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Research

Thresholds in seascape connectivity: the spatial arrangement of nursery habitats structure fish communities on nearby reefs

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Ecosystems are linked by the movement of organisms across habitat boundaries and the arrangement of habitat patches can affect species abundance and composition. In tropical seascapes many coral reef fishes settle in adjacent habitats and undergo ontogenetic habitat shifts to coral reefs as they grow. Few studies have attempted to measure at what distances from nursery habitats these fish migrations (connectivity) cease to exist and how the abundance, biomass and proportion of nursery species change on coral reefs along distance gradients away from nursery areas. The present study examines seascape spatial arrangement, including distances between habitats, and its consequences on connectivity within a tropical seascape in Mozambique using a seascape ecology approach. Fish and habitat surveys were undertaken in 2016/2017 and a thematic habitat map was created in ArcGIS, where cover and distances between habitat patches were calculated. Distance to mangroves and seagrasses were significant predictors for abundance and biomass of most nursery species. The proportions of nursery species were highest in the south of the archipelago, where mangroves were present and decreased with distance to nurseries (mangroves and seagrasses). Some nursery species were absent on reef sites farthest from nursery habitats, at 80 km from mangroves and at 12 km from seagrass habitats. The proportion of nursery/non-nursery snapper and parrotfish species, as well as abundance and biomass of seagrass nursery species abruptly declined at 8 km from seagrass habitats, indicating a threshold distance at which migrations may cease. Additionally, reefs isolated by large stretches of sand and deep water had very low abundances of several nursery species despite being within moderate distances from nursery habitats. This highlights the importance of considering the matrix (sand and deep water) as barriers for fish migration.

Keywords: coral reef, fish migrations, habitat configuration, habitat connectivity, habitat shifts, landscape ecology, ontogenetic

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Introduction

Ecosystems are linked by the movement of organisms across habitat boundaries and the arrangement of habitat patches can therefore affect species abundance, biomass and composition (Baguette et al. 2013). These movements are often caused by changes in animal needs in terms of food and shelter and may result in ontogenetic changes of habitat use. This can lead to spatial separation between juveniles and adults within populations (Werner and Gilliam 1984). Species that require resources from multiple habitat types in order to complete their life cycle will be vulnerable to disturbances that disrupt functional connectivity (Huijbers et al. 2013). Climate change, extensive fishing and habitat alterations may disrupt connectivity through i.e. fragmentation by changing the spatial arrangement of habitat patches across the seascape (Layman et al. 2004, Thrush et al. 2008). Habitat fragmentation is associated with a loss of habitat, reduced patch size, increasing distances between patches and may have consequences on survivorship and/or dispersal of organisms (Andrén 1994). Theory predicts that the effects of fragmentation on connectivity and, ultimately, on population persistence are non-linear and that beyond a predictable threshold an abrupt change will occur in system behaviour (Andrén 1994, With and Crist 1995, Mönkkönen and Reunanen 1999). Despite the ecological implications at stake, the consequences of fragmentation and habitat loss on connectivity in the marine environment have however received little attention. Furthermore, thresholds where abrupt changes in abundance and biomass of organisms may occur have rarely been estimated (Grober-Dunsmore et al. 2009, Boström et al. 2011). Studying seascapes with varying habitat configurations and distances between habitat patches can increase our understanding of potential thresholds related to fragmentation. Although little is known about seascape thresholds in marine systems, it is a potential factor in structuring marine communities and lends important information for ecosystem-based management.

Coastal ecosystems around the world are highly productive and important as nurseries for numerous fisheries species. However, these ecosystems suffer the highest rates of degradation from human impacts. In tropical regions about 35% of the world's mangrove forests (Alongi 2002), 29% of seagrasses (Waycott et al. 2009) and 27% of coral reefs (Cesar et al. 2003) have disappeared, and are continuing to decline with rise in sea water temperatures, eutrophication and overharvesting. Within these coastal ecosystems a number of fish and invertebrate species undergo ontogenetic, foraging and/or spawning migrations between habitats, connecting habitats within seascapes (Berkström et al. 2012). Many coral reef fishes reside in mangroves and seagrass beds as juveniles before migrating to coral reefs as large juveniles or sub-adults to join the adult populations (Gillanders et al. 2003, Nagelkerken et al. 2015). This post-settlement connectivity results in food–web interactions across habitat boundaries and ultimately effects ecosystem functioning (Clark et al. 2009, Sheaves 2009, Harborne et al. 2016).

Community structure of fishes on coral reefs have been found to differ with increased distance to nursery habitats including mangroves and seagrass beds (Dorenbosch et al. 2005, Berkström et al. 2013). Studies have also found that abundances of fish species on coral reefs, known to use seagrass or mangrove as nursery habitat, were very low or that the species were not observed in the absence of these nursery habitats (Nagelkerken et al. 2002, Mumby et al. 2004, Dorenbosch et al. 2005). Furthermore, seascape composition (i.e. abundance and variety of patch types) and configuration (i.e. the spatial arrangement of habitat patches) has been found to influence fish assemblages in seagrasses (Pittman et al. 2004, Gullström et al. 2008, Staveley et al. 2016), mangroves (Green et al. 2012) and coral reefs (Dorenbosch et al. 2007, Pittman et al. 2007, Grober-Dunsmore et al. 2008, Kendall et al. 2011, Nagelkerken et al. 2017), highlighting that seascape structure affects fishes at multiple spatial scales across multiple habitats. The structure of spaces between preferred habitat patches (e.g. unvegetated sand or deep water), sometimes referred to as the matrix, can have profound consequences for connectivity across the seascape by forming barriers that prevent or impede movements for some species (Pittman et al. 2004, Turgeon et al. 2010, Watling et al. 2011, Santos et al. 2018). However, there is still a lack of understanding of how far young post-settlement (juvenile and sub-adult) coral reef fishes may disperse within tropical seascapes and at what distances nurseries cease to affect adult communities on coral reefs (Nagelkerken et al. 2017). Few formal tests exist on the decrease of reef fish population replenishment away from nurseries, measured in actual distances or isolation (Huijbers et al. 2013, Nagelkerken et al. 2017, Gilby et al. 2018). In order to effectively manage seascapes and mitigate effects of fragmentation and habitat loss, we need to understand patterns of connectivity and identify distances or thresholds where interconnections diminish. These findings are essential in order to predict ecological implications of connectivity on population sizes and community structure. Seascape configuration and connectivity have become important aspects of marine spatial planning and the design of marine protected areas (MPAs), where protecting seascapes with high connectivity is recommended (Beger et al. 2010, Edwards et al. 2010).

