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Drivers of fish diversity and size spectra across lagoonal habitats of the Toliara reef system (SW Madagascar)

Henitsoa Jaonalison [a,*], Marilaure Grégoire [b], Jamal Mahafina [c], James Mwaluma [d], Helga Berjulie Ravelohasina [a,c], Aina Le Don Nomenisoa [c], Toky Justino Mory [c], Lantoasinoro Ranivoarivelo [c], Dominique Ponton [e], Bruno Frédérich [a]

[a] Laboratory of Evolutionary Ecology, FOCUS, Université de Liège, Belgium
[b] Modeling for Aquatic Systems (MAST), FOCUS, Université de Liège, Belgium
[c] Institut Halieutique et des Sciences Marines (IH.SM), Université de Toliara, Madagascar
[d] Kenyan Marines Sciences and Fisheries Institute (KMFRI), Mombasa, Kenya
[e] ENTROPIE (IRD, University of La Reunion, CNRS, University of New Caledonia, Ifremer), c/o CRIOBE, Université de Perpignan, Perpignan, 66860 France

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ABSTRACT

Size-spectra and taxonomic diversity are important indicators to study the dynamics of communities and to inform conservation in aquatic ecosystems. To date, few studies aimed at modelling the distribution of reef fish diversity at small spatial scales (~10 km) have been done. Based on a one-year fish sampling using trawl nets, we described and modeled the distribution of fish diversity and their size spectra across various coastal habitats in the Toliara reef system (SW Madagascar). Our data revealed a significant spatial and seasonal change of taxonomic diversity. Beta-diversity was mainly driven by species turnover with up to 75 %, indicating the important conservation value of the sampled sites. Fish size spectra slope emphasized the high dominance of small-sized fish on the sites close to the shoreline indicating their potential nursery zones. By combining environmental and geographic data with the use of the machine learning algorithm Random Forest, we demonstrated the geographic position of sites and associated habitat features were the foremost drivers of alpha-diversity and size spectra patterns (50–64 % of variation). The use of Generalized Dissimilarity Models revealed sediment cover was the main predictor of species turnover patterns (62 % of explained variation), with a rapid increase of species replacement within the first 2 km from the coast. Beyond a confirmation of the role of habitat features on biodiversity, our study emphasized the importance of distance to the shoreline on the distribution of fish diversity across the lagoon. This unexpected driver is discussed in the light of various anthropogenic factors including fisheries and sedimentation.

1. Introduction

Coral reefs are highly productive marine ecosystems from tropical zones (Sheppard et al., 2017). In many regions, they are ecologically connected to other coastal systems including seagrass beds and mangroves through varied fluxes of materials and energy (e.g. ontogenetic habitat shifts of organisms, daily movements of fishes …), and they collectively support high biomass and diversity of fish (Honda et al., 2013; Moura et al., 2021). These coastal ecosystems are always considered as complex due to the large network of biotic and abiotic components (Fonnesu et al., 2004). Unfortunately, they are also highly threatened due to their location in the most densely populated areas, experiencing anthropogenic degradation and exploitation (Harley et al., 2006; Graham et al., 2007; He and Silliman, 2019). In addition to such local pressures, global rising sea surface temperatures drove habitat degradation, further compromising the ecological functioning of the coastal systems (Hughes et al., 2017). In developing countries, these ecosystems are particularly facing overfishing and destructive fishing practice leading to significant ecological changes and drastic decline of the coastal areas-associated fishes (Ahmad et al., 2024; Barrilli et al., 2021). This highlights the important need of investigating the associated biodiversity metrics of such impacted marine ecosystems to provide baselines for evaluating conservation effectiveness, further biodiversity loss and designing science-based robust network of marine protected

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* Corresponding author.
E-mail address: henitsoa.jaonalison@uliege.be (H. Jaonalison).

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areas (Socolar et al., 2016).

Several biodiversity metrics exist to assess changes of fish diversity over time and space, but their choice relies on the question to be addressed and importantly on the specificity of the ecosystems (Galuppo et al., 2007). The variation of two taxonomic diversity components, alpha-diversity and beta-diversity, are generally used to understand biodiversity changes in coastal ecosystems (Karkarey et al., 2022). The alpha-diversity describes the number and abundance of species within areas or communities (Whittaker, 1972), while beta-diversity captures the information on the pattern of connectivity with relevant conservation implications (Socolar et al., 2016). Typically, beta-diversity describes the change in species compositions of assemblages across areas by considering the spatial species turnover (a result of species replacement among sites) and the nestedness of the assemblages (based on species loss in each site) (Whittaker, 1960; Baselga, 2010). More precisely, turnover happens when species present at one location are absent at another one but are replaced by other species absent from the first location. Nestedness corresponds to species which present at one site are absent at another, but are not replaced by additional species (Dornelas et al., 2014).

