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Where the grass is greenest in seagrass seascapes depends on life history and simple species traits of fish

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ABSTRACT

Tropical seagrass meadows are critical habitats for many fish species, yet few studies have investigated the influence of multiple scale-dependent factors and marine protected areas on seagrass fish species of differing life histories. We assessed the influence of fine-scale seagrass meadow characteristics and seascape-scale variables on the abundance of fish in a seagrass-dominated seascape in the Bazaruto Archipelago, Mozambique, particularly examining patterns of nursery- vs. resident species as well as mobile- vs. sedentary species. We found that fish distribution patterns in this seagrass-dominated seascape were dependent on species' life history characteristics; nursery taxa showed lower abundance in seagrass meadows further from adult reef habitats, while resident species within seagrass meadows occurred in higher abundances far from reefs. For taxa utilizing both mangroves and seagrass meadows as nursery habitat, proximity to mangroves was an important factor. Fish abundances were generally influenced by variables at the seascape scale (km), while sedentary species were predominantly influenced by area variables, and smaller seascapes (<500 m in radius) better explained distribution patterns. The influence of marine protected areas was taxon-specific, with the strongest effects of protection on resident species. Our results indicate that protection efforts in seagrass-dominated seascapes can have varying impacts on fish distribution, depending on the life history of the species present, and the geographical placement of the reserve within the seascape. Further, we suggest that simple species attributes can be utilised to describe generalized abundance patterns of fish in seagrass seascapes.

1. Introduction

In nature, organisms tend to be distributed in patches or along spatial gradients depending on environmental conditions (Legendre and Fortin, 1989). In particular, the arrangement of habitat patches in the landscape can influence ecological processes and the distribution of species (Wiens et al., 1993). Optimal conditions generally vary across species, and are in many cases linked to life-history traits (Thornton et al., 2011; Zarnetske et al., 2017). Simple attributes, such as body size and life history traits, may therefore be useful factors to consider when seeking to understand distributions of organisms (Thornton et al., 2011). This applies to both terrestrial and marine environments, although the factors that are ecologically relevant to distribution patterns may differ between terrestrial and marine ecosystems (Wedding et al., 2011; Pittman,

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2018).

Many marine fish species use several habitats throughout their life, and seascape context (i.e. the organization of different habitats in the surrounding seascape) therefore affects the structuring of fish communities in multi-habitat coastal seascapes and the ecological functions performed by them (Gilby et al., 2019; Martin et al., 2018; Staveley et al., 2017). In tropical seascapes, most work involving fish has been on the effects of distance to seagrass and mangroves on coral reef fish assemblages. Less is understood about the effects of mangroves and coral reef arrangement on fish assemblages in seagrass meadows and there is still a need for information on how seascape context influences fish communities in seagrass-dominated areas and on which spatial scales these seascape variables operate (Wedding et al., 2011; Berkström et al., 2012).

Tropical seagrass systems are important fish habitats comprising diverse fish assemblages representing varying life histories (Weinstein and Heck, 1979; Dorenbosch et al., 2005a,b; Hemingson and Bellwood, 2017). Despite the homogeneous appearance of seagrass habitats, associated fish assemblages may vary substantially among seagrass meadows located in different geographical contexts, such as near or far from reefs, rivers, land or deep water (Perry et al., 2018; Bradley et al., 2019; Sambrook et al., 2019). Life history traits, such as ontogenetic movement patterns and dietary requirements, affect a species' relationship with the seascape and therefore influence distribution patterns (Huijbers et al., 2013; Kimirei et al., 2015; Parsons et al., 2015). Consequently, distribution patterns vary between species, and are shaped by environmental variables on multiple spatial and temporal scales (Hori et al., 2009).

The influence of seascape configuration on fish distributions may be observed at a scale of tens or hundreds of meters for small-sized, sedentary species, while movement of large mobile species may occur over kilometres (Pittman et al., 2007; Olds et al., 2012; Green et al., 2015; Nagelkerken et al., 2017; Staveley et al., 2019). Furthermore, the length of migrations of a given species can vary by factors such as geographic location, seascape configuration, and local hydrology (Lowe et al., 2003; Martin et al., 2015; Sievers et al., 2016). As such, fish distribution patterns can be expected to be region-specific in addition to species-specific, making habitat-specific generalizations about fish distributions and ecosystem function challenging and possibly misleading (Boström et al., 2011). Depending on their size and mobility, distribution of species may be structured by variables on different spatial scales (Wedding et al., 2011; Goodell et al., 2018; Sievers et al., 2020). Grouping fish into broad categories based on simple attributes, such as habitat use, life stage, body size, or home range, may therefore be a useful approach when seeking to describe distribution patterns.

Seagrass meadows are important fishing grounds globally (Nordlund et al., 2018a) and are ecologically connected to coral reef fisheries in many regions of the tropics. Ecologically sound management of seagrass systems is therefore important (Torre-Castro et al., 2014). Despite the importance of seagrass meadows as fishing grounds, few studies have looked at fish distribution patterns related to life histories and protection from fishing in seagrass-dominated seascapes (but see Henderson et al., 2017). Understanding such patterns has implications for fisheries management, not only for spatial management, i.e. placement of marine protected areas (MPAs), but also for species-specific regulations. Due to the importance of seascape arrangement for fish distributions, it can be assumed that geographic placement of MPAs in seagrass-dominated seascapes would influence the outcomes of protection, especially for multi-habitat use taxa such as nursery and transient species. However, there is still limited information on which variables influence fish distributions across seagrass-dominaed seascapes (Nordlund et al., 2018b). Locations within the seascape and, for some species, the structural complexity of seagrass has been found to influence herbivory rates (Swindells et al., 2017; Berkström et al., 2020) and fish assemblage composition (Gullström et al., 2008; Henderson et al., 2017; Henderson et al., 2017). A better understanding of the factors that shape fish

distribution patterns in seagrass-dominated seascapes is essential for effective design of MPAs that would meet management objectives.

Seascape ecology is the science of landscape ecology adapted to the marine environment (Pittman, 2018). This study applies a seascape ecology approach to identify inter-patch proximity variables and within-patch variables that structure seagrass fish assemblages composed of resident and nursery species, and thereby help guide MPA placement in seagrass-dominated seascapes. Here, we define *nursery species* as those that spend their early life stages in seagrass meadows and shift to adult habitats when they outgrow the benefits to fitness and survival provided by their nursery habitat (Parrish, 1989; Dahlgren and Eggleston, 2000; Kimirei et al., 2013; Huijbers et al., 2015). In contrast, *resident species* spend all life stages in seagrass habitats, while *transient species* perform shorter temporal tidal or nocturnal migrations between habitat types, e.g. to forage in seagrass meadows during high tide or at night (Meyer and Schultz, 1985; Gullström et al., 2002; Hammerschlag et al., 2010). Many nursery and transient species are coral reef-associated and form an important ecological link between seagrass and reef ecosystems, via ontogenetic and feeding migrations (Meyer and Schultz, 1985; Nagelkerken et al., 2000; Pittman and McAlpine, 2003; Dorenbosch et al., 2005a; Harborne et al., 2016).

Specifically, based on field surveys in the Bazaruto Archipelago in Mozambique, this study aimed to determine (1) whether drivers of fish distribution patterns in a Western Indian Ocean seagrass-dominated seascape differ in fish species with varying life histories (comparing nursery and resident fish taxa), (2) relevant spatial scales to explain distribution patterns of seagrass fish assemblages based on simple species attributes (mobile or sedentary species), and (3) whether the influence of protection (presence of MPAs) differs between resident and nursery fish species.

