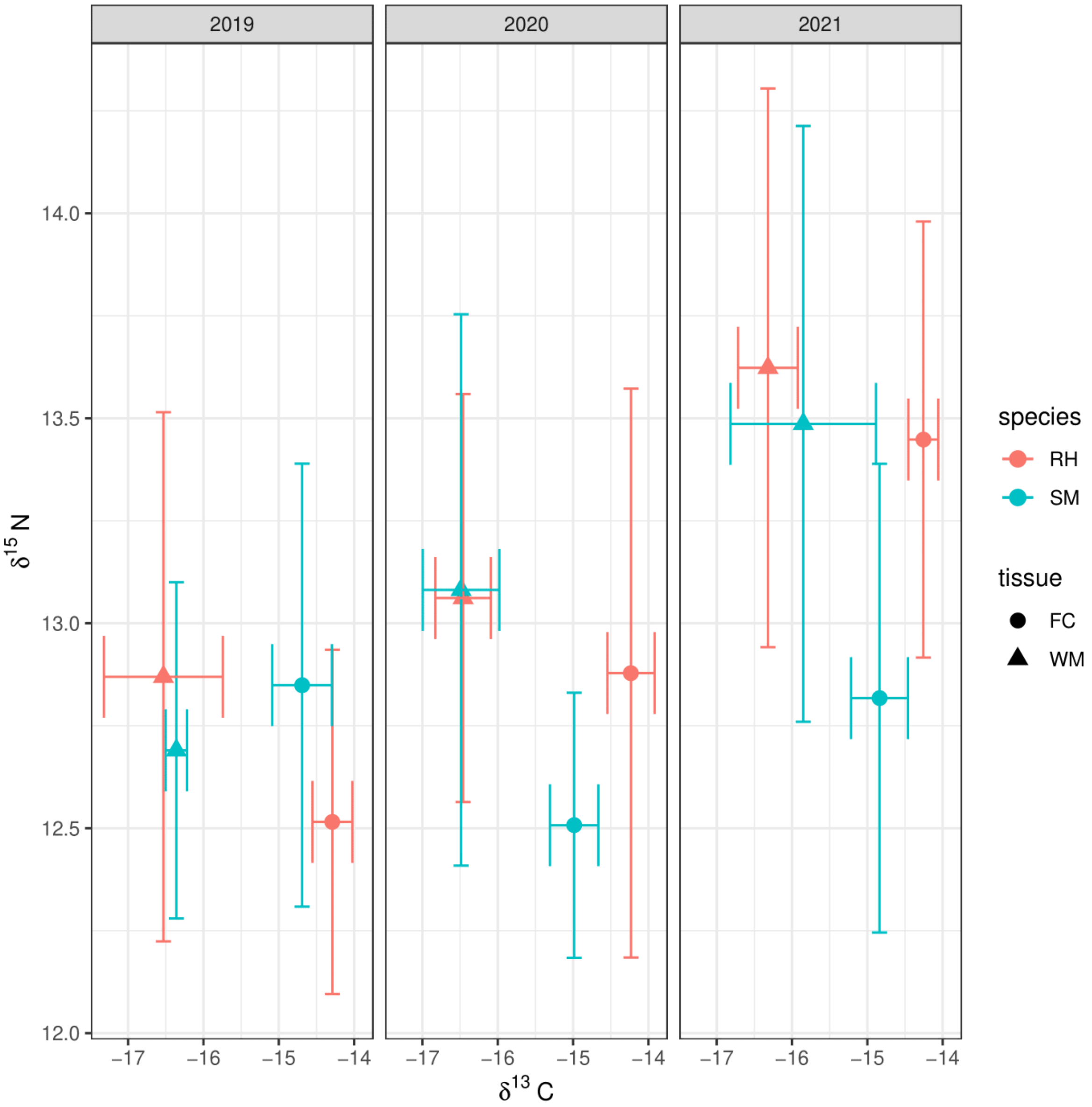


Figure 5.24 Biplot of the isotopic composition of fin clip (FC, circle) and white muscle (WM, triangle) samples of rock hind (RH, *Epinephelus adscensionis*) and spotted moray (SM, *Gymnothorax moringa*) collected in 2019 (May-August), 2020 (November, December) and 2021 (January – May). Biplots represent the mean ± 1 SD. Sample sizes of a given tissue are indicated inside the representative shape at the top of the figure (underneath the year label).

5.4 Discussion

We found evidence of resource partitioning via differences in horizontal and vertical space use of two coexisting mesopredators. While grouper exhibited high site fidelity and residency and occupied very small home ranges, moray eels were seen to undergo shifts in the area they occupied. Individual differences in vertical space within and between these two species may also facilitate coexistence. Dietary and trophic niche space from stomach content analysis and stable isotope analysis indicate a high level of niche overlap and potential for functional redundancy. Both species were identified as predominantly piscivorous predators consuming prey from the same trophic level. Minor differences in diet was identified over finer temporal scales (from fin tissue isotope data and stomach content); however, further work is required to confirm these observations given small sample sizes. Resource partitioning may facilitate coexistence, with differences in space use reducing competition for shelter and available prey, supported by a generalist diet and specialized morphology, which may enable these species to exploit seasonal prey pulses.

5.4.1 Residency and spatial overlap

This study utilized telemetry data generated over a range of spatial scales and array designs, from a tightly spaced gridded array of acoustic receivers to a linear curtain of receivers with >300 m spacing. These arrays overlapped across the study area, with tagging sites within the spatial constraints of all arrays, facilitating the tracking of grouper and moray across longitudinal scales. Data generated from three tagged grouper cohorts suggest temporally stable residency indices and a small home range. In contrast, moray eels were seen to undergo shifts in the area they occupied, which terminated periods of observed residency. However, it is uncertain whether this observed behaviour is due to emigration or the capture of animals at the edge of their home range. These results confirm that while there is some overlap in the spatial niche of these two species, differences in the occupied horizontal and vertical space used by these two species may facilitate coexistence.

High residency indices and small calculated home ranges confirm that rock hind grouper is a species exhibiting year-round site fidelity. While home range could only be calculated for four-tagged fish, clear residency patterns for most grouper across longitudinal time scales support that *E. adscensionis* have spatiotemporally distinct territories. Similarly, Koeck et al. (2014) identified the year-round residency of the dusky grouper (*E. marginatus*), which remained within a 0.65 km^2 marine reserve in Banyuls-Cerbère, France. Tracked *E. marginatus* occupied depths of <55 m and occupied rocky habitats, seagrass and coralligenous sea beds. Similarly, the grouper tracked within English Bay and Bates Point showed high site fidelity to rocky substrate. High fidelity and small home ranges have been widely reported for acoustically-tagged grouper in existing literature (Eklund & Schull 2001, Kiel 2004, Popple & Hunte 2005, Biesinger et al. 2013, Afonso et al. 2016). A long-term study of grouper tracked in and around a small marine reserve in the Azores calculated similarly small home ranges of <0.268 km^2 (*E. marginatus*) and <0.004 km^2 (*Serranus artricauda*) using COAs (5 y study; Afonso et al. 2016). The two species of abundant grouper tracked in this study exhibited high site fidelity, with differences in diel activity potentially facilitating their coexistence. Rowell et al. (2015) also observed prolonged residency periods in acoustically tracked Nassau grouper (*E. striatus*) and yellowfin grouper (*Mycteroperca venenosa*) within two marine reserves in the US Virgin Islands, which were subsequently detected >4 years after tagging, within the same capture site. This study explored the reproductive behaviour of these two species of grouper, and identified differences in the scale of space use which facilitate their coexistence during calling periods (vocalization to attract mates). While *E. striatus* remained within a small area, *M. venenosa* was detected across the two marine reserves (6 km apart).

Grouper have been recorded to co-exist with other mesopredators in other high biomass environments, with no relationship observed between areas of high density of mesopredator heterospecifics and the abundance of groupers (Valdivia et al. 2014). Food availability within Ascension's high biomass environment which experiences limited fishing pressure is analogous to that observed within marine protected areas (MPAs). Studies of serranid movement within MPAs suggest high fidelity to complex reef habitats (Popple & Hunte 2005); however, studies to date have not accounted for surrounding biomass and conspecific presence. Future work could incorporate measures of biomass using underwater video and observational surveys to capture the role of competition and food availability on animal movement. In addition, bathymetric, environmental and oceanographic data for Ascension's nearshore environment is limited and therefore could not be incorporated. Raw detections recorded across the Bates Point array (2021; Fig. 5.18) suggests grouper also occupy deeper (<50 m) sandy habitats with shelving depth gradients (not accurately captured on existing admiralty charts) which may be due to nutrient upwelling and available resources (Cheung et al. 2010). Research by Friedlander et al. (2014) found piscivores (including marbled coral grouper, *Plectropomus punctatus*) were more abundant in the leeward and upwelling areas, but abundance was not predicted by wave exposure around a remote atoll in the Seychelles. Observational SCUBA survey data conducted around the south (windward) and north (typically leeward) areas suggest grouper are prevalent around the entirety of the island (A. Richardson, *pers. comm.*, 8 April 2019). Whether grouper retain small home ranges across Ascension's range of environmental gradients (i.e. high wave action south of Ascension Island), habitats (rock, sand and rhodolith), depth gradients (nearshore versus offshore populations), areas of variable biomass (i.e. with fewer recorded conspecifics) and under risk of predation requires further investigation.

Groupers are ubiquitous mesopredators in warm-water reef ecosystems, which have been historically exploited throughout their range and form the basis of a billion-dollar global fishery (Mitchenson et al. 2011). Understanding an animal's home range is essential for effective fisheries management and basic ecological understanding (Lennox et al. 2019, Hays et al. 2019). Small home range and high residency estimates suggest that *E. adscensionis* populations around Ascension may also be vulnerable to overexploitation. From a management perspective, these results suggest that a local decline of this species could be ameliorated by the designation of small, appropriately located no-take zones. Similarly, Bryars et al. (2012) identified that 95% of tagged blue groper (Family Labridae, *Achoerodus gouldii*) activity space was situated along a 1.1 km stretch of coastline and proposed that a protected no-take zone several kilometers long and several kilometers wide would be sufficient to protect the aggregation of blue groper. Identifying whether nearshore populations of *E. adscensionis* function as discrete units with minimal movement or one homogenous population capable of localized replenishment will be central to estimating population replenishment potential. It has been speculated that fish spend less time foraging and may forage over smaller areas when the risk of predation is higher (Heithaus et al. 2008). While grouper and moray eels likely had few predators within Ascension’s nearshore environment, this has changed with the recent insurgence of Galapagos sharks (increased in numbers at the end of 2019, with continued presence observed into 2021 Kirsty Jones, *pers. comm.* 3 July 2022). Further investigation is required to confirm whether this relationship holds for Ascension’s grouper and moray eels.