To examine seascape arrangement and its consequences on connectivity in the marine environment a landscape ecology approach is appropriate since landscape ecology focuses on the link between spatial patterns and ecological processes. This framework applied to the marine environment, now known as seascape ecology, is a rapidly emerging field that holds great promise in ecological studies focusing on spatial patterns in coastal seascapes (Boström et al. 2011, Pittman 2018). Seascape ecology focuses explicitly on the geometric patterns of seascapes represented by patch-mosaics, gradients and terrains and their ecological consequences (Wedding et al. 2011, Pittman and Olds 2015). Where seascapes are represented as patch-mosaics of different habitats, seascape ecology typically investigates how the composition and spatial arrangement of these habitat patches affect species distribution and

abundance in time and space (Pittman et al. 2004). With this approach, reefs with high or low connectivity with other habitats can be identified, facilitating marine spatial planning and fisheries management in the study region. Additionally, the importance of seascape linkages for the replenishment of fish populations on reefs can be examined by studying community changes and corresponding changes in fish functional composition along distance gradients away from nurseries. Different sized seascapes may also be compared to determine if generalisations can be made in threshold values.

Using a seascape ecology approach, the present study aims to: 1) examine changes in fish abundance, biomass and species composition on tropical reefs along geographical distance gradients away from nursery areas (mangroves and seagrass); and 2) identify distance thresholds away from nursery habitats where abundances and biomasses of nursery fish species abruptly decline in a Mozambican archipelago. We hypothesise that the spatial arrangement of nursery habitat will affect nursery species abundance, biomass and composition on coral reefs and that nursery species on coral reefs will decline with increasing distance from nursery areas. We also hypothesise that at some distance away from fish nursery areas an abrupt change (threshold effect) in fish abundance and species composition on coral reefs will occur.

Methods

Study site

This study was conducted in January–March 2016 and March–April 2017 in the Bazaruto Archipelago (21°30′–22°10′S, 35°22′–35°30′E), Mozambique. The Bazaruto Archipelago encompasses a range of different habitats such as extensive seagrass beds, sandbanks, mangroves, channels and coral and rocky reefs (Everett et al. 2008). Mangroves are located primarily in the south of the archipelago, around the São Sebastião peninsula. The reefs on the east side of the islands are mainly submerged fringing reefs, with coral cover increasing towards the north of the archipelago, due to the more turbid waters in the south (Everett et al. 2008). Tidal range is approximately 3 m, which produces strong tidal currents in the channels between the islands ($< 1.6\,m\,s^{-1}$ (Hammar et al. 2012)). Climate is tropical with an average water temperature of 24–28°C throughout the year (Everett et al. 2008). The Archipelago include two protected areas; the Parque Nacional do Arquipélago de Bazaruto (PNAB), and the Santuario Bravio de Vilanculos (The Sanctuary). The PNAB was first created in 1971 to protect the resident dugong population (Díaz et al. 2016). In 2001, its boundaries were extended to encompass the current area of 1430 km^2, including seagrass beds, coral reefs and terrestrial environments. The PNAB is zoned for multiple use with fishing prohibited on all coral reefs within the park (Everett et al. 2008, Díaz et al. 2016). Fishing on coral reefs is allowed in the São Sebastião area, although fishing pressure is low due to the difficult access to the reefs and lack of motorized boats (D'Agata 2016).

Nine reefs spread across the archipelago were included in the study (Linene, Bangue, Baluba, Magaruque, Santa Carolina, 2 Mile, 5 Mile, Chilole/6 Mile and Lighthouse Reef, Fig. 1).

Spatial data

A thematic habitat map of the Bazaruto Archipelago was constructed. Polygons of different habitat types were manually delineated and visually interpreted from a satellite image (LANDSAT 8) in ArcMap 10.5 (resolution 10 m) (ESRI 2017). Habitat types were identified by georeferenced field observations (ground-truthing) using a handheld Global Positioning System receiver (Garmin eTrex Touch 25). Habitat types were categorised as: sand, channel, mudflat, dense mangrove, sparse mangrove, dense seagrass, sparse seagrass and reef, where 'sparse' was classified as $< 40\%$ cover, and 'dense' as $\geq 40\%$ cover (Fig. 1).

Distance from reef survey locations to channels and mangroves were generated with the 'Create Near Table' function in ArcMap 10.2 (ESRI 2017) using the thematic habitat map including main habitats in the wider Bazaruto Archipelago. Since many of the seagrass beds were located where the shortest distance measured would have crossed land, distance was measured manually in ArcMap, simulating the shortest route around land and tracing the channels.

Field data

The fish community was surveyed with underwater visual census (UVC) randomly placing line transects of 25 m length on coral reefs. Fish were recorded within 2 m of either side of the transect, i.e. a 25×4 m area. Larger-bodied mobile fish were recorded as the transect line was laid out and small and cryptic fish were recorded on the swim back. All fish were identified to lowest taxonomic level possible, and sizes (total length, TL) estimated to closest centimeter. Surveys were conducted in daylight, between 08: 00 and 15: 00. To avoid bias, the same two divers collected all fish data (L. Eggertsen and W. Goodell) and calibrated estimates of fish sizes continuously between the two divers by estimating size of the same fish and other objects during several occasions throughout the survey and verifying with a measuring tape. In total, 159 UVCs were conducted during the two years of field surveys.

In order to account for small-scale habitat variables (microhabitats) within habitat types, the benthic community was characterized by laying out 50×50 cm quadrats along each fish UVC, at 0, 5, 10, 15, 20 and 25 m distance from the starting point. Each quadrat was photographed, and then analyzed in the software photoQuad, using 30 points randomly spread within the quadrat, and identifying substrate under each point (Trygonis and Sini 2012). Substrate was classified into broad morphological groups (articulated coralline algae, colonial ascidians, solitary ascidians, branching coral, encrusting coral, massive coral, tabular coral, crustose coralline algae (CCA), coral rubble, epilithic algal matrix (EAM) on carbonate structure, EAM on rock, filamentous

