


Coexistence, resource partitioning, and fisheries management: A tale of two mesopredators in equatorial waters

Danielle L. Orrell¹  | Daniel Sadd² | Kirsty L. Jones² | Kate Chadwick² |
Tiffany Simpson² | Darcy E. Philpott² | Nigel E. Hussey¹

¹Department of Biological Sciences, University of Windsor, Windsor, Ontario, Canada

²Ascension Island Government Conservation & Fisheries Directorate, Ascension Island Government, ASN 1ZZ

Correspondence

Danielle L. Orrell, School of Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland; MaREI, The SFI Research Centre for Energy, Climate and Marine, Beaufort Building, Environmental Research Centre, University College Cork, Ringaskiddy, Cork, Ireland.
Email: danielle_orrell@live.co.uk

Present addresses

Danielle L. Orrell, School of Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, Cork, Ireland; and MaREI, The SFI Research Centre for Energy, Climate and Marine, Environmental Research Centre, University College Cork, Cork, Ireland.

Funding information

NSERC; Ontario Trillium Scholarship

Abstract

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, where they have significant cultural and subsistence value, but management of their non-commercial take is limited. This isolated volcanic system is home to high biomass and low species diversity, which poses two key questions: How can two mesopredators that perform similar ecological roles coexist? And if these two species are so ecologically similar, can they be managed using the same approach? Here, we combined acoustic telemetry, stomach content analysis, and stable isotope analysis to (i) explore space use and diet choices within and between these two species and (ii) to assess appropriate species-specific management options. Although rock hind had high residency and small calculated home ranges (0.0001–0.3114 km²), spotted moray exhibited shorter periods of residency (<3 months) before exiting the array. Vertical space use differed significantly across the 20-month tracking period, with individual differences in vertical space observed for both species. A hierarchical generalized additive model using 12-h averaged depth data identified that rock hind occurred lower in the water column than spotted moray, with both species occupying moderately deeper depths at night versus day (+1.6% relative depth). Spotted moray depth was also significantly predicted by lunar illumination. Aggregating samples by species and tissue type, Bayesian ecological niche modeling identified a 53.14%–54.15% and 78.02%–97.08% probability of niche overlap from fin clip and white muscle, respectively, whereas limited stomach content data indicated a preference for piscivorous prey. Variability in niche breadth between years suggests these species may exploit a range of prey items over time. These findings indicate that although these two species perform a similar ecological role by feeding on prey occupying the same trophic levels, subtle differences in movement behaviors between them suggest a one-rule-fits-all management approach is not likely the most effective option.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Authors. *Journal of Fish Biology* published by John Wiley & Sons Ltd on behalf of Fisheries Society of the British Isles.

KEYWORDS

acoustic telemetry, Ascension Island, coexistence, *Epinephelus adscensionis*, *Gymnothorax moringa*, resource partitioning

1 | INTRODUCTION

Species coexistence is central to maintaining biodiversity (Chesson, 2000); therefore, understanding the mechanisms that facilitate coexistence is pivotal to conservation and resource management. Resource partitioning describes how species with similar trophic roles can coexist, namely through differences in space use, or the resources they use over time (Bolnick et al., 2011). By identifying similarities and differences in space use and diet, appropriate and effective management options that preserve biodiversity and ensure ecosystem stability can be chosen, for example, in the wake of increased fishing pressure. In aquatic systems, resource partitioning often occurs via dietary segregation whereby individuals consume different dietary items or size spectra of prey to alleviate competition for resources (Higgins & Mehta, 2018; Meyer & Dierking, 2011; St-John, 1999). Behavioural strategies such as dietary generalism, whereby species consume a wide variety of available resources, including exploiting seasonal prey fluctuations (Gkenas et al., 2012; Ward et al., 2018), provide a further mechanism for coexistence. Various ecophysiological and morphological adaptations often facilitate dietary generalism. For example, flexible diel activity rhythms allow a species to make use of fluxes in available prey (Fox & Bellwood, 2011; Piet & Guruge, 1997; Sánchez-Hernández et al., 2020). Dietary generalism can also facilitate the maintenance of small home ranges, allowing individuals to readily acquire resources. At the same time, this minimizes the energy spent finding prey (in line with optimal foraging theory, MacArthur & Pianka, 1966).

Advancements in acoustic telemetry have enabled the tracking of multiple species across a plethora of habitats and environmental gradients (Hussey et al., 2015) 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 estimate residency, activity space, and home range (Heupel et al., 2006). When sensors are integrated into electronic tags, such as a pressure sensor to record depth, the vertical behavior of species can be quantified to estimate the degree of intra- and interspecific variation that occurs (Andrzejczek et al., 2022). Pairing acoustic telemetry with stomach content and stable isotope analysis can contextualize spatial data and identify differences in dietary choice over a range of temporal scales (Chan et al., 2022; Guzzo et al., 2016; Harmelin-Vivien et al., 1989). Stomach contents provide an immediate snapshot of an animal's diet but require lethal sampling. In contrast, stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) derived from minor invasive sampling can indicate habitat use and trophic level, respectively, based on the premise that “you are what you eat” (Kohn, 1999). By comparing tissues with differing turnover rates, that is, fast turnover tissues such as fin clip and blood plasma that show recent insights into diet, versus slow turnover tissues such as muscle that provide a measure of time-averaged insight of diet spanning months

(Church et al. 2009; Cunjak et al. 2005; Post, 2002), can improve our understanding of species' coexistence and resource partitioning in aquatic environments (Fry, 2006; Guzzo et al., 2016; Kristensen et al., 2010; Matich et al., 2017; Shipley & Matich, 2020).

Ascension Island (7.9467° S, 14.3559° W) is a young volcanic island situated in the central South Atlantic Ocean, with a high biomass but low species diversity nearshore environment (Wirtz et al., 2017) (Figure 1). In 2019, Ascension's entire exclusive economic zone (445,000 km²) was designated as a marine protected area (MPA), which forms part of a network of protection across British Overseas Territories, including Ascension, St Helena, and Tristan da Cunha (The Ascension Island Government, 2021). Pivotal to the effectiveness of this MPA and its nearshore monitoring and management strategy is gathering knowledge on key coastal species with a high cultural and subsistence value across the South Atlantic: rock hind (*Epinephelus adscensionis*) (Osbeck, 1765) and spotted moray (*Gymnothorax moringa*) (Cuvier, 1829) (The Ascension Island Government, 2020). Despite the prevalence of these two mesopredators and their importance in recreational and subsistence fishing, few published studies have explored their fine-scale movements, and current management measures do not take into account non-commercial fisheries take. If stocks appear to decline in the future, for example, due to fishing (Ferreira et al., 2018; Guabiroba et al., 2020; Sadovy, 1994; Sadovy et al., 2013) or climate change pressures (Brulé et al., 2022; Pratchett et al., 2017), this knowledge is central to identifying appropriate spatial management tools.

In the current study, we examined the movement and diet of these two morphometrically different mesopredators, the rock hind and spotted moray, which occur in high abundance in Ascension Island's nearshore environment. We assessed factors that facilitate coexistence and used these findings to deduce effective management options. We hypothesized that rock hind and spotted moray would exhibit a significant overlap in their observed spatial niche and high residency and site fidelity to the study area but would alleviate intra- and interspecific competition via resource partitioning through temporal differences in space use, facilitating coexistence. Additionally, due to high levels of resource competition among these predators, individuals would consume a wide variety of prey items, resulting in generalist diets and a broad trophic niche. This study addresses significant regional knowledge gaps and information necessary to inform practical marine management objectives.

2 | MATERIALS AND METHODS

2.1 | Range testing

Extensive range testing was undertaken prior to acoustic receiver deployment. Fixed-distance range tests were conducted in 2017 to

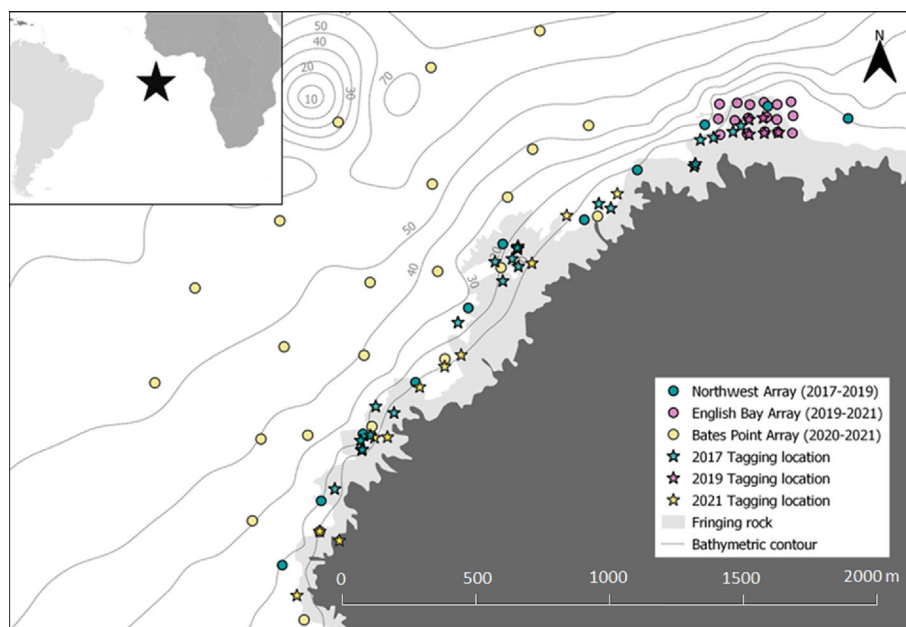


FIGURE 1 Ascension Island with the three acoustic arrays deployed between 2017 and 2021 includes the northwest linear array (n VR2W acoustic receivers = 11; 2017–2019 deployment, teal-fill circle), English Bay Vemco Positioning System (n acoustic receivers = 9–22, 2019–2021, pink-fill circles), Bates Point array (n acoustic receivers = 23, 2020–2021, yellow-fill circle). Fish were tagged in 2017 for the northwest array (n rock hind grouper = 20, indicated by teal stars), 2019 within the English Bay array (n rock hind grouper = 10; n moray eels = 10, pink stars), and 2021 within the Bates Point array (n rock hind grouper = 16; n moray eels = 5, yellow stars). The light, gray-filled polygon indicates rock substrate fringing the island (dark gray polygon). Bathymetric contour (dashed line) derived from Ascension Island Admiralty Chart 1691. Inset. Ascension Island (black star) in the South Atlantic Ocean (7.9467° S, 14.3559° W).

identify the receiver detection range and guide appropriate tag selection (n surface range tests from a kayak = 3, Ascension Island Government). Detection ranges for V9-2x, V13-1x, and V16-4x tags were calculated as 90% at 50 m and 30%–70% at 100 m. A second set of range tests were conducted in 2019 in English Bay to identify the role of substrate type on detection range (for each substrate type, namely sand and rock, n surface range tests from a kayak = 1, n benthic range tests on SCUBA = 1). Detection ranges were higher for sand (10%–70% at 50 m; 20%–40% at 100 m) than rock (10%–40% at 50 m; 0%–20% at 100 m). Further information on 2017 and 2019 range tests is provided in Orrell & Hussey 2023 Data S1. Sync tag data generated between September 1, 2019, and October 1, 2019, within the English Bay array were also used to determine the detection range and select appropriate receiver spacing for the Bates Point array deployed in 2020.

2.2 | Acoustic receiver deployments and data available for analysis

Movements of rock hind and spotted moray were identified using acoustic telemetry data from three different array designs with differing receiver spacing, which generated data over a range of spatial scales (see overview in Figure 1). All arrays were focused on the northwest coastline of Ascension Island. For additional technical information, see Data S1. All datasets were trimmed to remove any

detections recorded within the first 12 h of tagging to ensure the data generated reflected normal animal behavior and were not due to handling effects.

2.2.1 | Northwest linear array

In 2017, a single line of 11 acoustic receivers was deployed along the coastline moored at depths of 15–35 m and between 241 and 336 m apart. This work aimed to explore broadscale rock hind movements, with data collected between August 3, 2018, and April 14, 2019, made available and subsequently used in the analysis.

2.2.2 | English Bay Vemco positioning system

From August 7, 2019, to April 14, 2021, a grid of receivers with overlapping detection ranges were deployed in English Bay to track the fine-scale movements of rock hind and spotted moray. Receivers were moored at depths of 11–33 m and conservatively spaced 55–80 m apart. The total number of receivers within the English Bay array fluctuated between years, ranging from 23 from August 7, 2019, to January 14, 2020; to 20 from January 23, 2020, to May 18, 2020; to 9 from May 18, 2020, to April 14, 2021. The English Bay array data were trimmed to August 7, 2019–April 13, 2021 (inclusive).

TABLE 1 Transmitter information for the acoustic tags deployed in 2017, 2019, and 2021.

Species	Tagging year	Tag type	Number of tags	Tag diameter (mm)	Tag length (mm)	Tag weight in water (g)	Transmission rate (s)			Power (db)	Battery life (days)
							Nominal	Minimum	Maximum		
RH	2017	V13-1x	10	13	30.5	5.1	210	240	180	152	904
		V16-4x	10	16	68	12	210	240	180	158	3393
	2019	V16TP-6x	10	16	98	16.5	60	40	80	158	1236
	2021	V16-4x	10	16	68	12	210	240	180	158	3393
		V16P-6x	6	16	98	16.5	220	170	270	158	3650
SM	2019	V16TP-6x	10	16	98	16.5	60	40	80	158	1236
	2021	V16-4x	10	16	68	12	210	240	180	158	3393
		V16P-6x	6	16	98	16.5	220	170	270	158	3650

Abbreviations: RH, rock hind; SM, spotted moray.

2.2.3 | Bates Point array

In 2020, most receivers from English Bay had been recovered, and a grid of 23 receivers were deployed at Bates Point to track both the fine- and broadscale movements of rock hind and spotted moray. Receivers were moored at 13–71 m depth between 180 and 495 m apart, 1 km west of the original English Bay array. Acoustic detection data from this array for the present study were trimmed to January 7, 2021–April 15, 2021, when the full array was in place and fish tagged in 2021 were available for detection.