Recent work has shown that conventional home range estimation tools systematically underestimate home range estimates for autocorrelated relocation data (Fleming et al. 2015). AKDE incorporates an autocorrelation function alleviating this issue (Fleming & Calabrese 2021). It should be noted that AKDE is designed to work with true position fixes, not COA estimates, e.g. positions derived using TDOA VPS which provides an associated error for each position. As a result of using COA estimates, in two cases realistic home range values could not be obtained (detections were recorded on a single receiver leading to a model convergence failure). Despite these limitations, this approach offered the best method for estimating home range.

Tagged spotted moray exhibited a range of horizontal movement behaviours, including emigration after with residency of <1 month (which led to none or limited detections; 6 fish), or prolonged residency before emigration (1-12 months; 7 individuals). Only one tagged moray stayed within the study area for more than one year. During the observed residency periods, vertical data identified that several individuals moved to new areas (still within the constraints of the acoustic array). Other studies of moray eels confirmed these findings of short residency periods prior to emigration (Abrams et al. 1973, Young & Winn 2003, Bassett & Montgomery 2011). For example, Abrams et al. (1973) conducted a 6-week observational survey of *G. moringa* movements within Coki reef in the Caribbean and found that individuals were transient. *G. moringa* exhibited short residency periods, with some individuals returning to previously occupied dens. Similarly, an observational survey within English Bay (prior to acoustic tagging in 2019) identified that individuals had high fidelity for 10 days with some movement between dens along a 200 m transect. Residency patterns have been seen to differ between different moray species occupying the same reef (Abrams & Schein 1986). Abrams & Schein (1986) revisited Coki reef (where Abrams et al. 1973 conducted their previously mentioned research) and, using observational surveys, identified *G. moringa* was transient with lower residency than the goldentail moray, *Muraena miliaris*. A loss of coral reef following Hurricane David was associated with a reduction in the abundance of moray eels across the reef. Whether this is due to translocation by the storm, death, or loss of habitat is unclear. Existing research suggests that morays have high site fidelity to complex structures they use for refuge and feeding (Young & Winn 2003); the absence of complex structures may prompt emigration. The cues for moray eel emigration and movement is not established. However, research suggests that morays may compete for shelter. For example, Lozano-Álvarez et al. (2010) investigated interactions between Caribbean spiny lobster *Panulirus argus* and moray eels (*G. vicinus* and *G. moringa*) before and after the addition of lobster casitas. Morays were more likely to be sighted alone in small crevices than alongside other morays during observational surveys. The introduction of large shelters (casitas) increased the likelihood of cohabitation (casitas provide shelter large enough for multiple individuals). Competition for shelter with conspecifics and heterospecifics may therefore prompt movement. For example, a study by Higgins & Mehta (2018) identified distinct size structuring of California moray, *G. mordax,* across two coastal sites in Catalina Island, California. Research into the fine-scale social interactions of moray eels is limited and may provide insight into intra- and interspecific competition and the potential drivers of movement behaviour.

Literature on grouper suggests they are resilient to interference, i.e. stay within their home range after animal handling and tagging, and can return from a translocated location. For example, a displacement study by (Kaunda-Arara & Rose 2004) found that all greasy grouper (*E. tauvina*) translocated 0.5 and 2.6 km from their original capture site returned, and the majority returned within 1 d. Similar research has not confirmed site fidelity after translocation or handling for moray eels. Therefore, the stress associated with animal handling may have induced escape behaviour prompting tagged morays to emigrate. Additionally, whether morays are transient or were caught on the edge of their range is uncertain. Due to logistical constraints and difficulty catching morays at deeper sites in 2021, all individuals were caught <100 m from shore. None of the 5 individuals tagged in 2021 were subsequently detected after 1 week. Ideally, animals would have been tagged towards the center of the acoustic array to maximise detection likelihood and to allow estimation of home range. The cryptic shelter-dwelling behaviour of *G. moringa* may have also limited data yield due to acoustic shadowing and reduced line-of-sight between receivers preventing detection (Bassett & Montgomery 2011). Despite these limitations, these are the most comprehensive tracking data avilable for moray eels, owing to high data yield and longitudinal study duration. From a management perspective, these results suggest that a protected area which can accommodate emigration and the relocation of home ranges would be key to protection of *G. moringa*. However, the effective scale of this protected area is difficult to ascertain from these results.

5.4.2 Vertical movements

In general, vertical fish movements have received less attention to date than horizontal fish movements. Factors that drive individual differences in vertical fish movements have been linked to sea temperature (Freitas et al. 2016), diel cycles (Fox & Bellwood 2011), available prey depth (St-John 1999), predator avoidance (Power 1984), reproductive behaviour (Koeck et al. 2014), and the lunar cycle (Froehlich et al. 2021). Individuals of both species showed variable vertical movements, from static depth recordings with minimal change, a shift from shallow to deep habitats, a synchronised shift to depth for several days before return to a typical depth, and cyclical diurnal movements between shallow and deep habitats. These results support the acceptance of the alternate hypothesis (H2), temporal differences in space use within and between the two study species may facilitate their coexistence. Additional research is required to investigate this across finer-temporal scales (e.g. at an hourly resolution).

Ascension Island has an equatorial climate that experiences minimal seasonality. Relative to water temperature time series data recorded within the study area, temperature profiles from internal tag sensors suggest both species can withstand moderate temperature variation (>7°C) with no observed relationship between sea temperature and animal movement (i.e. moving to deeper or shallow depths). Due to an observed bias in the number of recorded detections during the day versus night on fixed tags (sync and ref tags, see Chapter 3), fine-scale diel activity was not assessed (similar issues with acoustic telemetry identified by Payne et al. 2010, Koeck et al. 2013). Modelled average 12-hour depth values identified that the depth of each species in the water column differed significantly between day and night, with a preference for moderately deeper depths at night. Whether deeper depth use is suggestive of rest or foraging behaviour is unclear from the resolution of acquired data.

Grouper are commonly described as diurnal predators (Koeck et al. 2014), however, several tagged individuals in this study were observed to undertake forays into deeper habitats at night. Similarly, while moray eels are known as nocturnal foragers, during observational surveys and capture attempts, morays were observed to actively hunt during daylight hours. Similar observations of active moray eel swimming during daylight hours have been reported on other remote tropical islands in the South Atlantic (St. Paul’s Rocks; Luiz-Júnior 2005). Plasticity of diel activity rhythms in tropical fishes can facilitate temporal niche partitioning and range expansion, e.g. to utilize different high-quality prey items or effectively exploit a high number of low-quality prey (Fox & Bellwood 2011, Sánchez-Hernández et al. 2020). For example, the diel activity of golden-lined rabbitfish (*Siganus lineatus*) within a tropical reef habitat differed depending on whether populations inhabited boulder-shoreline (active during daylight hours, static and resting in rest holes at night), or fringing reef habitats (active during the night, resting in rest holes in the day) (Fox & Bellwood 2011). Moray eels have been observed to initiate diurnal cooperative hunting forays alongside other groupers (Diamant & Shpigel 1985, Bshary et al. 2006, Vail et al. 2013), suggesting flexible diel activity rhythms. Whether a shift to slightly deeper in the water column at night is linked to resting or active behaviour requires further investigation.

Flexible diel activity may enable foraging on differing prey assemblages between day versus night; diel variation in prey assembalges have been previously reported in Ascension's waters (Brewin et al. 2016).

The significant predictor of day of year in the hGAM examining vertical space use may be due to the distribution of seasonal prey within the water column. Grouper are gape-limited feeders, whereby they will feed opportunistically on food items that their mouths are large enough to engulf (Reshetnikov et al. 1972). St-John (1999) found coral trout (*Plectropomus leopardus*, family Serranidae) depth selection varied with the depth of available prey items. Similarly, the occurrence of red snapper (*Lutjanus campechanus*) higher in the water column was thought to relate to spawning patterns and prey availability over diel and monthly periods (Williams-Grove & Szedlmayer 2017). Ascension has clear seasonal fluxes in prey occurrence which also vary with depth. For example, juvenile turtles (*Chelonia mydas*) on their first foray into the water from January to June (Ascension Island Government 2015a) are surface swimmers, which may stimulate surface feeding by predators. Mantis shrimp (suspected *Pseudosquillisma oculata*) are benthic crustaceans observed to spawn in April (from personal observation and wider food web sampling in 2021), which may induce opportunistic feeding lower in the water column. Opportunistic feeding strategies have been suggested to reduce interspecific competition and facilitate the coexistence of fishes across a variety of contexts (Mavuti et al. 2004, Friedlander et al. 2014, Flores-Ortega et al. 2020, Neves et al. 2021). Optimal foraging theory predicts that feeding on abundant prey, such as seasonal prey pulses of longjaw squirrelfish and mole crab would offer *E. adscensionis* and *G. moringa* a greater energetic benefit than searching for less abundant prey (MacArthur & Pianka 1966, Gerkings 1994).

Multiple grouper were observed to shift to deeper depths on 30 September 2019, indicative of spawning behaviour. Nolan et al. (2017) identified that Ascension rock hind grouper gonad maturity peaked with a seasonal decline in water temperature from March (28.1°C) to September (23.5°C), and gonad staging identified spawning occurred from July to November. On the 30th of September 2019, water temperatures within English Bay were 24°C, corresponding to a seasonal low, and a new moon was observed. Most groupers (genus Epinephelus) inhabiting subtropical and tropical waters exhibit reproductive changes with the lunar cycle, including changes to hormone levels and oocyte and ovulatory follicle development (Fukunaga et al. 2019). Existing research suggests groupers can perceive changes in the moonlight as evidenced by changes in melatonin content of the eye studied across the lunar cycle (Fukunaga et al. 2019). Spawning of groupers coinciding with the last lunar quarter and a new moon has also been documented (Chao & Lim 2004), with large spawning aggregations commonplace (Mitchenson et al. 2011). In addition, controlled lab studies have found that Epinephelus species are capable of multiple spawning events (Hussain & Higuchi 1980, Toledo et al. 1993, Chao & Lim 2004), which may explain the observed ‘yo-yo’ing to depth typically associated with spawning behaviour (4 – 8 m oscillations during spawning recorded by Koeck et al. 2014) at multiple times of the year by tracked grouper. Moray eel reproduction has not been as extensively studied. Samples collected off the southeast US suggest that spawning peaks between June and October, with spawning periodicity ranging from 24-31 days, and females potentially spawning between 9 and 12 times during the 278 d spawning season (Zokan et al. 2022). Additionally, *G. moringa* larvae have been collected throughout the year in the Caribbean, indicating that tropical populations may spawn throughout the year (Smith 1989). It has been suggested that, unlike anguillid, congrid and ophichtid eels, morays do not appear to migrate to spawn and instead spawn on the reefs they inhabit (Thresher 1984). Our data support this point given there was no clear shift in habitat observed during the potential spawning season.