In addition to taxonomic diversity, size-based metrics were often used to assess the effect of fishing on marine ecosystems, as increased fishing efforts reduce large-sized target fish species. However their variation was essentially studied at regional and global scales (Shin et al., 2005; Wilson et al., 2010). Size structure is also considered as an indicator of ecological status (Petchey and Belgrano, 2010) as variation in body size and distribution of ontogenetic stages reflect the ecosystem functioning like recruitment, predation and habitat use (Boll et al., 2023). In complex coastal environments such as lagoons, these metrics may additionally reveal habitat-specific ecological roles, including nursery functions. For instance, Romero-Berny et al. (2020) reported greater abundance of small-sized fish from several species and higher species richness in lagoonal habitat than in outer reefs due to the more sheltered and structured area. However, in tropical lagoonal systems, particularly at small spatial scales, empirical data on spatial variation in fish size structure and diversity remain limited. Understanding these variations is critical for disentangling the effect of environmental filtering, species turnover and anthropogenic pressure, such as non-selective mosquito net trawls, which may simultaneously affect both juvenile and adult individuals.

Investigating the relationship between indicators of ecological status (alpha- and beta diversity, and fish size structure) and different geographical and environmental variables is helpful for our understanding of the dynamics of fish communities (Devictor et al., 2010), as changes in diversity among areas may be attributed to environmental selection or spatial constraints (Qian et al., 2005). For example, determining the environmental drivers or spatial variables inducing changes in beta-diversity is ecologically important as higher beta-diversity produces greater species richness (Kraft et al., 2011). To date, the drivers of coral reef fish alpha- and beta-diversity have been solely tested at large spatial scales (i.e. a spatial scale comprised between 1000 to more than 2000 km) on adult fish communities (Mellin et al., 2014; Karkarey et al., 2022; González-Barrios et al., 2025). These studies revealed varied effects of environmental and geographical variables on fish diversity patterns. For example, Mellin et al. (2014) reported that reef fish diversity decreased with high latitudes and increased with the large distance from the coast. González-Barrios et al. (2025) stated a stronger and positive relationship of reef fish diversity with coral composition than coral cover. Reef fish diversity has also been found to be influenced by the distance among atolls (Karkarey et al., 2022). Recently, Coker et al. (2025) showed that the environmental gradient observed along the latitudinal distribution of the Red Sea affects the functional richness and diversity of fish. Other studies were conducted at smaller spatial scales and revealed the strong influence of reef-scale hydrodynamics such as current velocities and wave exposure on diversity of reef fish assemblages (Ceccarelli et al., 2023; Galbraith et al., 2023) as well as on the richness and abundance of reef fish larvae present on coral reefs (Jaonalison et al., 2020). Irawan and Hutabarat (2019) illustrated variation in fish diversity across various coastal habitats including seagrass beds, mangroves and coral reefs from Bontang, Indonesia, but they did not explore the potential drivers of these changes.

Our understanding of how substrate features (substrate type cover and composition), geographical variables (latitude and distance from the coast), food availability variation and hydrodynamics affect the diversity pattern of reef fish in lagoonal areas are still limited. The small-scale distribution pattern of fish diversity in a restricted system within 10 km with high fishing pressure from small-scale fishermen remains totally unexplored in Madagascar. This knowledge would be highly relevant for conservation purposes in defining the potential protection zones due to their ecological importance. Therefore, the objective of this study was to investigate the structure of fish assemblages from varied areas distributed across the lagoon of the largest barrier reef of the Indian Ocean (Great Reef of Toliara - GRT, SW Madagascar). The aims were to show (1) how various components of fish diversity (alpha-, beta diversity and size spectra) vary from the coast to the barrier reef, and (2) to determine the foremost variables driving spatial variation of diversity in connected areas. At a small spatial scale less than 10 km, latitude variation is negligeable, and general water mass conditions would have less impact on fish diversity patterns than the substrate features and the distance from the coast. However, due to the possible limited variation of the substrate features, they may also have less impact on fish diversity than the shoreline distance.

2. Methods

2.1. Study sites

Madagascar has two main seasons: a warm season from October–April with land surface temperature (LST) ranging from 25 to 35 °C and a cold season in May–September with LST between 15 and 25 °C. The study was conducted in the coral reef ecosystems of the Southwest of Madagascar, precisely in the large lagoon and the inner shelf of the Great barrier Reef of Toliara (GRT) (Fig. 1). These parts of the GRT are predominated by sediment (57 km^2) and seagrass beds (22 km^2) (Nomenisoa et al., 2024), and are characterized by tidal dynamics determined by the flows through the two passes (in the extreme north and south of GRT) and across the reef (Chevalier et al., 2015). These coastal areas, harboring at least 230 fish species (H. Jaonalison, unpubl.), are highly frequented and targeted by the small-scale fishers with 6.8 fishermen per day per km^2 (Andréfouët et al., 2013). They use different fishing gears including the potentially destructive gear known as the mosquito net trawls that catch juvenile fish. (Jaonalison, 2019).