2. Materials and methods

2.1. Study area

The present study was performed in the Bazaruto Archipelago, Mozambique (21.5°S, 35.4°E)(Fig. 1). The Bazaruto Archipelago consists of a vast, shallow bay with a string of islands bordered by fringing and patch coral- and sandstone reefs with varying coral cover (Everett et al., 2008). Extensive seagrass meadows exist in the bay, which is also characterized by shallow intertidal sandbanks and deeper tidal channels (<15 m depth). Strong tidal currents (up to 1.7 m s^{-1}) characterize the hydrology within the bay, with an average tidal amplitude of 3 m during spring tides (Everett et al., 2008; Hammar et al., 2012). Mangroves occur primarily to the south of the archipelago, around the São Sebastião Peninsula, which includes areas of both estuarine and marine conditions (Fig. 1).

Most of the reefs in the archipelago have been protected from fishing since the 1970s, and mangroves are rarely used as fishing areas (D'Agata, 2016). The most important fishing grounds for the local communities are the seagrass meadows, where seine netting and hook and line are the most common practices, targeting fish >5 cm in length (D'Agata, 2016). Two small no-take MPAs have been established in seagrass meadows of the São Sebastião peninsula in the private reserve Vilanculos Coastal Wildlife Sanctuary (VWCS): the Mazarete MPA (0.5 km^2) and the Marape MPA (5.2 km^2) (Fig. 1), both of which had been closed to fishing (for 0.5 and 4 years, respectively) at the time of the study. In addition to these protected areas, the Vilanculos District, which encompasses the entire archipelago except Bazaruto Island, also practices an annual temporary closure of the seine net fishery, usually from January to March (Díaz et al., 2016). Although relatively short, the temporary closure is perceived to have a positive effect on fish size and abundance (D'Agata, 2016).

All surveys were performed in January through March 2016 at 20 sites in 17 different seagrass meadows across the archipelago (Bazaruto Island, Vilanculos area, and São Sebastião Peninsula) (Fig. 1). There are
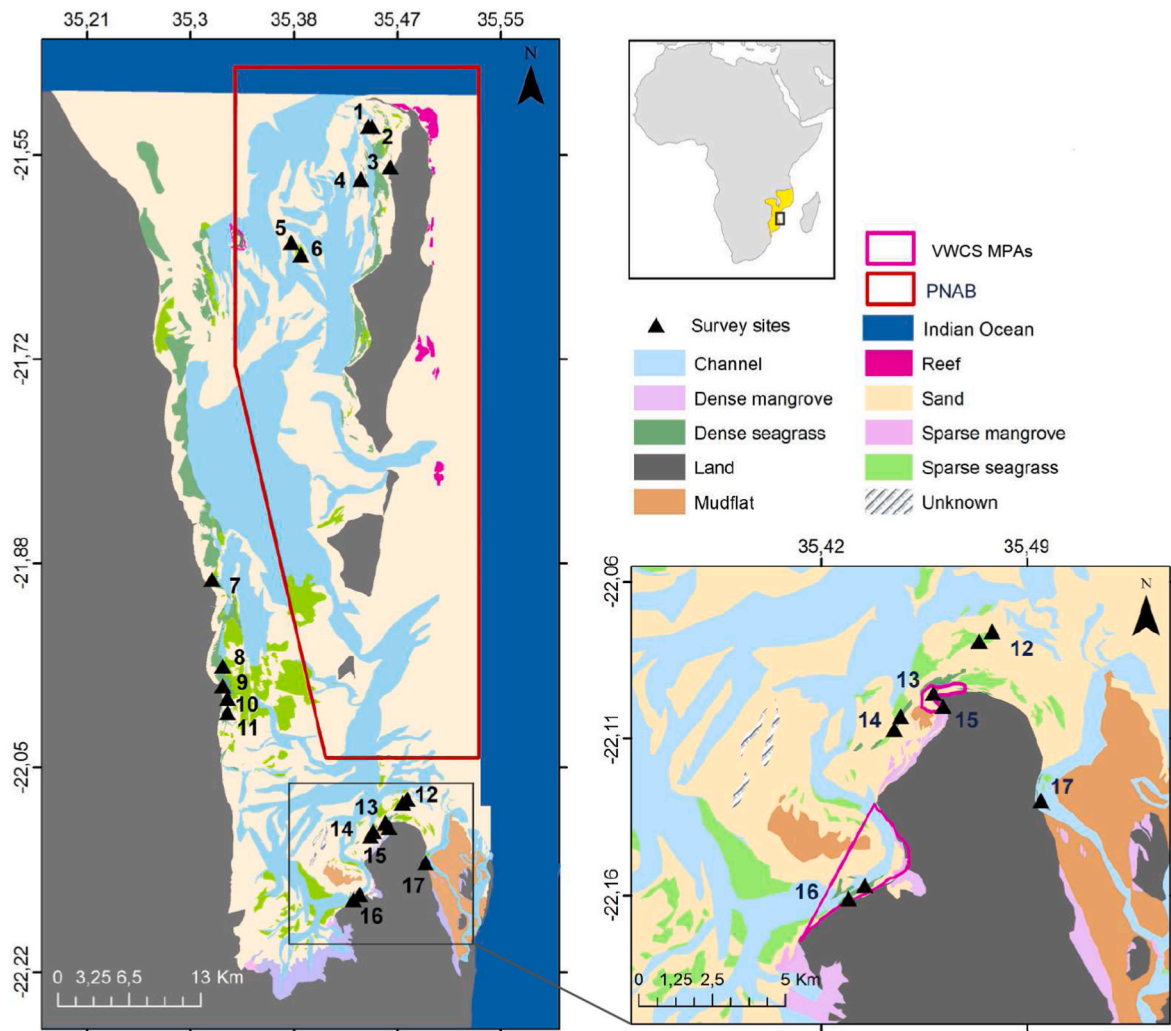
Fig. 1. *Map over the Bazaruto Archipelago showing main habitats and survey sites. Seagrass survey sites: 1 = Aguya, 2 = Murungulangene, 3 = Sitone, 4 = Matutuile, 5,6 = Canal de Deus 1 & 2, 7 = Vila do Indico, 8 = Mukoque, 9–11 = Vilanculos 1–3, 12 = Mazarete north 1 & 2, 13 = Mazarete 1 &2, 14 = Mazarete MPA 1, 15 = Mazarete MPA 2, 16 = Chinungwene and 17 = Marape MPA 1 & 2. PNAB = Parque Nacional de Bazaruto boundaries and VCWS = Vilanculos Coastal Wildlife Sanctuary.*

indications that juveniles are more abundant during this period compared to the austral winter (pers. comm A. Macia, Berkström et al., unpubl. data). All surveys were performed in seagrass habitats, with unvegetated sandy sediment as the only other present habitat. The three different areas were chosen based upon their differences in seascape context and available logistics (Supplementary data A, Table A1). The survey sites were situated along a distance gradient from mangroves, ranging from 0.7 to 64 km from mangrove habitats. Sites closest to coral reef habitats (i.e., sites 2–4, 7, 8, and 10) were situated within 5–8 km of reef habitats, while the two sites (1 and 6) located furthest from reef habitats were both >19 km from reefs (Supplementary data A, Table A1) (Fig. 1). All sites were subjected to marine conditions.

