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Seascape connectivity and the influence of predation risk on the movement of fishes inhabiting a back-reef ecosystem

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Abstract. The mangrove–seagrass–patch reef (MSP) ecosystem serves as the principal back-reef nursery for many reef fishes in the Caribbean, but the functional roles of habitats that form this seascape remain unclear. We assessed ecosystem and trophic connectivity of two common reef fishes (schoolmaster, *Lutjanus apodus*; white grunt, *Haemulon plumierii*) and one predator (great barracuda, *Sphyraena barracuda*) in a Caribbean MSP ecosystem using acoustic telemetry and natural dietary tracers. Triangulated positions from an acoustic positioning system indicated that *L. apodus* and *H. plumierii* relied on multiple habitats within this MSP ecosystem, occupying areas with more cover (lower risk) during the day and areas with less cover (higher risk) at night. During the day, both species exhibited limited movement away from structured habitats (e.g., mangroves, patch reef) and avoided the primary activity space of *S. barracuda* in the central channel over sand bottom or seagrass. At night, *L. apodus* moved into the channel and adjacent seagrass beds on the margin of this high-risk area when *S. barracuda* occurrence was reduced, suggesting that this species adjusts its foraging activities to minimize encounter rates with predators. *Haemulon plumierii* also displayed distinct day–night shifts with directed movements at twilight across higher risk habitat to nighttime locations in seagrass. Conspicuous changes in the rate of movement were also detected at different times of the day, and observed mismatches between movement rates of *S. barracuda* and our two potential prey species appeared to be a behavioral response to reduce their vulnerability. Dietary tracer analysis supported the premise that observed shifts to nocturnal habitats were associated with foraging, with significant contributions of organic matter derived from nighttime locations. Findings from this study clearly demonstrate that the configuration of habitats and spatiotemporal variability in predation risk are key determinants of movement and foraging activities for these species, indicating that an improved understanding of seascape connectivity is critical to the management of reef-dependent species.

Key words: acoustic telemetry; coral reef; foraging; habitat connectivity; migration; nursery habitat; stable isotopes.

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Introduction

Marine fishes commonly reside in complex seascapes, and their population dynamics are inherently linked to connectivity via movements at the habitat-, ecosystem-, and/or ocean-basin scale (Mumby and Hastings 2008, Rooker and Secor 2005, Rooker et al. 2008, Nagelkerken et al. 2015). Foraging success and survival of marine fishes are affected by their differential use of habitats (Clark et al. 2009, Hammerschlag et al. 2010), and spatiotemporal shifts are often assumed to be behavioral adjustments that optimize foraging success and minimize predation risk (Werner et al. 1983, Lima and Dill 1990). Given that many marine fishes require or utilize multiple habitats or ecosystems during ontogeny, the decline or loss of any component of a seascape can profoundly impact year-class strength (Dahlgren and Eggleston 2000). In response, an improved understanding of the causes of spatiotemporal shifts, including those linked to predator activity, is critically needed to determine the value and functional role of different components of a seascape.

Predation is a fundamental mechanism regulating the survival and dynamics of prey populations (Werner and Anholt 1993). Predators can influence the distribution and abundance of prey directly (consumptive) and indirectly through behavioral adjustments to predation risk (Trussell et al. 2006, Matassa et al. 2016), and the threat of predation typically varies in time and space across heterogeneous marine ecosystems (Wirsing et al. 2008). Vulnerability of prey within a seascape or landscape (i.e., terrestrial ecosystems) is determined by both the spatial configuration of the habitat patches and boundaries and the spatiotemporal distribution of both predators and conspecifics (Tambling et al. 2012). As a result, ranging (migration) and foraging behaviors of prey are presumably structured to some degree by the perceived risk associated with different components of a seascape (Rooker and Dennis 1991, Hammerschlag et al. 2010).

The mangrove–seagrass–patch reef (MSP) ecosystem serves as the principal back-reef nursery for a variety of reef-dependent species, and these shallow water seascapes are increasingly threatened by coastal development (Mumby et al. 2004, Nagelkerken et al. 2015). Spatially diverse assemblages of juvenile fishes within MSP ecosystems are common, with individuals frequently crossing multiple habitats or ecotones on a daily basis (Nagelkerken and van der Velde 2004, Adams et al. 2006, Nagelkerken et al. 2008). Spatial shifts by juvenile reef fishes are commonly assumed to be predator-mediated responses, with individuals moving between safe shelter areas of higher habitat complexity and more precarious open areas with lower complexity. Moreover, the nature and timing of spatial shifts appear to be influenced by predators, with prey altering their movements to minimize encounter rates with predators, following the "predation risk allocation hypothesis" of Lima and Bednekoff (1999). While directed habitat shifts within the MSP ecosystem are common and known to vary ontogenetically, the most conspicuous and predictable redistribution of fishes occurs between the day and night during twilight migrations (Helfman 1986, Rooker and Dennis 1991). Although general characterizations of diel distributions and habitat connectivity of juvenile fishes within MSP ecosystems have been previously published (Nagelkerken et al. 2000, Appeldoorn et al. 2009), the influence of predation—direct or perceived—on the habitat use and movement of juvenile reef fishes remains poorly understood.

The purpose of the current study was to assess the population connectivity of two reef fishes that commonly use the MSP ecosystem as nursery habitat: schoolmaster [snapper] (*Lutjanus apodus*) and white grunt (*Haemulon plumierii*). We characterized the movement and habitat use of juvenile *L. apodus* and *H. plumierii* using an emerging technology (acoustic positioning system) and then related fine-scale movement data of both species to predation risk by concurrently tracking a common predator in this MSP ecosystem, great barracuda (*Sphyraena barracuda*). The selected MSP ecosystem also included an open (deep channel with sand bottom) or higher risk habitat, which allowed us to further assess the influence of predation risk on both species. In addition, we incorporated dietary tracer data (stable isotopes) to investigate the link between spatiotemporal shifts within the MSP ecosystem and trophic connectivity for all three species. Similar to observations of preferential selection by prey to safer regions of terrestrial landscapes

(Valeix et al. 2009), we hypothesized that habitat use as well as the timing and magnitude of trans-boundary movements by *L. apodus* and *H. plumierii* was influenced by the presence of predators and/or the perceived predation risk associated with particular habitats or areas. Given that both species are known to display conspicuous day–night movements across seascapes, we anticipated that these directed and predictable habitat shifts were related to foraging.