To explore the spatial distribution of taxonomic and size diversity of fish, the lagoon was partitioned into four areas considering both the distance from the coast and the structure of benthic substrates (i.e. substrate types). We monitored the catch of local fishermen who used mosquito net trawls in these four areas including: (a) mangrove areas without seagrass vegetation (called “mangrove area”), (b) seagrass beds near the mangroves (called “seagrass area”), (c) seagrass beds in the lagoon (called “intermediate area”), and (d) seagrass beds in the barrier reef system (called “reef area”) (Table 1).

2.2. Sampling and lab processing

We recorded the geographical position of each sampling station (longitude and latitude) and estimated their distance from the coast by using GIS. Sampling involved the collection of fish samples and associated environmental variables including epifaunal density. Environmental variables collected for each coastal area during fish sampling included the sea surface temperature, seas surface salinity and depth. Two specific campaigns to evaluate the effect of epifaunal density with seagrasses were conducted two months per season and a specific

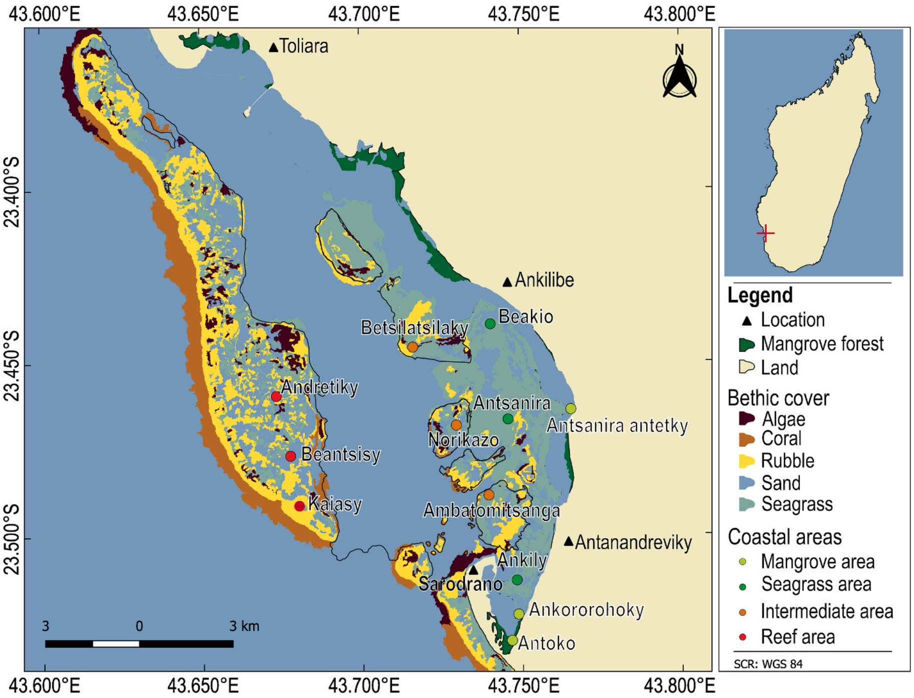


Fig. 1. Map showing the distribution of sample stations across different areas.

Table 1
Description of the sampled variables.

Category	Variables	Descriptions	Temporal resolution
Categorial variables	Mangroves area	Area close to mangroves without seagrass vegetation	monthly
	Seagrass area	Seagrass vegetation near the mangroves	monthly
	Intermediate area	Seagrass vegetations in the lagoon reef	monthly
	Reef area	Seagrass vegetations in the barrier reef	monthly
Continuous numerical variables	SST	Sea surface temperature during sampling	monthly
	SSS	Sea surface salinity during sampling	monthly
	Depth	Water depth during sampling	monthly
	Seagrass	Seagrass vegetations cover	once a year
	Sediment	Sediment cover (sand and/ or mud)	once a year
	Debris	Coral debris cover	once a year
	Algae	Macroalgae cover	once a year
	Live coral	Live coral cover	once a year
	Dead coral	Dead coral cover	once a year
	Epifauna density	Density of epifauna associated with the seagrass (m2)	twice per season
	Geographic	Longitude and latitude	
	Coast distance	Distance of each location from the coast	
Quantitative data	Size dataset	Original dataset comprising the individuals' size for each fish species per sample	monthly

campaign in a month to characterize the benthic substrate (coverage of seagrass vegetation, sediment, dead coral, live coral, debris and macroalgae) (Table 1). Benthic substrate for each coastal area was also characterized and used in relation to fish densities.