5.4.3 Dietary niche

Stomach content analysis has been historically used to identify dietary composition (Harmelin-Vivien et al. 1989) and, more recently, has been successfully used to contextualise foraging behaviours observed using acoustic telemetry (Young & Winn 2003). Similarly, stable isotopes can be used to investigate diet and offer a tool to identify diet choices over a range of scales using multiple tissues, i.e. “slow” turnover rate tissues from muscle and “fast” turnover rates from fin (Macneil et al. 2005, Phillips & Eldridge 2006). Stomach content and stable isotope data identified high dietary overlap between rock hind and spotted moray eel. Both species fed within the same trophic level and consumed primarily piscivorous prey. Tentative comparisons between years suggest niche width may fluctuate between species and that they consume seasonal prey sources; however, this requires further investigation due to low sample sizes.

Stomach content and stable isotope data found significant overlap in the dietary items consumed by *E. adscensionis* and *G. moringa*, which suggests potential functional redundancy. Functional redundancy describes how the role of one species is also fulfilled by another present within a system and is thought to dictate ecosystem resilience (Peterson et al. 1998, Mouillot et al. 2013). The prevalence of functional redundancy in high biomass systems has been explained by resource partitioning via the selection of different size spectra prey, ontogenetic shifts in diet, and temporal differences in foraging behaviour. Differences in the size spectra of selected prey items have been observed to shift with body size and age (Grouper: St-John 1999, Meyer & Dierking 2011, Condini et al. 2015; Moray eels: Higgins et al. 2018). Whether ontogenetic space and diet shifts promote predator-mediated coexistence for these two species as is commonly reported (Grouper: Wollrab et al. 2013, Artero et al. 2015; Moray eels: Kendall et al. 2021), or if differences in the size spectra of selected prey changes with body size and age remains to be investigated. For example, St-John (1999) identified that juvenile coral trout (*P. leopardus*) on the Great Barrier Reef, Australia, fed on a high proportion of benthic dwelling crustaceans whereas adults were almost entirely piscivorous. Prey selection may also vary according to jaw size, for example Higgins et al. (2018) identified a scaling relationship between California moray eel (*G. mordax*) head size and the size of their prey, the kelp bass (*Paralabrax clathratus*). Additionally, using a global stereo video dataset, moray eel (*G. flavimarginatus* and *G. javanicus*) were observed to opportunistically feed on available prey items, and the size of prey items varied ontogenetically (T. Lyons, *unpublished thesis* available from meeuwig.org). The observed overlap and preference for piscivorous prey items align with other studies of serranids (Stewart & Jones 2001, Artero et al. 2015) and moray eels (Young & Winn 2003, Higgins et al. 2018) within tropical reef environments. Both species were cannibalistic, as found in other studies of serranids (Hseu et al. 2003) and moray eels (Young & Winn 2003). Cannibalism in predatory species persists when resources are not limited, e.g. in laboratory trials providing food in excess to juvenile grouper (*E. coioides*) found that cannabilism continued to occur (Hseu et al. 2003). Whether the observed cannibalism in Ascension's mesopredators is a mechanism which reduces competition and facilitates coexistence or is a result of utilising available prey is unclear.

Diet studies typically span multiple years to enable comprehensive identification of annual and seasonal changes in prey availability and predator numbers (e.g. Dicken et al. 2017). Due to time constraints, diet analysis utilized opportunistic sampling across two field seasons (May-August 2019; November 2020 – May 2021), which coincidentally spanned unique seasons of prey availability. Seasonal prey pulses were noted during wider food web sampling and personal observations, including mole crab (Emerita spp) spawning November 2020 – February 2021, land crab (*Johngarthia lagostoma*) spawning January – May 2021) and green turtle (*C. mydas*) hatchling season January – June (Ascension Island Government

2015). In addition, an increase in bigeye scad (*Selar crumenophthalmus*) presence occurred in March – May 2021 as they were chased inshore by predatory game fishes, and mantis shrimp (suspected *P. oculata*) spawning and longjaw squirrelfish (*Neoniphon marianus*) spawning took place in April 2021. In 2021, attempts to catch and tag grouper at depths of >20m were largely unsuccessful and this could be linked to the turtle hatchling season. During hatchling season, grouper form "conveyor belts" close to shore ready to receive incoming turtles on their first foray into the ocean (R. Joshua, *pers. comm.* 3 January 2021). This prey-specific shift in behaviour may also explain the variability observed in animal depth over time. Seasonal prey fluxes have also been identified as a potential driver of movements and breeding success of Ascension's seabirds. Studies of Ascension's sooty tern (*Onychoprion fuscatus*) seabird population have identified an 8 to 10-month breeding interval since the 1870s (Reynolds et al. 2014; Chapin 1954), associated with a longer foraging period compared to other island colonies (The Seychelles, Feare 2009; Dry Tortugas, Dinsmore 1972) as they search for ephemeral food sources. In addition, local scientists have observed shifts in the timing of peak egg incubation by masked boobies (*Sula dactylatra*), i.e. from peak incubation in October 2016-2018 to December 2019-2021. The timing of peak incubation is thought to vary in accordance with food availability and sea turbulence (individuals are more likely to abandon nest attempts as they rely on sight to catch prey) (L. Shearer, *pers. comm.*, 28 June 2022).

Almost all sampled and tracked fishes were caught using rod and line or soaked lines, which may have driven the capture of hungry, risk-averse individuals (Lennox et al. 2017). To sample *G. moringa* stomach content Young & Winn (2003) caught individuals (*n* = 71) at their shelters during the day within a shallow backreef habitat in Belize, with moray eels sedated in water and subsequently sacrificed, or indigested prey captured during regurgitation (potentially triggered by sedation). This study had a higher yield of full stomachs (61%)

potentially due to the capture strategy. In addition, due to logistical constraints and personnel safety, all individuals were caught during daylight hours (9 am - 7 pm) which for nocturnal foragers such as moray eel may not coincide with typical foraging hours (Kendall et al. 2021). Stomach content analysis likely underestimated the number of prey items consumed, given that bones from a stomach were grouped and assigned to a single individual prey item. All tracked individuals were presumed to be adults based on size, and while a range of sizes were sampled for dietary analysis, small sample sizes limit inference.

To summarise, future diet analysis research over longitudinal scales could use several approaches to improve the generalisability of results in the context of coexistence, (1) use a variety of capture techniques, (2) sample at day and night, (3) collect samples across differing prey cycles, (4) capture a range of life stages to identify potential ontogenetic shifts in choice and size spectra of prey, (5) sample from sites with differing conditions, i.e. south of the island to compare the effect of differing habitat gradients (higher wave action), and (6) integrate contextual data on system biomass, e.g. from underwater video.

5.5 Conclusion

Our data provide new insights into the spatial and dietary niche of two recreationally important fisheries species found in Ascension's nearshore environment. These data suggest *E. adscensionis* exhibit a high degree of site fidelity and residency, whereas *G. moringa* are transient. Future work to identify island connectivity and potential replenishment of these species is key to ensuring the health of Ascension's fishes. Overlap in the dietary niche of these two mesopredators suggests they utilize similar prey, with a generalist diet enabling them to utilize ephemeral prey pulses. Exploring niche partitioning and the factors that enable coexistence can contribute to managing aquatic systems and assessing potential ecosystem resilience.

5.6 References

Abrams RW, Abrams MD, Schein MW (1973) Diurnal Observations on the Behavioral Ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean Coral Reef. Coral Reefs 1:185–192.

Abrams RW, Schein MW (1986) Individual movements and population density estimates for moray eels on a Caribbean coral reef. Coral Reefs 5:161–163.

Afonso P, Abecasis D, Santos RS, Fontes J (2016) Contrasting movements and residency of two serranids in a small Macaronesian MPA. Fish Res 177:59–70.

Artero C, Koenig CC, Richard P, Berzins R, Guillou G, Bouchon C, Lampert L (2015) Ontogenetic dietary and habitat shifts in goliath grouper *Epinephelus itajara* from French Guiana. Endangered Species Research.

Ascension Island Government (2015a) Green turtle species action plan. In: *The Ascension Island Biodiversity Action Plan*. Ascension Island Government Conservation Department, Georgetown, Ascension Island

Ascension Island Government (2015b) Shallow marine habitat plan. In: The Ascension Island Biodiversity Action Plan. Ascension Island Government Conservation Department, Georgetown, Ascension Island.

Bacheler NM, Shertzer KW, Runde BJ, Rudershausen PJ, Buckel JA (2021) Environmental conditions, diel period, and fish size influence the horizontal and vertical movements of red snapper. Sci Rep 11:9580.

Bassett D, Montgomery J (2011) Home range use and movement patterns of the yellow moray eel *Gymnothorax prasinus*. J Fish Biol 79:520–525.

Biesinger Z, Bolker BM, Marcinek D, Lindberg WJ (2013) Gag (*Mycteroperca microlepis*) space-use correlations with landscape structure and environmental conditions. J Exp Mar Biol Ecol 443:1–11.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Brewin PE, Brown J, Brickle P (2016) Diurnal variation of fish and macrobenthic invertebrate community structure in an isolated oceanic island of the South Atlantic. J Mar Biol Assoc UK 96:737–747.

Bryars S, Rogers P, Huveneers C, Payne N, Smith I, McDonald B (2012) Small home range in southern Australia’s largest resident reef fish, the western blue groper (*Achoerodus gouldii*): implications for adequacy of no-take marine protected areas. Mar Freshwater Res 63:552.

Bshary R, Hohner A, Ait-el-Djoudi K, Fricke H (2006) Interspecific communicative and coordinated hunting between groupers and giant moray eels in the red sea. PLoS Biology 4:2393–2398.

Burnham KP, Anderson DR (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33:261–304.

Carleton SA, Kelly L, Anderson-Sprecher R, del Rio CM (2008) Should we use one-, or multi-compartment models to describe 13C incorporation into animal tissues? Rapid Commun Mass Spectrom 22:3008–3014.