2.3 | Acoustic tag attachment

Adult rock hind (n 2017 = 20; n 2019 = 10; n 2021 = 16) were captured using conventional medium rig fishing rods or handlines with size 10/0 barbless circle hooks. Adult spotted moray (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). 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 induce anesthesia before handling. After anesthesia was induced, fish were measured, and total length (TL) and weight were recorded. Sex was not determined. A small non-lethal tissue sample was then taken from the front dorsal fin (posterior region, tip; 600–800 mg), and two bicolor T-bar tags (FD-94 Floy tag, Floy Inc., USA) were inserted into the body midway along the dorsal fin to aid future identification. An acoustic transmitter (InnovaSea Systems Inc., Boston, USA) was surgically implanted into the intraperitoneal cavity (see Table 1 for tag specifications and programming). The incision was closed with two independent sterile sutures (Ethicon 2–0 non-

absorbable suture used on rock hind; Ethicon 3–0 absorbable suture used on spotted morays; 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 then held for <30 min in a 25-L recovery container of fresh saltwater until a strong swim response was observed before release at their original capture site.

2.4 | Acoustic detection analysis: Calculating 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. Due to the variation in the array size and related difficulties inferring fate across the entire study period, fish tagged in English Bay in 2019 were assigned two fate categories. Stage 1 encapsulated fate during a 20–23 receiver array between August 2019 and May 2020, and stage 2 covered the period that the 9-receiver array remained (May 2020–April 2021). Fate classifications included resident, resident^F, emigrant, or predated (following Bacheler et al., 2021). Residents were defined by persistent detections within the study area, whereas residents on the edge (terminal line or “edge” of the receiver grid) of the array (resident^F) were classed as consistent detections across receivers at the edge of the array (applies to stage 1 with 23-receiver English Bay 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 moving rapidly 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 indicated by continuous detections on a single receiver with a depth variation of <1.3 m (\pm 0.5 m quoted tag accuracy, InnovaSea Systems Inc., 2021; plus 0.8-m average tidal range, Ascension Island Government, 2015b). For each individual,

TABLE 2 Summary data for rock hind (RH) *Epinephelus adscensionis* tagged in 2017 tracked from August 3, 2018, to April 14, 2021.

Animal ID	Capture date	TL (cm)	Weight (kg)	Tag type	Tracking data			Study duration (days)	No. detections	Fate	RD	RI (%)
					Tracking start date	First detection	Last detection					
RH01-2017	Aug 22, 2017	41.5	0.9	V13-1x	Aug 3, 2018	Aug 20, 2018	Nov 13, 2019	904	923	R	111	12
RH02-2017	Aug 25, 2017	33	0.7	V13-1x	Aug 3, 2018	Mar 1, 2019	Mar 16, 2019	904	6	R	2	0
RH03-2017	Aug 22, 2017	45	-recorded	V13-1x	Aug 3, 2018	Aug 3, 2018	Oct 12, 2018	904	2	R	2	0
RH04-2017	Aug 22, 2017	41	-recorded	V13-1x	Aug 3, 2018				0	UK	0	0
RH05-2017	Aug 22, 2017	36.5	-recorded	V13-1x	Aug 3, 2018				0	UK	0	0
RH06-2017	Aug 22, 2017	34.5	-recorded	V13-1x	Aug 3, 2018				0	UK	0	0
RH07-2017	Aug 17, 2017	40.5	1.0	V13-1x	Aug 3, 2018				0	UK	0	0
RH08-2017	Aug 17, 2017	37.5	1.1	V13-1x	Aug 3, 2018				0	UK	0	0
RH09-2017	Aug 17, 2017	37	1.0	V13-1x	Aug 3, 2018	Aug 25, 2018	Nov 21, 2018	904	5	R	3	0
RH10-2017	Aug 22, 2017	40.5	-recorded	V13-1x	Aug 3, 2018				0	UK	0	0
RH11-2017	Aug 22, 2017	51	-recorded	V16-4x	Aug 3, 2018	Aug 19, 2018	Oct 27, 2020	1330	2162	R	192	14
RH12-2017	Aug 22, 2017	49	-recorded	V16-4x	Aug 3, 2018				0	UK	0	0
RH13-2017	Aug 22, 2017	46	-recorded	V16-4x	Aug 3, 2018	Sep 14, 2018	Apr 4, 2021	1330	53	R	15	1
RH14-2017	Aug 22, 2017	50	-recorded	V16-4x	Aug 3, 2018	Jul 9, 2019	May 24, 2019	1330	163	R	103	8
RH15-2017	Aug 25, 2017	51	2.1	V16-4x	Aug 3, 2018	Feb 15, 2019	Apr 29, 2021	1335	22	R	16	1
RH16-2017	Aug 17, 2017	44	1.4	V16-4x	Aug 3, 2018	Nov 25, 2018	Mar 23, 2021	1327	140	R	20	2
RH17-2017	Aug 22, 2017	47	-recorded	V16-4x	Aug 3, 2018	Jul 11, 2018	Mar 21, 2021	1330	10	R	9	1
RH18-2017	Aug 22, 2017	49.5	-recorded	V16-4x	Aug 3, 2018	Jul 17, 2018	Jul 18, 2018	1330	2	R	2	0
RH19-2017	Aug 17, 2017	58	3.5	V16-4x	Aug 3, 2018	Sep 17, 2018	Apr 30, 2021	1327	61	R	22	2
RH20-2017	Aug 25, 2017	45.5	1.5	V16-4x	Aug 3, 2018				0	UK	0	0

Note: Data include capture date, animal total length (TL, recorded to an accuracy of 1 cm), animal weight (dash indicates this was not recorded, values rounded to one decimal place), acoustic tag type, tracking start date (date all receivers were deployed and recording), date of first and last detection, study duration (date animal tagged to either end of tag life, predation event, or until April 14, 2021), total number of detections, fish fate includes resident (R), resident^E (R^E), unknown (UK), and predated (P), residency days (RDs), and residency index (RI, %).

detection data were trimmed to the last detection of pre-predation event. Harvest events were not considered due to constant communication with the local fishing community and the absence of recapture reports.

Fish residence time was estimated using residency days (RD, number of days detected in the receiver array) and residency indices

(RI, number of days detected as a proportion of the total study period, RI). Tracking periods used to calculate RDs and RIs vary between the three arrays owing to different receiver deployment periods, and within an array owing to animal tagging dates (see Tables 2–4 for further details). The 2017 tagged rock hind detection period spanned a maximum of 903 days owing to tag battery limitations. For rock hind

TABLE 3 Summary data for rock hind (RH) *Epinephelus adscensionis* and spotted moray (SM) *Gymnothorax moringa* tagged in 2019 tracked from August 7, 2019, to April 14, 2021.

Animal ID	Capture date	TL (cm)	Weight (kg)	Tag type	Tracking start date	Tracking data		Study duration (days)	Total detections	Fate			RI (%)
						First detection	Last detection			S1	S2	RD	
RH02-2019	Jun 9, 2019	51	1.8	V16TP	Aug 7, 2019	Aug 7, 2019	Mar 21, 2021	605	131,253	R	R	436	72
RH03-2019	Jun 9, 2019	46	1.8	V16TP	Aug 7, 2019	Aug 7, 2019	Apr 7, 2021	605	119,217	R	R	509	84
RH04-2019	Jun 9, 2019	45	1.8	V16TP	Aug 7, 2019	Aug 7, 2019	Mar 15, 2021	605	121,775	R	R	430	71
RH05-2019	Jun 9, 2019	45	1.8	V16TP	Aug 7, 2019	Aug 7, 2019	Mar 20, 2021	605	107,338	R	R	505	83
RH06-2019	Jun 9, 2019	47	1.8	V16TP	Aug 7, 2019	Aug 7, 2019	Mar 20, 2021	605	82,450	R	R	507	84
RH11-2019	Aug 6, 2019	45	1.5	V16TP	Aug 7, 2019	Aug 7, 2019	Apr 2, 2021	605	40,644	R	R	592	98
RH12-2019	Aug 6, 2019	48	2.3	V16TP	Aug 7, 2019	Aug 7, 2019	Apr 14, 2021	605	521,502	R	R	605	100
RH13-2019	Aug 6, 2019	55	3.3	V16TP	Aug 7, 2019	Aug 7, 2019	Jan 29, 2021	605	213,341	E	UK	166	27
RH14-2019	Aug 6, 2019	47	1.8	V16TP	Aug 7, 2019	Aug 7, 2019	Apr 14, 2021	605	251,529	R	R	604	100
RH15-2019	Aug 6, 2019	46	1.8	V16TP	Aug 7, 2019	Aug 7, 2019	Apr 9, 2021	605	14,326	R	R	382	63
SM03-2019	Jun 17, 2019	74	1.1	V16TP	Aug 7, 2019	Aug 7, 2019	Dec 21, 2021	605	190,937	R	E	284	47
SM04-2019	Jun 17, 2019	85	1.6	V16TP	Aug 7, 2019	Aug 7, 2019	Apr 12, 2021	605	150,407	R	R	605	100
SM05-2019	Jun 18, 2019	120	3.6	V16TP	Aug 7, 2019	Aug 7, 2019	Dec 6, 2019	605	23,144	R ^E	R	122	20
SM06-2019	Jun 18, 2019	91	1.9	V16TP	Aug 7, 2019			605	0	UK	UK	0	0
SM07-2019	Jun 18, 2019	84	1.5	V16TP	Aug 7, 2019	Aug 7, 2019	Mar 29, 2020	605	58,909	R	E	226	37
SM08-2019	Aug 6, 2019	84	1.5	V16TP	Aug 7, 2019	Aug 7, 2019	Jan 20, 2021	605	45,855	R	R	262	43
SM09-2019	Aug 6, 2019	84	1.5	V16TP	Aug 7, 2019	Aug 7, 2019	Mar 31, 2020	605	10,390	R ^E	E	216	36
SM10-2019	Aug 7, 2019	107	4.0	V16TP	Aug 7, 2019	Aug 8, 2019	Feb 7, 2021	604	104,680	R	R	283	47
SM11-2019	Aug 7, 2019	105	3.0	V16TP	Aug 8, 2019	Aug 8, 2019	Sep 15, 2019	38	235 (1750)	P		38	100
SM12-2019	Aug 7, 2019	107	3.8	V16TP	Aug 8, 2019	Aug 8, 2019	Oct 26, 2020	604	22,273	R	R	169	28

Note: Animal total length (TL) is rounded to the nearest centimeter. Animal weight was recorded to an accuracy of 100 g. Study duration spans from the date the animal was tagged to a predation event, or until April 14, 2021; it excludes maintenance days during receiver recovery and redeployment from January 14, 2020, to January 24, 2020 (10 days). Fish tagged within the study period were given a 12-h recovery window, for example, SM11 and SM12. The total number of detections excludes detections within the 12-h recovery period after tagging and detections recorded after a predation event, with detections recorded post-predation event given in brackets. Fish fate describes resident (R), resident^E (R^E), unknown (UK), and predated (P) categorized for the two deployment periods, stage 1 (S1) during the 23-receiver array and stage 2 (S2) during the 9-receiver array. Also includes residency days (RDs), and residency index (RI, %).

and spotted moray tagged in 2019, calculations were based on a maximum detection period of 605 days. Rock hind and spotted moray tagged in 2020 were tracked for a maximum of 98 days. For any

individuals predated, the tracking period was calculated as the time between the tagging date (which included a 12-h recovery window) and the predation event. RIs were used to summarize the amount of

TABLE 4 Summary table for rock hind (RH) *Epinephelus adscensionis* and spotted moray (SM) *Gymnothorax moringa* acoustically tagged in 2021.

Tracking data																
Animal ID	Capture date	TL (cm)	Weight (kg)	Tag type	Tracking start date	First detection	Last detection	Study duration (days)	No. detections	Fate	RD	RI (%)	No. COA estimates	Home range (95% AKDE, km ²)		
RH56-2021	Jan 7, 2021	48	2.0	V16P	Jan 8, 2021	Jan 12, 2021	Mar 12, 2021	60 (82)	181 (192)	P	41	68				
RH57-2021	Jan 7, 2021	56	2.5	V16P	Jan 8, 2021	Jan 8, 2021	Apr 15, 2021	98	3150	R	98	100	815	0.0920		
RH58-2021	Jan 7, 2021	52	2.5	V16P	Jan 8, 2021	Mar 21, 2021	Mar 21, 2021	98	3	E	1	1				
RH59-2021	Jan 7, 2021	54	3.0	V16	Jan 8, 2021	Jan 9, 2021	Jan 12, 2021	98	21	E	2	2				
RH60-2021	Jan 9, 2021	53	2.0	V16P	Jan 9, 2021	Jan 13, 2021	Apr 14, 2021	97	83	R ^E	42	42				
RH61-2021	Jan 9, 2021	47	1.5	V16	Jan 9, 2021	Jan 15, 2021	Apr 14, 2021	97	25	E	20	20				
RH62-2021	Jan 11, 2021	52	2.0	V16P	Jan 11, 2021			95	0	UK	0	0				
RH63-2021	Jan 11, 2021	51	1.5	V16	Jan 11, 2021	Feb 15, 2021	Mar 26, 2021	95	6	E	3	3				
RH64-2021	Jan 11, 2021	57	1.5	V16P	Jan 11, 2021	Jan 11, 2021	Apr 15, 2021	95	8055	R	95	100	1799	0.0003		
RH65-2021	Jan 11, 2021	50	2.0	V16	Jan 11, 2021	Jan 11, 2021	Apr 15, 2021	95	4973	R	95	100	1328	0.0001		
RH66-2021	Jan 11, 2021	51	2.0	V16	Jan 12, 2021	Jan 13, 2021	Apr 10, 2021	94	66	R ^E	36	38				
RH67-2021	Jan 11, 2021	48	1.5	V16	Jan 12, 2021	Jan 18, 2021	Apr 15, 2021	94	43	R ^E	27	28				
RH68-2021	Jan 13, 2021	55	2.5	V16	Jan 13, 2021			0 (57)	0 (834)	P						
RH69-2021	Jan 15, 2021	56	2.5	V16	Jan 13, 2021	Mar 22, 2021	Mar 22, 2021	93	1	E	1	1				
RH70-2021	Jan 15, 2021	46	1.6	V16	Jan 16, 2021			90	0	UK	0	0				
RH71-2020	Jan 15, 2021	53	2.5	V16	Jan 16, 2021	Feb 16, 2021	Mar 8, 2021	90	592	E	21	21	166	0.3114		
SM18-2021	Jan 9, 2021	87	1.5	V16P	Jan 9, 2021			97	0	UK	0	0				
SM19-2021	Jan 15, 2021	82	1.0	V16P	Jan 15, 2021			91	0	UK	0	0				