Methods

Study area

The study was performed in a back-reef seascape in the Guanica Biosphere Reserve located off the southwestern coast of Puerto Rico (Fig. 1). The study site included two small mangrove keys within the Cayos de Caña Gorda and included all habitats typically found within the MSP ecosystem in the Caribbean: red mangrove (*Rhizophora mangle*), seagrass, and patch reefs. The mangrove keys within the study site were separated by a deeper channel (Fig. 1) with a sand bottom and mixed stands of seagrass, mainly turtle grass (*Thalassia testudinum*) with lesser amounts of manatee grass (*Syringodium filiforme*) and shoal grass (*Halodule wrightii*) present from the channel edge to the mangrove prop roots on each side of the channel. Large stands of *T. testudinum* were also present on the leeward side of each mangrove key in the northwestern region of the seascape. The southeastern region of the seascape contained several small patch

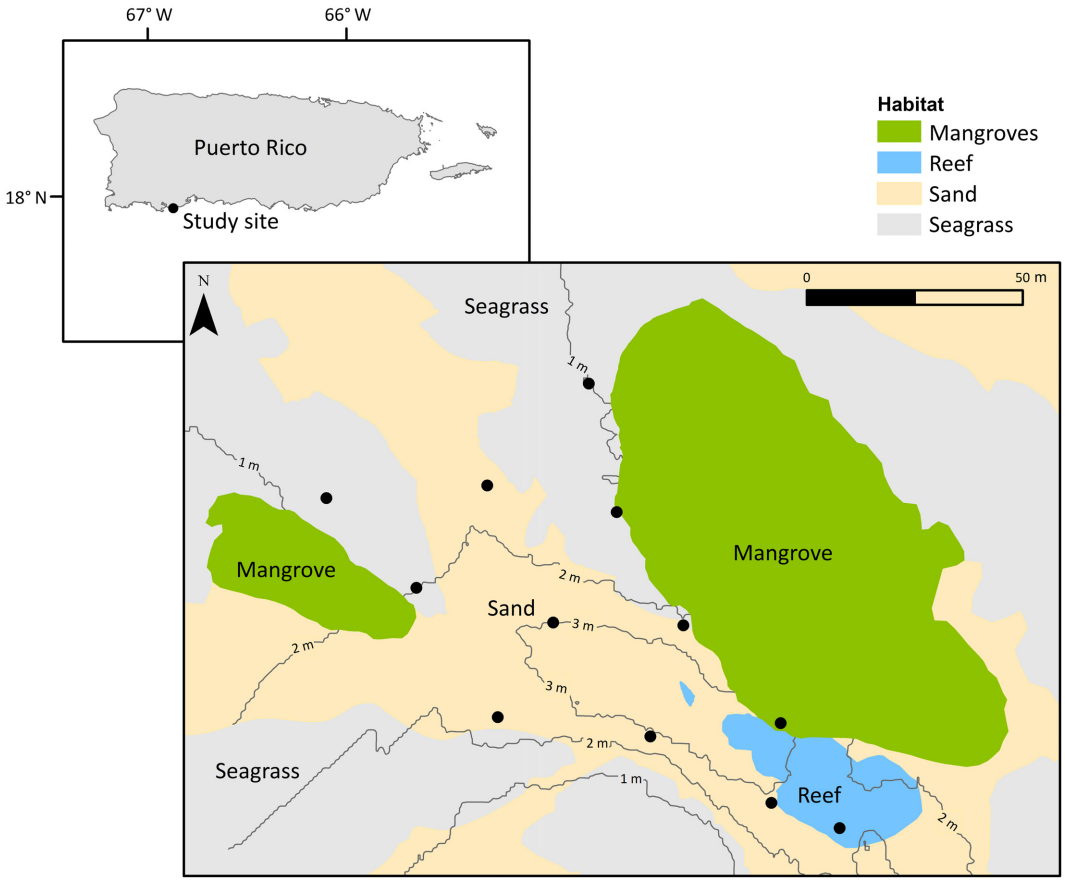

Fig. 1. Map of study site in the Guanica Biosphere Reserve located off the southwestern coast of Puerto Rico. Large inset map shows the spatial configuration of habitats within the mangrove–seagrass–patch reef ecosystem and the location of receivers (solid circles) in the acoustic positioning system. Bathymetry is also denoted with contour lines.

reefs, comprised primarily of *Porites astreoides*, *Porites porites*, *Siderastrea radians*, and *Siderastrea siderea*.

High-resolution bathymetric and benthic habitat maps were created using both ortho-rectified aerial imagery and in situ observation. Ortho-rectified aerial images (resolution 0.3 m; US Army Corps of Engineers 2006) were used to determine initial boundaries between habitats within the study area. The composition and boundary of each habitat patch were then classified in situ using a handheld GPS unit to both ground truth and refine the discrimination of benthic habitats. Habitats were then digitized in a geographic information system (ArcGIS 10.2.2, ESRI, Redlands, California, USA) for visualization and analysis purposes. Bathymetric maps were constructed from in situ depth observations recorded at 138 locations within the seascape. The majority of these locations were gridded at approximately 5-m intervals throughout the study area; however, locations were also strategically placed in areas of high bathymetric relief (i.e., channel edges) to ensure accurate representation of these features. Depth was then interpolated using ordinary kriging to create a continuous raster surface. Current measurements taken with a flowmeter (Model 2030R, General Oceanics, Miami, Florida, USA) at 15 locations within the seascape were used to classify areas of high or low current velocity within the study site.

Acoustic telemetry

Juvenile *Lutjanus apodus* (197.2 ± 22.7 mm total length [TL] ± 1 standard deviation [SD]) and *Haemulon plumierii* (190.4 ± 13.6 mm TL) were captured via underwater hook and line or trapped with a 30-m L × 1 m H seine net at the study site (Appendix S1: Table S1). Both species were captured in the mangroves or on patch reefs within 20 m from the mangrove edge. Our model predator, *Sphyraena barracuda* (390.8 ± 31.8 mm TL), was captured with a seine net from the study site. Vemco V8-4H transmitters (Vemco, Bedford, Nova Scotia, Canada) were surgically implanted into all three species: *L. apodus* (n = 10), *H. plumierii* (n = 10), and *S. barracuda* (n = 5). Each transmitter was inserted in the abdominal cavity through a small incision between anal and pelvic fins. Similar to Moulton et al. (2017), one or two interrupted stitches with absorbable sutures (4-0 Ethicon vicryl) were used to close the wound. Post-operative fish were placed in a holding tank with aeration for 15–30 min and then released at capture sites. All transmitters were programmed with a random delay of 80–160 s and tagging occurred from 21 May to 26 May 2014. Total number of tagged animals released into the array was restricted (n = 25) to minimize acoustic collisions based on recommended maximum capacity of the acoustic positioning system given our transmitter programming (short delays = increased collisions), receiver spacing, high site fidelity of study species, and limited seascape size.