2.2. Fish and habitat surveys

The fish community was surveyed with underwater visual census (UVC) using 25 × 4 m belt transects. This method is considered efficient and accurate, and is widely used in shallow-water environments, including seagrass meadows (Hill and Wilkinson, 2004; Alonso Aller et al., 2014). Surveys were conducted during daylight hours between 07:00 and 15:30 in low slack tide due to the wide tidal range and strong tidal currents. Eight UVCs were performed at each survey site, except at the two survey sites at 7 (n = 3 and 4), 8 (n = 5) and two of the sites at 6 (n = 6) due to the increasingly strong tidal current during field work

(Supplementary data A, Table A1, Fig. 1). Depth at the time of surveys ranged between 0.5 and 3 m (Supplementary data A, Table A2). Survey starting points were positioned >50 m apart to avoid overlap of survey areas. To avoid edge effects, care was taken to place all UVCs >20 m from the edges of seagrass meadows. All fish were identified to the lowest taxonomic level possible, and size (total length) of specimens was estimated to the closest centimetre. The geographical position of each transect was recorded (with a *Garmin eTrex Touch 25*).

Seagrass characteristics were assessed along each fish UVC transect by placing a 50 × 50 cm quadrat in two locations (at 15 and 20 m distance from the starting point) after the fish survey was completed. This resulted in a minimum of 14 replicates per seagrass survey site and a total of 288 quadrats. Seagrass was identified to species level and the percent cover of each of the different species in the quadrat was estimated. To measure shoot density, all seagrass shoots within one quarter of the quadrat (0.0625 m^2) were counted. To determine canopy height, the three tallest seagrass plants in each quadrat were measured. Metrics were then averaged across quadrats for each transect. Pronounced seasonal changes in seagrass cover or morphology for the species included in the study have not been recorded in the Bazaruto Archipelago (pers. comm. Dr. S. Bandeira).

Surveys were also performed in the two MPAs. Despite the young age of the newest MPA (4 months at the start of the study), the area was included due to that the 3-month fishing ban is perceived as having a

positive effect on both fish size and abundance (D'Agata, 2016).

2.3. Spatial configuration of the seascape

A thematic habitat map of the Bazaruto Archipelago was constructed by manually delineating polygons for different habitats and habitat patches, which were visually interpreted from a satellite image (LANDSAT 8) in ArcMap 10.5 (resolution 10 m) (ESRI, 2017). Habitat types were identified through georeferenced field observations using a handheld Global Positioning System receiver (*Garmin eTrex Touch* 25) and used for ground-truthing information. Habitat categories were Sand, Channel, Mudflat, Dense Mangrove, Sparse Mangrove, Dense Seagrass, Sparse Seagrass, and Reef, where "Sparse" was classified as <40% coverage, and "Dense" as ≥40% coverage. This was visually estimated in the field for seagrass, and from satellite imagery for mangroves.

Measures of inter-patch distances were derived in ArcMap. Euclidian distances from each UVC from the closest habitat features of "Land," "Mangrove", "Reef," and "Channel" were generated using the 'Near' tool (point to polygon distance) in the ArcMap toolbox, independent of "Dense" or "Sparse" designations (ESRI, 2017). When direct distances crossed land, the distance was traced manually to respective habitat feature and around land masses, so as to represent distances relevant to movement within the marine habitat. The UVCs were spread along gradients of 100 m to 10 km to most seascape features (Supplementary data A, Table A1).

2.4. Data analyses

2.4.1. General fish distribution patterns

To identify significant predictor variables explaining fish distribution patterns in the seascape, both seascape- and habitat variables were used (Supplementary data A, Table A2). Seascape variables were represented by the distances from each UVC to adjacent habitats identified in the habitat map, and the habitat variables by total seagrass cover, canopy height, percent cover *Thalassodendron ciliatum*, percent cover *Thalassia hemprichii* and/or *Cymodocea* spp, depth, and shoot density. The influences of predictor variables on fish assemblage structure were explored with Redundancy analysis (RDA) using abundance data of fish on UVC level separated into genus. Since the predictor variables contained variables measured on different scales (cm, m, and km), all predictor variables were standardized to z-score values with the 'decostand' function in 'vegan' (Oksanen et al., 2019). Data were checked visually for normal distribution and fish data transformed using the Hellinger transformation. Significance for models and constrained axes were determined with a permutation test (999 permutations) using 'anova.cca'. Analyses were then re-run using only the significant environmental variables as predictors. All multivariate analyses were performed with the 'vegan' package (Oksanen et al., 2019) in R (R core team 2017).

2.4.2. Fish abundance patterns of selected taxa

To understand the influence of small-scale habitat and large-scale seascape variables (distance) on fish distribution patterns, fish abundance of selected taxa was modelled with Boosted Regression Trees (BRTs), which is a classification algorithm in machine learning (Elith et al., 2008). BRT models combine regression trees with boosting, and stepwise build a combined predictive model (Elith et al., 2008). Both methods stepwise separate data based on threshold values, and the final model is an average of a large number of trees (Breiman, 2001; Cutler et al., 2007; Franklin and Miller, 2009). To improve accuracy, bagging is utilised, which means that a randomly selected proportion of the data is withheld in each step (Breiman, 1996). For the BRTs, optimal combinations of bagging, learning rate, and tree complexity can be achieved by testing all possible combinations of these parameters. These models can handle nonlinear interactions between predictors of different magnitudes and are robust to outliers (Leathwick et al., 2006; Elith and Leathwick, 2007).

Only resident and nursery species were included in the models to examine how different life histories influence spatial distributions of fish, since no transient species were detected. Resident species were represented by the seagrass parrotfish *Leptoscarus vaigiensis* (Labridae, tribe Scarinae) and the four-lined terapon, or trumpeter perch, *Pelates quadrilineatus* (Teraponidae). Nursery species included juvenile parrotfishes (mainly *Scarus ghobban*), emperors (*Lethrinus variegatus;* Lethrinidae), the dory snapper *Lutjanus fulviflamma* (Lutjanidae), and mojarras (*Gerres* spp., Gerreidae). The three former nursery taxa migrate to reefs when they grow large, while specimens of *Gerres* spp. are mainly found in unvegetated sandy areas as adults (Froese and Pauly, 2019; Lugendo et al., 2005) (Table 1). The *Gerres* taxon was modelled at genus level because *G. longirostris* and *G. filamentosus* occurred in low abundances and could not always be identified to species level. The species in this group are ecologically similar and possess the same functional attributes. All species used in the model belonged to the mobile group. All species included in the models have a wide distribution in the Western Indian Ocean (Froese and Pauly, 2019), and are targeted in the artisanal fishery in the Bazaruto Archipelago (D'Agata, 2016), highlighting the socioeconomic value of such data for conservation and management efforts.

To select appropriate variables for the BRT analysis, a CCA was performed using each UVC as a replicate and including all predictor variables. Data were transformed and standardized, and significance of the constrained axes was tested as described for the fish community data. Non-significant variables ($p < 0.05$) were removed from the BRT model dataset, which included percent cover of *T. ciliatum* and seagrass shoot density.