(Continues)

TABLE 4 (Continued)

Animal ID	Capture date	TL (cm)	Weight (kg)	Tag type	Tracking start date	Tracking data			Study duration (days)	No. detections	Fate	RD	RI (%)	No. COA estimates	Home range (95% AKDE, km ²)
						First detection	Last detection								
SM20-2021	Jan 21, 2021	88	1.5	V16P	Jan 21, 2021	Mar 25, 2021	Mar 25, 2021	85	3	UK	1	1			
SM21-2021	Jan 21, 2021	94	1.8	V16P	Jan 21, 2021			85	0	UK	0	0			
SM22-2021	Jan 21, 2021	122	4.7	V16	Jan 21, 2021	Jan 24, 2021	Jan 30, 2021	85	12	E	6	7			

Note: Animal total length (TL) is rounded to the nearest centimeter. Animal weight was recorded to an accuracy of 100 g. Tracking start date excludes a 12-h recovery period where relevant. Study duration spans from the date the animal was tagged to a predation event, with detection days post-predation event given in brackets, or detections until April 14, 2021, if not predated. The total number of detections includes those recorded until a predation event occurred, with detections recorded post-predation given in brackets. Fish fate describes resident (R), resident^E (R^E), unknown (UK), and predated (P) individuals. Residency days (RDs), residency index (RI), number of center of activity (COA) estimates, and home range estimates calculated using autocorrelated kernel density estimators (95% AKDE, rounded to four decimal places) are provided.

time a tagged animal was detected within the array 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.g., 2.9 km between the furthest west and east receivers) and limited coverage of the English Bay (cumulative listening area = 0.0984 km²) array prevented the calculation of additional spatial statistics beyond RD and RI.

2.5 | Investigating horizontal space use

For the Bates Point array, center of activity (COA) analysis was used to estimate space use of acoustic-tagged animals; 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). This approach disaggregates detection data from a receiver location, reducing the propensity for autocorrelation by subsampling data into a user-defined period (in this case, 60 min) (Matley et al., 2017). COA positions were calculated using the Animal Tracking Toolbox (ATT package; Udyawer et al., 2018). COA analysis was only calculated for fish with >100 detections; therefore, this metric was only calculated for four rock hind. These sequential average positions were then used to estimate rock hind home range (95% utilization distribution) using an autocorrelated kernel density (AKDE) 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).

2.6 | Modeling vertical space use

To investigate differences between in relative water column depth use between the species, hierarchical generalized additive models (hGAMs) were used. The English Bay detection data (*n* detected rock hind = 10; *n* detected spotted moray = 9) were trimmed to include only data recorded, whereas the 23-receiver array was in place (251 days, see Section 2.4). Raw depth sensor values were converted so that an individual's depth represented a value relative to the listening receiver's mooring depth ranging from 0 to 1 (i.e., a fish at 2 m depth relative to a 10-m water column depth would translate to a value of 0.2). This conversion was undertaken to account for how a fish's depth relative to the available water column may have different ecological impacts, given inherent variation in the conditions a fish is exposed to. For example, surface currents and tidal change 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, which was a result of the tagged fish sitting below a ledge where the listening receiver was moored. Values exceeding 1 were forced to 0.99 (reoccurring) due to the requirements of the selected beta regression distribution family, which can only accommodate values between 0 and 1. 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 day.

Within the hGAM models, relative depth (D) was modeled as response variable, whereas diel period (data retrieved using the *sunCalc* package in R, Thieurmel & Elmarhraoui 2019; day or night, DP as factor), percentage lunar illumination (retrieved using the *lunar* package, Lazaridis 2022; denoted as i), fish TL (z-score), and day of the year (denoted as DOY) were included as explanatory variables. hGAMs were fitted using the *bam* function in the *mgcv* package (Wood, 2011). Because lunar illumination cyclically fluctuated with month, this variable was fitted using a tensor product of a cubic spline function of lunar illumination i and a cyclic cubic spline function with a monthly cycle of t . Tensor products required two values for k and were set to $c(10, 5)$ to explain the interaction between lunar illumination and month across the 10 months of the study. A smoothing parameter of $k = 6$ was selected for simple smooths such as fish TL. A higher $k = 30$ was selected for DOY given the range of values (0–285). The unique fish ID (FishID) was considered a random effect in the model and therefore fitted with the smooth term “re.” 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 *gam.check* function in *mgcv* was used to evaluate whether an optimal value for k was selected. The full model with all terms and candidate subset models was evaluated using AIC values. Models with ΔAIC scores within 10 units of the best model were deemed informative and to have reasonable support (Burnham & Anderson 2004). The model intercepts were log transformed to convert this value to relative fish depth.

The most complex model of those deemed informative included the following terms:

$$D \sim \text{Species} + s(DP, \text{by} = \text{species}) + s(TL, \text{by} = \text{species}) \\ + s(f_{i, \text{month}}(i, t), \text{by} = \text{species}) + s(DOY, \text{by} = \text{species}) \\ + s(\text{FishID}, \text{by} = \text{species})$$

2.7 | Estimating diet using stomach content analysis

Stomachs were collected from euthanized fish caught using targeted rod-and-line angling and opportunistic sampling during local fishing competitions. Collected stomachs were stored in individual Whirl-Pak bags and chilled (for immediate dissection) or frozen (processed within 1 month of collection). During stomach processing, the full and empty weight of the stomach was recorded, and stomach contents were weighed to the nearest 0.01 g and identified to family level. Digested material that could not be identified was removed from subsequent analysis. Percentage weight (%W), number (%N), and frequency occurrence (%F) were calculated for all identified prey (Hyslop, 1980).

2.8 | Estimating diet using stable isotope analysis

Fin clips were collected from acoustic-tagged animals and lethally sampled animals (as described in Section 2.2), with 600–800 mg taken

from the posterior region of the front dorsal fin. White muscle and stomach content data were collected using lethal sampling. After euthanasia, 2 g of white muscle was collected from the dorsal anterior surface, which was subsequently rinsed with fresh water and stored in 2-mL cryovials in a freezer at -18°C .

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 removed, and the sample was left to dry for 48 h in a fume cupboard to evaporate any remaining solvent. All samples were lipid extracted, and between 400 and 600 μg of each sample was then weighed into a tin capsule and analysed using a continuous-flow isotope ratio mass spectrometer (IMRS, Finnigan MAT Delta^{plus}, Thermo Finnigan, San Jose, CA, USA), equipped with an elemental analyser (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:

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000$$

where X is ^{13}C or ^{15}N , and R is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Isotope ratios are expressed per mille (‰) relative to a secondary standard, which includes Pee Dee Belemnite carbonate for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$.

Samples with percentage carbon to nitrogen ratios of >4 were removed prior to analysis as lipids were likely still present within the sample (three rock hind white muscle tissue samples excluded). 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 $\delta^{13}\text{C}$ (CR) and $\delta^{15}\text{N}$ (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).

2.9 | Ethics statement

All research was conducted under appropriate research permits provided by the Ascension Island Government. Experimental procedures were also approved under license AUPP #19//10 issued by the University of Windsor, Canada. Animal handling followed best practice guidelines for the focal species.

3 | RESULTS

3.1 | Tagged animal total length and tag burden

In total, 46 rock hind ranging from 33 to 58 cm TL (mean \pm SE = 47.1 ± 0.853) and 15 spotted morays ranging from 74 to 122 cm TL (mean \pm SD = 94.2 ± 3.749) were equipped with acoustic tags and released into the three respective arrays. Tag burden (weight of the tag in the air in relation to animal mass) was calculated as <2.4% for tagged rock hind (note weights of 11 rock hind were not recorded in 2017 and were therefore not included) and <3.6% for tagged spotted moray.

3.2 | Fish fate and residency

Of the rock hind tagged in 2017 ($n = 20$), 12 (60%) were detected on the northwest 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%) were detected across the Bates Point array (2020–2021). Calculated RIs ranged from 0% to 15% (RH11) (Table 3). Seven tagged rock hind were recorded over 1-year post-tagging near their original tagging location. For example, 3549 detections were recorded for RH01 across 2018–2020 (Figure 2a), with most of the detections within 50 m of the original tagging location (Figure 2b).

Of the 10 rock hind tagged in 2019, 9 (90%) remained within the monitored region for $\geq 50\%$ of the study period, and of these, 6 (60%) for $\geq 75\%$ of the study period. On average, tagged rock hind remained in the array for a total period of 474 ± 132 days, which corresponded to RIs between 27% and 100% (mean \pm SD = 78.2 ± 22.05) (Table 4; Figure 3a). Of the 10 tagged spotted moray, 9 (90%) were detected. Of these, one spotted moray was predated 38 days after tagging as shown by a continuous static vertical movement profile. In total, eight (89% of those detected) remained within English Bay for $>25\%$ of the study period, and two (22%) were detected for $\geq 75\%$ of the study period. Residency ranged from 0 to 605 days, which equated to RIs ranging from 0% to 100% (Table 4; Figure 3b).

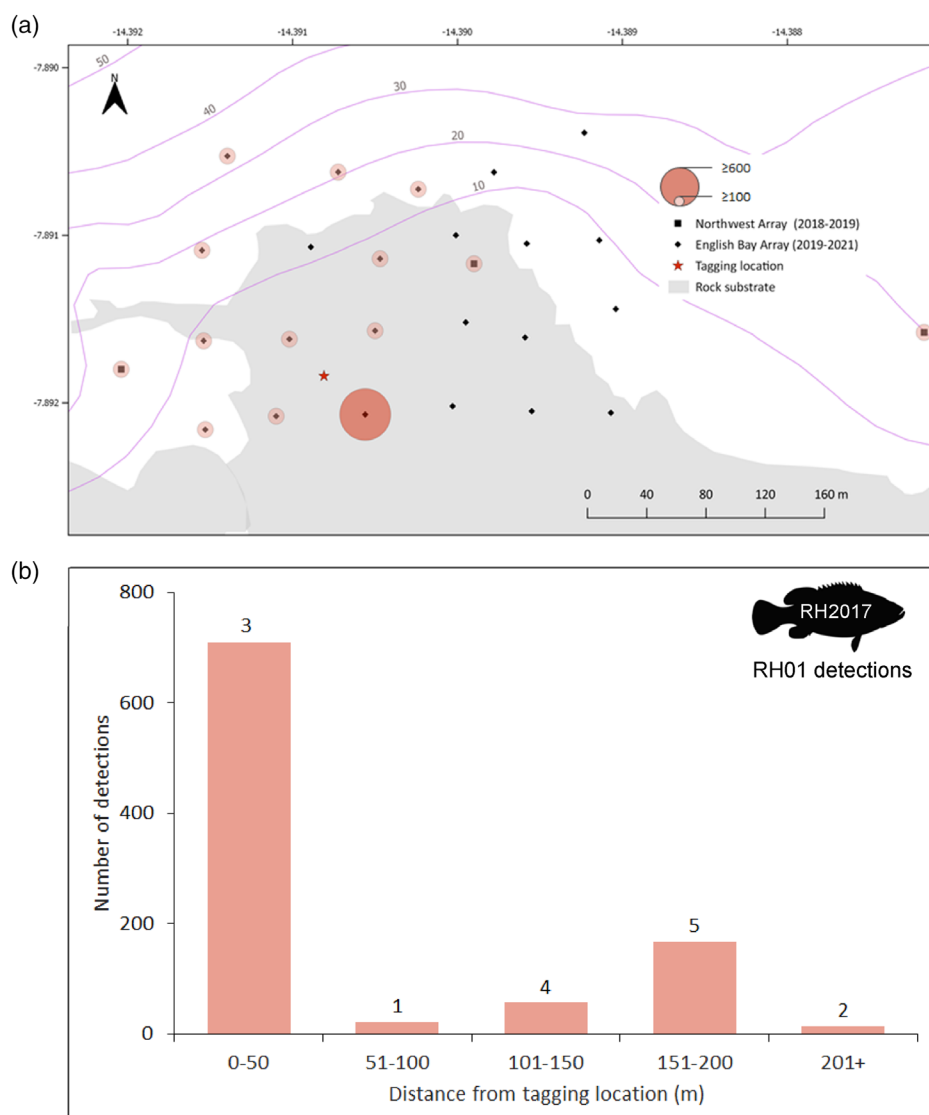
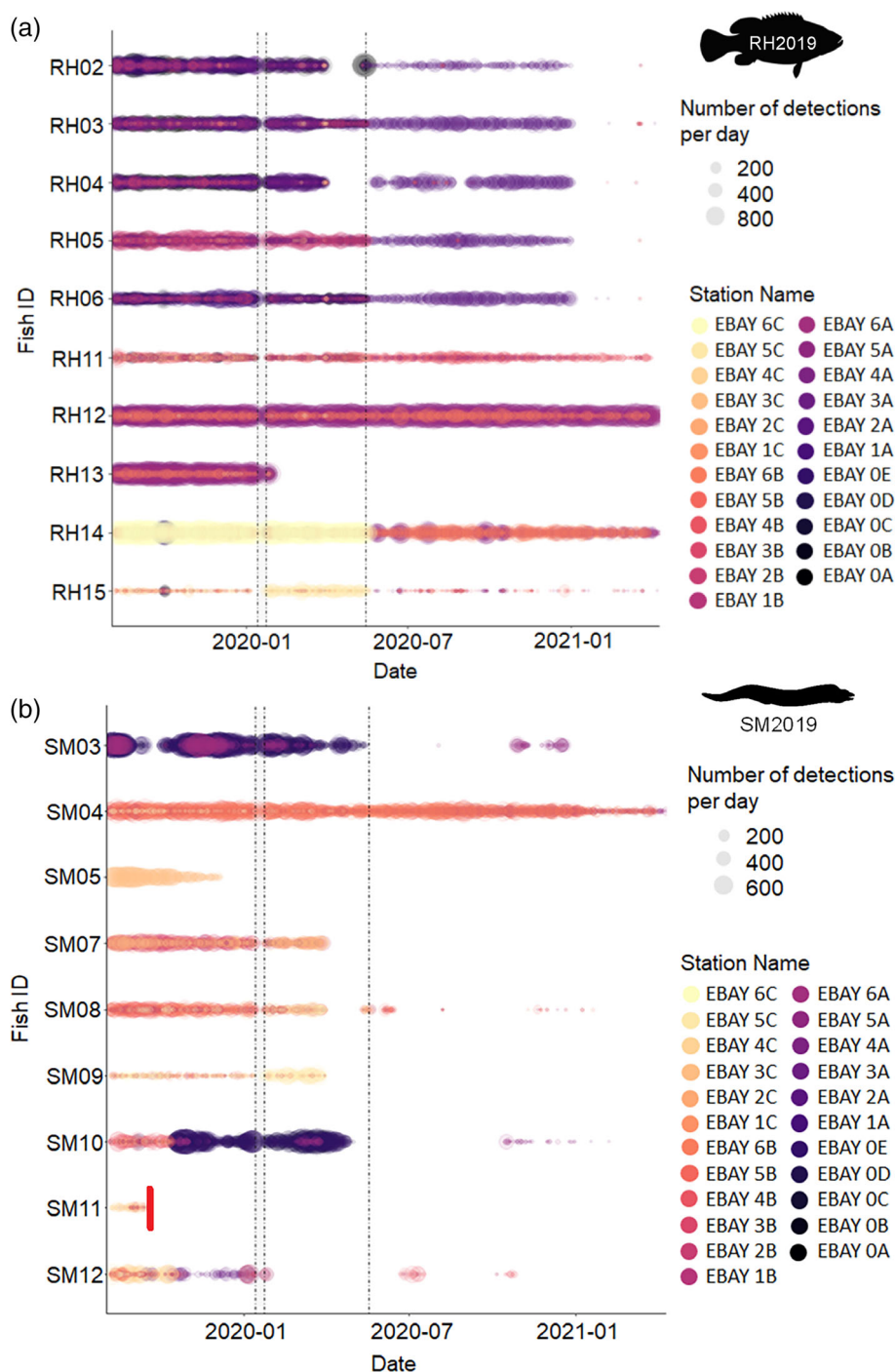