Chan AJ, Raoult V, Jaine FRA, Peddemors VM, Broadhurst MK, Williamson JE (2022) Trophic niche of Australian cownose rays (R*hinoptera neglecta*) and whitespotted eagle rays (*Aetobatus ocellatus*) along the east coast of Australia. J Fish Biol 100:970–978.

Chao T, Lim LC (2004) Natural spawning of three species of grouper in floating cages at a pilot broodstock facility at Komodo, Flores, Indonesia. Singapore Journal of Primary Industries 19:78–93.

Chapin JP (1954) The calendar of Wideawake Fair. Auk:1–15.

Chesson P (2000) Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31:343–366.

Church MR, Ebersole JL, Rensmeyer KM, Couture RB, Barrows FT, Noakes DLG (2009) Mucus: a new tissue fraction for rapid determination of fish diet switching using stable isotope analysis. Can J Fish Aquat Sci 66:1–5.

Cheung W, Lam V, Sarmiento JL, Kearney K, Watson R, Zeller D, Pauly D (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Glob Chang Biol 16:24–35.

Collins AB, Heupel MR, Motta PJ (2007) Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. J Fish Biology 71:1159–1178.

Condini MV, Hoeinghaus DJ, Garcia AM (2015) Trophic ecology of dusky grouper *Epinephelus marginatus* (Actinopterygii, Epinephelidae) in littoral and neritic habitats of southern Brazil as elucidated by stomach contents and stable isotope analyzes. Hydrobiologia 743:109–125.

Cunjak RA, Roussel JM, Gray MA, Dietrich JP, Cartwright DF, Munkittrick KR, Jardine TD (2005) Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. Oecologia 144:636–646.

Diamant A, Shpigel M (1985) Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Agaba). Environ Biol Fishes 13:153–159.

Dicken ML, Hussey NE, Christiansen HM, Smale MJ, Nkabi N, Cliff G, Wintner SP (2017) Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from South African waters. PLoS One 12:e0177897.

Dinsmore JJ (1972) Sooty tern behavior. University of Florida, Gainesville.

Eklund A-M, Schull J (2001) A Stepwise Approach to Investigating the Movement Patterns and Habitat Utilization of Goliath Grouper, *Epinephelus itajara*, Using Conventional Tagging, Acoustic Telemetry and Satellite Tracking. 189–216.

Emmanuel L (2014) Lunar: Lunar Phase & Distance, Seasons and Other Environmental Factors.

Farmer NA, Ault JS (2011) Grouper and snapper movements and habitat use in Dry Tortugas, Florida. Mar Ecol Prog Ser 433:169–184.

Feare C (2009) The breeding of the Sooty Tern Sterna fuscata in Seychelles and the effects of experimental removal of its eggs. Journal of Zoology 179:317–360.

Fleming CH, Calabrese JM (2021) Ctmm: Continuous-Time Movement Modeling.

Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96:1182–1188.

Flores-Ortega JR, Godínez-Domínguez E, González-Sansón G, Flores-Ortega JR, Godínez-Domínguez E, González-Sansón G (2020) Trophic interactions between the 11 most abundant demersal fish species on the Pacific coast of central Mexico. Ciencias marinas 46:101–117.

Fox RJ, Bellwood DR (2011) Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*: Diel activity plasticity in a rabbitfish. Funct Ecol 25:1096–1105.

Freitas C, Olsen EM, Knutsen H, Albretsen J, Moland E (2016) Temperature-associated habitat selection in a cold-water marine fish. J Anim Ecol 85:628–637.

Friedlander AM, Obura D, Aumeeruddy R, Ballesteros E, Church J, Cebrian E, Sala E (2014) Coexistence of low coral cover and high fish biomass at Farquhar Atoll, Seychelles. PLOS ONE 9:e87359.

Froehlich CYM, Garcia A, Cintra-Buenrostro CE, Hicks DW, Kline RJ (2021) Structural differences alter residency and depth activity of red snapper (*Lutjanus campechanus*) at two artificial reefs. Fisheries Research 242:106043.

Fry B (2006) Stable isotope ecology. Springer, New York, NY.

Fukunaga K, Yamashina F, Ohta N, Mizuno H, Takeuchi Y, Yamauchi C, Takemura A (2019) Involvement of melatonin in transducing moon-related signals into the reproductive network of the female honeycomb grouper *Epinephelus merra*. Gen Comp Endocrinol 282:113211.

Gerkings SD (1994) Feeding ecology of fish. Academic Press, San Diego.

Gkenas C, Oikonomou A, Economou A, Kiosse F, Leonardos I (2012) Life history pattern and feeding habits of the invasive mosquitofish, *Gambusia holbrooki*, in Lake Pamvotis (NW Greece). J Biol Res-Thessalon 17:121–136.

Guzzo MM, Blanchfield PJ, Chapelsky AJ, Cott PA (2016) Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. J Great Lakes Res 42:276–285.

Hardin G (1960) The Competitive Exclusion Principle. Science 131:1292–1297.

Harmelin-Vivien ML, Kaim-Malka RA, Ledoyer M, Jacob-Abraham SS (1989) Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. J Fish Biology 34:715–734.

Harrison J, Higgins B, Mehta R (2017) Scaling of dentition and prey size in the California moray (*Gymnothorax mordax*). Zoology 122.

Hays GC *et al.* (2019) Translating marine animal tracking data into conservation policy and management. Trends Ecol Evol 34:459–473.

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–210.

Heupel MR *et al.* (2006) Automated Acoustic Tracking of Aquatic Animals: Scales, Design and Deployment of Listening Station Arrays. Mar Freshw Res 57:1.

Higgins BA, Law CJ, Mehta RS (2018) Eat whole and less often: ontogenetic shift reveals size specialization on kelp bass by the California moray eel, *Gymnothorax mordax*. Oecologia 188:875–887.

Higgins BA, Mehta RS (2018) Distribution and habitat associations of the California moray (*Gymnothorax mordax*) within Two Harbors, Santa Catalina Island, California. Environ Biol Fish 101:95–108.

Hseu JR, Lu FI, Su HM, Wang LS, Tsai CL, Hwang PP (2003) Effect of exogenous tryptophan on cannibalism, survival and growth in juvenile grouper, *Epinephelus coioides*. Aquaculture 218:251–263.

Hussain N, Higuchi M (1980) Larval rearing and development of the brown spotted grouper, *Epinephelus tauvina* (Forskal). Aquaculture 19:339–350.

Hussey NE, Dudley SFJ, Mccarthy ID, Cliff G, Fisk AT (2011) Population - Isotopic tracking through food web. 2045:2029–2045.

Hussey NE, Hedges KJ, Barkley AN, Treble MA, Peklova I, Webber DM, Ferguson SH, Yurkowski DJ, Kessel ST, Bedard JM, Fisk AT (2017) Movements of a deep-water fish: Establishing marine fisheries management boundaries in coastal Arctic waters. Ecol Appl 27:687–704.

Hutchinson GE (1957) Concluding Remarks. In: *Quantitive Biology*.

InnovaSea Systems Inc. (2021) Coded transmitters - 69 kHz. Available from: https://www.innovasea.com/uploads.

Johnston TA, Ehrman AD, Hamilton GL, Nugent BK, Cott PA, Gunn JM (2019) Plenty of room at the bottom: niche variation and segregation in large-bodied benthivores of boreal lakes. Can J Fish Aquat Sci 76:1411–1422.

Kaunda-Arara B, Rose GA (2004) Homing and site fidelity in the greasy grouper *Epinephelus tauvina* (Serranidae) within a marine protected area in coastal Kenya. Mar Ecol Prog Ser 277:245–251.

Kendall MS, Siceloff L, Ruffo A, Winship A, Monaco ME (2021) Green morays (*Gymnothorax funebris*) have sedentary ways in mangrove bays, but also ontogenetic forays to reef enclaves. Environ Biol Fish 104:1–15.

Koeck B, Alós J, Caro A, Neveu R, Crec'hriou R, Saragoni G, Lenfant P (2013) Contrasting Fish Behavior in Artificial Seascapes with Implications for Resources Conservation. PLoS One 8:e69303.

Koeck B, Pastor J, Saragoni G, Dalias N, Payrot JÔ, Lenfant P (2014) Diel and seasonal movement pattern of the dusky grouper *Epinephelus marginatus* inside a marine reserve. Mar Environ Res 94:38–47.

Kristensen DK, Kristensen E, Mangion P (2010) Food partitioning of leaf-eating mangrove crabs (Sesarminae): Experimental and stable isotope (^{13}C and ^{15}N) evidence. Estuar Coast Shelf Sci 87:583–590.

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48.

Leibold MA (1995) The niche concept revisited: mechanistic models and community context. Ecology 76:1371–1382.

Lennox RJ, Alós J, Arlinghaus R, Horodysky A, Klefoth T, Monk CT, Cooke SJ (2017) What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. Fish Fish 18:986–1010.

Lennox RJ, Engler-Palma C, Kowarski K, Filous A, Whitlock R, Cooke SJ, Auger-Méthé M (2019) Optimizing marine spatial plans with animal tracking data. Can J Fish Aquat Sci 76:497–509.

Lozano-Álvarez E, Briones-Fourzan P, Alvarez-Filip L, Weiss H, Negrete-Soto F, Barradas-Ortiz C (2010) Influence of shelter availability on interactions between Caribbean spiny lobsters and moray eels: Implications for artificial lobster enhancement. Marine Ecology Progress Series 400:175–185.

Luiz-Júnior OJ (2005) Unusual behaviour of moray eels on an isolated tropical island (St. Paul's Rocks, Brazil). Coral Reefs 24:501–501.

Lysy M, Stasko AD, Swanson HK (2014) NicheROVER: (Niche) (R)egion and Niche (Over)lap Metrics for Multidimensional Ecological Niches. *v* 1.1.0.

Macarthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377–385.

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609.

Macneil A, Skomal G, Fisk A (2005) Stable isotopes from multiple tissues reveal diet switching in sharks. Mar Ecol Prog Ser 302:199–206.

Martinez RB, Wolf BO (2005) Mass-balance models for animal isotopic ecology. In: *Physiological and ecological adaptations to feeding in vertebrates*. Starck JM, Wang T (eds) Science Publishers, Enfield, NH.

Matich P, Ault JS, Boucek RE, Bryan DR, Gastrich KR, Harvey CL, Heithaus MR, Kiszka JJ, Paz V, Rehage JS, Rosenblatt AE (2017) Ecological niche partitioning within a large predator guild in a nutrient-limited estuary: Niche partitioning among estuarine predators. Limnol Oceanogr 62:934–953.