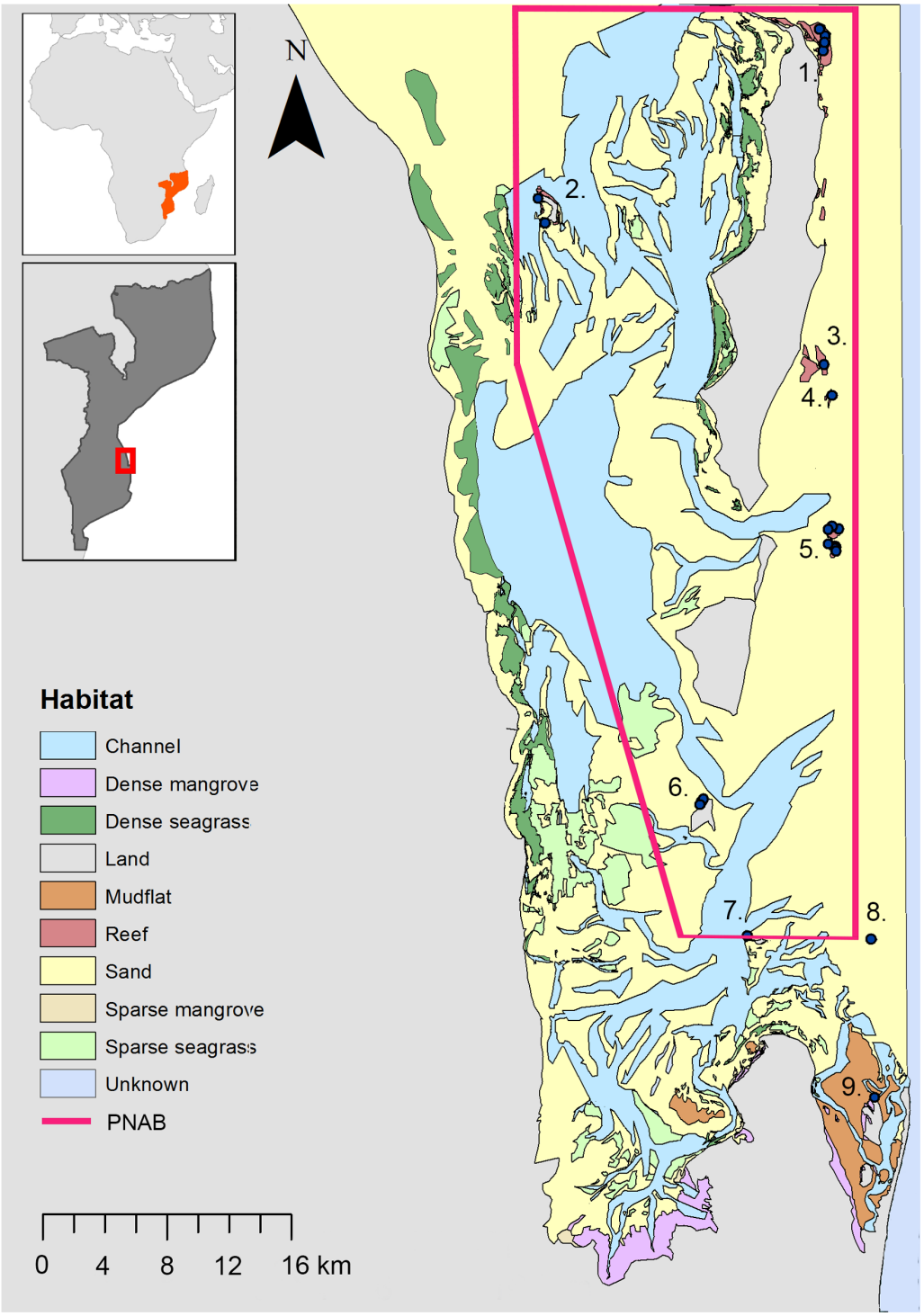

Figure 1. Study sites in the Bazaruto Archipelago, Mozambique. PNAB = Parque Nacional de Bazaruto and 1 = Lighthouse reef, 2 = Santa Carolina, 3 = 6 Mile reef, 4 = 5 Mile reef, 5 = 2 Mile reef, 6 = Magaruque, 7 = Bangue, 8 = Baluba and 9 = Linene reef.

algae, foliose algae, thick-leathery algae, rock, sand, sponges, soft coral, zoanthidae and other). An average of the proportions of each benthic morphological group was calculated for each UVC. In total, 700 photo quadrats were analysed.

To estimate topographic complexity, photographs were taken at the start and end point of each fish UVC, and later categorized on a scale of 1–4, where 1 corresponded to low topographic complexity and 4 to high complexity. Depth

was measured with a dive computer at the beginning of each UVC, irrespective of tide.

Data analyses

To investigate if the fish assemblage was affected by environmental variables, redundancy analysis (RDA) ordinations were performed for selected abundant fish taxa relevant to the study aims. Species were categorised as nursery species or non-nursery species where possible, following Froese and Pauly (2019) (Supplementary material Appendix 1 Table A1). The following taxa were included; *Acanthurus* spp., *Chaetodon auriga*, *Chaetodon* non-nursery species, *Chlorurus sordidus*, *Chromis fieldi*, *Chromis viridis*, *Gnathodentex aurolineatus*, *Halichoeres scapularis*, *Lethrinus* nursery-species, *Lutjanus* nursery species, *Lutjanus* non-nursery species, *Mulloidichctys* spp., *Naso* spp., *Parupeneus* spp., Haemulidae nursery species, Haemulidae non-nursery species, *Scarus ghobban*, *Scarus rubroviolaceus*, *Siganus sutor* and *Upeneus tragula*.

Fish data was transformed using Hellinger transformation (Legendre and Gallagher 2001) and the environmental variables were transformed to z-scores using the 'standardize' transformation since variables were measured on different scales. Significance of axes was tested with the function anova.cca in R (ver. 3.3.4), using 999 permutations.

The ordinations were performed in the package 'vegan' in R (ver. 3.3.4) using each UVC as a replicate and variables on habitat level (depth, topographic complexity, proportion sand, proportion bare rock, coral rubble and cover of thick leathery algae, branching coral, tabular coral, massive coral, CCA and EAM cover on carbonate and on rocky substrate), combined with distance to mangroves, seagrass beds and channels.

To understand how relationships of proximity to nurseries structured fish assemblages on the reefs and identify thresholds where abrupt changes in fish abundance, biomass or proportion nursery and non-nursery species occurred, generalized additive models (GAMs) were performed for fish families that include both nursery and non-nursery species, and that were fairly abundant in the data set (Francesco Ficetola and Denoël 2009). These included Scarinae, Lutjanidae and Haemulidae. For all models, each UVC was used as a replicate. Collinearity of predictors was tested with variance inflation factor (VIF), and predictors with a value larger than three were excluded from the models. Correlation of variables was investigated using the correlation chart function in the 'PerformanceAnalytics' package in R. The GAMs were performed with the 'logit' function, and REML as smoothing parameter estimation method, using proportion (binomial distribution) and abundance (Poisson distribution) of nursery species for the three families, with distance to mangroves, seagrass and/or channels and complexity, depth, coral and EAM cover as predictor variables for initial models.

To investigate distribution patterns in relation to nursery habitat use, abundance and biomass were also modelled for fish grouped into different nursery categories (seagrass, mangrove, occasional and non-nursery species). All variables were scaled since they were measured on different scales, and both abundance and biomass were modelled using a Gaussian distribution with the 'identity' function. The final models were chosen based on lowest AIC values, when $\Delta AIC > 2$ between models (Burnham and Anderson 1998). All GAMs were executed with the 'mgcv' package (Wood 2017) in R (R Core Team).

Results

In total, 10 468 individual fish from 296 species representing 50 different families were recorded on the 9 reefs. Pomacentridae was the most abundant family (2332 individuals), followed by Acanthuridae (1657 individuals) and Labridae (1478 individuals). Benthic composition differed between the surveyed reef sites. Hard coral cover ranged between an average of 53% (Santa Carolina Island) and 0% (Bangue and Linene reef), with the southern reefs in general having less coral cover and having a benthic community mainly composed of EAM. However, there was no correlation found between coral cover and distance to mangroves or seagrass. Correlation coefficient between total coral cover and distance to mangroves and distance to seagrass was 0.22 and 0.18 respectively (Supplementary material Appendix 1 Fig. A1). Coral cover was low in some sites (i.e. Lighthouse reef) far from nursery habitats (Supplementary material Appendix 1 Fig. A2).