FIGURE 2 Detections of a rock hind grouper, fish ID “RH01,” tagged in 2017 within English Bay, northwest of Ascension Island. (a) Proportional circles represent the cumulative number of detections across the two discrete arrays. Grouper tagging location indicated by red star. (b) Cumulative number of detections grouped by distance from the original 2017 tagging location (number of unique stations expressed above the respective bar).

FIGURE 3 Horizontal movements of individual fish acoustically tagged in 2019 across the English Bay array (“EBAY”) between August 7, 2019, and April 14, 2021. Dashed lines indicate maintenance periods where receivers were out of the water for battery replacements, with the gray 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 (RH, *Epinephelus adscensionis*, $n = 10$) and (b) spotted moray (SM, *Gymnothorax moringa*, $n = 9$). A solid red line indicates a mortality event.



Of the rock hind tagged in 2021 ($n = 16$), 14 (87%) were detected within the Bates Point array across the <98-day study period. Of these individuals, three (19%) were detected for the full study duration (100% residency), and eight (50% tagged) remained in the array for >25% of the study (Table 4). Rock hind home range (95% AKDE) estimates ranged from 0.0001 to 0.3114 km² (n individuals = 4; mean \pm SE = 0.1013 ± 0.07 ; Figure 4). Of the five spotted morays tagged in 2021, only two (20%) were detected across the 3-month study period with a total of three and 12 detections each. Corresponding RIs were low and ranged from 1% to 7%.

3.3 | Vertical movements

Rock hind occupied a mean depth of 17.2 ± 4.8 m SD (one decimal place), with depths ranging from the water's surface to the seafloor (n tagged in 2019 = 10; maximum recorded depth = 38.1 m) (Figure 5a). The mean depth of detected spotted morays was 15.2 ± 10.9 m SD (one decimal place) (Figure 6a); however, animal depth ranged from 2.4 to 38.1 m. Both species exhibited individual variability in their vertical position over time (Figures 5b and 6b). Individuals of both species performed frequent short-duration movements to

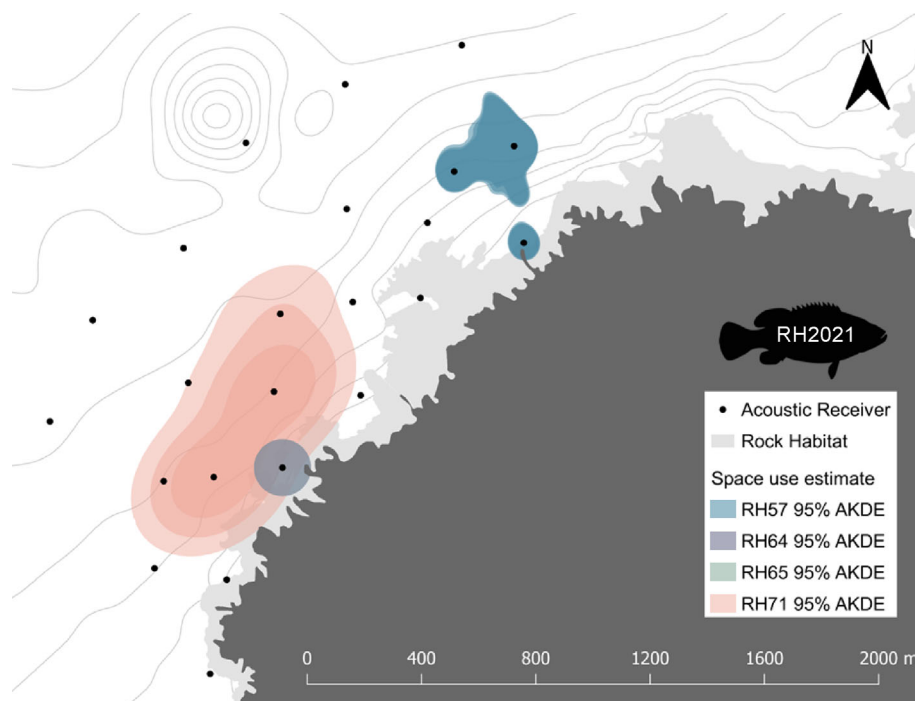


FIGURE 4 Space use estimates (95% autocorrelated kernel density estimate [AKDE]) of rock hind (RH), *Epinephelus adscensionis* ($n = 4$) tagged in 2021 off of Bates Point, northwest of Ascension Island (RH57, RH71). Two fish (RH64 and RH65) with 95% AKDE estimates overlap and appear as a single circle. 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 CIs on the magnitude of the calculated area.

depth, whereas several tracked spotted morays undertook a directional shift to deeper habitats.

In the hGAM depth model, all terms except fish TL were chosen ($R^2 = 0.69$, deviance explained = 87.2%), given that the additional term did not improve the model fit (most complex model AIC = $-24,525$; model excluding TL AIC = $-24,525$). The 0.125 intercept indicating relative water column depth calculated for rock hind was significantly different from the intercept for spotted moray at 0.082 relative water column depth ($t = -3.21$, $p < 0.001$). However, there was a significant random effect of individual fish ID on relative fish depth in the water column, with a large component of the variation explained by this effect ($F = 844.82$, $p < 0.001$). Time of the day (day or night) had a significant effect for both species ($t = 9.00$, $p < 0.001$); however, the effect size was small, 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 the depth of spotted moray within the water column was significantly different across the lunar cycle ($F = 0.73$, $p < 0.001$); however, no effect was observed for rock hind ($F = 0.12$, $p = 0.08$). DOY was a significant predictor of depth for rock hind ($F = 1.65$, $p < 0.05$), with deeper depths occupied in February to July and in October. Depth of spotted moray fluctuated greatly with the DOY ($F = 20.17$, $p < 0.001$); deeper depths were observed in March and June and shallower depths in late April and September to October. Smoothers are visualized in Data S2.

3.4 | Temperature data

Integrated tag temperature sensors showed that the temperature of fish tagged in English Bay (n detected rock hind = 10, n detected

spotted moray = 9) ranged from 21.99 to 29.52°C across the study period (Data S3). These profiles matched the measured seasonal variation in sea temperature recorded in English Bay with an external environmental logger, which ranged from 23.61°C to 29.20°C (August 7, 2019–April 13, 2021, mean \pm SD = 26.15 ± 1.48). Several fish occupied variable temperatures. However, these individuals predominantly occupied deeper moored receiver stations; for example, A-line receivers and O-line receivers moored at >20 m in English Bay.

3.5 | Stomach content data

The majority of sampled rock hind ($n = 46$, 87%) and spotted moray ($n = 14$, 70%) had empty stomachs upon collection (Data S4). Of the rock hind sampled ($n = 53$), only individuals caught in 2020 had identifiable stomach contents ($n = 7$, 13% of all sampled rock hind). Of identifiable rock hind stomach contents, teleost fish were the most commonly consumed (54.55% of stomachs) followed by crustaceans (36.36%F). Of the sampled spotted moray ($n = 20$), only six had identifiable stomach contents (n 2019 = 2; n 2021 = 4). Teleost fish were the most common prey items in both 2019 (50%F) and 2021 (97.67%F) and accounted for the largest proportion of prey mass (98.42%W in 2019; 98.39%W in 2021) and number (86.67%N in 2019, 97.67%N in 2021).

3.6 | Stable isotopes

Muscle tissue and fin clip $\delta^{13}\text{C}$ values were variables ranging from -15.7‰ to -13.8‰ for spotted morays and -18.3‰ to -13.6‰ for rock hind, respectively. Additionally, $\delta^{15}\text{N}$ values ranged from

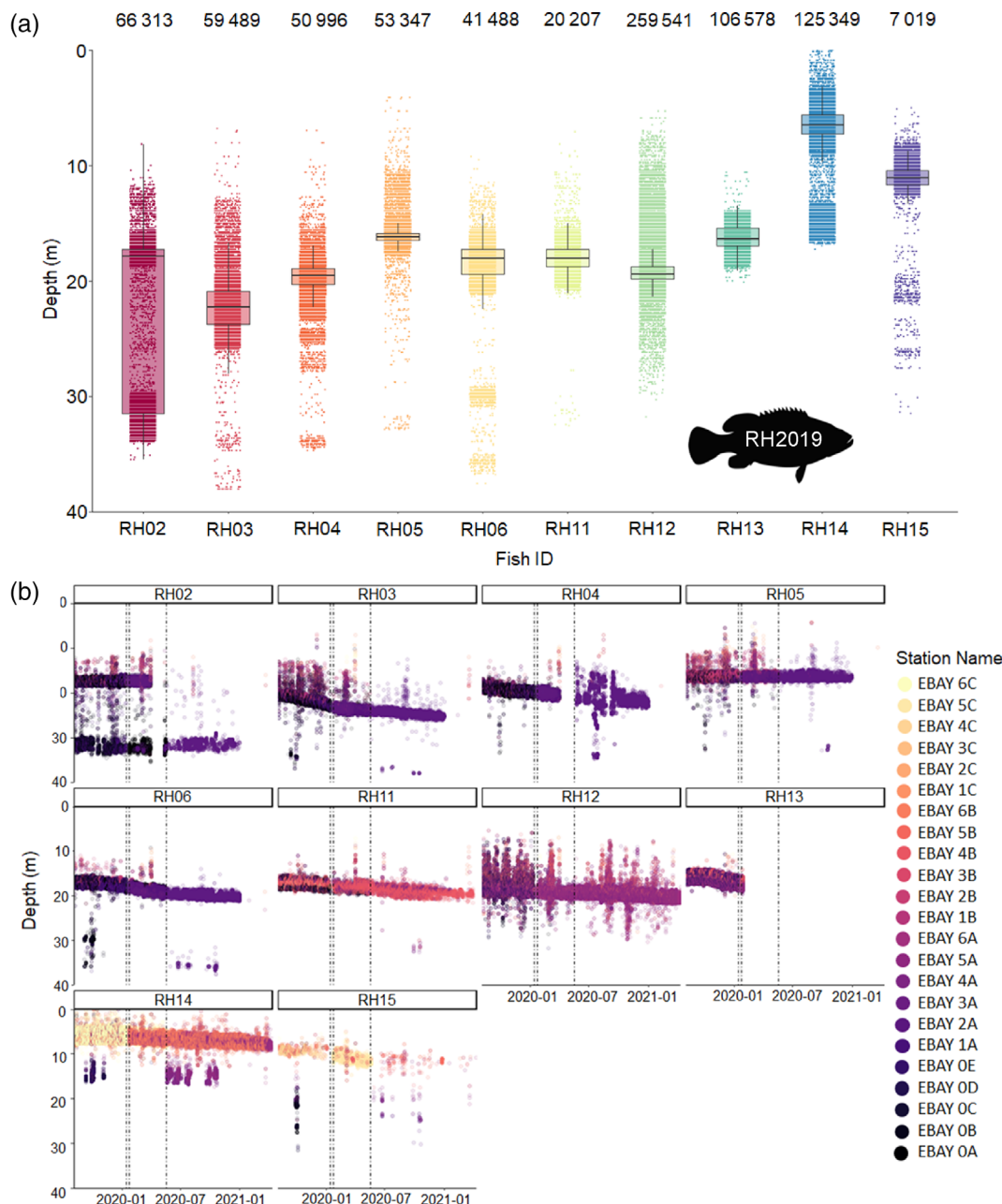


FIGURE 5 Rock hind (RH, $n = 10$) pressure sensor detections recorded across the English Bay array between August 7, 2019, and April 14, 2021. Excludes a 10-day receiver maintenance period (January 14–24, 2020). (a) The total number of pressure detections per tagged individual is given above the corresponding boxplot, with data presented indicating the mean \pm 1 SD. (b) Raw pressure detections. Dashed lines indicate changes in receiver configuration, for example, maintenance period (January 2020) or reduction in array size (reduced from 23 to 9 receivers on May 18, 2020.)