Matley JK, Fisk AT, Tobin AJ, Heupel MR, Simpfendorfer CA (2016) Diet-tissue discrimination factors and turnover of carbon and nitrogen stable isotopes in tissues of an adult predatory coral reef fish, *Plectropomus leopardus*. Rapid Communications in Mass Spectrometry 30:29–44.

Matley JK, Heupel MR, Fisk AT, Simpfendorfer CA, Tobin AJ (2017) Measuring niche overlap between co-occurring *Plectropomus* spp. using acoustic telemetry and stable isotopes. Mar Freshw Res 68:1468–1478.

Mavuti KM, Nyunja JA, Wakwabi EO (2004) Trophic ecology of some common juvenile fish species in Mtwapa Creek, Kenya. West Indian Ocean J Mar Sci 3:179–188.

Mehta RS, Wainwright PC (2007) Biting releases constraints on moray eel feeding kinematics. J Experim Biol 210:495–504.

Meyer A, Dierking J (2011) Elevated size and body condition and altered feeding ecology of the grouper Cephalopholis argus in non-native habitats. MEPS 439:203–212.

Mitchenson YS, Craig MT, Cheung W, Choat JH, Mitcheson YSD, Craig MT, Bertoncini AA, Carpenter KE, William WL (2011) Fishing groupers towards extinction : A global assessment of threats and extinction risks in a billion dollar fishery Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. Fish Fish 14:119–136.

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177.

Neves M, Kratina P, Delariva R, Jones J, Fialho C (2021) Seasonal feeding plasticity can facilitate coexistence of dominant omnivores in Neotropical streams. Rev Fish Biol Fisheries. doi:10.1107/s11160-021-09648.

Nolan ET, Downes KJ, Richardson A, Arkhipkin A, Brickle P, Brown J, Mrowicki RJ, Shcherbich Z, Weber N, Weber SB (2017) Life-history strategies of the rock hind grouper *Epinephelus adscensionis* at Ascension Island. J Fish Biol 91:1549–1568.

Noonan MJ *et al.* (2019) A comprehensive analysis of autocorrelation and bias in home range estimation. Ecol Monogr 89:e01344.

Payne N, Gillanders B, Webber D, Semmens J (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. Mar Ecol Prog Ser 419:295–301.

Pedersen EJ, Miller DL, Simpson GL, Ross N (2019) Hierarchical generalized additive models in ecology: an introduction with mgcv. PeerJ 7:e6876.

Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. ecosystems. Res J Environ Sci 1:6–18.

Peterson BJ, Fry B (1987) Stable Isotopes in Ecosystem Studies. Annual Reviews 18:293–320.

Phillips DL, Eldridge PM (2006) Estimating the timing of diet shifts using stable isotopes. Oecologia 147:195–203.

Piet GJ, Guruge WAHP (1997) Diel variation in feeding and vertical distribution of ten co-occurring fish species: consequences for resource partitioning. Environ Biol Fishes 50:293–307.

Polovina JJ (1984) Model of a coral reef ecosystem. Coral Reefs 3:1–11.

Popple ID, Hunte W (2005) Movement patterns of *Cephalopholis cruentata* in a marine reserve in St Lucia, W.I., obtained from ultrasonic telemetry. J Fish Biol 67:981–992.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Power ME (1984) Depth distributions of armored catfish: Predator-induced resource avoidance? Ecology 65:523–528.

Randall JE, Golani D (1995) Review of the moray eels (Anguilliformes: muraenidae) of the Red Sea. Bull Mar Sci 56:849–880.

RBR Ltd. (2021) RBR CT and CTD data loggers.

Reshetnikov YS, Claro R, Silva A (1972) The pattern of feeding and the rate of digestion in some tropical predatory fish. J Ichthyol 12:818–824.

Reynolds SJ, Martin GR, Dawson A, Wearn CP, Hughes BJ (2014) The sub-annual breeding cycle of a tropical seabird. PLOS ONE 9:e93582.

Rowell TJ, Nemeth RS, Schärer MT, Appeldoorn RS (2015) Fish sound production and acoustic telemetry reveal behaviors and spatial patterns associated with spawning aggregations of two Caribbean groupers. Mar Ecol Prog Ser 518:239–254.

RStudio Team (2021) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA.

Sanchez Henao A, García Álvarez N, Silva F, Estevez P, Gago-Martinez A, Martín F, Ramos-Sosa M, Fernandez A, Diogène J, Real Valcárcel F (2020) Presence of CTXs in moray eels and dusky groupers in the marine environment of the Canary Islands. Aquat Toxicol 221:105427.

Sánchez-Hernández J, Vieira-Lanero R, Servia MJ, Cobo F (2020) Feeding habits of four sympatric fish species in the Iberian Peninsula: keys to understanding coexistence using prey traits. Aquat Toxicol 221.

Shipley ON, Matich P (2020) Studying animal niches using bulk stable isotope ratios: an updated synthesis. Oecologia 193:27–51.

Simpfendorfer CA, Heupel MR, Collins AB (2008) Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Can J Fish Aquat Sci 65:482–492.

Simpfendorfer CA, Heupel MR, Hueter RE (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can J Fish Aquat Sci 59:23–32.

Smith DG (1989) Family Congridae. In: *Fishes of the Western North Atlantic*. Foundation for Marine Research, New Haven, CT. 460–567

Stewart BD, Jones GP (2001) Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. Mar Biol 138:383–397.

St-John J (1999) Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus* (Serranidae): Patterns in taxa, size and habitat of prey. Mar Ecol Prog Ser 180:233–246.

Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist JD (2015) A new probabilistic method for quantifying *n*-dimensional ecological niches and niche overlap. Ecology 96:318–324.

Thieurmel B, Elmarhraoui A (2019) Suncalc: compute sun position, sunlight phases, moon position and lunar phase. *v* 0.5.0. https://CRAN.R-project.org/package=suncalc.

Thresher RE (1984) Reproduction in reef fishes. T.F.H. Publications Inc., Neptune City, NJ.

Toledo JD, Nagai A, Javellana D (1993) Successive spawning of grouper, *Epinephelus suillus* (Valenciennes), in a tank and a floating net cage. Aquaculture 115:361–367.

Udyawer V, Dwyer RG, Hoenner X, Babcock RC, Brodie S, Campbell HA, Harcourt RG, Huveneers C, Jaine FRA, Simpfendorfer CA, Taylor MD, Heupel MR (2018) A standardised framework for analysing animal detections from automated tracking arrays. Anim Biotelemetry 6:1–14.

Vail A, Manica A, Bshary R (2013) Referential gestures in fish collaborative hunting. Nat Commun 4:1765.

Valdivia A, Bruno JF, Cox CE, Hackerott S, Green SJ (2014) Re-examining the relationship between invasive lionfish and native grouper in the Caribbean. PeerJ 2:e348.

Walker BH (1992) Biodiversity and ecological redundancy. Conservation Biology 6:18–23.

Ward JN, Hinton JW, Johannsen KL, Karlin ML, Miller KV, Chamberlain MJ (2018) Home range size, vegetation density, and season influences prey use by coyotes (*Canis latrans*). PLoS One 13:e0203703.

Wickham H (2016) Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Williams-Grove LJ, Szedlmayer ST (2017) Depth preferences and three-dimensional movements of red snapper, Lutjanus campechanus , on an artificial reef in the northern Gulf of Mexico. Fish Res 190:61–70.

Wirtz P, Bingeman J, Bingeman J, Fricke R, Hook TJ, Young J (2017) The fishes of Ascension Island, central Atlantic Ocean-new records and an annotated checklist. J Mar Biol Assoc UK 97:783–798.

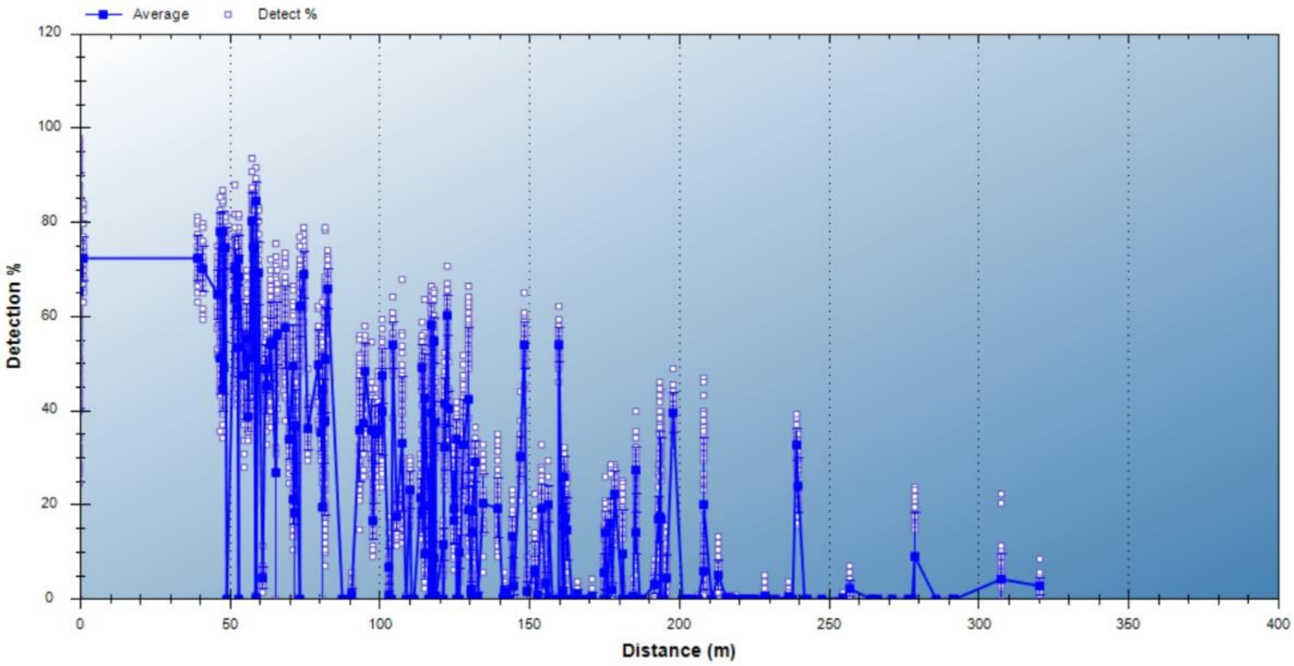
Wollrab S, de Roos AM, Diehl S (2013) Ontogenetic diet shifts promote predator-mediated coexistence. Ecology 94:2886–2897.