An acoustic positioning system comprised of 12 Vemco VR2W omnidirectional receivers was deployed within the selected seascape, encompassing a detection area of approximately 30,000 m^2. Acoustic receivers within the array were closely spaced (~50 m) with overlapping detection ranges, which allowed us to triangulate fish positions (Dance and Rooker 2015). To minimize the effects of internal transmitter placement on detection range (Dance et al. 2016), receiver spacing was determined from a priori range testing using an internally tagged *H. plumierii* placed at several locations within the study area. Twelve synchronizing transmitters or sync tags (Vemco V13-1H, 69 kHz) with a nominal delay of 600 s (range: 500–700 s) were co-located with receivers within the acoustic positioning system to synchronize the internal clocks of the VR2W receivers and act as reference tags. Acoustic receivers were either attached to 2″ diameter PVC poles inserted in the sediment or in poles cemented into cinder blocks (e.g., receivers in the channel). The array was in place until 30 June 2014, and the minimum duration of the tracking trial for any tagged fish was 35 d (maximum = 41 d).

Dietary tracers

The potential carbon contribution of four primary producers (phytoplankton, seagrass, mangroves, and benthic microalgae [BMA]) was investigated for *L. apodus*, *H. plumierii*, and *S. barracuda*. Surface water samples for particulate organic matter (POM), a proxy for phytoplankton, were collected in 4-L containers and vacuum-filtered (<130 kPa) immediately upon returning to the laboratory onto precombusted 0.7-μm GF/F filters, and then frozen (−20°C). Sediment collections of BMA were taken using a

grab sampler, and the vertical migration technique (Wells et al. 2008) was used to separate BMA from the substrate. Benthic microalgae were filtered and frozen for stable isotope analysis. Mangrove leaves and seagrass blades were carefully collected by hand at the study site and stored in ziplock bags in a cooler until returning to the laboratory. This plant material was then scraped with a spatula to remove all encrusting organisms and epiphytic algae and stored frozen (−20°C). *Lutjanus apodus*, *H. plumierii*, and *S. barracuda* used for diet analysis were collected with pole spears after the completion of the tagging trial.

Samples from all primary producers and fishes were thawed and then dried at 60°C for 24–48 h. Dried filters for POM were packed into tin capsules. Muscle tissue from fishes and plant tissue (blades, leaves) were dried and then powdered using a mortar and pestle, and approximately 1.0 mg was packaged in tin capsules. All samples were analyzed for stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) at the Stable Isotope Facility at the University of California at Davis, CA, USA. Isotopic ratios are reported relative to Vienna PeeDee belemnite for carbon and atmospheric N_2 for nitrogen. Lipids were not extracted from fish tissue; however, C:N ratios were low (<4) across the size spectrum of fishes, indicating a low lipid content and little influence of lipids on fish tissue $\delta^{13}C$ values (Post et al. 2007). Isotopic values are expressed using the standard δ notation, as parts per thousand (‰).

Data analysis

Time-indexed, triangulated positions from the acoustic positioning system were filtered by horizontal position error (HPE) following Dance and Rooker (2015). Based on analysis of 12 in situ static transmitters within the array, we observed that triangulated positions with HPE <12 generally correspond to positioning errors of <2 m. In response, further analysis of position data was limited to HPEs below this threshold. Also, positions obtained within the first 30 min of the fish being released into the seascape were omitted to minimize the effect of release location on resulting patterns of habitat use. The influence of time of day on location in the seascape was investigated by partitioning triangulated positions among day, night, and crepuscular (twilight) periods. Given that the timing of sunrise and sunset changed over the course of the trial, a midpoint for sunrise and sunset between observed times on 26 May and 26 June was used. Periods 50 min before sunrise (05:52 h) and 50 min after sunset (19:01 h) approximated the beginning and end of twilight (civil and nautical) and were used here to denote the pre-sunrise and post-sunset twilight periods.

Triangulated positions were first classified to habitat (mangrove, seagrass, patch reef, sand) to estimate the proportion of detections for tagged *L. apodus*, *H. plumierii*, and *S. barracuda* for each habitat type within the seascape during three time periods (day, night, and twilight) in ArcGIS 10.22. Multivariate analysis of variance (MANOVA) was used to determine whether daily occurrence within a specific habitat (percent of detection by habitat by day) varied among the three time periods (day, night, and twilight). Univariate contrasts (ANOVAs) based on daily percent occurrence by time period within each habitat were also performed, but given that all models were significant, only MANOVA results are presented. The primary activity space of *S. barracuda* (i.e., predator) was defined as the 75% isopleth of a kernel density estimate (kde) from all triangulated positions using Geospatial Modeling Environment (GME, Beyer 2012). Initially, a mean 75% kde for *S. barracuda* was generated to define high use areas during each time period; however, the number of triangulated positions for this species was very low at night and habitat use did not vary among the three time periods. Thus, an overall activity space (75% kde) was used to denote the high use area of the model predator kde in our study area. In turn, the spatial configuration of the predator kernel density plot was then used to assess whether habitat use and movements of *L. apodus* and *H. plumierii* were linked to predator activity. Although direct predation by *S. barracuda* on our two potential prey species was not observed, predation on grunts and snappers by this predator is known to occur (Randall 1967, Foss 2016). It should also be noted that our model predator co-occurred with larger conspecifics in the seascape and also used similar habitats (sand bottom in the center of channel with higher current velocity) to other piscivores found in the Caribbean, including jacks, groupers, and sharks (Bohlke

and Chaplin 1993). This indicates that the activity space derived for tagged *S. barracuda* (<430 mm TL) likely applies to both larger conspecifics and other predators that frequent shallow water ecosystems in the Caribbean.

Locations of *L. apodus* and *H. plumierii* within the seascape were further analyzed using Euclidean distance-based analysis (EDA; Conner et al. 2003) to investigate the possible influence of predation threat on position and movement within the seascape. This approach is commonly used to evaluate habitat selectivity and important movement corridors in marine ecosystems (Furey et al. 2013, Dance and Rooker 2015). Here, EDA ratios were used to describe habitat use of *L. apodus* and *H. plumierii* relative to the high use areas of a potential predator (i.e., 75% kde of *S. barracuda*). Euclidean distance-based analysis ratios were calculated by first estimating distances of all triangulated positions to the nearest border of the predator activity space (i.e., 75% kde), with all positions inside the predator kde assigned a distance of 0. Distances of 1000 random positions to the nearest border of the predator activity space were also determined. For each individual, the mean distance of all fish positions relative to the predator activity space was divided by the mean distance of all random points to the predator activity space, and EDA ratios were estimated for day, night, and twilight. Analysis of variance (ANOVA) was used to determine whether *L. apodus* or *H. plumierii* displayed non-random use of the seascape, with values >1 indicating that fish positions were farther from the predator zone than predicted by chance, which is indicative of predator avoidance.