The BRT models were performed with the gbm.step function in the 'dismo' package (Hijmans et al., 2011) in R (version 3.3.1.). Poisson error distribution was used for all taxa. Model fitting was performed with 10-fold cross-validation, testing all possible combinations of the model parameters, including tree complexity (tr; 2, 3, 4, 5 and 10), learning rate (lr; 0.05, 0.005 and 0.001), and bag fraction (0.5 and 0.75). The best models were chosen based on the lowest cross-validation deviation and number of trees. Models with less than 1000 trees were discarded, and models with very high numbers of trees were avoided due to over-fitting (Elith et al., 2008). To evaluate the BRT models, percent deviance explained (PDE) was calculated for each modelled fish taxon. Both the PDE for the cross-validated models and the test PDE for the withheld data were used to estimate model performance. Substantially lower test PDE indicates overfitting (Costa and Kendall, 2016). In addition, mean absolute error (MAE) and root mean square error (RMSE) were used to evaluate the BRT models. These errors describe how well predicted values conform to observed values, and are frequently used in modelling (Knudby et al., 2011; Costa et al., 2014;

Table 1

Attribute table over the taxa modelled with Boosted Regression Trees (Lugendo et al., 2005, Froese and Pauly 2019).

Taxa	Trophic guild	Life history	Nursery habitat	Adult habitat
Gerres oyena	Invertivore	Nursery	Seagrass, mangroves	Unvegetated
Gerres filamentosus	Invertivore	Nursery	Seagrass, mangroves	Unvegetated
Gerres longirostris	Invertivore	Nursery	Seagrass, mangroves	Unvegetated
Leptoscarus vaigiensis	Herbivore	Resident	Seagrass	Seagrass
Lethrinus variegatus	Invertivore	Nursery	Seagrass	Reef
Lutjanus fulviflamma	Invertivore/piscivore	Nursery	Seagrass, mangroves	Reef
Pelates quadrilineatus	Invertivore	Resident	Seagrass, mangroves	Seagrass
Scarus ghobban	Herbivore/detritivore	Nursery	Seagrass	Reef

Sayegh et al., 2014).

2.4.3. Importance of scale for mobile and sedentary fish species

On which scale a landscape (i.e., how much of a landscape we need to incorporate in our study) describes the distribution of species, or "effect of scale", is a fundamental question in landscape ecology studies. Simple species traits, such as species mobility and body size, have been used to test hypotheses of effect of scale (Bird Jackson and Fahrig, 2012; Miguet et al., 2016). We used mobility as a trait to test the scale at which seascape variables exerted the strongest influence on fish abundance, and separated species into sedentary and mobile species according to Froese and Pauly (2019). All nursery and transient species were classified as mobile species, while the resident species group contained both mobile and sedentary species. The proportional areas of all the different habitats were calculated within concentric circles of 20, 50, 100, 200, 500, 1000, 1500, and 2000 m radii from each survey point. Areas were calculated using the "Buffer" and "Intersect" tools in the ArcMap toolbox, overlaying the categorical habitat map. To test which spatial scale explained most of the variance in fish abundance, a redundancy analysis (RDA) was performed for each radius value, in addition to distance variables and seagrass cover. Data were transformed as described above. Significance of the constrained axes was tested with a permutation test (999 permutations) using the anova.cca function in the 'vegan' package in R. The significant variables and obtained F-values were then compared. Buffer rings around transects had increasing overlap with increasing radius, as will happen at increasing spatial coverage in any constrained geographical area (Pearman, 2002). Removal of data from overlapping buffers would result in a dataset too reduced to detect statistical significance, and previous studies have found consistent results between datasets including and excluding overlap when testing the influence of scale on fish assemblages (Goodell et al., 2018). In our case, the analysis was performed on a mix of overlapping (area) and non-overlapping (distance) variables, and we proceeded with full datasets.

2.4.4. Influence of protection

The influence of MPAs on fish abundances was investigated for the São Sebastião area. The analysis was restricted to this area since fishing pressure in the seagrass meadows open to fishing could be considered equally strong (D'Agata, 2016). Five fish taxa commonly caught in local fisheries were used in these analyses: the resident and mobile seagrass-associated species *P. quadrilineatus* and *L. vaigiensis*, and the nursery species *L. fulviflamma*, *Gerres* spp., and *Lethrinus* spp. The lethrinids were treated on genus level to increase number of individuals in surveys, based on that they possess very similar species traits (*Lethrinus lentjan*, *Lethrinus nebulosus* and *L. variegatus*). Linear mixed models were used with site as a random factor, and "protected" or "non-protected" from fishing as a fixed factor using the "lme4" package (Bates et al., 2015) in R. Relative contributions of fixed and random variables for explained variance were obtained using the function "VarCorr" from the "lme4" package. Fish abundance data were log- or square-root transformed to meet assumptions of normality.

The seascape and habitat characteristics of each survey site (i.e., distance from reef, distance from mangroves, distance from channel, distance from land, depth, and seagrass cover) were individually standardized based on their range (functions "decostand" and method "range" in the "vegan" package), by transforming data to relative values between 0 and 1, and then visualized as radial plots.

3. Results

3.1. General fish distribution patterns

In total, 144 UVCs were performed, in which 88 fish species representing 32 families were recorded. The majority of individuals were juveniles and sub-adults of species that reside in reef habitats during the adult stage, i.e. nursery species (Fig. 2, Supplementary data B, Table B1). No transient species were detected in the surveys, which resulted in all analyses on life history being restricted to nursery- and resident species. The most frequently occurring fish taxa were *Lethrinus variegatus* (in 67.4% of all UVCs), *Cryptocentrus cryptocentrus* (39.6%), *Leptoscarus vaigiensis* (35.4%), *Pelates quadrilineatus* (31.9%), and *Lutjanus fulviflamma* (30%) (Supplementary data B, Table B1). Few adults (2% of the total abundance of observed fish) were recorded, except for small cryptic species. Juveniles of certain coral reef-associated species, such as *Oxycheilinus bimaculatus*, *Stethojulis* spp, *Naso brevirostris*, and *Coris caudimacula*, occurred only at sites close to reefs and in low abundances.

Abundance of seascape residents increased with distance from reefs, while abundance of nursery species decreased (Fig. 2 e and f). Total abundance of fish was similar across the seascape regardless of distance to reef (Fig. 2 i).

Seascape- and within-habitat variables influenced fish abundance and distributions in seagrass meadows across the seascape and did jointly explain 17.8% of the variance of fish abundance per site (R^2 value, RDA; Fig. 3) when analysing the whole fish community on genus level. The four first axes were significant and all variables were significantly related to general fish assemblage composition (RDA, anova permutation test, $p < 0.05$; Fig. 3). A low degree of explanation was expected since each UVC was used as a replicate and variation was high between replicates. Abundances of taxa associated with mangroves, such as *Neopomacentrus* sp., were negatively influenced by increasing distance from mangroves, while abundances of seagrass residents, such as *Cryptocentrus* spp., were positively influenced by distance from reefs (Fig. 3).

3.2. Abundance patterns of selected taxa

The BRT models provided a clearer understanding compared to the RDA with regard to variables that were important for the distribution of certain taxa. In general, seascape variables were more important than within-habitat variables, although the importance of predictors was highly taxa-specific (Fig. 4). Distance from reef was the most important variable for the reef-associated nursery species *L. variegatus* (explaining 57.8% of the variation), which decreased in abundance with increasing distances to reefs. Abundance of *L. variegatus* was negatively correlated with distance from reef, and there seemed to exist a threshold drop in abundance at an approximate distance of 6 km from the reef (Fig. 4). Distance from reef was also a strong predictor for the seagrass resident species *P. quadrilineatus* (32.1%), which showed a positive correlation with this variable. Distance from mangroves showed a negative correlation with abundance of all taxa, except for *L. variegatus*, which had no association with this variable. For all other taxa, except the Gerreids, a threshold at 3 km from mangroves was found where abundances abruptly declined. Distance from channels was highly correlated with abundances of most taxa, except for *S. ghobban* and *L. variegatus*. The distribution of *Gerres* spp. was in general affected on a broader spatial scale than the other taxa (with the effect of scale between habitats/features visible at distances of 1 km compared to only 200 m for the other taxa).