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc 73:3–36.

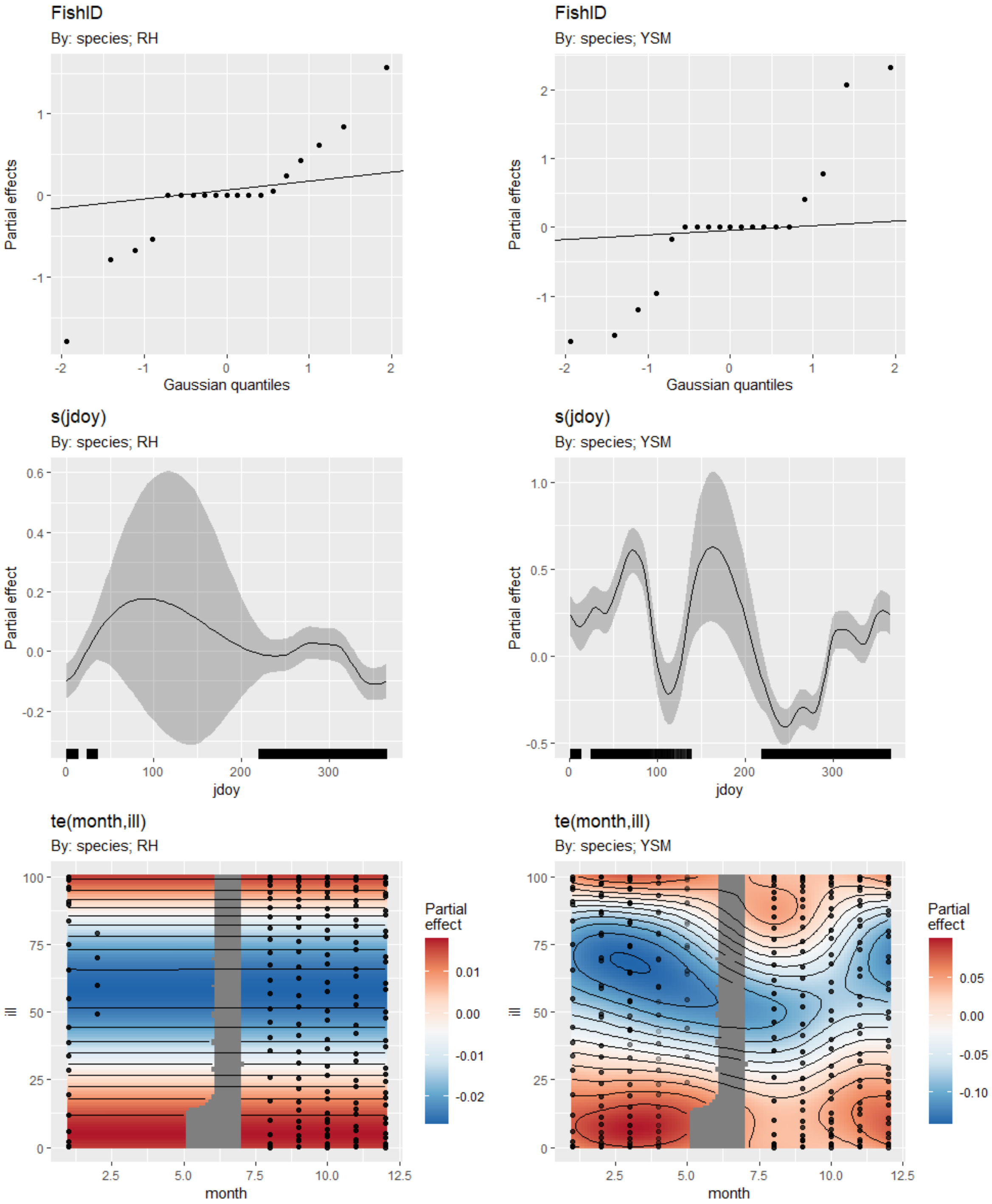
Young RF, Winn HE (2003) Activity Patterns, Diet, and Shelter Site Use for Two Species of Moray Eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. Ichthyol Herpetol 2003:44–55.

Zokan MA, Wyanski DM, White DB, Sedberry GR (2022) Life history of the spotted moray (*Gymnothorax moringa*) off the Atlantic coast of the southeastern United States: age, growth, and reproduction - ProQuest. Fishery Bulletin 120.

Supplementary Material for Chapter 5



Supplementary Figure 5.1 Summarised detection efficiency (%) of synchronisation tags (*n* = 13) at increasing distances from acoustic receivers (VEMCO VR2W, *n* = 22) deployed in a gridded array with 55 m (rock) to 80 m (sand) spacing. The solid blue line represents the average hourly detection efficiency (%) across the array, with raw detection efficiency for each receiver station shown by the hollow white square. Output generated using the VEMCO Range Test software available from the Innovasea website (https://support.vemco.com/s/downloads).



Supplementary Figure 5.2 Comparisons of smooths used in best fit hierarchical generalized additive model, drawn using *gratia* package in R (Simpson 2022). Row 1 indicates partial effect of fish ID, row 2 the partial effect of day of year, and row 3 the tensor product smoother relationship between lunar illumination (ill) and month of study.

Chapter 6. General Discussion

6.1 Introduction

This thesis explores the current progress in investigating spatial niche and applies acoustic telemetry alongside dietary tools in a complex equatorial system to explore coexistence. Acoustic telemetry offers unique insight into aquatic animal movements and behaviour. By integrating positioning algorithms, this technology shifts from defining animal presence/absence within a receiver's detection range (typically hundreds of metres) to estimating an animal's location with potential sub-metre precision. Improving the resolution of acquired positions facilitates more precise basic movement metrics (i.e. the rate and direction of movement) used to reconstruct movement trajectories, from which space use estimates, including home range, can be made. The utility of positioning algorithms also greatly improves our potential to identify fine-scale movements that directly affect animal energy budgets, therefore, population persistence and growth. However, the rapid advancement of this technology (including increased transmission rates and integrative data streams) must be met by an awareness of user considerations and intrinsic study system properties which drive system performance (high data yield, low positioning error). Critical decision-making must go hand-in-hand with transparent reporting at all stages of telemetry work, from initial design considerations, exploring detection data yield, deriving positions from detections, and filtering positions using positioning error thresholds. Validation of telemetric findings through direct observation, remote underwater cameras and in-situ sampling can help piece together patterns in telemetric data and improve explanatory power. In the case of elucidating home range, tools which can explore the original conceptualization of home range, "*the area traversed by the individual in its normal activities of food gathering, mating and caring for young*" (Burt 1943), could include dietary measures (i.e. stomach content analysis and chemical tracers). Together with acoustic telemetry, this user toolbox of traditional and modern techniques can provide essential insight into aquatic underwater landscapes and conditions constraining an animal’s realized niche.

6.2 Summary of research

A systematic review identified the current applications, analytical approaches, and future directions of a popular commercial fine-scale positioning system (the Vemco Positioning System, VPS). Like one of the first published acoustic telemetry studies, this system uses a Time Difference of Arrival (TDOA) algorithm to generate animal positions (with potential sub-meter accuracy) from simultaneous detections of a tag on three or more listening acoustic receivers. Fine-scale telemetry offers the potential to explore spatial niche and classic ecological concepts, including coexistence, resource partitioning and competition in a real-world experimental setting. This technology has been used to track a range of taxa and life stages. Most research has focused on demersal and reef-associated species of IUCN Least Concern residing within marine biomes in the northern hemisphere. Studies have focused on questions concerning behavioural ecology (e.g., habitat and space use and behavioural states), conservation (responses to prevalent anthropogenic stressors and assessing remedial techniques), land use management, methodological studies of the technology, animal reproductive ecology, fisheries management strategies and other drivers of animal movement. Incorporating additional data streams such as video, environmental sensors, and historical records has enabled the development of holistic movement models. Fine-scale acoustic arrays paired with positioning algorithms have vast potential to improve our understanding of fundamental aspects of aquatic animal ecology and spatial niche.

While the factors limiting data yield from discontinuous (presence-absence) acoustic telemetry arrays have been discussed in several seminal papers, this has yet to be synthesized for fine-scale telemetry. To guide new and existing users embarking on a VPS study, I synthesized the factors that have limited data yield in published VPS studies. I then generated a framework of pre- in-situ and post-study steps to help improve study success (increase data yield and reduce the error associated with derived animal positions). This framework is exemplified through the description of a real-world VPS case study which was ultimately compromised. By highlighting factors that can limit a fine-scale positioning study, it is hoped that this framework will encourage standardized reporting of essential steps and checks that will improve transparency and generalisability of findings, enable comparisons between studies, and facilitate the advancement of this field.

VEMCO High Residency (HR) technology is the newest iteration of technology that can be paired with the VPS. HR tags use binary phase-shift keying transmissions to facilitate higher attainable transmission rates and shorter transmission intervals (e.g., HR detections every 3 s versus every 30 s using pulse per modulation technology formerly paired with VPS). These features reduce the probability of signal collision (which occurs when part of the signal is lost and the tag ID cannot be encoded) and enable larger cohorts of animals to be effectively tracked. To guide new and existing users, I outline steps that can be used to evaluate raw detection data before deriving positions, including assessing tilt, signal-to-noise ratios, and simultaneous data yield from fixed and animal tags. With this knowledge, users can make informed decisions on processing steps and appropriate analyzes. Commercial position processing from VPS arrays using the TDOA algorithm may be preferable over user-led positioning when time and expertise are fundamental project constraints. The steps VPS analysts undertake to derive positions are unclear and have led to a famed “black box” of analysis. Transparency in this stage is key to empowering researchers and informed decision-making at all study phases, from planning fine-scale arrays and reviewing data acquisition in-situ to filtering data given derived position error values. While the case study component of this work focuses on the newest iteration of VPS, an HR-VPS system, these steps are translatable across both PPM and HR VPS arrays. By providing these tools, outlining user-led data checks, and demystifying the “black box” of analysis, it is hoped this work will encourage critical data exploration and improve transparency in the steps used to derive positions.