Rate of movement (m/min) was calculated for all three species to determine whether reactive movement and/or escape response (e.g., maximum swimming) varied as a function of time period (day, night, and twilight) using ANOVA. Our movement metric was calculated as the linear distance between two triangulated positions divided by the time elapsed between the successive detections. Rate of movement estimates were limited to successive detections occurring within a 10-min period to reduce the possibility of underestimating distance traveled due to missing locations.

For dietary tracers, the contribution of primary producers (i.e., sources) to *L. apodus*, *H. plumierii*, and *S. barracuda* was estimated with Bayesian mixing models using stable isotope analysis in the software R (SIAR) version 4.0 (Parnell et al. 2010). The purpose of using SIAR was to quantify contributions of primary producer categories to consumers in order to specify consumer–resource relationships that may not be possible to calculate otherwise (Phillips et al. 2014). Because seagrass and BMA maintained similar $\delta^{13}C$ and $\delta^{15}N$ values, we excluded BMA from SIAR with the understanding that a fraction of the seagrass contribution may be due to BMA production. Bayesian mixing models combining seagrass/BMA into a single source were similar to our three-source model that did not include BMA, justifying the approach adopted. For each three-source mixing model, a carbon trophic enrichment factor of 1.0‰ (SD ± 0.3‰) was used (DeNiro and Epstein 1978, Fry and Sherr 1984). $\delta^{15}N$ enrichment values range from 2.5‰ to 3.5‰ (SD ± 0.6‰) in aquatic systems (Vander Zanden and Rasmussen 2001, Vanderklift and Ponsard 2003), and therefore, a nitrogen enrichment value of 3.0‰ was used per trophic position (Fry and Sherr 1984, Wells et al. 2017). Model inputs for SIAR included no concentration dependence, 500,000 iterations, and 50,000 discards.

Results

Habitat use within the seascape

All *Lutjanus apodus*, *Haemulon plumierii*, and *Sphyraena barracuda* tagged with V8 transmitters were detected on multiple days within the MSP seascape. Over a half million fish detections were recorded during the trial, yielding a total of 29,018 triangulated positions with HPE <12: *L. apodus* (15,348), *H. plumierii* (11,438), and *S. barracuda* (2232). Although triangulated positions were available for all tagged fish, certain individuals within each species accounted for a large fraction of the estimated positions, with multiple individuals having a minimum of 1000 triangulated positions: *L. apodus* (#04, 05, 08), *H. plumierii* (#04, 06, 09; Appendix S1: Table S1). Positions for each species partitioned among day, night, and twilight indicated conspicuous diel shifts in habitat use by both *L. apodus* and *H. plumierii* (MANOVAs, $P < 0.001$; Fig. 2).

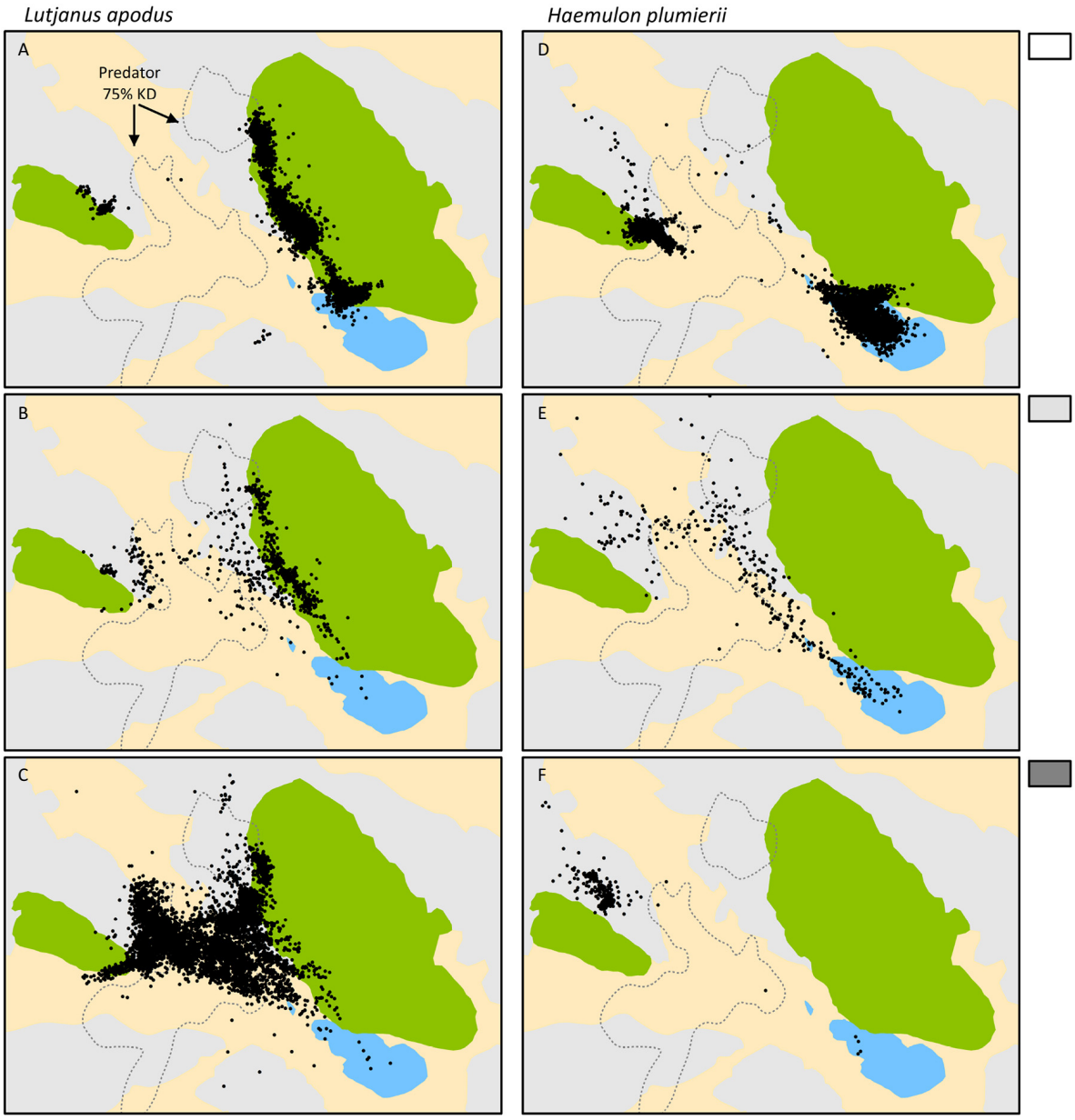

Fig. 2. Summary of all triangulated position estimates (based on acoustic positioning system) for tagged schoolmaster (*Lutjanus apodus*; A–C) and white grunt (*Haemulon plumierii*; D–F) during day, dawn/dusk, and night within the mangrove–seagrass–patch reef ecosystem. Mean 75% kernel distributions of great barracuda (*Sphyraena barracuda*) also shown as indicated by areas outlined with dashed line. Time periods shown with different background fills on right margin of plot: day (white; A, D), dawn/dusk (light gray; B, E), night (dark gray; C, F).