Effects of within-habitat variables were not consistent among species. Seagrass canopy height was of notable importance only for *S. ghobban* (70.2%), which showed a sharp increase in abundance in meadows where the mean seagrass canopy was taller than 35 cm. Seagrass cover generally had a weak positive influence on fish abundances, but a negative influence on *L. variegatus* abundance (8.2%) that occurred in higher abundances in meadows with less than 20% seagrass cover (Fig. 4).

Model performance of the BRTs was moderate, except for the less abundant taxa (*L. vaigiensis* and *S. ghobban*), for which the models performed poorly (Supplementary data B, S Table B3). These models showed signs of overfitting (i.e. low MAE and test PDE) and should be interpreted with care (Supplementary data B, S Table B3).
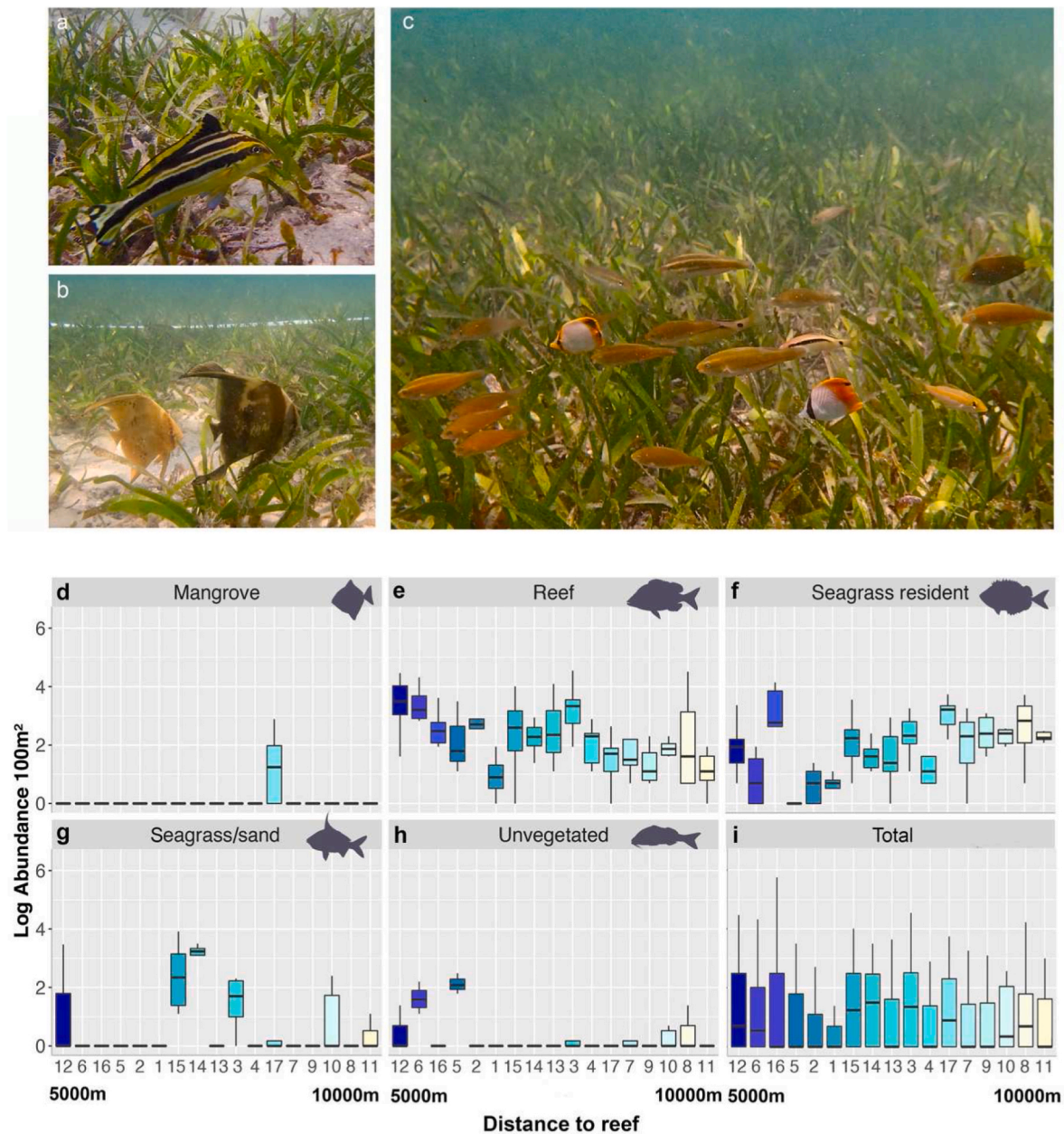
Fig. 2. *Common fish species in the seagrass surveys; a) a juvenile* Diagramma pictum*, b) juvenile* Platax orbicularis*, and c) a group of juveniles, including* Chaetodon*,* Scarus*,* Parupeneus*,* Acanthuridae *and* Lethrinus*. Boxplots show abundance of fish at the surveyed seagrass sites grouped by their adult habitat and ordered by distance to closest reef. Numbers on the x axis represent survey sites as in* Fig. 1*. Horizontal lines represent median values and the whiskers the range of data. Photo credits: Marcos Lucena and Whitney Goodell, and fish images by the 'fishualize' package in R, and adapted from efishalbum.com.*

3.3. Effect of scale for mobile and sedentary fish species

Effect of scale on fish abundance differed between the mobile and sedentary groups. Abundance of mobile species was mainly explained by distances from adjacent habitats rather than by area of habitat, especially at large 'seascapes' (buffer radii <1 km) (RDA and permutation test anova.cca, Table 2). Area of dense seagrass within buffers was only significantly influencing abundances at larger seascapes/buffers (radii of ≥1 km) (Table 2). At smaller seascapes/scales (radii of <500 m), the only area variable that was significant for mobile fish abundance was area of channel habitat (Table 2). Small and sedentary species were influenced significantly by area of habitat within both small and large seascapes (20 m–2000 m radii), while distance from other main habitats was rarely significant (RDA and permutation test, Table 2).

The models explained very little of the variance in abundance of the cryptic and sedentary species ($R^2 < 0.07$), while for the mobile species they performed better ($R^2 < 0.17$). R^2 values increased with seascape size for mobile species, but not for the cryptic and sedentary species (Table 2).