Variables structuring the fish assemblage

Both seascape and within-habitat patch variables influenced the fish assemblage, but effects were different depending on taxa. All distance/seascape variables (distance to mangroves, to seagrass and to channels) and cover of massive coral, EAM on carbonate structure, topographic complexity, sand and thick-leathery algae were significant predictors for distribution of the selected taxa (RDA, $p < 0.05$, $R^2 = 0.21$, 999 permutations, Supplementary material Appendix 1 Fig. A3).

Pomacentrids were associated with high complexity and coral cover, Acanthurids to high cover of thick-leathery algae and distance from mangroves and the excavator *Chlorurus sordidus* (Labridae: Scarinae) with high coral cover. The nursery species *Scarus ghobban* was negatively correlated with distance to seagrass beds. The RDA also separated the nursery and non-nursery Haemulids and Lutjanids from each other along the first axis.

Seascape arrangement effects on reef fish assemblages with regard to nursery habitat use

Proportions of fish species utilising coastal nursery habitats were larger in the south of the archipelago, where mangroves are present, and distances to seagrass beds were shorter (Fig. 2). Proportions of the fish assemblage comprised of nursery species were smallest at the reefs farthest from seagrass and mangrove habitats, and where distances to channels

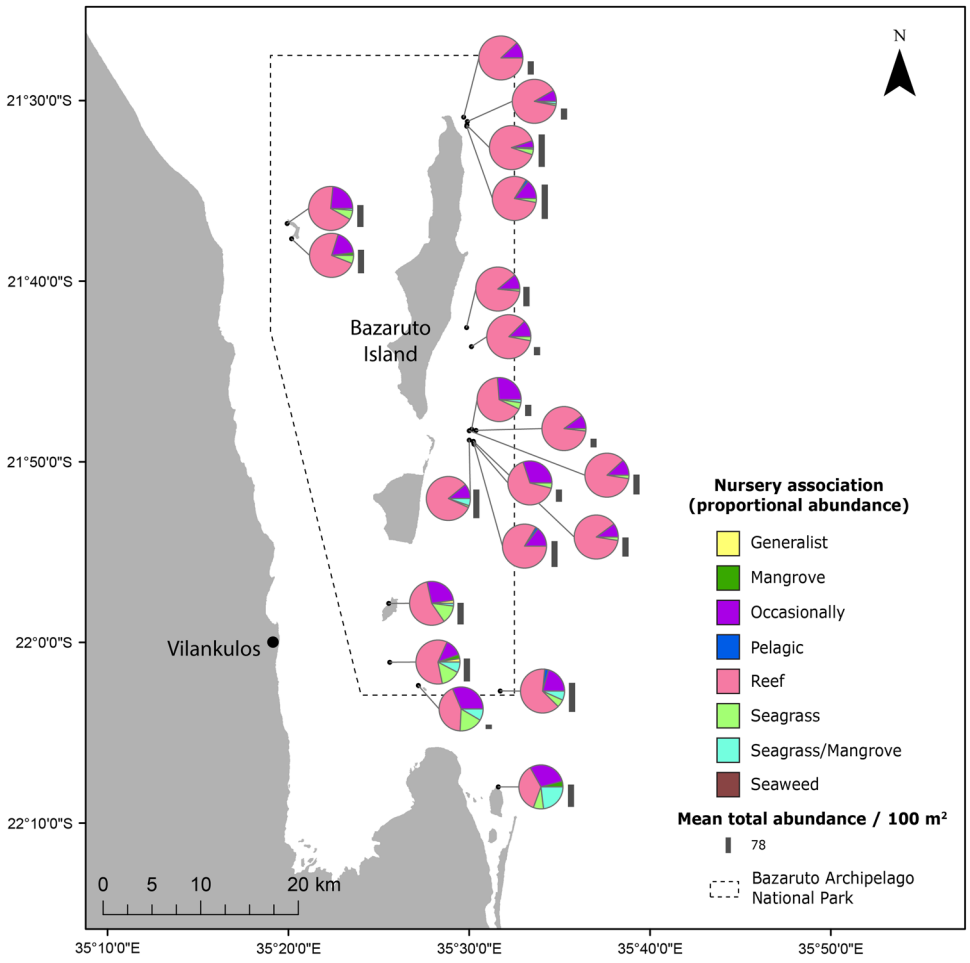

Figure 2. Proportion of fish species recorded on all study sites shown by main nursery habitat association in the Bazaruto Archipelago, Mozambique.

were large (e.g. 5 and 6 Mile and the Lighthouse reefs). Biomass of seagrass-nursery species decreased with distance to seagrass, while biomass for mangrove-nursery species and non-nursery (reef) species remained similar throughout the seascape (Fig. 3). Both proportion and abundance of nursery species (Scarinae, Lutjanidae and Haemulidae) on coral reefs decreased with distance to nurseries (Fig. 4, 5). No nursery species of Haemulidae and Scarinae were recorded at the reef sites farthest from mangroves (80 km) and the same pattern was found for Lutjanidae and Scarinae in relation to distance to seagrass habitats (12 km) (Fig. 4).

'Distance to channels' and 'distance to seagrass' could not be used in the same models due to high collinearity (following the variable inflation factor test). None of the other variables showed any strong correlation (> 0.70) to each other (Supplementary material Appendix 1 Fig. A1). Separate models were generated and the variable that generated the lowest AIC value was used in the final models. Abundance and biomass of seagrass-associated species were significantly correlated with distance to seagrass and mangroves and abundance abruptly declined at 8 km from seagrass habitats (Table 1, Supplementary material Appendix 1 Fig. A4). Both abundance and biomass decreased with distance to these two habitats. Additionally, abundance was also significantly correlated with % EAM cover (Table 1, Supplementary material Appendix 1 Fig. A4). For mangrove-associated species, abundance but not biomass was correlated with distance to both mangroves and seagrass with abundance decreasing with distance. Biomass was only correlated with topographic complexity (Table 1, Fig. 5, Supplementary material Appendix 1 Fig. A4). Biomass of neither the 'occasional', nor the 'non-nursery' category were correlated with any seascape variable, but depth was significant for the 'occasional' category (Table 1, Supplementary material Appendix 1 Fig. A4). Abundance of the 'non-nursery' category was correlated with distance to mangroves, coral cover and topographic complexity, but compared to nursery species, increased with distance to mangroves. Abundance of the 'occasional' category was correlated with distance to seagrass, topographic complexity and EAM cover (Table 1, Supplementary material Appendix 1 Fig. A4).