Triangulated positions for *L. apodus* were nearly all within the mangrove prop roots during the day, and the mean proportion of daytime positions in this habitat was 91.7% (Figs. 2, 3). Although *L. apodus* was detected in other habitats, daytime occurrence in these habitats was very limited (seagrass 2.5%, patch reef 5.4%, sand 0.4%). Daytime occurrence of juvenile *H. plumierii* was highest in the patch reef (51.4%) habitat, but a large fraction of our daytime

detections for this species also occurred in the mangrove prop roots (30.3%), with more limited use of seagrass (14.5%) and sand (3.8%) habitat. In contrast to *L. apodus* and *H. plumierii*, nearly all *S. barracuda* daytime positions were located within the sand (channel) or seagrass habitats (62.8% and 36.0%, respectively), which is in accord with our hypothesis that the sand habitat within the channel and seagrass beds on the margin of the channel represent a predator hotspot within this MSP ecosystem.

At night, occurrence of *L. apodus* and *H. plumierii* shifted and nocturnal areas used by both species were markedly different from daytime locations. Triangulated positions for *L. apodus* were predominantly in the sand (channel) habitat (59.9%); however, individuals were also present in seagrass (27.4%) and mangrove (12.6%) habitats (Fig. 2). In contrast, nearly all positions for *H. plumierii* at night were in seagrass (97.4%), suggestive of highly consistent movements into this habitat from daytime refuge or foraging areas. Similar to the daytime pattern, over 90% of the positions of *S. barracuda* at night were in the sand habitat, but triangulated positions at night were very limited and insufficient to characterize diel shifts in habitat use.

Conspicuous day–night shifts in habitat use by both *L. apodus* and *H. plumierii* indicated directed movement away from daytime resting or foraging areas. Triangulated positions during twilight (dawn/dusk denoted as 50 min before sunrise or 50 min after sunset) showed that such movements occurred during this time period, particularly for *H. plumierii*, with individuals often present in transitional areas between daytime and nighttime locations (Fig. 2). As a result, positions during dawn/dusk also represented twilight migration pathways or corridors used by individuals. Positions of *H. plumierii* during twilight showed increased occurrence in the sand habitat (17.9%), signifying a common migration pathway (crossing to channel) taken by this species. Even though individuals traversed the sand (channel) habitat during twilight migrations to seagrass beds, the chosen pathway or movement corridor across the channel minimized overlap with *S. barracuda* activity space, which may represent a behavioral response to reduce predation risk. For *L. apodus*, the majority of positions during dawn/dusk were in seagrass (36.9%) and mangrove (41.9%) habitats, showing that movement into the sand habitat within the channel occurred after civil or nautical twilight (i.e., later at night; Fig. 3).

Predator–prey associations within the seascape

Mean EDA ratios (±1 standard error [SE]) of *L. apodus* and *H. plumierii* indicated non-random use of the area used primarily by the tagged *S. barracuda*. *Lutjanus apodus* were significantly closer to the predator 75% kde at night (EDA 0.29 ± 0.12) and to a lesser degree during dawn/dusk (EDA 0.40 ± 0.11) when individuals moved away from the mangrove prop roots into adjacent seagrass and sand habitat within or near the channel (Fig. 2, ANOVA, $P < 0.05$). During the day, the mean EDA ratio for *L. apodus* (EDA 0.84 ± 0.29) was at least twofold higher than other periods (ANOVA, $P < 0.01$), indicating that individuals significantly increased their distance from areas heavily used by *S. barracuda* (Fig. 4). Similar to *L. apodus*, *H. plumierii* were farthest from the predator 75% kde during the day (EDA 1.84 ± 0.09; Fig. 4). The mean EDA ratio was also high during the nighttime period (EDA 1.49 ± 0.35) and again indicative of predator avoidance by *H. plumierii* as individuals moved to the interior of seagrass beds on the leeward side of the seascape (Fig. 2). The lowest mean EDA ratio for *H. plumierii* was present during crepuscular periods (EDA 1.21 ± 0.04), which is not unexpected because twilight migrations often crossed the channel or areas commonly frequented by *S. barracuda*. Although diel shifts in association with the predator activity space were observed for both species, results were not significant (ANOVA, $P > 0.05$), which is possibly due to the fact that triangulated positions were only available for a fraction of tagged *L. apodus* ($n = 5$) and *H. plumierii* ($n = 3$) during all three time periods.

Rate of movement within the seascape

Conspicuous changes in the rate of movement were detected at different times of the day for both *L. apodus* and *H. plumierii*. Mismatches in movement rates between our model predator and both *L. apodus* and *H. plumierii* were observed, possibly leading to lower detection or encounter rates (Fig. 5). A conspicuous diel change in the rate of movement was observed for