Using acoustic telemetry and dietary tools, I explore the mechanisms that facilitate the coexistence of two highly abundant mesopredators in a complex nearshore environment. Results from acoustic telemetry suggest rock hind grouper, *Epinephelus adscensionis* have high site fidelity and small home ranges, a finding supported by other studies on horizontal movements of serranids (March et al. 2010, Koeck et al. 2014, Afonso et al. 2016). Data from tracked spotted moray (*Gymnothorax moringa*) is consistent with studies that this species has short residency periods with relatively constrained movements at a site before occupying new dens (Abrams et al. 1973, Young & Winn 2003). These data suggest that differences in intra- and inter-individual depth use may facilitate coexistence. On average, grouper occupied deeper sites than moray eels. Significant predictors of vertical space use include (1) time of day, with a slight shift to deeper habitat at night for both species, (2) lunar illumination, but only for moray eels, (3) day of the year, which may link to the distribution of seasonal prey pulses, and (4) the individual studied. Visualizations of detection profiles indicate a potential synchronized new moon spawning event by *E. adscensionis* captured for the first time using acoustic telemetry. Chemical analysis of slow (white muscle) and fast (fin) turnover tissues found these species feed within the same trophic level. Differences in niche breadth between years suggest these two species utilize a range of prey items over time, which may be opportunistic or related to prey composition within their occupied range. This research provides the first glimpse into the movement behaviour of these two recreationally important fishery species around Ascension Island and differs in spatial and dietary niche which may facilitate coexistence.

6.3 Utility of this thesis and future frontiers of exploration

Literature reviews and conceptual frameworks are key to reviewing the current progress in a specific area and identifying future frontiers of exploration. For example, Nathan et al. (2008) devised a conceptual framework to integrate the basic components and processes involved in animal movement, namely: (1) interval drivers (why move?), (2) motion capacity (how?) and (3) navigation capacity (when and where to move?). This movement paradigm simplified movement into singular components, highlighting facets of movement ecology that remain poorly understood. Following this publication, Holyoak et al. (2008) reviewed a subset of 1,000 movement papers across 496 unique journals and applied Nathan's framework, it was found that few studies had explored navigation capacity, and those that did were primarily focused on vertebrates. Following this, Demšar et al. (2021) reviewed movement-focused research in ecology, GIS, geography, social science, public health, transportation, computer science, and physics. This review aimed to bridge gaps between disciplines through unifying terminology and methodology. Demšar combined Nathan's (2008) framework with a four-step model typically used to forecast future demand and performance of transport systems (i.e. Miller & Shaw 2001). Navigational capacity was split into two subunits: where to move and what route to take. Movement space was conceptualized in Demšar's framework, which defines where these movements occur, e.g., in a two- or three-dimensional physical space and whether movements are constrained (e.g., vehicle mobility is bound to roads akin to anadromous fish bound to migrate through rivers and streams), or unconstrained (i.e., in avian movement in x, y, z space). Reviews of current research are integral to evaluating progress in a given field to drive future research frontiers.

In this thesis, I provide user frameworks and recipes for success, supported by reviewing literature and case studies highlighting the difficulties faced using commercial fine-scale positioning systems (namely the VEMCO VPS) in an experimental setting. While the factors limiting data yield from discontinuous (presence/absence) telemetry arrays are detailed in several seminal review papers (Heupel et al. 2006, Kessel et al. 2014), this has not yet been synthesized for fine-scale telemetric approaches. By synthesizing existing research in this field and the factors that can limit performance, I highlight areas of future exploration that require further understanding. Several core components of this thesis are methodological and the result of compromised field experiments. Reporting and publishing “null” findings and flawed experiments is not common practice. However, dissecting why field experiments fail is crucial to evidence-based research and paving the way to exploring limiting factors that can be faced when using new technologies and approaches (Levinn & Pluth 2020).

Collectively this work demonstrates the utility of using acoustic telemetry to study spatial niche in the aquatic realm and offers a window of opportunity to explore animal behaviour and space use. While this work reviews the application of one commercial positioning system which uses the TDOA positioning algorithm, an effort has been made in this field to support open-access user-led methods to derive animal positions. For example, open-access code to conduct TDOA analysis (Trancart et al. 2019, ~1 m accuracy using home-brewed TDOA analysis) and time of arrival positioning (Yet Another Positioning Solver, *YAPS* package; Baktoft et al. 2017). The YAPS model uses maximum likelihood analysis of a state-space model framework applied to the time of arrival of acoustic detections (Baktoft et al. 2017). More data is retained by only requiring detections on two receivers (Baktoft et al. 2017). YAPS can also accommodate tags produced by various manufacturers, making it versatile. Cabled autonomous systems can also be used to derive precise animal locations. Cabled systems improve the ease of clock synchronisation between receiver clocks by directly connecting receivers to a universal GPS clock (using a GPS card). In doing so, cabled systems can achieve an estimated detection time accuracy of 250 ns across a single system, equating to very precise high-resolution animal tracks (Deng et al. 2011). While cabled systems can be incredibly precise, they are constrained by attainable cable lengths (O'Dor et al. 2001, Cooke et al. 2005) and the conditions in which the system can safely operate within, e.g. avoiding high wave action areas. Other signal encoding types, including code division multiple access can also be used to track potentially hundreds of animals carrying tags transmitting at high sampling rates (i.e., 5 s) (Niezgoda et al. 2002). Continued innovations in telemetry technology such as tag miniaturization, battery life improvements, and on-the-fly filtering by listening receivers will facilitate diversification in the aquatic taxa that can be studied and ecological topics addressed. Due to technological limitations and cost, fine-scale high-resolution tracks are currently limited by scale, as animal positions can only be derived while within range of the acoustic array. Incorporating additional tags that also track animals outside the range of the acoustic array, e.g. using satellite tags (coarse data is relayed via passing satellites), is currently the best option for capturing large-scale movements (Nathan et al. 2022).

This thesis addresses the navigation capacity component of Nathan's movement framework (when and where to move) but does not explore intrinsic drivers of movement, i.e., cognition, memory, and internal drivers of movement. Generating a holistic view of niche in accordance with Hutchinson's realized niche requires additional detail on the environment (biotic and abiotic conditions) a species inhabits, which was not captured in this thesis, including available refuge and prey and species interactions. Contextual information on substrate rugosity and corresponding refuge space, for example, using observational or multibeam surveys to map bathymetric complexity, could help build a more comprehensive picture of the surrounding environment. Moray eel den preference is driven by the size of the crevice opening, with larger animals occupying dens with larger openings (Abrams et al. 1973). Given the difficulty of acoustic tracking morays due to cryptic behaviour and shelter dwelling, in future work, telemetry could be paired with routine observational surveys as seen in Abrams et al. (1973) and Young & Winn (2003) to validate and contextualize results. Intra- and interspecific competition and food availability may also play a role in space use. Grouper and moray eels coinhabit crevices within Ascension's rocky substrate, with a mixed-species moray eel assemblage commonplace (Kate Chadwick, *pers. comm.*, 29 June 2022). Abrams et al. (1973) identified that *G. moringa* has a strong tendency to inhabit a hole previously used by a muraenid, and that space was not a limiting factor. Future research into the chemical and tactile cues used by morays to identify appropriate dens may provide perspective on this observed behaviour, and what drives movement between areas (as observed in telemetric data from English Bay). Moreover, this thesis focuses on the coexistence of 1 species of moray, *G. moringa,* with grouper. However, there are 11 species of moray eels found in the nearshore waters of Ascension Island (Wirtz et al. 2017). Future work could explore if different species of moray interact differently with grouper and whether this cohabitation changes with maturity or animal density. Additionally, in-situ telemetry data downloads (i.e., every 2-months) and larval trapping at suspected spawning periods of both moray and grouper could be used to validate spawning events inferred from telemetric data (as seen in Buchinger et al. 2017).

Dietary tools used in this thesis include stomach content analysis and chemical tracers. While data grouped by species across the three years suggests dietary overlap, visualizations of diet choice split by year suggest that there may be intra-annual variation in diet. Stomach content data hints that some individuals may be specialized to feed on certain prey. For example, one sampled moray abundantly consumed mole crab. Whether this diet choice was selective or driven by availability, e.g. the moray eel was coincidentally closer to shore, where mole crabs are commonly distributed, is unclear. However, the latter is likely true, given the high abundance of the two species and their generalist nature. Larger sample sizes and longitudinal data collection would augment and clarify these dietary findings.

Moray eels possess a variety of morphological adaptations which facilitate opportune generalist feeding, including curved piercing teeth, a second set of jaws, an anguilliform body shape, and specialized mucal glands. Often described as durophagous (Mehta 2009), this essentially translates to “nature’s nutcrackers” and describes their ability to crush the hard shells of invertebrates such as crustaceans. Their large mouth contains a single row of teeth in the upper and lower jaw and several vomerine teeth on the roof of the mouth to prevent prey from escaping (Böhlke 2002). Moray eels cannot generate suction when feeding. When striking prey, the oral jaws seize prey, and the pharyngeal jaw (nested in its throat) draws the prey back into the body (Mehta & Wainwright 2007). The elongate, laterally compressed moray body shape facilitates movement within and between rocky crevices while disguised by their mottled colouration. The outermost layer of moray eel skin contains mucal glands making the eels more resilient to time spent on land and able to consume semi-terrestrial prey (Mehta & Donohoe 2021).

Similarly, groupers are host to various ecomorphological adaptations, including ram and suction feeding strategies, the ability to swallow prey whole, and camouflage via colour change. Goliath grouper (*E. itajara*) are observed to modulate feeding behaviour based on position and mobility of prey. For example, Collins & Motta (2017) found that mobile epibenthic food elicits larger maximum gapes, faster capture rates and ram feeding behaviour. In contrast, *E. itajara* exhibits slower approaches and suction feeding to capture immobile prey, seemingly minimising energy expenditure (Collins & Motta 2017). A grouper’s blunt teeth enable them to swallow prey whole, which minimizes the chance of evasion (St-John 1999). Grouper can also change colour to enable them to camouflage on an array of background types (Watson et al. 2014), beneficial within a heterogeneous environment such as Ascension’s nearshore environment. These adaptations suggest that both species can utilize a range of resources tied to the habitat they occupy and could exploit seasonal prey pulses. However, future research is required to contextualize current findings, i.e., larger sample sizes and longitudinal time scales for dietary sampling.