2.2.1. Fish sampling

Fish sampling was conducted monthly in the four connected coastal areas from July 2021 to June 2022 covering both the warm season (October–April) and cold season (May–September). Sampling solely focused on catches obtained from 3 pirogues operated by fishermen using mosquito trawl nets (100 m width, 2 m height and 3 mm mesh operated by three fishers per pirogue) in the fixed fishing grounds (Fig. 1). Their catches were collected from the four coastal areas for three days a month (with one sample per area per day) for 12 months covering the two seasons in Madagascar (i.e. warm and cold seasons). In each coastal area, sampling was conducted in three different fixed stations (with one station per day and per coastal area) during the spring tide of full-moon period. To quantify the effort in terms of fishing haul duration, we recorded from the boat the time related to sampling gears deployment (i.e. by recording the beginning and the end of trawl though our research assistants) as well as the local water mass conditions.

At the laboratory, samples were first sorted by morphospecies before putting them on the graduated Plexiglas plate to be photographed using Olympus TG6. These images (called "morphospecies photo") permitted to get information on size distribution among morphospecies per sample, per area, per day, per month, and per season using ImageJ software. Secondly, for each morphospecies photo, one specimen was randomly selected for having high-definition image with camera Nikon D90. The camera was connected to a computer using ControlMyNikon software, which automatically imported the captured photos into Adobe Lightroom® for processing. The software was used to assign species names to the imported images by comparing them with an existing database of previously identified specimens, most of which were identified at the species level. These previous image databases were also from the lagoon of the great barrier reef of Toliara and identified using molecular tools (Jaonalison et al., 2022). Finally, a tissue fragment from each photographed specimen was sampled and preserved into 90 % ethanol and stored at −20 °C for future genetic analyses.

A total of 144 samples were collected across four coastal areas for the mixed seasons within a year, with 36 samples per area. Specifically, 60 samples were collected during the cold season and 84 samples during the warm season.

2.2.2. Epifaunal sampling

The sampling of epifauna associated with the aboveground eelgrass shoots was performed in nine stations where seagrasses were present. We used a 60 μm mesh bag with mouth dimension of 0.15 m^2 to collect the eelgrass shoots and associated epifauna (Duffy et al., 2015). We collected three samples per seagrass species and per station, by sampling only the dominant monospecific meadow. In the laboratory, epifaunal invertebrates were separated from the seagrass blades and other organisms by scraping with a glass slide. We identified and counted the epifaunal invertebrates after extraction using a 320-μm sieve and preserving with 70 % ethanol (Al-Wedaei et al., 2011; Momota and Nakaoka, 2018). Epifauna abundance on the seagrass was measured as the number of individual epifauna per station.

2.2.3. Benthic substrate characterization

Benthic substrate characterization was conducted through underwater surveys along three transects during neap tide periods, ensuring better visibility and lower wave exposure. A 50-m transect was used, with 50 × 50 cm quadrats placed every 4 m. Each quadrat was photographed and analyzed using PhotoQuad software following the protocol in Trygonis and Sini (2012). To estimate the average proportion of benthic morphological groups (sand, rubble, macroalgae, seagrass, dead coral, live coral) and individual seagrass species, we randomly distributed 40 points within each photo-quadrat. The proportion of each seagrass species was then used to calculate a supplementary explanatory variable, referred to as "seagrass diversity," using the Shannon diversity index (see formula below). Using the proportion of substrate features, we also estimated the habitat heterogeneity index (HHI) through the following formula:

$$HHI = \sum (Substrate\ Type\ i\ x\ Proportional\ Cover\ i)$$

2.3. Response data processing

Our study focused on five response variables including species richness, Shannon diversity index, Simpson diversity index, beta-diversity and size spectra (Table 2). Our size dataset comprised individual sizes (in cm) of all fish taxa per sample. For each selected species per sample the number of individuals were estimated for creating abundance dataset. Presence-absence dataset was derived from the size dataset by grouping the size by taxa and sample. The abundance dataset was used for estimating the alpha-diversity (Species richness, Shannon diversity, and Simpson diversity), while the presence-absence dataset and the size dataset were used for calculating the beta-diversity and size spectra, respectively.

As the duration of mosquito net trawling (effort) differed among samples, the abundance dataset was standardized by calculating the Catch Per Unit Effort (CPUE) using the effort in terms of trawling duration of each sample, before estimating the corresponding CPUE for half-hour corresponding to the mean duration of trawling.

CPUE = (Individual number per species per sample/Trawling duration) x 0.5 h.

Table 2
Computed response variables from the sampled data.