For nursery taxa of Scarinae (mainly represented by *Scarus ghobban*) distance to mangroves and seagrass had significant effects on both proportion of nursery versus non-nursery taxa and abundance and abundance abruptly declined at

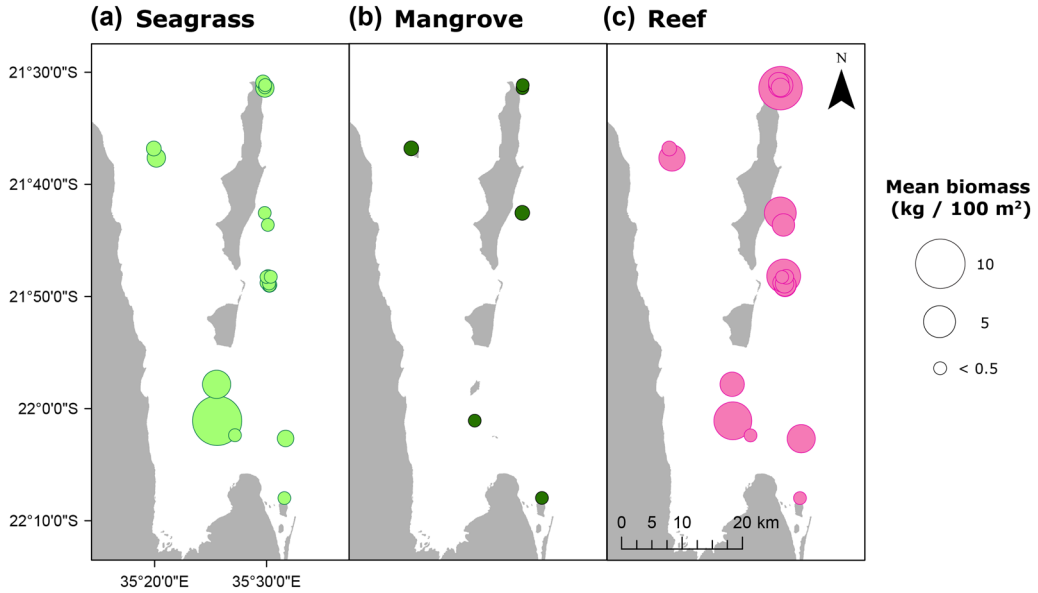

Figure 3. Biomass of (a) seagrass-associated nursery species, (b) mangrove-associated nursery species and (c) non-nursery species on reefs within the Bazaruto Archipelago, Mozambique.

8 km from seagrass habitats (Fig. 5, Table 1). Abundance of Scarinae was also significantly correlated with depth and % cover of EAM (Fig. 5, Table 1). Abundance of Lutjanid nursery taxa was significantly correlated with distance to mangroves and seagrass, depth, coral and % of EAM cover and similar to Scarinae, abundance abruptly declined at 8 km from seagrass habitats (Fig. 5, Table 1). Depth was, however, the only variable that had any effect on the proportion of Lutjanid nursery and non-nursery species. Abundance of Haemulid nursery species and the proportion nursery and non-nursery Haemulid species were significantly correlated with distance to seagrass and distance to mangroves. Additionally, Haemulid abundance was significantly correlated with % cover of EAM (Fig. 5, Table 1).

Discussion

As hypothesised, seascape spatial arrangement where reefs existed at varying distance away from nursery habitats had an effect on nursery fish species abundance, biomass and composition on reefs. Distance to mangroves and seagrasses were significant for most nursery species. Furthermore, both proportion and abundance of nursery species of parrotfishes (Scarinae), snappers (Lutjanidae) and grunts (Haemulidae) were highest in the south of the archipelago, where mangroves were present, and decreased with distance from nurseries (mangroves and seagrasses). No nursery species of grunts were recorded at the reef sites farthest from mangroves (80 km), and the same pattern was found for snappers and parrotfishes in relation to distance to the farthest seagrass habitat (12 km). Threshold distances were found where abrupt changes in nursery species abundance and biomass occurred. Distance to seagrass was significant for seagrass nursery species abundance and biomass, while biomasses for mangrove and non-nursery species were similar throughout the seascape. Like abundance, biomass of seagrass nursery species was highest in the south and west of the archipelago, where seagrass beds are closer to the reef habitats, and decreased with distance from seagrass habitat.

Few studies have explicitly tested abrupt changes in densities and biomasses of fish nursery species with distance away from nursery areas (but see Nagelkerken et al. 2017, Shideler et al. 2017). Furthermore, threshold distances have rarely been estimated. In the present study, the abundance and biomass of seagrass nursery species and nursery snappers and parrotfishes abruptly declined on coral reefs at distances greater than 8 km from seagrass habitats. Some species were also absent at the reef farthest away from mangroves (80 km) and seagrasses (12 km). These patterns are likely the result of uni-directional movement from natal to adult habitat by coral reef fishes utilising mangrove and seagrass beds as nursery habitat (Berkström et al. 2012, Litvin et al. 2018). Movement patterns in the last stage of nursery habitat occupancy are poorly known (Gillanders et al. 2003, Nagelkerken et al. 2015). There are still large knowledge gaps in the understanding of how far young fish disperse and up to what distances nurseries affect adult community structure (Nagelkerken et al. 2017). Patterns were found to differ among families, suggesting that responses to habitat arrangement are family and even species specific and may be related to home ranges and different traits exhibited among species. Large-bodied species often have larger home ranges and are found at greater depths than their smaller counterparts (Mouillot et al. 2014). Indeed, there was a significant relationship between fish biomass and depth on the Bazaruto reefs. Size might also explain the different threshold values found among these families in Bazaruto. Maximum size of