12.1‰ to 13.9‰ for spotted morays and 12.1‰ to 15.9‰ for rock hind (Data S5). Ecological niche modeling indicated an overlap in isotopic niches of rock hind and spotted moray for both fin clips and white muscle (Figure 7). For fin clips, the 95% mean posterior probability that an individual rock hind would be present in the niche of spotted moray was estimated as 53.1%. On the contrary, the mean posterior probability that an individual spotted moray would be found in the niche of rock hind was 54.2%. The 95% mean posterior overlap probability was higher for white muscle tissue. The mean posterior

probability that rock hind would be present in the niche space of spotted moray was 97.08%. In comparison, there was a 78.02% mean posterior probability that spotted moray would be found in the niche space of rock hind. The niche size of rock hind was estimated as 3.3 ± 0.5 (mean \pm SE) and spotted moray as 2.5 ± 0.5 based on fin clips and 5.7 ± 0.7 (rock hind) and 9.6 ± 1.8 (spotted moray) for white muscle.

When isotope data were visualized by year, fin tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the two species varied slightly over the three study

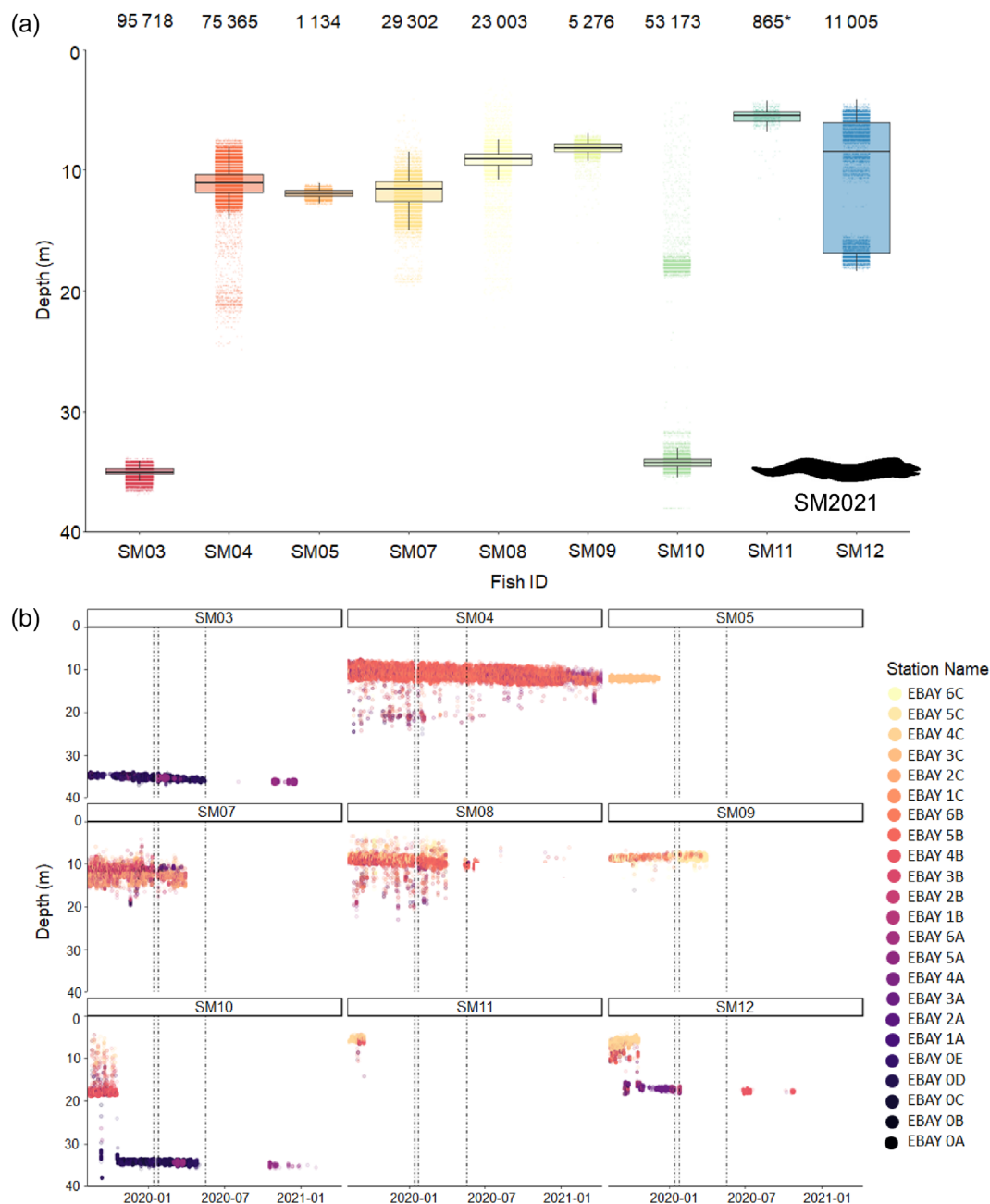


FIGURE 6 Spotted moray (SM, $n = 9$) pressure sensor detections recorded across the English Bay array between August 7, 2019, and April 14, 2021. Excludes detections post-predation (SM11) and during the 10-day receiver maintenance period (January 14–24, 2020). (a) The total number of pressure detections per tagged individual is given above the corresponding boxplot, the asterisk (*) indicates cumulative detections pre-predation with data presented indicating the mean ± 1 SD. (b) Raw pressure detections. Dashed lines indicate changes in receiver configuration, for example, maintenance period (January 2020) or reduction in array size (reduced from 23 to 9 receivers on May 18, 2020).

years (2019, 2020, and 2021), whereas white muscle showed consistent overlap (Figure 8).

4 | DISCUSSION

Differences in predominantly horizontal and, to a lesser degree, vertical space use of two coexisting mesopredators provide evidence of resource partitioning. Although rock hind exhibited high site fidelity

and residency and occupied very small home ranges, moray eels were seen to undergo spatial shifts, that is, lower residency and emigration from the array areas. Individual differences in vertical space within and between these two species were extremely high and are likely the key factor facilitating coexistence. Dietary and trophic niche space from stomach content and stable isotope analysis indicated a level of niche overlap with both species identified as predominantly piscivorous predators consuming prey across the same two trophic levels. Minor differences in diet were identified over finer temporal scales

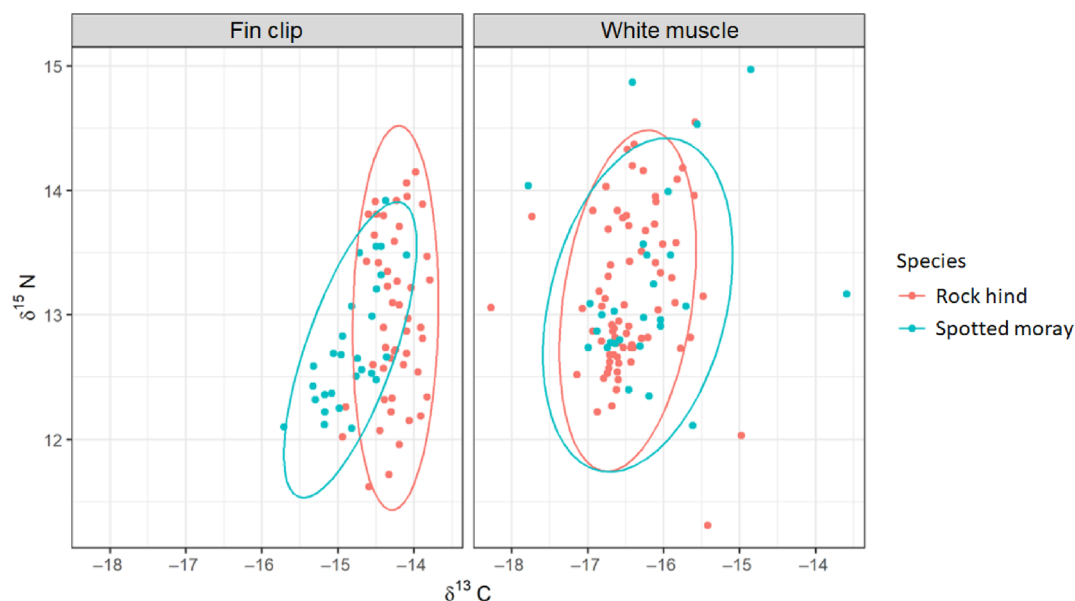


FIGURE 7 Fin clip (FC) and white muscle (WM) isotopic compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of rock hind (*Epinephelus adscensionis*, red points; n FC samples = 38, n WM samples = 76) and spotted moray (*Gymnothorax moringa*, blue points; n FC samples = 28, n WM samples = 28). Points represent values for individual fish, and ellipses represent the species' isotopic niche.

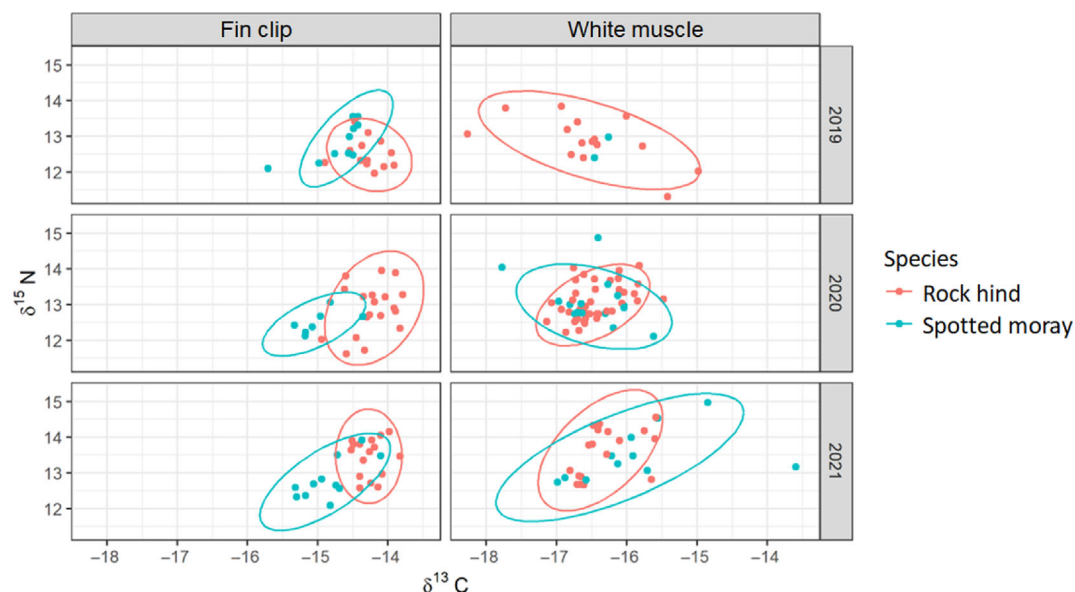


FIGURE 8 Fin clip (FC) and white muscle (WM) isotopic compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of rock hind (RH, *Epinephelus adscensionis*, red points) and spotted moray (SM, *Gymnothorax moringa*, blue points). Points represent values for individual fish, and ellipses represent the species' isotopic niche. In the absence of enough data, ellipses were not generated. Data span 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).

(from fin tissue isotope data and stomach contents); however, further work is required to confirm these observations, given the small sample sizes. These data suggest that although these two species perform similar ecological roles, differences in space use and residency identify the need for species-specific management, that is, no-take protected areas for grouper and fisheries management measures for spotted moray.

4.1 | Horizontal space use and home range

Resource partitioning alleviates competition for resources, with differences in space use reducing competition for shelter and available prey. This study used telemetry data generated over a range of spatial scales and array designs, from a linear curtain of receivers with 300-m spacing to a tightly spaced gridded array of acoustic receivers. These

arrays overlapped across the study area, with tagging sites within the spatial constraints of all arrays, facilitating the tracking of rock hind and spotted moray across longitudinal scales. Data generated from three cohorts of tagged rock hind suggest temporally stable RIs and a small home range across this multi-year study. High fidelity and small home ranges have been widely reported for acoustically tagged grouper in existing literature (Afonso et al., 2016; Biesinger et al., 2013; Eklund & Schull, 2001; Kiel, 2004; Koeck et al., 2014; Popple & Hunte, 2005). For example, in the Azores, dusky grouper (*Epinephelus marginatus*) were detected almost every day for 5 years at their initial capture site (Afonso et al., 2016).

Rock hind home ranges spanned 0.0001 to 0.3114 km² (calculated for AKDE from COAs of four fish tracked in 2021). This is similar to the home ranges of dusky grouper (*E. marginatus*) and blacktail comber (*Serranus atricauda*) in and around a small marine reserve in the Azores positioned using COA and estimated using kernel utilization distribution areas (KUD). Home range estimates were <0.268 and <0.004 km², respectively, across a 5-year study period (Afonso et al., 2016). It should be noted that AKDE was developed based on positions derived using fine-scale tracking approaches, which provide an associated error for each position. As a result, for two additional rock hind in this study where sufficient detection data were available, realistic home range values could not be estimated, given that detections were recorded on a single receiver leading to model convergence failure. Despite these limitations, we suggest AKDE offers the best approach as conventional methods have been shown to systematically underestimate home range for autocorrelated relocation data (Fleming et al., 2015). This metric was chosen to illustrate the high residency of rock hind and demonstrate the potential for spatial management measures. Owing to the limited number of spotted moray detections on the Bates Point array (within the specified 60 minute time bin for COA), it was not possible to estimate home range using AKDEs.