Category	Variables	Long name of variables	Temporal resolution
Response variables	Shannon diversity	Shannon diversity indices of fishes	monthly
	Simpson diversity	Simpson diversity indices of fishes	monthly
	Species richness	Species richness of fishes	monthly
	Beta-diversity	Total beta-diversity of fishes	monthly
	Nestedness	Compositional nestedness of fishes	monthly
	Turnover	Compositional turnover of fishes	monthly
	Size slope	Size spectra of fish	monthly

Using the CPUE data, we calculated Shannon diversity and Simpson diversity indices for each station per area and across both seasons using the following equations:

- Shannon Diversity $\mathrm{H}' = -\sum_{i=1}^{S} (\boldsymbol{pi} \cdot \mathbf{ln}\, \boldsymbol{pi})$

With $\boldsymbol{S}$ is the total number of species

and $\boldsymbol{p}\ \boldsymbol{i}$ the proportion of individuals belonging to species $\boldsymbol{i}$ (calculated as the CPUE of species $\boldsymbol{i}$ divided by the total CPUE of all species).

- Simpson Diversity $\mathbf{D} = 1 - ((\sum \boldsymbol{n}(\boldsymbol{n} - \mathbf{1}))\ /\ \boldsymbol{N}(\boldsymbol{N} - \mathbf{1}))$

With $\mathbf{n}$ = the total CPUE of a particular species.

$\mathbf{N}$ = the total CPUE of all species.

From Presence-Absence data, we calculated Sorensen's beta-diversity, nestedness and turnover components. The three dissimilarities matrices (beta-diversity, nestedness and turnover) were plotted to visualize their variation among areas and between seasons. We also estimated the proportional contribution of nestedness and turnover components for each area and season to determine their influence on beta-diversity dissimilarities across the areas and the seasons. The components contributing the most to the variation of beta-diversity were retained for the modeling. The percentage of species overlaps between areas were estimated to support the interpretation of beta-diversity component dissimilarities.

- Beta-diversity $\beta_{S\phi r} = (B + C)/(2A + B + C)$
- *Species turnover* $\beta_{SIM} = \min (B,C)/(A + \min(B,C)$
- Nestedness $\beta_{nested} = \beta_{S\phi r} - \beta_{SIM}$

Where:

A = number of species common to both areas
B = number of species unique to the first area
C = number of species unique to the second area

Finally, we transformed the original size dataset into size frequency data to analyses fish size distribution. Size class with bin size of 1.5 cm and size frequency were log-transformed before fitting the models using linear regression by following the approach in Seitz et al. (2020). The fitted slopes of size spectra from linear regression model were plotted using boxplots, showing the size slope patterns across areas and seasons. A decrease in the slope (becoming more negative) indicates an increase of small-sized fish (i.e. juvenile) and a decrease of large fish (Yemane et al., 2004).

2.4. Statistical analyses and models fitting

We first examined the spatial and temporal distribution of the environmental and geographical variables by using a Principal Components Analysis (PCA). The environmental data was first z-score normalized so that the mean of all the values is 0 and the standard deviation is 1 before running PCA. The biplot of the first two principal components were presented to visualize if the environmental gradient differs across the coastal areas and seasons.

Then, we assess spatial and temporal variation of fish diversity and size spectra by performing a two-way ANOVA testing the independent and interactive effects of areas and seasons on species richness, Shannon diversity, Simpson diversity and slope of size spectra. When significant effects were detected, we conducted Tukey's Honest Significant Difference (TukeyHSD) test to identify the factors contributing to the significant effects.

Before processing model fitting to identify major factors driving fish diversity, selections of variables were performed by removing the highly correlated variables ($r > 0.8$) which always led to model overfitting. The original dataset (including the response and explanatory variables) was split into two datasets (Train-data and Test-data). The train-data representing 75 % of the original dataset was used for fitting the model, while the test-data (25 %) for assessing the performance of the fitted model. We performed 10-fold cross-validation to prevent model overfitting. Models for species richness, Shannon and Simpson diversity, and fish size were run with Random forest algorithm (Breiman, 2001). We compared the capacity of the fitted models to explain the pattern of the response variables through the *pseudo-R*^{2} values, while the model accuracies with the coefficient of determination R^2. We used Generalized Dissimilarity Modelling (GDM) to link the spatial variation of taxonomic beta-diversity with the environmental gradient and spatial variables. This non-linear statistical approach explains better the variation of taxonomic diversity than linear models and is used to model and understand how biological dissimilarity between sites changes as a function of environmental and geographical distance (Glassman et al., 2017). The partial contribution of each predictor in explaining the pattern of the response variables were assessed using RF-overall and the gdm-coefficient. All the statistical analyses and modeling were conducted with R version 4.4.2 (R Core Team, 2024), using randomForest and gdm packages (Breiman et al., 2018; Fitzpatrick et al., 2022).