3.4. Influence of protection

Protected areas had higher abundances of *P. quadrilineatus* compared to non-protected areas, but this relationship was not significant (Linear mixed models, p = 0.09; Table 3). There were no significant effects of protection on any fish taxa (Fig. 5). For all species assessed, abundance was influenced by site, with the effect of site being taxa-specific (Table 3). Lethrinids occurred in highest abundance at the seagrass meadow located closest to the reefs in non-protected areas (Site 8, Fig. 5). Juvenile *Lutjanus fulviflamma* was most abundant in one of the
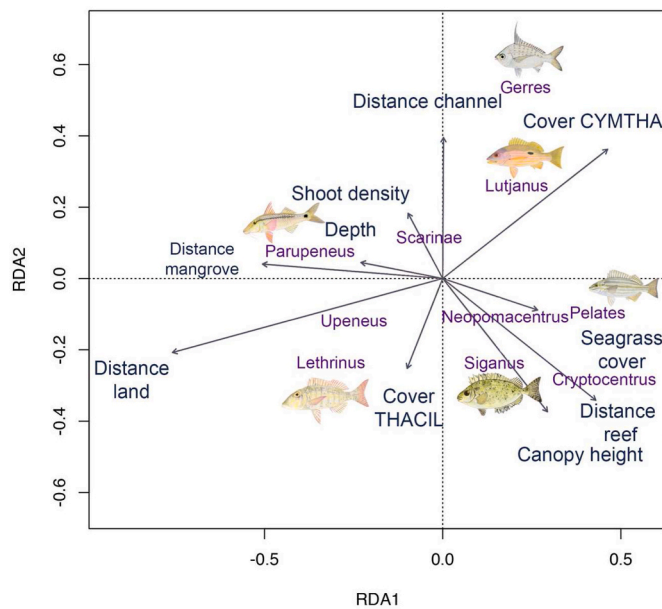
Fig. 3. *Redundancy Analysis (RDA) showing the influence of predictor variables on the abundance of fish genera in the seagrass-dominated seascape. Length of arrow is proportional to strength of variable. Abbreviations: CYMTHA= Cymodocea spp. and Thalassia hemprichii cover, THACIL = Thalassodendron ciliatum. Genera that showed little influence from predictor variables were removed from the image (i.e.* Acanthurus, Amblyogobius, Ctenogobiops, Gnatholepis *and* Plectorhinchus*). Fish images from* www.efishalbum.com.

MPAs in Mazarete (3d, Fig. 5), but occurred in low abundance in the Marape MPA (1a & b, Fig. 5), which was situated furthest from the reefs (Fig. 5).

4. Discussion

Distributions of organisms in a mosaic landscape are influenced by patch size and arrangement, and can be described both by distance- and area variables (Bender et al., 2003; Calabrese and Fagan, 2004). This study identified important seascape variables in structuring the fish assemblage of a tropical seagrass-dominated landscape using simple species attributes, including life history traits and mobility. We also determined the scale of effect (e.g. extent of landscape that is relevant for distribution studies) on fish distribution using mobility as a trait. Distance variables on broad (km) scales generally explained mobile species' abundances and distributions (across species of varying life histories) better than area variables, while sedentary/cryptic species (which all, except two species, belonged to the resident species group) were mainly influenced by area variables in smaller (<500 m in radius) seascapes.

Seascape variables, such as distance from reef, influenced abundances of taxa but in opposite directions depending on the species' life history (nursery vs. resident). Consequently, categorizing fish as nursery or resident species allows for certain generalizations of distribution patterns. For example, nursery species are expected to occur in higher densities in meadows close to their adult habitats, while resident species display the opposite pattern; they are more abundant in meadows further from reef habitats. This may be explained by higher abundances of transient predatory reef fish closer to reefs. Studying the response of the whole fish community to key variables influencing fish abundance and distribution in seagrass-dominated systems can generate results that are strongly biased by the most abundant species.

Species-specific patterns have been suggested as one of the main reasons why it is difficult to generalize the influence of seascape attributes on fish distributions in seagrass systems (reviewed by Connolly

and Hindell, 2006). Differences in species-specific characteristics, such as life-histories and mobility, can lead to different responses to predictor variables. Grouping species in broad categories related to habitat use and mobility, as in the present study, may however allow for broader generalizations on distributions while still retaining a certain degree of accuracy of such generalizations. For example, we found that Lethrinids were more abundant in seagrass meadows close to reefs (i.e. their adult habitat), but in contrast to earlier results (Henderson et al., 2017; Henderson et al., 2017) abundance was not related to distance from mangroves. Juvenile Lethrinids occur in low densities in the mangroves in Bazaruto (Eggertsen et al. unpubl. data), suggesting low dependency on mangroves as a nursery habitat. In contrast, the strong negative influence of increasing distance from mangroves on the abundances of *L. fulviflamma, P. quadrilineatus,* and *Gerres* spp. may be related to their use of mangroves as nursery habitats (Dorenbosch et al., 2004; Lugendo et al., 2005; Berkström et al., 2013).

Location of a seagrass meadow in relation to land emerged as a strong predictor for all taxa except Lethrinids. In a range of different marine systems, shallow vegetated areas close to shore often hold high abundances of juvenile fish, perhaps due to low densities of predators (Gullström et al., 2011; Kraufvelin et al., 2018). The results from this study indicate that distance from land is an important variable for seagrass fish distribution, regardless of mangrove presence, and highlights the importance of meadows located close to shore.

Tidal channels are a prominent feature of the Bazaruto seascape. Abundance patterns related to configuration of the channels are difficult to interpret since the ecological significance of the tidal channels is complex. These features can serve as foraging migration routes for predators (Krumme, 2009), thus serving as corridors with implications for predation processes. Tidal channels also facilitate ontogenetic migrations of nursery species to their adult habitats (Gibson, 2003). For juvenile *L. fulviflamma,* which displayed higher abundances close to channels, shores, or mangroves, proximity to channels could be advantageous as a migration corridor since these nurseries are located at large distances from their adult reef habitat. In contrast, *Gerres* spp., which were negatively influenced by proximity to channels, perform shorter ontogenetic migrations by shifting from seagrass habitats to deeper sandy habitats when they grow larger, and may benefit from nurseries located further away from channels and thus avoiding potential predators. Consequently, the importance of channels for fish distributions would be expected to be taxa-specific and may depend on the spatial configuration of surrounding habitats within the seascape.

The strength of seascape variables on fish distribution may vary with geographic location, fish size, and focal habitat (Kramer and Chapman, 1999; Connolly and Hindell, 2006; van Lier et al., 2017). We found that effects on fish abundance occurred at larger distances in Bazaruto compared to multi-habitat seascapes in Tanzania (Gullström et al., 2011; Berkström et al., 2013) and the Pacific (Martin et al., 2015). This was particularly true for the seascape variable "distance from reef". In the present study, thresholds in distance from reefs, where abundances drastically decreased for Lethrinids, were located at about 6 km from reefs (BRT models, Fig. 4). Previous studies have found threshold distances for multi-habitat species of fish (including nursery species) between seagrass meadows, mangroves and reefs in the Indo-Pacific at less than 1 km (Berkström et al., 2013; Martin et al., 2015), while in the Bazaruto seascape at about 8 km (Berkström et al., 2020). The Bazaruto seascape is larger in extent compared to the seascapes in the previous studies, with extensive seagrass meadows and larger distances between different habitats (e.g. between reefs and seagrass meadows or mangroves). Our study therefore provides an example of how fish are influenced by these variables in a broader-scale seagrass-dominated seascape, and shows that fish can be plastic in their migrations.