Spotted morays tracked in this study were seen to undergo shifts in the area they occupied, which terminated periods of observed residency. An observational survey conducted in 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 (D. Orrell, unpublished data). Similar den-swapping behavior has been identified by moray eel tracking and observational studies (Abrams et al., 1973; Bassett & Montgomery, 2011; Kendall et al., 2021; Young & Winn, 2003). Abrams et al. (1973) conducted a 6-week observational survey of spotted moray movements within the Coki reef in the Caribbean and found that individuals exhibited short residency periods, with some returning to previously occupied dens. Whether the observed behavior in the Ascension telemetry study described here is due to emigration or the capture of animals at the edge of their home range is uncertain. Due to logistical constraints and difficulty in catching spotted morays at deeper sites in 2021, all individuals were captured <100 m from the shore. None of the five individuals tagged in 2021 were subsequently detected after one week. Ideally, animals would have been tagged toward the center of the acoustic array to maximize detection likelihood and therefore

enable home range estimation. The cryptic shelter-dwelling behavior of spotted moray may also have limited data yield due to acoustic shadowing and reduced line-of-sight between receivers preventing detection (Bassett & Montgomery, 2011; Orrell, Webber & Hussey, 2023). Additionally, although the spotted moray are the most important moray species locally to recreational fishers (recreational, cultural, and for consumption) and one of the most abundant, 11 moray species are found in Ascension's waters (Wirtz et al., 2017). Future work should aim to characterize residency and movement behaviors among moray species or capture larger cohort sizes to identify inter- and intraspecific differences in movement behaviors. Despite these limitations, this study provides the most comprehensive tracking data available for this species, owing to high data yield and longitudinal study duration.

Intra- and interspecific differences in residency and space use of spotted moray and rock hind could be linked to several factors, including internal state, personality, sex, local population dynamics, or other biological factors (Hollins et al., 2018; Killen et al., 2016; Nilsson et al., 2014). For example, all tracked fish were caught using baited lines, which may have led to the capture of hungry or risk-averse individuals (Thomsen et al., 2010). Additionally, sex and population dynamics may have also played a role in the movements of these species. For example, rock hind are protogynous hermaphrodites that form harem social structures with a single dominant male defending a territory containing one or several females (Kline et al., 2011; Marques & Ferreira, 2018). Removal of a dominant male can trigger the transition of the largest female (Kline et al., 2011). Given that it was not possible to identify the sex of tagged rock hind and their hermaphroditic ability, this may have led to inherent differences in behavior between individuals or the same individual throughout the study period. However, the high RIs and small home ranges estimates calculated for rock hind suggest they are amenable to spatial protection. In contrast, low RIs suggest that spotted moray may be more effectively managed using a fisheries management-based approach.

4.2 | Vertical space use

Individuals of both species showed variable vertical movements, including static depth recordings with minimal change (see RH06 and RH11 in Figure 5b and SM03 and SM09 in Figure 6b), a shift from shallow to deep habitats (SM10, SM12, Figure 6b), a synchronized shift to depth for several days before return to a typical depth (almost all grouper, Figure 5b; SM04, Figure 6b), and cyclical diurnal movements between shallow and deep habitats (RH02, Figure 5b; SM06, Figure 6b). 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 behavior (Koeck et al., 2014), and the lunar cycle (Froehlich et al., 2021). Our results suggest that temporal differences in individual space use within and between the two study species may facilitate their coexistence.

Due to an observed bias in the number of recorded detections during the day versus night on fixed tags (synchronization and reference tags co-deployed in English Bay) owing to high ambient nocturnal noise, fine-scale diel activity was not assessed (similar issues previously identified by Payne et al., 2010; Koeck et al., 2014). However, the average depth of both species in the water column (12-h averaged relative depths) differed significantly between day and night, with a preference for slightly deeper depths at night. Grouper are commonly described as diurnal predators (Koeck et al., 2014). However, several tagged individuals in this study undertook forays into deeper habitats at night. Similarly, although moray eels are known as nocturnal foragers (Young & Winn, 2003) during observational surveys and capture attempts, spotted 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). The plasticity of diel activity rhythms in tropical fishes can facilitate temporal niche partitioning, for example, 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, Fox and Bellwood (2011) found that the diel activity of golden-lined rabbitfish (*Siganus lineatus*) differed depending on the habitat they occupied within a tropical reef. Individuals occupying the boulder shoreline were active during daylight hours and rested in rest holes at night. Conversely, individuals occupying fringing reef habitats were active at night and rested in rest holes during the day. Additionally, moray eels have been observed to initiate diurnal cooperative hunting forays alongside other groupers (Bshary et al., 2006; Diamant & Shpigel, 1985; Vail et al., 2013), suggesting flexible diel activity rhythms. It should be noted that more detections were recorded for both species across day than night in our study. This is a common limitation of acoustic tracking owing to increased biological noise at night on reefs (How & de Lestang, 2012; Huveneers et al., 2016; Stocks et al., 2014; Swadling et al., 2020) and the nature of cryptic diurnal species that hide among complex structures preventing signal reception (Zhang et al., 2015).

Lunar illumination significantly affected the depth of spotted morays within the water column. However, no effect was observed for rock hind. This association could be due to intrinsic differences in reproductive behavior. Although moray eels spawn throughout the year (Zokan et al., 2022), rock hind are seasonal spawners (Nolan et al., 2017). Samples collected off the southeast United States suggest that female spotted moray spawning periodicity ranges from 24 to 31 days, which suggests that females could spawn 12 times during the 278-day spawning season (Zokan et al., 2022). Additionally, spotted moray larvae have been collected throughout the year in the Caribbean, indicating 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. Site fidelity during spawning may explain how this behavior could be captured despite the small area of the array (Thresher, 1984) and may explain some of the variation in vertical behavior observed for this species.

The significant predictor of the DOY in the depth model could 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, Williams-Grove and Szedlmayer (2017) found the occurrence of red snapper (*Lutjanus campechanus*) higher in the water column was tied to spawning patterns and prey availability over diel and monthly periods. Ascension has clear seasonal fluxes in prey occurrence, which also vary with depth. For example, green turtles (*C. mydas*) hatch from January to June (Ascension Island Government, 2015a) and are surface swimmers, which may stimulate surface feeding by predators. Mantis shrimp (suspected *Pseudosquilla oculata*) are benthic crustaceans observed to spawn in April (D. Orrell, personal observation), which may prompt opportunistic feeding lower in the water column. Opportunistic feeding strategies can reduce interspecific competition and facilitate the coexistence of fishes across a variety of contexts (Flores-Ortega et al., 2020; Friedlander et al., 2014; Mavuti et al., 2004; Neves et al., 2021). Additionally, optimal foraging theory predicts that feeding on abundant prey, such as seasonal prey pulses of longjaw squirrelfish and mole crab, would offer rock hind and spotted moray a greater energetic benefit than searching for less abundant prey (Gerking, 1994; MacArthur & Pianka, 1966).

Significant individual differences in vertical space use within and between these two species suggest they can exploit available resources, which may facilitate coexistence. Future research is required to identify other relevant drivers of vertical space use, for example, seasonal prey availability and fluxes and the abundance of (non-tagged) individuals of each species within the study area. Validating the observed behaviors using underwater cameras and routine sampling across a range of depths and habitats would be beneficial, so to confirm the findings reported here.

4.3 | Dietary composition and overlap

The observed overlap and preference for piscivorous prey items, accepting our small sample size, aligns with other studies of serranids (Artero et al., 2015; Stewart & Jones, 2001) and moray eels (Higgins et al., 2018; Young & Winn, 2003) within tropical reef environments. There was a high incidence of empty stomachs for both rock hind and spotted moray, which could be a result of several factors, including the capture method, time of sampling, and food availability. Fish capture occurred exclusively during daylight hours using baited lines; therefore, fish may have been caught in the interval between evacuation of their last meal and successful capture of their next prey (Rindorf & Lewy, 2004). Future research could focus on using a range of capture techniques (e.g., SCUBA or spearfishing), sampling across a range of temporal scales (day and night, repeated across several seasons and years) and use supplementary techniques, such as environmental DNA (eDNA), to identify diet in an absence of identifiable

material. 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, for example, laboratory trials providing food in excess to juvenile orange-spotted grouper (*Epinephelus coioides*) found that cannibalism continued to occur (Hseu et al., 2003). Whether the observed cannibalism in rock hind reduces competition and facilitates coexistence or results from exploiting available prey remains unclear.

Similar to previous studies that have integrated stomach contents and stable isotope analyses (Artero et al., 2015; Conдини et al., 2015; Reñones, Polunin & Goni, 2002), this complementary approach allowed the identification of diet items across a range of time scales. Although no controlled diet feeding trials have been conducted for rock hind, or in general for moray eels, work by Matley et al. (2016) suggests tissue turnover rates of 37 days for fin and 126 days for white muscle (based on adult leopard coral grouper, *P. leopardus*). These turnover rates would suggest that we captured a snapshot of diet across several seasons of seasonally abundant prey resources.

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), coincidentally spanning several unique prey pulses. 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, 2015b). In 2021, attempts to catch and tag rock hind at depths of >20 m were largely unsuccessful, and this could be linked to the turtle hatchling season. During hatchling season, rock hind form “conveyor belts” close to shore, ready to receive incoming turtles on their first foray into the ocean (R. Joshua, personal communication; January 3, 2021).

The overlap in dietary niche between these two species is expected if they both consume seasonally abundant prey resources (Cusa Berge & Varpe, 2019). The more variable $\delta^{13}\text{C}$ value in fin clips suggests that spotted moray exploits a broader range of basal sources, accepting the small sample size by year. Some separation in trophic niche may result from generalist feeding behavior (Wantzen et al., 2002) and spatially explicit available prey exploitation. Variation in both carbon and nitrogen isotope data suggests variable individual feeding strategies between individuals and species, similar to the individual-specific movement behaviors observed. Tentative comparisons of stable isotope values between years suggest niche width may fluctuate to some degree between species. However, this requires further investigation due to low sample sizes.

4.4 | Management implications

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 a basic ecological understanding of the species and determining effective fisheries management measures (Hays et al., 2019; Lennox et al., 2019). The Ascension Island's MPA prohibits large-scale commercial fishing within 200 nm of the island, and recreational fishing is only permitted within 12 nm of the island (The Fisheries [Conservation and Management] Ordinance, 2015, Ascension Island Government Conservation and Fisheries Directorate, 2021). However, currently, there are no restrictive measures on non-commercial rock hind fishing practices except for individuals to hold a permit to export fish off the island (Customs [Export Control] Regulations, 2010). Nonetheless, given the isolated nature of the stock, we encourage considering proactive management and addressing several key research areas.

Multi-year tracking data collected across a range of spatial scales find rock hind have small home ranges and high residency to near-shore areas. These findings indicate that Ascension rock hind populations are vulnerable to overexploitation and local extirpation. However, high site fidelity and small home ranges suggest that rock hind are amenable to spatial protection measures. Owing to potential increases in fishing pressure linked to the island's runway reopening in 2023, we suggest several proactive management measures to ensure population stability and health. Note that although several measures are suggested here, their actualization would only be reached after careful consideration, engagement, and discussion by the local government alongside the fishing community.

Management options for rock hind could include the following:

1. Small no-take zones covering a range of depths and habitats. No-take MPAs have proved effective in conserving grouper populations elsewhere. For example, juvenile dusky grouper numbers were much higher in a no-take zone than in a fishing zone in an MPA at Ustica Island off the Sicilian coast of Italy (Vacchi et al., 1999). This recommendation echoes the call Choat and Robertson (2008) made for the neighboring island of St Helena, whereby small no-take zones would effectively protect populations from perilous declines. Identifying local oceanographic conditions and prevailing currents may aid in selecting no-take protected areas that are not typically fished at present but could provide an opportunity for replenishment owing to the rock hind's planktonic larval stage.
2. Bag and vessel limits, with lower limits imposed on visitors (< 6-month trip duration), may be necessary if the population or recreational fishery on the island substantially increases with improved access. Bag limits are a well-established management tool to ensure reef fish population health and are in place for grouper, gag, and snapper species in the USA and the Gulf of Mexico.
3. A minimum landing size could ensure that individuals can spawn before removal from the system. Nolan et al. (2017) identified rock hind reach sexual maturity on Ascension Island at 28.9 cm TL for females and 35.1 cm for males. Therefore, a minimum size of 29 cm could ensure a healthy reproductive stock for population

replenishment. However, current evidence suggests rock hind are protogynous hermaphrodites; therefore, removal of only larger individuals could also lead to an altered sex ratios and timing of maturation and protogyny (Choat & Robertson, 2008; Nolan et al., 2017), a factor that requires consideration when selecting an appropriate management strategy.

Moray eel ecology and space are understudied, despite their vital role in the structure of tropical reefs (Moretto, Stahl & Mehta, 2022). Spotted moray is locally consumed on Ascension Island and are culturally and recreationally significant. There is no monitoring or management of spotted moray besides limiting exports off-island through a permit system (Customs [Export Control] Regulations, 2010). Acoustic telemetry data presented here do not conclusively suggest that spatial management is an appropriate tool to manage this species. Owing to these findings, an alternate approach should be evaluated to manage spotted moray populations, for example, using bag limits and minimum landing sizes.