3. Results

3.1. Description of environmental and spatial variables

The proportion of substrate features (seagrass, sediment, coral, algae, …), the water mass conditions (SST, SSS), the geographical position of the fishing areas (coast distance) and the density of epifauna varied among areas and explained 52 % of the spatial and seasonal variability of environmental data. The mangrove areas differed from the others mainly by a higher sediment proportion; the seagrass areas by the higher seagrass vegetation proportion and the associated epifauna density; and the intermediate areas and reef areas by the combination of seagrass cover with other features (macroalgae and live corals …). Among the ecological and geographic features, only sea surface salinity (SSS), live coral cover and algae cover showed correlation coefficients (r) higher than 0.8 where their values increased with an increasing distance to shoreline. Accordingly, we removed SSS and algae cover from the environmental dataset before models fitting.

3.2. Alpha-diversity and size spectra patterns

Overall, a total of *30,978* individuals belonging to 190 taxa and 55 families were recorded over the surveyed areas and periods. A total of 135 taxa from 47 families were recorded during the cold season, while 164 taxa from 48 families were recorded during the warm season. Labridae and Gobiidae were by far the most represented in our sampling, during both seasons. Species from Serranidae, Ephippidae, Leiognathidae, Sparidae, Priacanthidae, Engraulidae, and Caesionidae occurred only during the warm period (Fig. 3). The species richness of Gobiidae, Acanthuridae, Apogonidae, Pomacentridae, Carangidae, Chaetodontidae, Siganidae, Teraponidae and Blenniidae was higher during the warm period than during the cold period.

The two-way ANOVA revealed that both areas and seasons had significant independent effects on species richness ($p \leq 0.001$) and Shannon diversity ($p < 0.05$) (Table 3). Seasonal effect indicated significantly higher species richness during the warm season compared to the cold season (Tukey HSD, $p \leq 0.001$). Species richness was the lowest in the mangrove area, and the highest in the reef area (Fig. 4). Based on median values, species richness was higher during the warm season than in cold season (Fig. 4). Pairwise comparisons showed no significant differences in species richness among seagrass, intermediate, and reef areas (Table 3). However, these three areas exhibited significantly higher species richness than the mangrove area. The season effect on Shannon diversity was marginally significant ($p = 0.054$). The area effect on Shannon diversity was primarily driven by its lower values in the mangrove area compared to the reef area (Table 3, Fig. 4). The low Shannon diversity in the mangrove and seagrass areas, both near the coast, suggests species dominance by a few taxa. In contrast, the reef area is characterized a more balanced species distribution, corresponding to the highest Shannon diversity values (Fig. 4).

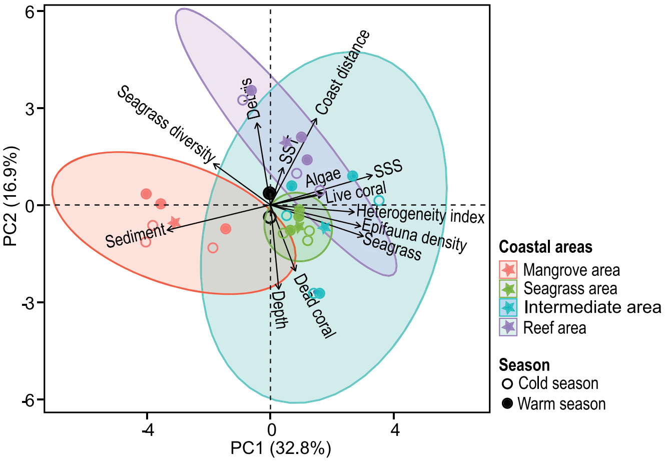


Fig. 2. PCA showing the seasonal and spatial variability of the environmental variables in the lagoon of the great barrier reef of Toliara. See Table 1 for a description of every explanatory variable and Supporting Information S1 Table 1 for their mean values across seasons at each sampling site.

Fig. 4 suggested spatial and seasonal variation in the Simpson diversity index but the two-way ANOVA revealed an absence of significant differences (Table 3). The low values of Simpson index in mangroves highlighted fish communities from these areas were dominated by a few species, particularly during the cold season (Fig. 4). Finally, the interaction between areas and seasons did not significantly affect the variation in both alpha-diversity indices ($p > 0.7$, Table 3).