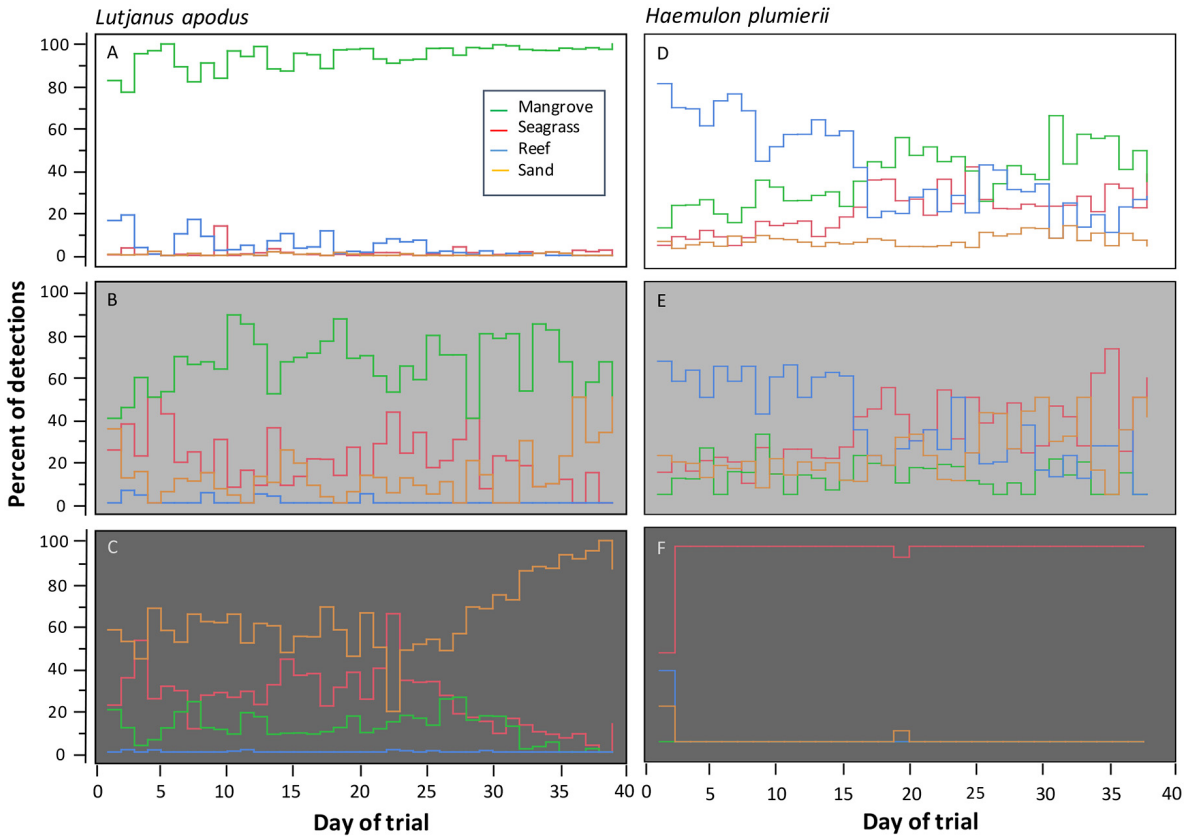

Fig. 3. Mean percentage of detections (based on all points each day) for schoolmaster (*Lutjanus apodus*; A–C) and white grunt (*Haemulon plumierii*; D–F) by habitat type within the mangrove–seagrass–patch reef ecosystem. Occurrence at each time period and day denoted with step plots that connect a horizontal line from each point to the *x* value of the following point and then a vertical line to that point. Estimates of percent occurrence shown for each habitat type (mangrove, seagrass, patch reef, and sand channel), and time periods denoted with different background fills on plots: day (white), dawn/dusk (light gray), night (dark gray).

L. apodus with significantly lower movement during the day (1.92 m/min ± 0.04) relative to night or twilight where mean rates of movement were nearly double the rate observed during the day (ANOVA, $P < 0.01$). Mean rate of movement (m/min ± 1 SE) for *H. plumierii* was relatively similar between the day (1.48 m/min ± 0.04) and night (1.92 ± 0.02), but increased significantly at both dawn (4.69 m/min ± 0.07) and dusk (5.77 m/min ± 0.08) when individuals transitioned from daytime to nighttime areas (ANOVA, $P < 0.01$). Although the daytime period was characterized as having the lowest rate of movement for both *L. apodus* and *H. plumierii*, the mean rate of movement by *S. barracuda* peaked during the day (4.70 m/min ± 0.20) as well as during crepuscular periods (dawn: 4.82 m/min ± 0.41, dusk: 4.89 m/min ± 0.85), indicating an apparent mismatch in activity and/or timing of movement (i.e., habitat shifts) by predator and prey within this MSP ecosystem (Fig. 5).

Dietary signatures and links to habitat selection

Mixing models based on producer and consumer $\delta^{13}C$ and $\delta^{15}N$ values indicated that the primary source(s) of organic matter supporting *L. apodus* and *H. plumierii* was different (Fig. 6). For *L. apodus*, the mean contribution estimate of POM was 80.0% (±17.3 SD), implying that phytoplankton-based production was essential to lower trophic levels (i.e., prey) supporting this

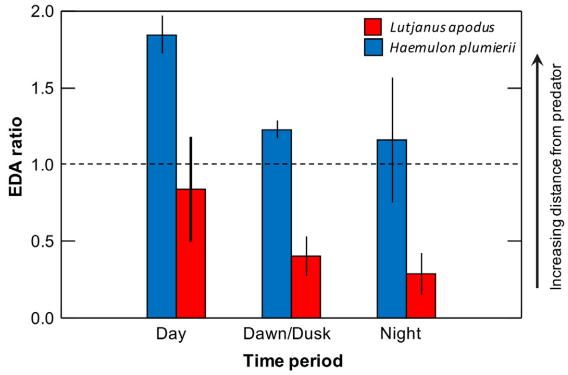

Fig. 4. Mean Euclidean distance-based analysis (EDA) ratios for schoolmaster (*Lutjanus apodus*) and white grunt (*Haemulon plumierii*) in relation to 75% kernel density of great barracuda (*Sphyraena barracuda*). Ratios given by time period (day, dawn/dusk, night) relative to each high-risk area. Larger ratios indicate that fish positions were farther from the boundary of the predator activity space. Error bars denote ±1 standard error.

species (Fig. 6). More limited contributions were predicted from mangrove (10.6% ± 9.4 SD) and seagrass/BMA (9.4% ± 9.9 SD) production. In contrast, mean contribution estimates for *H. plumierii* highlighted the importance of

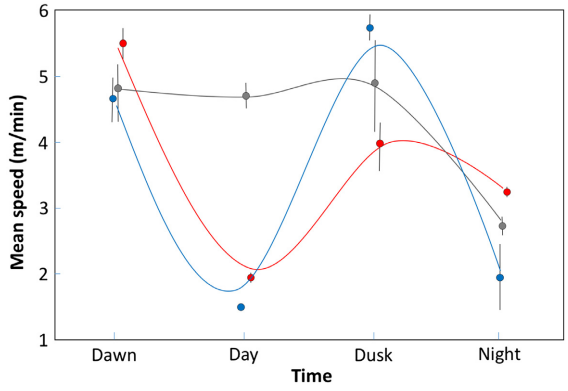

Fig. 5. Mean rate of movement (m/min) by schoolmaster (*Lutjanus apodus*; red), white grunt (*Haemulon plumierii*; blue), and great barracuda (*Sphyraena barracuda*; gray) in relation to time period (dawn, day, dusk, night). Lines represent locally weighted scatterplot smoothing (LOWESS) applied to mean speed value for each time period. Error bars denote ±1 standard error.

seagrass/BMA as an important source of carbon (40.7% ± 6.2 SD), but phytoplankton-based production remained important (POM = 54.2% ± 10.3 SD). Again, mangrove-derived carbon was limited (5.1% ± 4.3 SD). Mean contribution estimates for *S. barracuda* (POM 52.1% ± 20.7 SD, seagrass 33.8% ± 12.5 SD, mangrove 14.1% ± 9.0 SD) were more similar to values observed for *H. plumierii*, confirming that seagrass- or BMA-associated production is important to both species.