Overall, the results for rock hind and spotted moray support several key research areas that would help guide fisheries management decisions for these species, including the following:

1. **Use of low-cost tools to improve population monitoring and stock size estimates.** Previously, annual dive surveys (2010–2020) focused on the north side of the island were used to assess grouper age structure and abundance; however, restrictions on dive activities have prevented their continuance. Rock hind and spotted moray population monitoring could include conducting routine video surveys to estimate abundance and biomass, and through increased participation in the voluntary logbook programme to identify current catch rates. Genetic sampling and use of close-kin mark-recapture (Casas & Saborido-Rey, 2023) may be a low-cost option to build upon this dataset and estimate population sizes and genetic connectivity.
2. **Studying island-wide animal movements.** Building upon the existing telemetry work, using an island-wide array of receivers could identify whether nearshore populations function as discrete units with minimal movements or one homogenous population that is capable of high localized replenishment facilitated by island circumnavigation.
3. **Identification of rock hind and spotted moray spawning aggregations and spawning areas.** Ascension's grouper spawning season spans July–November and peaks in August (astral winter) as identified using monthly gonad staging (Nolan et al., 2017). However, although grouper are predominantly aggregate spawners, it is not currently reported whether they do so in Ascension's waters and if so, where. Routine ichthyoplankton monitoring through water sampling may be helpful in identifying aggregate spawning areas.
4. **Detailed bathymetric mapping of nearshore areas.** Bathymetric and relief maps could help determine suitable habitats for these species and may also aid in identifying probable areas for spawning.
5. **Identification of key prey fluxes and their annual timing.** Developing a long-term opportunistic diet sampling programme using

stomach content and stable isotope analysis could elucidate diets across seasons and with ecosystem change. Additionally, pairing local ecological knowledge with eDNA could identify species not isolated from stomach contents. Because prey movements are a key driver in the nearshore movements of recreational and sport fishes, this knowledge could be used to evidence perceived seasonal differences in predator population abundance.

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. High individual variation in vertical movements and observed range in isotopic values suggest that individuals of both species feed on prey occupying the same trophic levels but may feed opportunistically on available prey. The high residency and high site fidelity of rock hind tracked across multiple years, in tandem with small home ranges of individuals tracked in 2021, suggest spatial management measures would be an effective tool to managing this species. In contrast, variable residency and site fidelity of spotted moray highlight that an alternate non-spatial management approach, including bag limits and minimum landing size, may be more effective. These results highlight that although rock hind and spotted moray occupy a similar ecological role across a nearshore environment, differences in space use suggest that a one-rule-fits-all management approach is not appropriate to managing these two coexisting species.

AUTHOR CONTRIBUTIONS

Danielle L. Orrell and Nigel E. Hussey conceived the study. Danielle L. Orrell, Daniel Sadd, Kirsty L. Jones, Kate Chadwick, Tiffany Simpson, and Darcy E. Philpott conducted the fieldwork. Danielle L. Orrell performed the data analyses. Danielle L. Orrell and Nigel E. Hussey wrote the manuscript with contributions from Daniel Sadd, Kirsty L. Jones, Kate Chadwick, Tiffany Simpson, and Darcy E. Philpott. All authors read and approved the final manuscript.

ACKNOWLEDGMENTS

This work was made possible, thanks to the support of the Ascension Island community and fishing community, including Jaco Ferriera, Clay Brogdon, Richie Joshua, Dwayne Joshua, Shaun Scipio, Alex Knipe, Adrienne Levknecht, Rick Lutman, James Richards, Mike Greentree, Richard Cook, Alex Brittan, Hugh Carville, Geston Wayne Burckhalter, Eugene Bennett, Siobhan Stewart, Ken Williams, Ollie Jones, and Gary Picky. Additionally, Ascension Island Government staff, including Victoria Knight, Andrew Richardson, Alys Perry, Marcia Blyth, Diane Baum, and Jolene Sim. Thank you also to the Schuyler Line Navigation Company for supporting the equipment deployment and data collection that made this work possible. Thanks also extends to the Ocean Tracking Network R coding group for their guidance and scintillating data discussions. Particular thanks are given to Robert Lennox, Mike O'Brien, and Jack Hollins for their guidance on spatial analysis and modeling.

FUNDING INFORMATION

Danielle L. Orrell was supported by the Ontario Trillium Scholarship and Nigel E. Hussey by the NSERC Discovery Grant Program.

ORCID

Danielle L. Orrell  <https://orcid.org/0000-0002-9449-3920>

REFERENCES

- Abrams, R. W., Abrams, M. D., & Schein, M. W. (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, R. S., & Fontes, J. (2016). Contrasting movements and residency of two serranids in a small Macaronesian MPA. *Fisheries Research*, 177, 59–70.
- Andrzejczek, S., Lucas, T. C. D., Goodman, M. C., Hussey, N. E., Armstrong, A. J., Carlisle, A., Coffey, D. M., Gleiss, A. C., Huvneers, C., Jacoby, D. M. P., Meekan, M. G., Mourier, J., Peel, L. R., Abrantes, K., Afonso, A. S., Ajemian, M. J., Anderson, B. N., Anderson, S. D., Araujo, G., ... Curnick, D. J. (2022). Diving into the vertical dimension of elasmobranch movement ecology. *Science Advances*, 8(33), eabo1754. <https://doi.org/10.1126/sciadv.abo1754>
- Artero, C., Koenig, C. C., 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*, 27(2), 155–168.
- 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, N. M., Shertzer, K. W., Runde, B. J., Rudershausen, P. J., & Buckel, J. A. (2021). Environmental conditions, diel period, and fish size influence the horizontal and vertical movements of red snapper. *Scientific Reports*, 11, 9580.
- Bassett, D., & Montgomery, J. (2011). Home range use and movement patterns of the yellow moray eel *Gymnothorax prasinus*. *Journal of Fish Biology*, 79, 520–525.
- Biesinger, Z., Bolker, B. M., Marcinek, D., & Lindberg, W. J. (2013). Gag (*Mycteroperca microlepis*) space-use correlations with landscape structure and environmental conditions. *Journal of Experimental Marine Biology and Ecology*, 443, 1–11.
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183–192.
- Brulé, T., Renán, X., & Colás-Marrufo, T. (2022). Potential impact of climate change on fish reproductive phenology: A case study in Gonochoric and hermaphrodite commercially important species from the southern Gulf of Mexico. *Fishes*, 7(156). <https://doi.org/10.3390/fishes7040156>
- 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, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261–304.
- Casas, L., & Saborido-Rey, F. (2023). A review of an emerging tool to estimate population parameters: The close-kin mark-recapture method. *Frontiers in Marine Science*, 10. <https://www.frontiersin.org/articles/10.3389/fmars.2023.1087027>
- Chan, A. J., Raoult, V., Jaine, F. R. A., Peddemors, V. M., Broadhurst, M. K., & Williamson, J. E. (2022). Trophic niche of Australian cownose rays (*Rhinoptera neglecta*) and whitespotted eagle rays (*Aetobatus ocellatus*) along the east coast of Australia. *Journal of Fish Biology*, 100, 970–978.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Choat, J. H., & Robertson, R. D. (2008). An ecological survey of the St Helena and Ascension Island populations of the Jack (*Epinephelus adscensionis*) with a review of management options.
- Church, M. R., Ebersole, J. L., Rensmeyer, K. M., Couture, R. B., Barrows, F. T., & Noakes, D. L. G. (2009). Mucus: A new tissue fraction for rapid determination of fish diet switching using stable isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1–5.
- Collins, A. B., Heupel, M. R., & Motta, P. J. (2007). Residence and movement patterns of cownose rays *Rhinoptera bonasus* within a south-west Florida estuary. *Journal of Fish Biology*, 71, 1159–1178.
- Concini, M. V., Hoeinghaus, D. J., & Garcia, A. M. (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 analyses. *Hydrobiologia*, 743(1), 109–125. <https://doi.org/10.1007/s10750-014-2016-0>
- Cunjak, R. A., Roussel, J. M., Gray, M. A., Dietrich, J. P., Cartwright, D. F., Munkittrick, K. R., & Jardine, T. D. (2005). Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*, 144, 636–646.
- Cusa, M., Berge, J., & Varpe, Ø. (2019). Seasonal shifts in feeding patterns: Individual and population realized specialization in a high Arctic fish. *Ecology and Evolution*, 9(19), 11112–11121. <https://doi.org/10.1002/ece3.5615>
- Diamant, A., & Shpigel, M. (1985). Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Agaba). *Environmental Biology of Fishes*, 13, 153–159.
- Dicken, M. L., Hussey, N. E., Christiansen, H. M., Smale, M. J., Nkabi, N., Cliff, G., & Wintner, S. P. (2017). Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from south African waters. *PLoS One*, 12, e0177897.
- 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. In *Electronic Tagging and Tracking in Marine Fisheries: Proceedings of the Symposium on Tagging and Tracking Marine Fish with Electronic Devices* (pp. 189–216). Springer.
- Ferreira, B., Bertoni, A. A., & Choat, J. H. (2018). *Epinephelus adscensionis*. In *The IUCN red list of threatened species 2018* (e. T132819A46918058). <https://doi.org/10.2305/IUCN.UK.20182.RLTS.T132819A46918058.en>
- Fleming, C. H., & Calabrese, J. M. (2021). Ctm: Continuous-Time Movement Modeling.
- Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator. *Ecology*, 96, 1182–1188.
- Flores-Ortega, J. R., Godínez-Domínguez, E., González-Sansón, G., Flores-Ortega, J. R., 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, R. J., & Bellwood, D. R. (2011). Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*: Diel activity plasticity in a rabbitfish. *Functional Ecology*, 25, 1096–1105.
- Freitas, C., Olsen, E. M., Knutsen, H., Albrechtsen, J., & Moland, E. (2016). Temperature-associated habitat selection in a cold-water marine fish. *The Journal of Animal Ecology*, 85, 628–637.