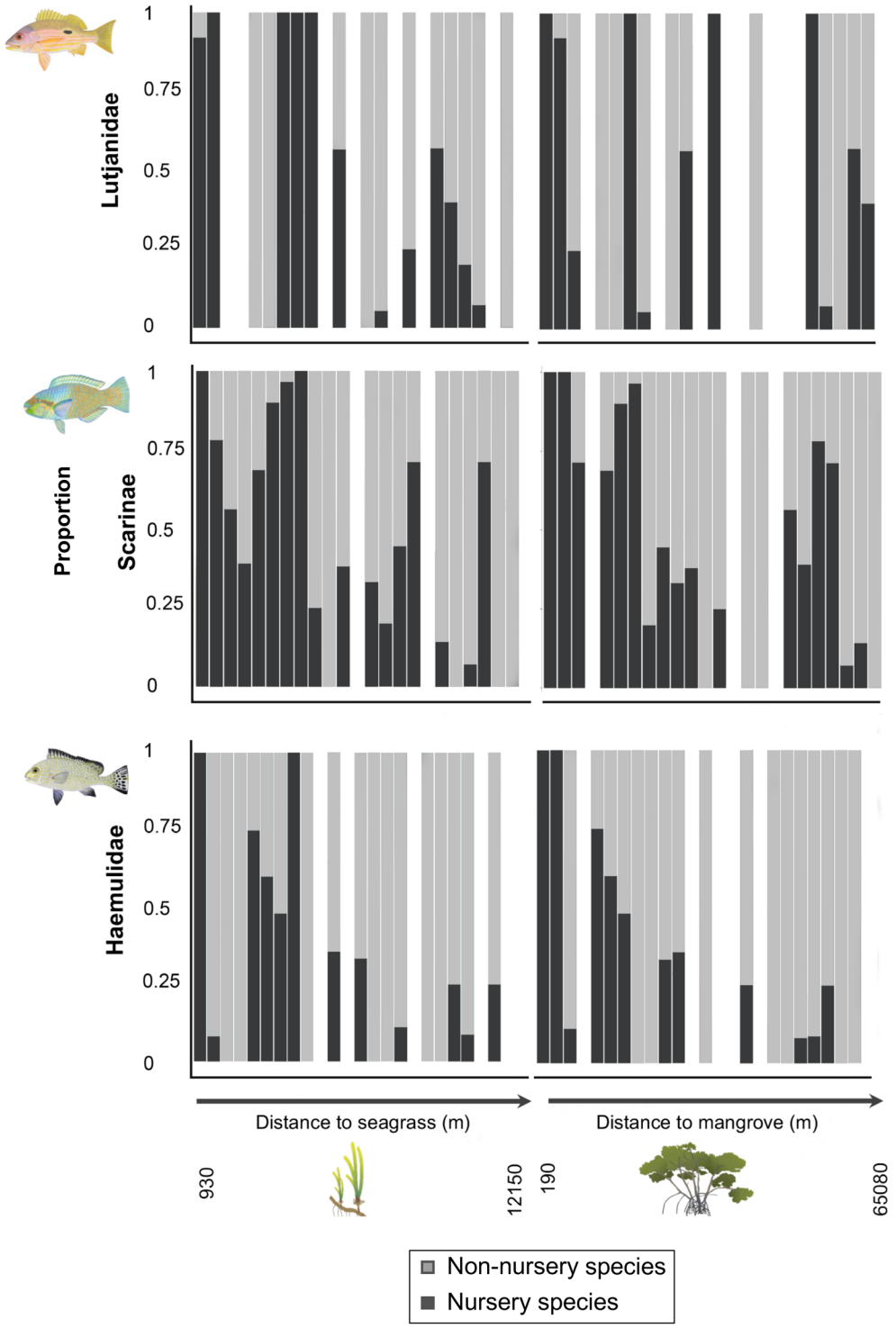

Figure 4. Proportion nursery species and non-nursery species of Haemulids, Lutjanids and Scarinae at all survey reef sites in the Bazaruto Archipelago, Mozambique, ordered in increasing distance to seagrass and mangroves. Each bar represents a surveyed reef. Empty bars indicate that fish from respective family were absent on that reef.

most nursery species of snappers are rather small and similar in size (< 35 cm), while grunts have a wider range of sizes among nursery species. Also, biomass of mangrove-associated nursery species were similar throughout the seascape compared to seagrass-associated nursery species and may also be explained by different species traits. For instance the grunt *Plectorhinchus plagiodesmus* is a mangrove-associated nursery species which grows rather large as an adult on reefs (<

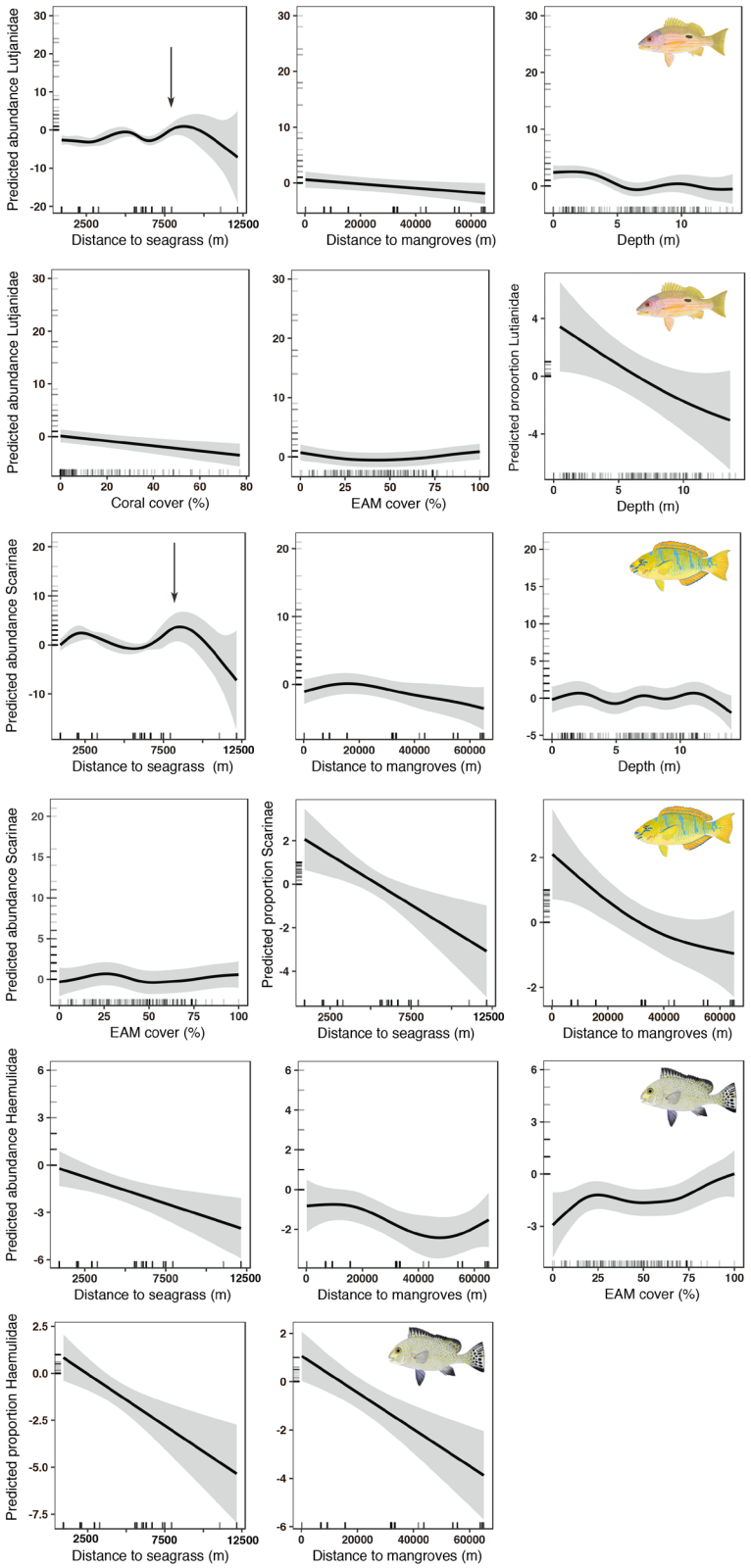

Figure 5. Partial dependence plots showing the relationships between abundance and proportion of Haemulid, Lutjanid and Scarinae nursery species and significant habitat variables modelled with generalized additive models (GAMs). Shaded areas indicate 95% confidence intervals. Arrows indicate a threshold distance (8 km) where abrupt changes in fish abundance occurred. Image courtesy of <www.efishalbum.com>.

Table 1. GAM results for abundance and proportion of nursery species of Haemulidae, Lutjanidae, Scarinae and non-nursery species that use reef as juvenile habitat related to habitat variables. Results for abundance and biomass of different nursery categories of reef fish (seagrass, mangrove, occasional) and non-nursery species are also displayed. Significant values are shown in bold. – = variable was excluded in the final model.