Habitat area has been found to be a good predictor of the distribution of organisms in mosaic landscapes, if measured on relevant scales (Bender et al., 2003). What is a relevant scale may, however, differ depending on traits of the studied species (Bird Jackson and Fahrig,
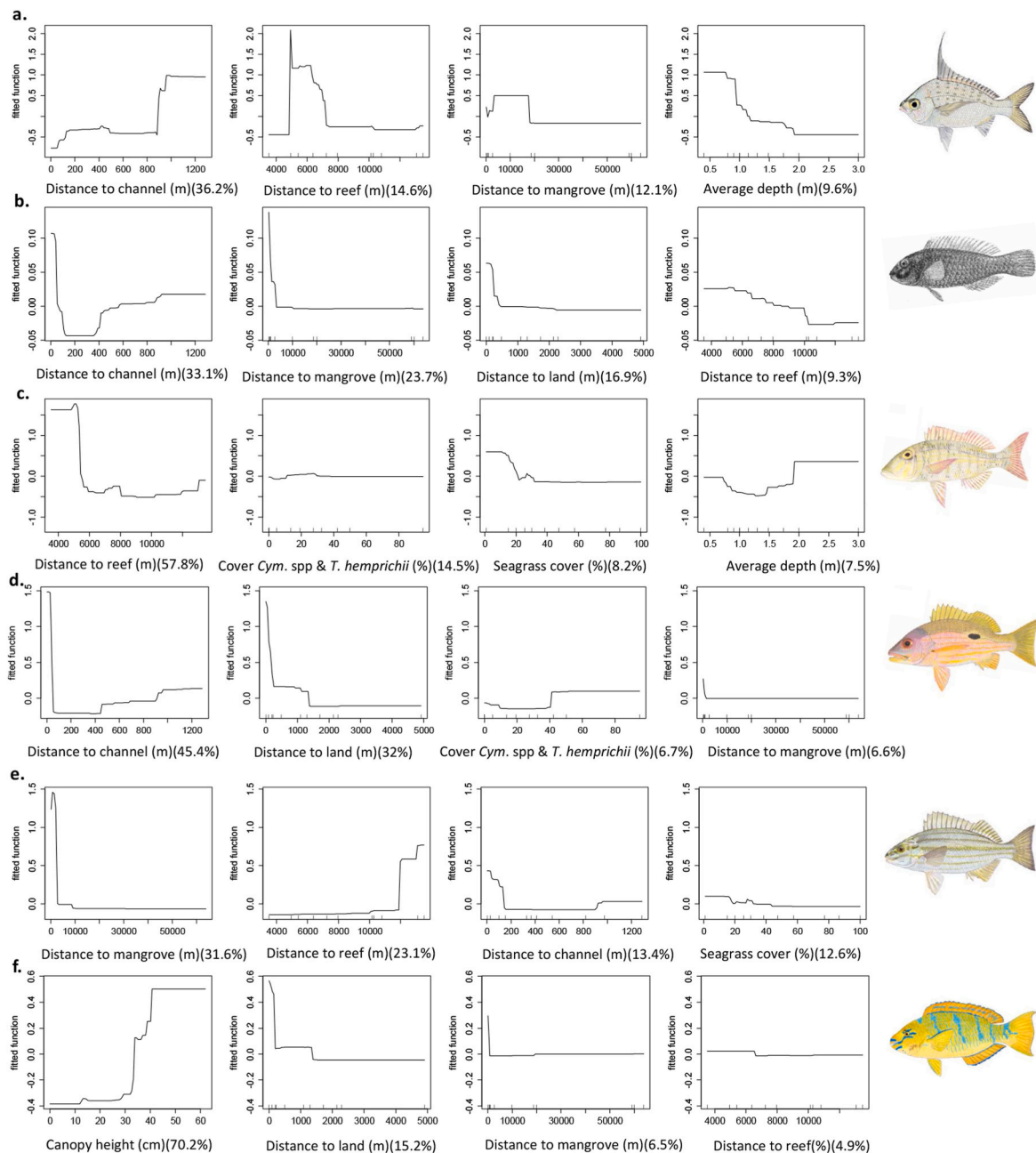
Fig. 4. *Fitted functions for the* 4 *most influential predictor variables for abundance of a)* Gerres spp.*, b)* Leptoscarus vaigiensis*, c)* Lethrinus variegatus*, d)* Lutjanus fulviflamma*, e)* Pelates quadrilineatus*, and f)* Scarus ghobban *modelled with Boosted Regression Trees. Percentages in brackets show relative influence of each variable. Abbreviation: Cym* = Cymodocea. *Image courtesy of* www.efishalbum.com *except for* L. vaigienis *(Sir Francis Day, Fauna of British India).*

2012). Mobility has in many cases been suggested as a trait influencing the effects of scale, although little scientific evidence has supported this theory (Miguet et al., 2016). We found clear differences in effect of scale between mobile and sedentary species, and that larger seascapes explained distribution of mobile species better than small seascapes. For mobile species (including both resident and nursery species), distances from different habitats explained species distributions better than area of habitat within seascapes. If many species are multi-habitat use species, distance variables may provide more accurate predictions of distributions than area measurements, especially in seascapes where different habitats are located far apart. Area variables derived from smaller seascapes may better explain distributions of sedentary species that do not migrate and thus have limited home ranges (Kramer and Chapman, 1999; Bird Jackson and Fahrig, 2012). A separation of species into mobile and sedentary groups gave clear results, while using

additional traits, such as life history, would probably further improve the performance of models. It should also be considered that seascapes of distinctly patchy habitat configurations may entail spatially-clustered sampling, as in this study, which inherently leads to spatial overlap when evaluating habitat variables extracted from larger seascapes. This limitation should be acknowledged when interpreting results, but we feel our results convey valuable patterns for broad groups of seagrass-dwelling fish.

Within-patch variables, such as habitat cover and complexity, have in some studies shown less importance compared to seascape variables (e.g. Pittman et al., 2007; Wedding et al., 2011). Our results generally also support the importance of seascape variables, although seagrass cover had a negative influence on abundance of Gerreidae and Lethrinidae, and canopy height a positive effect on abundance of juvenile *S. ghobban*. The negative effect of seagrass cover may be linked to

Table 2
Importance of predictor variables for abundance of cryptic/sedentary and mobile fish species recorded in seagrass meadows. P and R^2 values were obtained through a permutation test using the axes of the RDA.

Fish category	Circle radii (m)	Distance				Area						R^2
		Channel	Mangrove	Land	Reef	Channel	Mangrove	Mudflat	Dense seagrass	Sparse seagrass	Sand	
Sedentary	20	-	-	-	-	-	-	-	*	*	-	0.07
Sedentary	50	-	-	-	-	*	-	-	*	-	-	0.02
Sedentary	100	-	-	-	-	*	-	-	*	-	-	0.02
Sedentary	200	-	-	-	-	*	-	-	*	-	-	0.02
Sedentary	500	-	-	-	*	*	-	-	*	*	*	0.07
Sedentary	1000	-	-	-	-	-	-	*	*	*	-	0.07
Sedentary	1500	-	-	-	-	-	-	*	*	-	-	0.06
Sedentary	2000	-	*	-	*	-	-	*	-	*	-	0.03
Mobile	20	*	-	*	*	-	-	-	-	-	-	0.12
Mobile	50	*	*	*	*	*	-	-	-	-	-	0.12
Mobile	100	*	-	*	*	*	-	-	-	-	-	0.15
Mobile	200	-	-	*	*	*	-	-	-	-	-	0.10
Mobile	500	-	-	*	*	*	-	-	-	*	-	0.13
Mobile	1000	*	-	*	*	-	*	*	*	-	-	0.16
Mobile	1500	*	-	*	*	-	*	*	*	-	-	0.16
Mobile	2000	*	*	*	*	-	-	*	*	-	-	0.17

Significance (p < 0.05) is indicated with an *.