- Friedlander, A. M., 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, C. Y. M., Garcia, A., Cintra-Buenrostro, C. E., Hicks, D. W., & Kline, R. J. (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.
- Gerking, S. D. (1994). *Feeding ecology of fish*. Academic Press.
- 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). *Journal of Biological Research-Thessaloniki*, 17, 121–136.
- Guabiroba, H. C., Santos, M. E. A., Pinheiro, H. T., Simon, T., Pimentel, C. R., Vilar, C. C., & Joyeux, J. C. (2020). Trends in recreational fisheries and reef fish community structure indicate decline in target species population in an isolated tropical oceanic island. *Ocean & Coastal Management*, 191, 105194. <https://doi.org/10.1016/j.ocecoaman.2020.105194>
- Guzzo, M. M., Blanchfield, P. J., Chapelsky, A. J., & Cott, P. A. (2016). Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. *Journal of Great Lakes Research*, 42, 276–285.
- Harmelin-Vivien, M. L., Kaim-Malka, R. A., Ledoyer, M., & Jacob-Abraham, S. S. (1989). Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. *Journal of Fish Biology*, 34, 715–734.
- Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., Casale, P., Chiaradia, A., Costa, D. P., Cuevas, E., Nico de Bruyn, P. J., Dias, M. P., Duarte, C. M., Dunn, D. C., Dutton, P. H., Esteban, N., Friedlaender, A., Goetz, K. T., Godley, B. J., ... Sequeira, A. M. M. (2019). Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution*, 34, 459–473.
- Heupel, M. R., Semmens, J. M., Hobday, A. J., Arendt, M. D., Lucy, J. A., Munroe, T. A., Arendt, M. D., Lucy, J. A., Evans, D. A., Bégout, M.-L., Lagardère, J.-P., Bégout-Anras, M.-L., Lagardère, J.-P., Lafaye, J.-Y., Boettcher, R., Haig, S. M., Bridges, W. C., Clark, P. J., Evans, F. C., ... Batten, S. D. (2006). Automated acoustic tracking of aquatic animals: Scales, design and deployment of Listening Station arrays. *Marine and Freshwater Research*, 57, 1.
- Higgins, B. A., & Mehta, R. S. (2018). Distribution and habitat associations of the California moray (*Gymnothorax mordax*) within two harbors, Santa Catalina Island, California. *Environmental Biology of Fishes*, 101, 95–108.
- Higgins, B. A., Law, C. J., & Mehta, R. S. (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.
- Hollins, J., Thambithurai, D., Koeck, B., Crespel, A., Bailey, D. M., Cooke, S. J., Lindström, J., Parsons, K. J., & Killen, S. S. (2018). A physiological perspective on fisheries-induced evolution. *Evolutionary Applications*, 11, 561–576.
- How, J. R., & de Lestang, S. (2012). Acoustic tracking: Issues affecting design, analysis and interpretation of data from movement studies. *Marine and Freshwater Research*, 63, 312–324.
- Hseu, J. R., Lu, F. I., Su, H. M., Wang, L. S., Tsai, C. L., & Hwang, P. P. (2003). Effect of exogenous tryptophan on cannibalism, survival and growth in juvenile grouper, *Epinephelus coioides*. *Aquaculture*, 218, 251–263.
- Hussey, N. E., Dudley, S. F. J., McCarthy, I. D., Cliff, G., & Fisk, A. T. (2011). Stable isotope profiles of large marine predators: viable indicators of trophic position, diet, and movement in sharks? *Canadian Journal of Fisheries and Aquatic Sciences*, 68(12), 2029–2045.
- Hussey, N. E., Hedges, K. J., Barkley, A. N., Treble, M. A., Peklova, I., Webber, D. M., Ferguson, S. H., Yurkowski, D. J., Kessel, S. T., Bedard, J. M., & Fisk, A. T. (2017). Movements of a deep-water fish: Establishing marine fisheries management boundaries in coastal Arctic waters. *Ecological Applications*, 27, 687–704.
- Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Flemming, J. E. M., & Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, 348, 1255642.
- Huveneers, C., Simpfendorfer, C. A., Kim, S., Semmens, J. M., Hobday, A. J., Pederson, H., Stieglitz, T., Vallee, R., Webber, D., Heupel, M. R., Peddemors, V., & Harcourt, R. G. (2016). The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution*, 7, 825–835.
- Hyslop, E. J. (1980). Stomach contents analysis—A review of methods and their application. *Journal of Fish Biology*, 17(4), 411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>
- InnovaSea Systems Inc. (2021). Coded transmitters -69 kHz.
- Kendall, M. S., Sicheloff, L., Ruffo, A., Winship, A., & Monaco, M. E. (2021). Green morays (*Gymnothorax funebris*) have sedentary ways in mangrove bays, but also ontogenetic forays to reef enclaves. *Environmental Biology of Fishes*, 104(8), 1–15. <https://doi.org/10.1007/s10641-021-01137-0>
- Kiel, B. L. (2004). Homing and spatial use of gag grouper, *Mycteroperca microlepis*. (Doctoral dissertation, University of Florida).
- Killen, S. S., Adriaenssens, B., Marras, S., Claireaux, G., & Cooke, S. J. (2016). Context dependency of trait repeatability and its relevance for management and conservation of fish populations. *Conservation Physiology*, 4, cow007.
- Kline, R. J., Khan, I. A., & Holt, G. J. (2011). Behavior, color change and time for sexual inversion in the Protogynous grouper (*Epinephelus adscensionis*). *PLoS One*, 6, e19576.
- Koeck, B., Pastor, J., Saragoni, G., Dalias, N., Payrot, J. Ô., & Lenfant, P. (2014). Diel and seasonal movement pattern of the dusky grouper *Epinephelus marginatus* inside a marine reserve. *Marine Environmental Research*, 94, 38–47.
- Kohn, M. J. (1999). You are what you eat. *Science*, 283(5400), 335–336. <https://doi.org/10.1126/science.283.5400.335>
- Kristensen, D. K., Kristensen, E., & Mangion, P. (2010). Food partitioning of leaf-eating mangrove crabs (Sesarinae): Experimental and stable isotope (^{13}C and ^{15}N) evidence. *Estuarine, Coastal and Shelf Science*, 87, 583–590.
- Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88, 42–48.
- Lazaridis, E. (2022). Lunar: Lunar phase & distance, seasons and other environmental factors. *Version 0.2-01*.
- Lennox, R. J., Engler-Palma, C., Kowarski, K., Filous, A., Whitlock, R., Cooke, S. J., & Auger-Méthé, M. (2019). Optimizing marine spatial plans with animal tracking data. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 497–509.
- Luiz-Júnior, O. J. (2005). Unusual behaviour of moray eels on an isolated tropical island (St. Paul's rocks, Brazil). *Coral Reefs*, 24, 501.
- Lysy, M., Stasko, A. D., & Swanson, H. K. (2014). nicheROVER: (Niche) (R) egion and Niche (Over)lap Metrics for Multidimensional Ecological Niches.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100, 603–609.
- Marques, S., & Ferreira, B. P. (2018). Sexual development and demography of the rock hind *Epinephelus adscensionis*, a protogynous grouper, in the south-west Atlantic. *Marine and Freshwater Research*, 69, 300.
- Matich, P., Ault, J. S., Boucek, R. E., Bryan, D. R., Gastrich, K. R., Harvey, C. L., Heithaus, M. R., Kiszka, J. J., Paz, V., Rehage, J. S., & Rosenblatt, A. E. (2017). Ecological niche partitioning within a large predator guild in a nutrient-limited estuary: Niche partitioning among estuarine predators. *Limnology and Oceanography*, 62, 934–953.
- Matley, J. K., Fisk, A. T., Tobin, A. J., Heupel, M. R., & Simpfendorfer, C. A. (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, J. K., Heupel, M. R., Fisk, A. T., Simpfendorfer, C. A., & Tobin, A. J. (2017). Measuring niche overlap between co-occurring *Plectropomus* spp. using acoustic telemetry and stable isotopes. *Marine and Freshwater Research*, 68, 1468–1478.
- Mavuti, K. M., Nyunja, J. A., & Wakwabi, E. O. (2004). Trophic ecology of some common juvenile fish species in Mtwapa Creek, Kenya Western Indian Ocean. *Journal of Marine Science*, 3, 179–188.
- Meyer, A., & Dierking, J. (2011). Elevated size and body condition and altered feeding ecology of the grouper *Cephalopholis argus* in non-native habitats. *Marine Ecology Progress Series*, 439, 203–212.
- Mitchenson, Y. S., Craig, M. T., Cheung, W., Choat, J. H., Mitcheson, Y. S. D., Craig, M. T., Bertoncini, A. A., Carpenter, K. E., & William, W. L. (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 and Fisheries*, 14, 119–136.
- Moretto, W. I., Stahl, A. K., & Mehta, R. S. (2022). Effects of acute temperature change on California moray prey manipulation and transport behavior. *Zoology*, 154, 126030. <https://doi.org/10.1016/j.zool.2022.126030>
- Neves, M., Kratina, P., Delariva, R., Jones, J., & Fialho, C. (2021). Seasonal feeding plasticity can facilitate coexistence of dominant omnivores in Neotropical streams. *Reviews in Fish Biology and Fisheries*, 31, 417–432.
- Nilsson, J.-Å., Brönmark, C., Hansson, L.-A., & Chapman, B. B. (2014). Individuality in movement: The role of animal personality. In L.-A. Hansson & S. Åkesson (Eds.), *Animal movement across scales* (pp. 90–109). Oxford University Press.
- Nolan, E. T., Downes, K. J., Richardson, A., Arkhipkin, A., Brickle, P., Brown, J., Mrowicki, R. J., Shcherbich, Z., Weber, N., & Weber, S. B. (2017). Life-history strategies of the rock hind grouper *Epinephelus adscensionis* at Ascension Island. *Journal of Fish Biology*, 91, 1549–1568.
- Noonan, M. J., Tucker, M. A., Fleming, C. H., Akre, T. S., Alberts, S. C., Ali, A. H., Altmann, J., Antunes, P. C., Belant, J. L., Beyer, D., Blaum, N., Böhning-Gaese, K., Cullen, L., Jr., de Paula, R. C., Dekker, J., Drescher-Lehman, J., Farwig, N., Fichtel, C., Fischer, C., ... Calabrese, J. M. (2019). A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs*, 89, e01344.
- Orrell, D., Webber, D., & Hussey, N. (2023). A standardised framework for the design and application of fine-scale acoustic tracking studies in aquatic environments. *Marine Ecology Progress Series*, 706, 125–151. <https://doi.org/10.3354/meps14254>
- Payne, N., Gillanders, B., Webber, D., & Semmens, J. (2010). Interpreting diel activity patterns from acoustic telemetry: The need for controls. *Marine Ecology Progress Series*, 419, 295–301.
- Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, 7, e6876.
- Piet, G. J., & Guruge, W. A. H. P. (1997). Diel variation in feeding and vertical distribution of ten co-occurring fish species: Consequences for resource partitioning. *Environmental Biology of Fishes*, 50, 293–307.
- Popple, I. D., & Hunte, W. (2005). Movement patterns of *Cephalopholis cruentata* in a marine reserve in St Lucia, W.I., obtained from ultrasonic telemetry. *Journal of Fish Biology*, 67, 981–992.
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703–718.
- Power, M. E. (1984). Depth distributions of armored catfish: Predator-induced resource avoidance? *Ecology*, 65, 523–528.
- Pratchett, M. S., Cameron, D. S., Donelson, J., Evans, L., Frisch, A. J., Hobday, A. J., Hoey, A. S., Marshall, N. A., Messmer, V., Munday, P. L., Pears, R., Pecl, G., Reynolds, A., Scott, M., Tobin, A., Tobin, R., Welch, D. J., & Williamson, D. H. (2017). Effects of climate change on coral grouper (*Plectropomus* spp.) and possible adaptation options. *Reviews in Fish Biology and Fisheries*, 27(2), 297–316. <https://doi.org/10.1007/s11160-016-9455-9>
- Reñones, O., Polunin, N. V. C., & Goni, R. (2002). Size related dietary shifts of *Epinephelus marginatus* in a western Mediterranean littoral ecosystem: An isotope and stomach content analysis. *Journal of Fish Biology*, 61(1), 122–137. <https://doi.org/10.1111/j.1095-8649.2002.tb01741.x>
- Reshetnikov, Y. S., Claro, R., & Silva, A. (1972). The pattern of feeding and the rate of digestion in some tropical predatory fish. *Journal of Ichthyology*, 12, 818–824.
- Rindorf, A., & Lewy, P. (2004). Bias in estimating food consumption of fish by stomach-content analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 2487–2498.
- RStudio Team. (2021). RStudio: Integrated Development Environment for R.
- Sánchez-Hernández, J., Vieira-Lanero, R., Servia, M. J., & Cobo, F. (2020). Feeding habits of four sympatric fish species in the Iberian Peninsula: Keys to understanding coexistence using prey traits. *Aquatic Toxicology*, 221, 186–195.
- Sadovy de Mitcheson, Y., Craig, M. T., Bertoncini, A. A., Carpenter, K. E., Cheung, W. W. L., Choat, J. H., Cornish, A. S., Fennessy, S. T., Ferreira, B. P., Heemstra, P. C., Liu, M., Myers, R. F., Pollard, D. A., Rhodes, K. L., Rocha, L. A., Russell, B. C., Samoilys, M. A., & Sanciango, J. (2013). Fishing groupers towards extinction: A global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries*, 14(2), 119–136. <https://doi.org/10.1111/j.1467-2979.2011.00455.x>
- Sadovy, Y. (1994). Grouper stocks of the Western Central Atlantic: The need for management and management needs. In M. H. Goodwin, G. T. Waugh, & M. J. Butler (Eds.), *Proceedings of the 43rd gulf and Caribbean fisheries institute* (pp. 43–64). Gulf and Caribbean Fisheries Institute.
- Shipley, O. N., & Matich, P. (2020). Studying animal niches using bulk stable isotope ratios: An updated synthesis. *Oecologia*, 193, 27–51.
- Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 23–32.
- Smith, D. G. (1989). Family Congridae. In *Fishes of the Western North Atlantic* (Vol. 9, pp. 460–567). Ears Foundation for Marine Research.
- 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.
- Stewart, B. D., & Jones, G. P. (2001). Associations between the abundance of piscivorous fishes and their prey on coral reefs: Implications for prey-fish mortality. *Marine Biology*, 138, 383–397.
- Stocks, J. R., Gray, C. A., & Taylor, M. D. (2014). Testing the effects of nearshore environmental variables on acoustic detections: Implications on telemetry Array design and data interpretation. *Marine Technology Society Journal*, 48, 28–35.
- Swadling, D. S., Knott, N. A., Rees, M. J., Pederson, H., Adams, K. R., Taylor, M. D., & Davis, A. R. (2020). Seagrass canopies and the performance of acoustic telemetry: Implications for the interpretation of fish movements. *Animal Biotelemetry*, 8, 8.
- Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., & Reist, J. D. (2015). A new probabilistic method for quantifying *n*-dimensional ecological niches and niche overlap. *Ecology*, 96, 318–324.
- The Ascension Island Government. (2020). *Ascension Island marine protected area monitoring, evaluation, and research strategy*. Ascension Island Government Conservation and Fisheries Directorate.
- The Ascension Island Government. (2021). *The Ascension Island marine protected area management plan 2021–2026*. Ascension Island Government Conservation and Fisheries Directorate.
- Thieumel, B., & Elmarhraoui, A. (2019). Suncalc: Compute sun position, sunlight phases, moon position and lunar phase. *R package version 0.5.0*. <https://CRAN.R-project.org/package=suncalc>

- Thomsen, B., Humborstad, O.-B., & Furevik, D. M. (2010). Fish pots: Fish behavior, capture processes, and conservation issues. In *Behavior of marine fishes* (pp. 143–158). John Wiley & Sons, Ltd.
- Thresher, R. E. (1984). *Reproduction in reef fishes*. T.F.H. Publications Inc.
- Udyawer, V., Dwyer, R. G., Hoenner, X., Babcock, R. C., Brodie, S., Campbell, H. A., Harcourt, R. G., Huveneers, C., Jaine, F. R. A., Simpfendorfer, C. A., Taylor, M. D., & Heupel, M. R. (2018). A standardised framework for analysing animal detections from automated tracking arrays. *Animal Biotelemetry*, 6, 1–14.
- Vacchi, M. (1999). Protection measures and juveniles of dusky grouper, *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae), in the Marine Reserve of Ustica Island (Italy, Mediterranean Sea). *Mar. Life*, 9 (2), 63–70.
- Vail, A., Manica, A., & Bshary, R. (2013). Referential gestures in fish collaborative hunting. *Nature Communications*, 4, 1765.
- Wantzen, K. M., de Arruda Machado, F., Voss, M., Boriss, H., & Junk, W. J. (2002). Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. *Aquatic Science*, 64(3), 239–251.
- Ward, J. N., Hinton, J. W., Johannsen, K. L., Karlin, M. L., Miller, K. V., & Chamberlain, M. J. (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*.
- Williams-Grove, L. J., & Szedlmayer, S. T. (2017). Depth preferences and three-dimensional movements of red snapper, *Lutjanus campechanus*, on an artificial reef in the northern Gulf of Mexico. *Fisheries Research*, 190, 61–70.
- Wirtz, P., Bingeman, J., Bingeman, J., Fricke, R., Hook, T. J., & Young, J. (2017). The fishes of Ascension Island, central Atlantic Ocean—new records and an annotated checklist. *Journal of the Marine Biological Association of the UK*, 97, 783–798.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*, 73, 3–36.
- Young, R. F., & Winn, H. E. (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.
- Zhang, Y., Xu, Q., Alós, J., Liu, H., Xu, Q., & Yang, H. (2015). Short-term Fidelity, habitat use and vertical movement behavior of the black rockfish *Sebastes schlegelii* as determined by acoustic telemetry. *PLoS One*, 10, e0134381.
- Zokan, M. A., Wyanski, D. M., White, D. B., & Sedberry, G. R. (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, 195–204.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Orrell, D. L., Sadd, D., Jones, K. L., Chadwick, K., Simpson, T., Philpott, D. E., & Hussey, N. E. (2025). Coexistence, resource partitioning, and fisheries management: A tale of two mesopredators in equatorial waters. *Journal of Fish Biology*, 106(5), 1377–1399. <https://doi.org/10.1111/jfb.15744>