	Nursery Haemulidae		Nursery Lutjanidae		Nursery Scarinae	
	Abundance	Proportion	Abundance	Proportion	Abundance	Proportion
	p	p	p	p	p	p
Predictor variables						
Distance to seagrass	**0.005****	**< 0.001*****	**< 0.001*****	p > 0.05	**< 0.001*****	**0.003****
Distance to channels	–	–	–	–	–	–
Distance to mangrove	**0.028***	**< 0.001*****	**< 0.017***	–	**< 0.001*****	**0.01****
Average complexity	–	–	–	–	–	–
Depth	p > 0.05	–	**< 0.001*****	**0.02***	**< 0.001*****	p > 0.05
Coral cover	–	p > 0.05	**< 0.001*****	p > 0.05	p > 0.05	p > 0.05
EAM cover	**0.014***	–	**< 0.001*****	p > 0.05	**< 0.001*****	p > 0.05
n	164	78	164	77	204	125
r^2	0.315	0.686	0.523	0.688	0.602	0.431
Deviance explained %	40.1	53.5	67.8	64.2	61.0	41.6

	Seagrass nursery sp.	Mangrove nursery sp.	Occasional	Non-nursery
Abundance 100 m^2				
Distance to seagrass	**0.022***	**0.005****	p > 0.05	p > 0.05
Distance to channels	–	–	–	–
Distance to mangrove	**0.003****	**< 0.001*****	p > 0.05	**0.002****
Average complexity	p > 0.05	p > 0.05	**0.017***	**0.008****
Depth	p > 0.05	–	p > 0.05	p > 0.05
Coral cover	–	–	–	**0.004****
EAM cover	**0.035***	p > 0.05	p > 0.05	p > 0.05
n	144	144	144	144
r^2	0.45	0.342	0.138	0.254
Deviance explained %	50.9	39.3	19.6	31.4
Biomass g × 100 m^2				
Distance to seagrass	**0.037***	–	p > 0.05	–
Distance to channels	–	–	–	–
Distance to mangrove	**0.035***	p > 0.05	p > 0.05	–
Average complexity	–	**0.030***	p > 0.05	p > 0.05
Depth	p > 0.05	–	**0.009****	p > 0.05
Coral cover	–	p > 0.05	–	p > 0.05
EAM cover	–	–	p > 0.05	–
n	156	156	156	156
r^2	0.358	0.114	0.070	0.054
Deviance explained %	40.2	16	10.5	7.6

90 cm, Froese and Pauly 2019). Although abundances of *P. plagiodesmus* were lower on reefs compared to their young in mangroves, the large size of the adults resulted in a more uniform pattern of biomass throughout the seascape.

An alternative explanation to the observed patterns may be changes in live coral and EAM cover, which are known to modify fish densities (Jones and Syms 1998), with distance away from nursery habitats. However, abundances and biomasses of nursery species (seagrass and mangrove) were not correlated with these habitat variables, with the exception of seagrass nursery abundance and % cover EAM. Instead, non-nursery species settling on reefs, were highly correlated with coral cover and topographic complexity. Furthermore, some sites on reefs far away from seagrasses and mangroves, i.e. Lighthouse reef, had low coral cover and low abundances of nursery species. Although we did not tag fish in the current study, others have shown that most of the dispersal from nursery habitats to reefs by juveniles and sub-adults are concentrated at their nearest nursery habitat (Huijbers et al. 2013, Kimirei et al. 2013), despite adults being capable of long distance dispersal (Kaunda-Arara and Rose 2004, Meyer et al. 2010).

Threshold distances also seem to differ between study regions and even between different seascapes within regions, suggesting that regional differences in terms of tidal regimes (Igulu et al. 2014) and seascape settings are important to consider. For example, fish nursery species in the Caribbean were found to rapidly decline at a distance of 4 km from nurseries and most nursery species were absent at locations 14 km away from nurseries (Nagelkerken et al. 2017). Additionally, Shideler et al. (2017) found that species richness on Caribbean coral reefs declined with decreasing mangrove extent at

scales < 20 km^2. A larger proportion of Caribbean juvenile reef fishes utilise mangroves compared to seagrass as nursery habitat, while seagrass beds are utilised by a larger number of species as nursery habitat by Indo-Pacific reef fishes, the major driver of this phenomena being the differences in tidal amplitudes (Igulu et al. 2014). Additionally, herbivores utilise mangrove areas as nurseries in the Caribbean (Mumby et al. 2004, Harborne et al. 2016), while they are nearly absent in Western Indian Ocean (WIO) mangroves as juveniles (Nagelkerken et al. 2000, Mwandya et al. 2010, Berkström et al. 2012). These regional differences likely explain some of the disparities found in threshold values between studies in the Caribbean and the present study in the WIO. However, the spatial setting or seascape context must be explicitly considered in studies of fish ecology. Even within the same regions, differences in seascape setting can lead to variable patterns in ecological thresholds. In Menai Bay, Zanzibar, Berkström et al. (2013) found a positive relationship between seagrass connectivity (distance and area) and invertebrate feeder/piscivore fish abundance on coral reefs at the scale of 750 m. This was especially apparent for adult snappers and differs from our results in the Bazaruto archipelago, a seascape that is more expansive than Menai Bay. In the Bazaruto archipelago, the greatest distance from mangroves to reefs was 80 km, while in Menai Bay it was approximately 20 km. Furthermore, in Menai Bay most reefs were in close proximity to seagrass beds (> 10 m, Berkström et al. 2013), while in the Bazaruto archipelago reefs tended to be located farther from seagrass habitats (> 1000 m). Areal extent, spatial distribution of habitat patches and geographical isolation within a matrix of sand and deep water seems to affect ecological threshold distances, where abrupt changes in nursery species abundance, biomass and composition occur.

The matrix, habitat imbedded between focal habitat patches, should not be ignored since it is of great importance when explaining movement patterns in animals (Watling et al. 2011, Pagès et al. 2014). Watling et al. (2011) found in their meta-analysis that matrix matters for connectivity in patchy terrestrial landscapes across a wide variety of taxa and geographic contexts. The relevance of patch isolation is a major theme in the Theory of Island Biogeography and has received much attention in landscape ecology (Ricketts 2001). This may also be true in aquatic systems. In the Bazaruto Archipelago, 5 and 6 Mile Reef are surrounded by deep water and sand, often considered hostile environments for many fish species. Open sandy areas act as barriers for movement because of increased risk of predation (Chapman and Kramer 2000, Lowe et al. 2003, Turgeon et al. 2010). Although other reefs were farther away from mangrove nurseries than 5 and 6 mile, they had the lowest number of mangrove and seagrass associated nursery species, likely a result of them being farthest away from seagrass habitats as well as being isolated by large stretches of sand and deep water. This highlights the need to include the matrix and also consider the 'isolation' of reefs, rather than only focusing on distance away from nurseries. Lowe et al. (2003) found that kelp bass followed the margin of rocky reefs and kelp patches and never crossed the 200 m sand stretch between two marine reserve boundaries. However, they did move across sandy areas if they were interspersed with kelp. Similarly, Davis et al. (2017) noted that small stretches of seagrass within large sandy areas functioned as corridors for fishes migrating between deeper areas and shallow intertidal reefs during incoming tides. These findings and the results from the present study suggest that habitat loss and fragmentation may affect the migration by large juvenile and subadult fish to coral reefs. When stretches of hostile habitat (e.g. sand) become too large migration is likely to cease, with effects on reef fish replenishment. However, fragmentation may have either negative or positive effects on fish migrations as exemplified by Pittman et al. (2004) and Santos et al. (2018) and needs further investigation.