Table 3
Relative variance explained by fixed and random factors from the linear mixed models on effects of protection and site on abundance on five fish taxa.

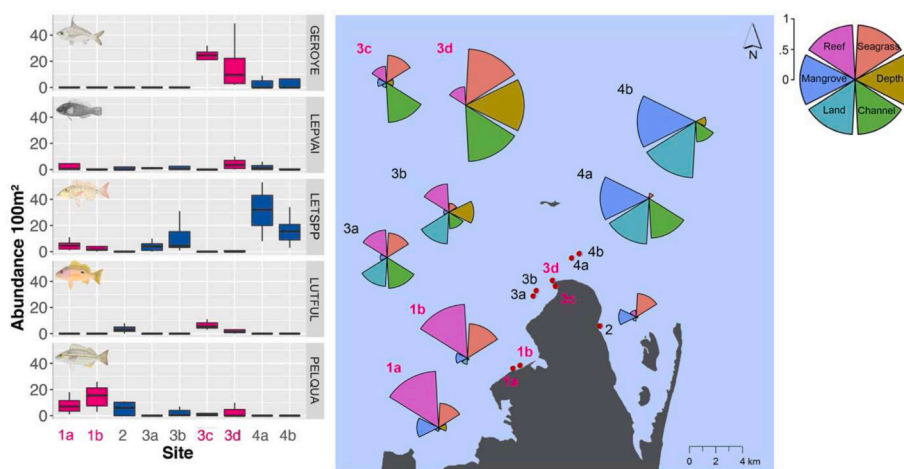| Taxa	Fixed (Protection)	Random (Site)	Residuals	Correlation fixed effect (R^2)	p-value (fixed effect)
Pelates quarilineatus	0.306	0.268	0.425	−0.662	0.089
Gerres spp.	0.29	0.331	0.379	−0.664	0.162
Lethrinus spp.	0.432	0.332	0.236	−0.665	0.083
Lutjanus fulviflamma	0.3	0.419	0.28	−0.665	0.46
Leptoscarus vaigiensis	0.038	0.102	0.86	−0.665	0.845

Fig. 5. *Abundance per 100 m^2 of five species targeted in the small-scale fishery and survey site characteristics. The map shows the surveyed sites in São Sebastião and their different characters with size of triangle proportional to variable value (distance from named habitats, except for "seagrass" that corresponds to seagrass cover and "depth" that corresponds to depth at the survey point). Survey points with letters in magenta indicate no-take marine protected areas. 1 a and b = Marape MPA, 2 = Chinungwene, 3 a and b = Mazarete non-protected seagrass, 3 c and d = Mazarete MPA, 4 a and b = Mazarete North. GEROYE = Gerres oyena, LEPVAI = Leptoscarus vaigiensis, LETSPP = Lethrinus spp., LUTFUL = Lutjanus fulviflamma, PELQUA = Pelates quadrilineatus. Image courtesy of* www.efishalbum.com *except for* L. vaigienis *(Sir Francis Day, Fauna of British India).*

feeding strategy, since both Lethrinids and Gerreids feed on sediment infauna (Froese and Pauly 2018), and dense seagrass beds can hinder foraging efficiency (Heck and Thoman, 1981). How within-patch variables and seascape variables interact and together influence fish abundances are important to disentangle, for instance when identifying essential fish habitats and for spatial management of the seascape. Seagrass cover can be extracted from satellite images and is therefore a relatively easy variable to incorporate in models and to use when identifying potential important seagrass habitats.

Spatial placement of MPAs has been recognized as an important factor for the success of coral reef protection, in many cases with regard to connectivity with other habitats (Almany et al., 2009; Grober-dunsmore et al., 2009; Olds et al., 2012). If MPAs are to be effective, life history and mobility of species should be considered in reserve design (Batista et al., 2015). Both protected areas examined in our study cover dense seagrass meadows and are located in close proximity to mangroves and channels, while far from reefs. Our results indicate that these characteristics are not optimal for all the species in the study, particularly not for the majority of the nursery species. If maintaining high connectivity with reef habitats would be the main focus of an MPA, the MPA should be placed as to incorporate seagrass meadows within threshold distances from reefs.

We speculate that fishing pressure within seagrass habitats exerts a stronger effect on resident species than on nursery species, as nursery species are subjected to fishery-related mortality only during their juvenile life stage, a stage characterized by naturally high mortality rates (Lorenzen, 1996; White, 2015). For example, high abundances of seagrass resident Siganids were previously common in the Bazaruto

Archipelago (pers. comm. S. Bandeira). However, in our study, larger Siganids were extremely rare, which may be related to the seine net fishery. Contrary to common theories on management of fisheries (but see Kolding et al., 2016), a fishery that targets reef fish only in the juvenile stage may not necessarily be unsustainable (White, 2015), particularly if adult habitats are protected or otherwise experience low extraction pressure. The positive relationship between abundance of *P. quadrilineatus* and protection status is likely a combined result of optimal reserve placement and restricted fishing on a species subjected to intense fishing pressure during all life stages. Similarly, *L. fulviflamma* occurred in higher abundance in the young (6 months) MPA (closer to reefs) compared to the MPA in Marape (4 years; far from reefs). This suggests that geographical position can exert a stronger effect than protection *per se.*

Some potential limitations of this study are important to mention. We are aware that the MPAs in this study are very young, and that the results in this study are based on a single-occasion survey (three months). Recruitment patterns may vary substantially between years, but we believe that the scales and variables identified here should be useful in seagrass-dominated seascape studies. Since the nursery species are represented mainly by juveniles, even a young MPA could possibly have positive effects on fish abundance (considering that the three-month seasonal fishing ban in Bazaruto is perceived to have a positive effect on fish abundance and size). Further, it is not clear if fish migrate between the different seagrass meadows, or if the areas of sand between them function as barriers, as has been found elsewhere (Lowe et al., 2003). This is a subject for future studies, as well as the understanding of recruitment patterns on larger temporal scales.

5. Conclusions

Our results emphasize that marine spatial planning efforts should benefit from considering fish distribution patterns based on simple attributes, such as life-history and mobility, in combination with seascape metrics. The design of a spatial management plan should be based on the management objectives and distribution patterns of the species of interest, a point demonstrated by the opposing effects that some variables had on abundance of different taxa. Ideal seascape size and the use of distance or area measurements as predictor variables can be designed depending on the taxa of interest and seascape configuration. By carefully considering geographical placement of reserves, protected areas can boost the abundance of fish species or groups, benefitting the surrounding fishery via spillover effects of adults or increased export of larvae (Nagelkerken et al., 2012). The species examined in this study are all targeted in the local fishery, and we therefore stress the need for knowledge of seascape influence for a multi-species fishery.

CRediT authorship contribution statement

Linda Eggertsen: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Whitney Goodell:** Investigation, Writing – original draft, Writing – review & editing, Methodology. **Cesar A.M.M. Cordeiro:** Investigation, Formal analysis, Writing – review & editing. **Damboia Cossa:** Investigation, Funding acquisition, Writing – review & editing. **Marcos de Lucena:** Investigation, Writing – review & editing. **Charlotte Berkström:** Funding acquisition, Supervision, Writing – review & editing. **João N. Franco:** Investigation, Writing – review & editing. **Carlos E.L. Ferreira:** Supervision, Writing – review & editing. **Salomão Bandeira:** Writing – review & editing. **Martin Gullström:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107738.

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