Discussion

Habitat use by both *Lutjanus apodus* and *Haemulon plumierii* indicated reliance on complex back-reef ecosystems comprised of mangroves, seagrass, and coral patch reefs, which is well reported in the literature (Nagelkerken et al. 2015). Both species were common constituents of mangrove prop roots during the day, and several studies have documented the importance of mangroves to the replenishment of snapper and grunt populations (Nagelkerken et al. 2002, Mumby et al. 2004, Serafy et al. 2015). The mangrove nursery paradigm suggests that for certain species this habitat, often in conjunction with seagrass beds, disproportionately contributes to the production of associated species (Kimirei et al. 2013). Juvenile *L. apodus* and *H. plumierii* showed strong dependence on both mangroves and seagrass within the MSP ecosystem, and the value and functional role of each habitat on the foraging success or survival potential of each species appears to be distinctly different.

Several studies have observed shifts in habitat use (i.e., connectivity) within MSP ecosystems for grunts and snappers (Dorenbosch et al. 2007, Hitt et al. 2011*a*, Nagelkerken et al. 2015), and salient changes in habitat use by these taxa are presumably linked to predation risk (Hammerschlag et al. 2010). Direct or indirect behavioral adjustments due to predation risk are known to strongly influence the distribution and abundance of both aquatic (Hixon and Carr 1997, Almany and Webster 2006, Stier et al. 2014) and terrestrial (DeCesare et al. 2014, Chudzińska et al. 2015) fauna. Moreover, predation risk is known to shape migration patterns of prey, with individuals often altering their movement, habitat use, and foraging activity to avoid encounters

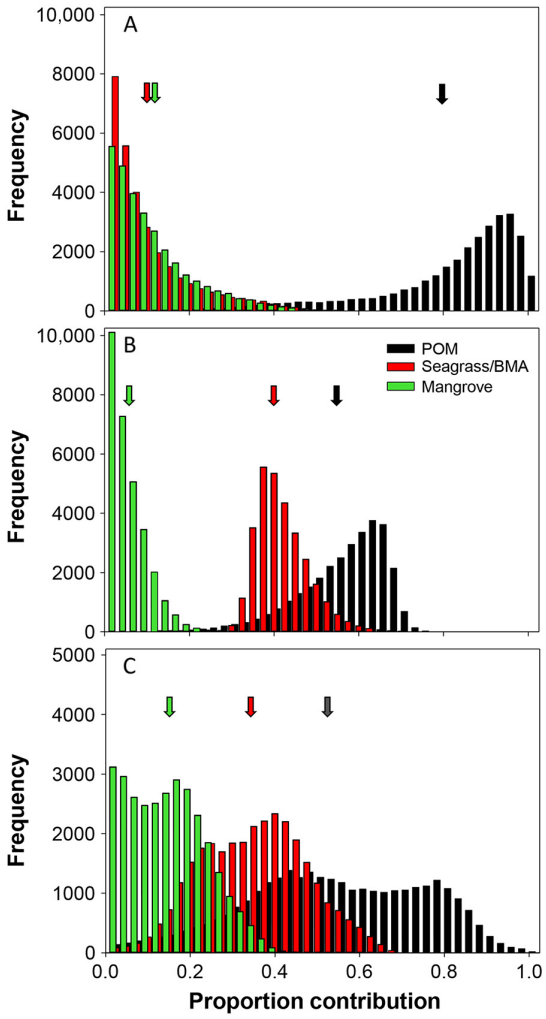

Fig. 6. Source (producer) contribution estimates for (A) schoolmaster (*Lutjanus apodus*), (B) white grunt (*Haemulon plumierii*), and (C) great barracuda (*Sphyraena barracuda*). Mean $\delta^{13}C$ and $\delta^{15}N$ values (±1 standard deviation) used in SIAR for producers and consumers denoted below: mangrove ($\delta^{13}C$: −28.3 ± 1.1, $\delta^{15}N$: 1.4 ± 0.6), particulate organic matter (POM) (−16.5 ± 0.6, 5.0 ± 0.4), seagrass (−7.1 ± 0.9, 0.9 ± 0.7), benthic microalgae (BMA) (−8.9 ± 0.8, 3.4 ± 0.4), *L. apodus* (−15.9 ± 3.3, 9.2 ± 0.4), *H. plumierii* (−12.1 ± 0.5, 9.0 ± 0.4), *S. barracuda* (−13.7 ± 0.8, 9.6 ± 0.2). $\delta^{15}N$ for each producer and each consumer was between 5 and 10 samples, and BMA was not included as a source in SIAR results shown.

with predators (Catano et al. 2017). In the present study, we observed conspicuous shifts for *L. apodus* from daytime locations within the mangrove prop roots to nighttime areas in the channel over sand bottom or adjacent seagrass beds near the edge of this feature. A striking, albeit different type of day–night shift was observed for *H. plumierii* with individuals moving from mangroves or patch reefs to seagrass beds on the leeward sides of both mangrove keys at night.

Nocturnal shifts in distribution are often attributed to tradeoffs between foraging success and predation risk (Creel and Christianson 2008). In response, habitat selection by both *L. apodus* and *H. plumierii* at night is likely a function of both food resources and the spatial distribution of predators in the seascape. For *L. apodus*, most of the positions at night were in the sand (channel) and seagrass habitats on the margin of the channel, which were the areas commonly frequented by *Sphyraena barracuda* during the day. Movement by *L. apodus* into the sand (channel) habitat explains why observed EDA ratios were lowest for this species during the night, implying that individuals moved closer to the predator and, in turn, increased their predation risk. However, the activity space of *S. barracuda* was based primarily on daytime positions and detections at night were limited. This appears to indicate movement by this predator away from the channel or seascape at night and potentially outside the detection range of the receivers. Nocturnal movements by *S. barracuda* away from the sand (channel) appear to lead to lower risk in this habitat, possibly resulting in more unrestricted foraging opportunities for *L. apodus*. Although salient day–night shifts in habitat use were also present for *H. plumierii*, nocturnal locations for this species were predominately in seagrass beds located on the leeward side of both mangrove keys and often several hundred meters from daytime locations. Interestingly, *H. plumierii* commonly crossed the high-risk sand (channel) habitat during twilight periods on the way to nighttime locations, and directed movement of grunts into seagrass beds are assumed to be linked to foraging (Rooker and Dennis 1991, Burke 1995, Nagelkerken et al. 2008).