The Bazaruto archipelago is also penetrated by a network of sand channels which may impede movement between patches for small fishes, but could potentially facilitate the movement of fishes that travel along habitat edges into which they can hide when larger predators approach. The channels may indeed increase movement patterns of some species and explain some of the differences found between Bazaruto and Menai Bay. In the Caribbean, Rooker et al. (2018) found that snappers and grunts exhibited limited movement away from structured habitats during the day when their main predator (*Sphyraena barracuda*) was active. In contrast, they moved into high-risk areas like sandy channels at night, when predators were less active. Similarly, Hitt et al. (2011) also noted that snappers and grunts moved into less structured habitats at night to feed. The fish followed continuous habitat edges during twilight migrations, likely to avoid predation and to facilitate navigation.

The ontogenetic niche shifts related to post-settlement migration alter community structures in recipient ecosystems (Heck et al. 2008, Hyndes et al. 2014). Carbon is transferred throughout the system in a trophic relay process where intertidal production is moved from nursery areas to coral reefs (Kneib 1997). Additionally, the change in proportion of nursery versus non-nursery species with distance and isolation from nursery habitats may have profound effects on the functional group composition of fishes on coral reefs and ultimately ecosystem function (Mumby et al. 2004, Sheaves 2009, Berkström et al. 2012). Nursery and non-nursery species of grunts have similar diets (invertebrate feeders/piscivores) and hence changes in their proportion on reefs may not have major trophic implications (Berkström et al. 2012, Froese and Pauly 2019). However, regarding functional traits (following Mouillot et al. 2014), Lutjanid nursery and non-nursery species differ in several aspects. The majority of non-nursery Lutjanids have a larger distribution in depth (1–265 m), while the most abundant nursery species (*L. fulviflamma* and *L. ehrenbergii*) are restricted to shallower water (< 35 m, Froese and Pauly 2019). The more abundant non-nursery species also have a wider range of maximum sizes, with several species reaching large maximum sizes (e.g. *Aprion virescens* and *Lutjanus bohar*, Froese and Pauly 2019). Of the

recorded nursery Lutjanid species, only *Lutjanus argentimaculatus* which is a mangrove-associated nursery species, has a large maximum size (150 cm, Froese and Pauly 2019). In this case, presence of seagrass beds would therefore not contribute with large Lutjanids to the reef fish community. The implications of this for reef ecosystem functioning is a subject for future studies.

Parrotfish feeding modes also differ between nursery and non-nursery species suggesting that important browser, scraper and excavator functions by these species may change with increasing distance from mangrove and seagrass nurseries. Considering functional traits related to the different nursery and non-nursery species of parrotfishes, reefs close to nurseries were dominated by scrapers (nursery species) while reefs further away from nurseries were dominated by excavators which are non-nursery species (Bonaldo et al. 2014). Mumby and Hastings (2008) found that herbivores that undergo ontogenetic migrations enhanced the resilience of coral reefs close to mangroves. Building on these results, Harborne et al. (2016) demonstrated that high nursery connectivity was correlated to changes in grazing pressure by parrotfishes on nearby reefs, potentially leading to differences in coral cover of 3–4% when compared to low connectivity reefs. Furthermore, Martin et al. (2018) also showed that proximity of habitat mattered for herbivory and predation on coral reefs in Australia. The differences in replenishment of certain species may therefore alter communities on coral reefs, suggesting that isolated reefs may be more vulnerable to disturbance than more connected reefs. Connected reefs will have a more continues supply of young fish while isolated reefs may have a more limited supply. If reefs have a wide array of species with multiple functions they are likely less vulnerable to disturbance since there are multiple species that can serve the same function. However, if a reef has a less diverse fish assemblage and is subjected to disturbances such as fishing, the need for replenishment of recruits from other habitats may be essential. Vulnerability to disturbances may, however, depend on local conditions and the ecological effects of nursery parrotfish feeding. In the present study, the reefs closer to nursery habitats are subjected to higher turbidity and have less coral cover compared to more distant ones (Everett et al. 2008, this study). The scraper function seems to be more dominant on reefs connected to seagrass and mangroves, and connectivity may therefore not increase the excavating function on reefs in the WIO.

Marine spatial planning and the construction and implementation of MPAs is challenging, particularly in countries where scientific information is scarce and where local fishers are highly dependent on accessing habitats on a regular basis. Finding connectivity thresholds between habitats can therefore benefit the planning and construction of MPAs. By creating very large MPAs to include as much habitat as possible you also exclude or restrict local fishers. Instead, a network of MPAs or habitat types based on functional connectivity and biodiversity hotspots can be established making the use of habitats more effective. Mangroves and seagrass beds are often overlooked and rarely managed together with coral reefs (Berkström et al. 2012), despite that they can be equally or even more at risk from habitat degradation and loss (Weeks 2017). Only recently have scientists showed that proximity to nursery areas, such as mangrove and seagrass beds, has a positive effect on reef fish abundance promoting the effectiveness of MPAs (Olds et al. 2013, 2016). Pittman et al. (2007) also highlighted the urgent need to incorporate information on the influence of seascape structure in marine resource management activities. Different types of seascapes provide different fish assemblages and hence focus on identifying and characterising seascape types may be more relevant than focusing on individual focal habitat types (Pittman et al. 2007, Nagelkerken et al. 2017, Shideler et al. 2017). Considering the threshold values being different in the present study compared to a smaller seascape in the WIO and seascapes in the Caribbean, generalisations may be difficult. However, threshold distances were identified and may still be used as a tool in similar seascape settings. They may facilitate the placement of MPAs and the design of habitat restoration in fragmented areas were distances of hostile habitat (e.g. sand) for post-settlement juveniles are too large to cross (Pittman et al. 2007). Future studies comparing threshold distances in seascapes of varying sizes would aid in finding commonalities, useful for a wider management community. Furthermore, finding threshold distances in larval dispersal and foraging migrations would also be highly useful.

Conclusion

The present study shows that the spatial arrangement of nursery habitats alters the broader reef fish community and that certain distances (thresholds) can be found where abrupt changes in nursery species abundance, biomass and species composition occur. These threshold values indicate distances at which ontogenetic fish movements from nurseries to reefs decrease abruptly or cease. These distances, however, are likely region and seascape specific and dependant on tidal amplitudes as well as seascape sizes, urging the need to take generalisations with caution. Networks of MPAs in all three habitats (mangroves, seagrass and coral reefs) coherent with the mobility of migrating coral reef fishes are thus recommended.

Data availability statement

Data available from Figshare Digital Repository: <https://doi.org/10.17045/sthlmuni.11920242.v1> (Berkström et al. 2020).

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Supplementary material (available online as Appendix ecog-04868 at <www.ecography.org/appendix/ecog-04868>). Appendix 1.

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