Future research could also investigate whether the findings of Higgins et al. (2018) apply to this system, namely whether there is an ontogenetic shift in diet choice. A possible avenue of study would be to examine the size spectra of prey consumed by the two species across a range of ontogenetic stages. Groupers are “gape-limited”, which describes how they do not mechanically reduce their prey before ingestion and, therefore, only feed on prey that can fit inside their gape (St-John 1999, Jayne et al. 2002). In contrast, moray eels use prey manipulation behaviours to consume larger prey (Mehta & Wainwright 2007). Differing prey size spectra may be selected at different ontogenetic size classes owing to these differing feeding strategies, which may also facilitate coexistence. In contrast, generalist feeding exhibited by both species may lead to the selection of a wider array of less profitable dietary items based on what is available (in line with Optimal Foraging Theory, MacArthur & Pianka 1966). In addition, future research could investigate whether diet choices differ between fish caught within high and low biomass areas (identified through routine surveys or remote underwater video) and across different habitats (in general, Ascension’s rock habitats have higher biomass and diversity of potential prey than sand). This biomass-diet comparison may provide insight into the effects of heightened fishing activity in certain areas, for example, due to increased tourism and an associated increase in recreational fishing activity, and how this may impact local food-web dynamics. Context-specific studies of both *E. adscensionis* and *G. moringa* are limited, therefore, future research in remote island systems could provide novel insight into their ecology and conservation.

Understanding spatial niche is integral to species conservation (Lennox et al. 2019, Brownscombe et al. 2022). For example, the scale of animal movement dictates the spatial extent of effective protected areas (Lea et al. 2016), which can be used to conserve vulnerable species. While groupers (family *Epinephelidae*) are ubiquitous across warm-water reef ecosystems, a review by Mitchenson et al. (2011) identified that 12% of grouper species face extinction if the current population trends continue. Data on grouper population sizes and distribution are limited, with 30% of grouper species identified by Mitchenson et al. (2011) as IUCN Data Deficient. International conservation targets currently strive to conserve 30% of the ocean using no-take marine protected areas (MPAs, and networks of MPAs) by 2030 (Sandwith et al. 2014). Central to the delineation and designation of MPAs is the accurate identification of animal aggregations, areas of residency, migratory corridors and hotspots (i.e. spawning grounds or nursery habitat), which can be provided using biotelemetry (Lennox et al. 2019). To date, this technology has vastly improved our current understanding of animal distributions, with fine-scale positioning offering the next lens of resolution into animal interactions and fine-scale behaviour within the underwater world.

6.4 Conclusion

My dissertation research provides insight into the current tools and techniques used to explore the spatial niche of aquatic animals. It provides a comprehensive review of existing applications of a commercial positioning system, VPS, technology which has the potential to redefine our current understanding of fine-scale animal behaviour, species interactions and individual idiosyncrasies in movement. I provide a detailed framework that can maximize data yield and accuracy using this system, applied to a real-world case study to guide new and existing users embarking on fine-scale telemetry research. I then describe the latest iteration of technology that can be paired with VPS and detail pre-positioning steps that can be used to evaluate detection data exemplified using a real-world HR-VPS dataset. I also detail the steps a VPS analyst will follow to derive TDOA positions. Using acoustic telemetry to explore space use and traditional and modern tools to investigate dietary niche, I then investigate coexistence of two coexisting mesopredators in a complex equatorial system.

These data suggest that generalist diets enable individuals to utilize available prey within small home ranges, facilitating high species abundance and coexistence. I also identified for the first time using acoustic telemetry synchronized spawning activity of the rock hind grouper.

6.5 References

Abrams RW, Abrams MD, Schein MW (1973) Diurnal Observations on the Behavioral Ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean Coral Reef. Coral Reefs 1:185–192.

Afonso P, Abecasis D, Santos RS, Fontes J (2016) Contrasting movements and residency of two serranids in a small Macaronesian MPA. Fish Res 177:59–70.

Baktoft H, Gjelland KØ, Økland F, Thygesen UH (2017) Positioning of aquatic animals based on time-of-arrival and random walk models using YAPS (Yet Another Positioning Solver). Sci Rep 7:14294.

Böhlke EB (2002) Bony fishes part 1 (Acipenseridae to Grammatidae). In: *The living marine resources of the Western Central Atlantic*. Special publication no. 5, FAO Species Identification Guides for Fisheries Purposes. Copeia.

Brownscombe JW, Shipley ON, Griffin LP, Morley D, Acosta A, Adams AJ, Boucek R, Danylchuk AJ, Cooke SJ, Power M (2022) Application of telemetry and stable isotope analyzes to inform the resource ecology and management of a marine fish. J Appl Ecol 59:1110–1121.

Buchinger TJ, Marsden JE, Binder TR, Huertas M, Bussy U, Li K, Hanson JE, Krueger CC, Li W, Johnson NS (2017) Temporal constraints on the potential role of fry odors as cues of past reproductive success for spawning lake trout. Ecol Evol 7:10196–10206.

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352.

Collins AB, Motta PJ (2017) A kinematic investigation into the feeding behavior of the Goliath grouper *Epinephelus itajara*. Environ Biol Fish 100:309–323.

Cooke SJ, Niezgoda GH, Hanson KC, Suski CD, Phelan FJS, Tinline R, Philipp DP (2005) Use of CDMA acoustic telemetry to document 3-D positions of fish: relevance to the design and monitoring of aquatic protected areas. Mar Technol Soc J 39:31–41.

Demšar U. *et al.* (2021) Establishing the integrated science of movement: bringing together concepts and methods from animal and human movement analysis. International Journal of Geographical Information Science 35:1273–1308.

Deng ZD, Weiland MA, Fu T, Seim TA, LaMarche BL, Choi EY, Carlson TJ, Eppard MB (2011) A cabled acoustic telemetry system for detecting and tracking juvenile salmon: Part 2. Three-Dimensional Tracking and Passage Outcomes. Sensors (Basel) 11:5661–5676.

Heupel MR *et al.* (2006) Automated Acoustic Tracking of Aquatic Animals: Scales, Design and Deployment of Listening Station Arrays. Mar Freshw Res 57:1.

Higgins BA, Law CJ, Mehta RS (2018) Eat whole and less often: ontogenetic shift reveals size specialization on kelp bass by the California moray eel, *Gymnothorax mordax*. Oecologia 188:875–887.

Holyoak M, Casagrandi R, Nathan R, Revilla E, Spiegel O (2008) Trends and missing parts in the study of movement ecology. PNAS 105:19060–19065.

Jayne B, Voris H, Ng P (2002) Snake circumvents constraints on prey size. Nature 418:143.

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish 24:199–218.

Koeck B, Pastor J, Saragoni G, Dalias N, Payrot JÔ, Lenfant P (2014) Diel and seasonal movement pattern of the dusky grouper *Epinephelus marginatus* inside a marine reserve. Marine Environmental Research 94:38–47.

Lea JSE, Humphries NE, von Brandis RG, Clarke CR, Sims DW (2016) Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. Proc R Soc B 283.

Lennox RJ, Engler-Palma C, Kowarski K, Filous A, Whitlock R, Cooke SJ, Auger-Méthé M (2019) Optimizing marine spatial plans with animal tracking data. Can J Fish Aquat Sci 76:497–509.

Levinn C, Pluth M (2020) Learning from Our Mistakes: We Have a Scientific and Fiscal Obligation to Publish Failed Results. ChemRxiv.

MacArthur RH, Pianka ER (1966) On Optimal Use of a Patchy Environment. The American Naturalist 100:603–609.

March D, Palmer M, Alós J, Grau A, Cardona F (2010) Short-term residence, home range size and diel patterns of the painted comber *Serranus scriba* in a temperate marine reserve. Mar Ecol Prog Ser 400:195–206.

Mehta RS (2009) Ecomorphology of the moray bite: relationship between dietary extremes and morphological diversity. Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches 82:90–103.

Mehta RS, Donohoe KR (2021) Snowflake morays, *Echidna nebulosa*, exhibit similar feeding kinematics in terrestrial and aquatic treatments. Journal of Experimental Biology 224:jeb234047.

Mehta RS, Wainwright PC (2007) Biting releases constraints on moray eel feeding kinematics. J Exp Biol 210:495–504.

Miller HJ, Shaw S-L (2001) Geographic Information Systems for transportation: Principles and applications. Oxford University Press.

Mitchenson YS, Craig MT, Cheung W, Choat JH, Mitcheson YSD, Craig MT, Bertoncini AA, Carpenter KE, William WL (2011) Fishing groupers towards extinction: A global assessment of threats and extinction risks in a billion dollar fishery Fishing groupers towards extinction : a global assessment of threats and extinction risks in a billion dollar fishery. Fish Fish 14:119–136.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–19059.

Nathan R *et al.* (2022) Big-data approaches lead to an increased understanding of the ecology of animal movement. Science 375:eabg1780.

Niezgoda G, M.C. B, Sisak M, Anson P (2002) Tracking acoustic transmitters by code division multiple access (CDMA)-based telemetry. Hydrobiologia 483:275–286.

O'Dor RK, Aitken JP, Babcock RC, Bolden SK, Seino S, Zeller DC, Jackson GD (2001) Using Radio-Acoustic Positioning and Telemetry (RAPT) to define and Assess Marine Protected Areas (MPAs). In: *Electronic Tagging and Tracking in Marine Fisheries*. Reviews: Methods and Technologies in Fish Biology and Fisheries, Sibert JR, Nielsen JL (eds) Springer Netherlands, Dordrecht, 147–166.

Sandwith T *et al.* (2014) The Promise of Sydney: An editorial essay. Parks 20.1:7–18.

St-John J (1999) Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus* (Serranidae): Patterns in taxa, size and habitat of prey. Marine Ecology Progress Series 180:233–246.

Trancart T, Carpentier A, Acou A, Danet V, Elliott S, Feunteun É (2019) Behaviour of endangered European eels in proximity to a dam during downstream migration: Novel insights using high accuracy 3D acoustic telemetry. Ecol Freshw Fish:eff.12512.

Watson AC, Siemann LA, Hanlon RT (2014) Dynamic camouflage by Nassau groupers *Epinephelus striatus* on a Caribbean coral reef. J Fish Biol:1634–1649.

Wirtz P, Bingeman J, Bingeman J, Fricke R, Hook TJ, Young J (2017) The fishes of Ascension Island, central Atlantic Ocean-new records and an annotated checklist. J Mar Biol Assoc UK 97:783–798.

Young RF, Winn HE (2003) Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. Ichthyol Herpetol. 44–55.

Vita Auctoris

Name: Danielle Orrell

Place of Birth: Torquay, England, United Kingdom.

Year of Birth: 1994

Education: Torquay Girls Grammar School
Torquay, England, United Kingdom. 2013

University of Liverpool
B.Sc. Marine Biology
Liverpool, England, United Kingdom. 2016

University of Glasgow
M.Res., Ecology and Environmental Biology
Glasgow, Scotland, United Kingdom. 2017

University of Windsor
Ph.D.
Windsor, Ontario, Canada. 2022