Fish size ranged from 1 to 61 cm, with an increase of body size being observed from the mangrove areas to the adjacent reef (Fig. 4). An average of 3.4 ± 1.4 cm in the mangrove area, 3.9 ± 2.5 cm in the seagrass area, 4.8 ± 2.6 cm in the intermediate area and 5.6 ± 3.0 cm in the reef area was observed in the lagoon of GRT. The distribution in size structure of fish communities, expressed as the size spectra slope, varied significantly among areas (Two-way ANOVA: $F = 3.22$, $p = 0.035$), especially driven by the significant difference of size slope between the seagrass area and the reef area (Tukey HSD, $p = 0.03$). The size slope was most negative in the seagrass area where the mean size of fish was also small (Fig. 4), indicating a higher abundance of small-sized fish and a decline in large-sized fish in the seagrass area than in the reef area. No significant differences were detected between seasons or in the interaction between areas and seasons. However, a larger proportion of small-sized fish was more obvious in the mangrove area during the cold season.

The 15 most dominant species belonging to the most species-rich fish families accounted for 70 % of all individuals observed in the lagoon. Fish assemblages were strongly dominated by juvenile individuals (Supporting Information S1 Table 2). *Siganus sutor* was the most abundant species (19.4 % of total individuals), with a mean size of 3.3 ± 1.7 cm, far below its maturity threshold (15 cm; Woodland, 1990), indicating that all individuals were juveniles. Similarly, individuals of *Scarus psittacus*, *Naso brevirostris*, *Parupeneus barberinus* and *Fistularia commersonii* having juvenile proportions exceeded 94 % of abundance. Additionally, 22 % of the individuals from *Stethojulis strigiventer* and *Calotomus spinidens* showed juvenile proportions. In total, more than half of the dominant species were composed primarily of immature individuals.