Twilight migrations between daytime to nighttime areas are common for constituents of tropical reefs and MSP ecosystems (Hobson 1975, Helfman 1986, Hitt et al. 2011*a*, *b*), despite the fact that predator activity often peaks during

twilight periods (Catano et al. 2017). Coral reef fishes appear to anticipate and respond to diel shifts in predation risk (Rizzari et al. 2014, Catano et al. 2016), and taxa investigated here (i.e., grunts) are known to migrate over limited time intervals before or after civil twilight to ostensibly reduce encounters with predators (Rooker and Dennis 1991, Danilowicz and Sale 1999). In the present study, an acoustic positioning system was used to further evaluate diel migrations with the goal of clarifying relationships between predation risk and three components of these migrations: time/duration, migration pathway, and speed of movement. *Haemulon plumierii* displayed directed and consistent twilight movements with individuals commonly crossing the high-risk channel in the same location on successive nights.

Interestingly, movement by juvenile *H. plumierii* across the channel was rapid, and the highest rate of movement (mean: 13.1 m/min) by this species occurred during limited time intervals before (dawn) or following (dusk) the beginning of civil twilight. Previous research has shown that reactive movement and escape response (e.g., mean or maximum swimming speed/acceleration) of teleost and amphibian prey are faster in response to a perceived predation risk (Ramasamy et al. 2015, Weterings et al. 2016). The higher swimming speed of *H. plumierii* displayed during the twilight period is likely a learned response from past experiences with predators or an innate behavior associated with movement into an unprotected area (i.e., less cover) that lowers the probability of encountering or being captured by *S. barracuda* or other predators (e.g., carangids) that were observed in the channel. Moreover, the timing of crepuscular migrations by *H. plumierii* occurred within a very restricted period and nearly all (>90%) of the observed channel crossings transpired during the first 12 min following civil twilight at sunset or the 12 min before the start of civil twilight at dawn. "Anti-predation windows" can occur during brief intervals at dawn and dusk at intermediate levels of light intensity, and movements during these periods have been shown to reduce the risk of predation (Clark and Levy 1988). Thus, the brief twilight intervals used by *H. plumierii* to cross the channel coincide with periods immediately after light levels drop (dusk) or immediately before light levels increase (dawn), and these short time periods appear to represent anti-predation windows where predation risk may be lower than other times of the day.

Movements to nocturnal areas during twilight were less pronounced for *L. apodus*, with a large proportion of the triangulated positions 30 min or more after sunset still in the mangrove prop roots. Similarly, Hitt et al. (2011*b*) observed that *L. apodus* transitioned more slowly from structured daytime habitats to sand and seagrass at night, with individuals often departing diurnal resting areas after twilight or up to 1-h post-sunset (astronomical twilight). In the present study, observed positions at twilight for *L. apodus* outside the mangroves were predominantly in the higher risk channel over sand bottom. Unlike the directed channel crossings by *H. plumierii* at twilight, the reliance on anti-predation windows appears less important for *L. apodus* given the more gradual and protracted movements displayed by this species at dawn and dusk. Nevertheless, the rate of movement by this species also peaked during twilight, and increased step length (i.e., speed) during dawn and dusk has also been observed for this species in the U.S. Virgin Islands (Hitt et al. 2011*b*). Increased rates of movement during twilight may be related to predation risk by *S. barracuda* or other predators moving into the channel during transition periods. Observed shifts in the spatial distribution of *L. apodus* at twilight and into the night appear to be a resource selection response to take advantage of higher flow rates (~30 cm/s) in the channel compared to more protected areas in mangroves and seagrass habitats (~0–2 cm/s) in this MSP ecosystem. Increased flow often leads to greater encounter rates with midwater prey, enhancing the foraging efficiency of consumers (MacKenzie and Kiorboe 1995, Lewis and Pedley 2001), which may offset the risk of occupying the higher risk channel over relatively open sand bottom habitats with limited or no cover (DeCesare et al. 2014).

Trophic relationships of *L. apodus* and *H. plumierii* were examined concurrently with the acoustic telemetry trial and support the hypothesis that shifts to nocturnal habitats within the MSP ecosystem were associated with foraging. Muscle tissue $\delta^{13}C$ and $\delta^{15}N$ values for *L. apodus* and *H. plumierii* indicated that signatures of

both species were linked to producer signatures associated with habitats occupied at night. This finding is consistent with observations that both species rely heavily on nocturnal habitats for prey (Nagelkerken et al. 2000, Nagelkerken and van der Velde 2004). *Lutjanus apodus* most closely matched POM (phytoplankton) values observed in the sand (channel), while seagrass/BMA was identified as an important source of organic matter to *H. plumierii*. Because both species are known to feed opportunistically during the day (Rooker 1995, Verweij et al. 2006), it is not surprising that predicted source estimates from SIAR also included producers associated with habitats frequented during the day. $\delta^{13}C$ and $\delta^{15}N$ values and estimated source contributions for *S. barracuda* were similar to *H. plumierii*, which appears to show increased habitat overlap between these two species. This may result in higher predation risk for *H. plumierii* or possibly indicate the consumption of other seagrass-dependent species by *S. barracuda*.

In conclusion, habitat characteristics such as cover and complexity are often key determinants of predation risk and survival (Rogers et al. 2014), and both model prey species (*L. apodus*, *H. plumierii*) occupied areas with generally more cover (lower risk) during the day and areas of less cover (higher risk) at night. This suggests that the mangrove prop roots and/or patch reefs represent daytime resting sites for *L. apodus* and *H. plumierii*, while the more open channel over sand substrate or seagrass served as nighttime foraging areas for the two species, respectively. The spatial configuration of habitats within this seascape influenced the distribution of both predator and prey species investigated with *L. apodus* and *H. plumierii* generally avoiding high-risk areas (i.e., channel) during the day when *S. barracuda* were common in this habitat. Mismatches between movement rates of our model predator (*S. barracuda*) relative to both *L. apodus* and *H. plumierii* may be an adaptive response to reduce detection or encounter rates, although different feeding behaviors (e.g., sit-and-wait vs. active foraging) of selected predator and prey species may also contribute to observed disparities in movement rates. Our findings clearly demonstrate interconnections between predator and prey activities and suggest that migration pathways, foraging success, and survival of juvenile fishes inhabiting these back-reef ecosystems may be shaped significantly by seascape configuration and the spatial distribution of predators. Since an improved understanding of seascape connectivity is essential to conservation prioritization (Weeks 2017), approaches similar to the one used here are necessary to fully assess the causes and scope of these linkages.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2200/full