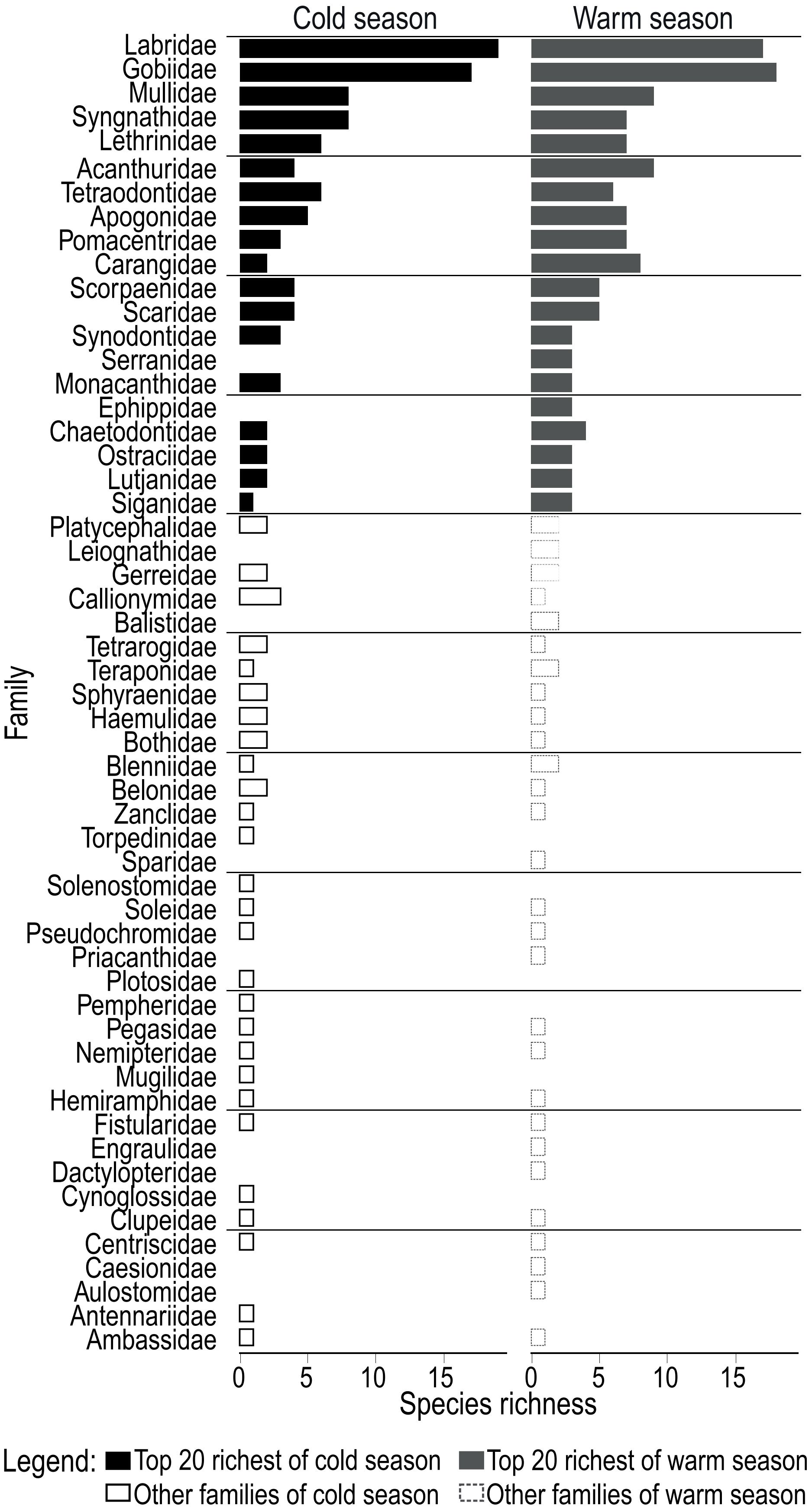


Fig. 3. Seasonal distribution of species richness among families in the lagoon of the great barrier reef of Toliara.

Table 3
Results of two-way ANOVA Test and TukeyHSD test for testing the effect of areas and seasons on alpha-diversity index and size spectra of fish.

Responses	Factors	ANOVA	TukeyHSD test	
		p	Variable Combinations	*adj. p*
Species richness	Areas	**< 0.0001**	Seagrass area – Mangrove area	**0.001**
			Intermediate area – Mangrove area	**0.001**
			Reef area- Mangrove area	**0.000**
			Other combinations	>0.3
	Seasons	**0.001**	Warm-Cold	**0.001**
	Interaction	0.802		
Shannon diversity	Areas	**0.042**	Reef area vs Mangrove area	**0.042**
			Other combinations	>0.2
	Seasons	0.054		
	Interaction	0.905		
Simpson diversity	Areas	0.281		
	Seasons	0.163		
	Interaction	0.731		
Mean size	Areas	**0.003**	Seagrass vs Mangrove area	**<0.001**
			Intermediate vs Mangrove area	**<0.001**
			Reef area vs Mangrove area	**<0.001**
			Seagrass vs Reef area	**<0.001**
			Other combinations	>0.052
	Seasons	0.881		
	Interaction	0.632		
Size slope	Areas	**0.035**	Seagrass vs Reef area	**0.035**
			Other combinations	>0.08
	Seasons	0.97		
	Interaction	0.486		

3.3. Beta-diversity patterns

Beta-diversity and its two components (nestedness and turnover) varied among the coastal areas (Fig. 5a). Beta-diversity among areas ranged from 0.2 to 0.7 with the highest dissimilarities found between mangroves and the areas closest to the barrier reef (i.e. Intermediate area and Reef area). The dissimilarity in fish communities was mainly linked to species turnover with up to 75 % (Fig. 5b) and similar pattern was observed for both warm and cold season (Fig. 5a). The main contribution of species turnover on beta-diversity indicated the dissimilarity of fish composition was linked to a low species overlap (11–15 %) due to species replacement (Table 4).

3.4. Impact of environmental and geographical variables on the taxonomic diversity and fish size spectra

Random Forest models showed that the distance to shoreline, the sediment cover, the seagrass cover, the seagrass diversity, and the heterogeneity of the benthic substrate explained the spatial variation of the taxonomic (species richness, Shannon and Simpson indices) and the size diversity in fish community in the lagoon of Toliara. The fitted models better explained the species richness (*pseudo*-$R^2 = 0.64$) and Shannon diversity (*pseudo*-$R^2 = 0.58$) than the Simpson diversity (*pseudo*-$R^2 = 0.52$) and mean size (*pseudo*-$R^2 = 0.50$) (Table 5). Similarly, the accuracies of models were also higher for species richness ($R^2 = 0.65$) and Shannon diversity ($R^2 = 0.70$) than for Simpson diversity ($R^2 = 0.52$) and fish size ($R^2 = 0.54$) (Table 5).

Acknowledging that mangroves were characterized by a substrate comprising mainly of sediment, we repeated the analyses by removing mangroves from the dataset (Supporting information S1 Table 3). It was revealed that the distance from the coast remained the foremost driver in alpha-diversity and fish size even when mangroves were no longer considered. In this second set of analyses, the effects of live coral cover and sediment cover appeared to be more important in explaining the patterns of alpha-diversity and fish size decreased. However, the model accuracies were very low with R^2 ranging from 0.10 to 0.21.

The partial dependence plots indicated a positive relationship between distance from the coast and fish diversity. In other words, when the distance from the coast increases, species richness, Shannon index, Simpson index, and fish size also tend to increase (Fig. 6). High diversity and high cover of seagrasses also positively sustained taxonomic diversity and fish size. On the other hand, a negative impact on diversity was detected for sediment cover. An increase of sediment cover is generally associated with a decrease in species richness and Shannon index (Fig. 6).

GDM models revealed that the sediment cover and the distance from the coast were the main significant factors explaining variation in species turnover (Table 5). The model exhibited that about 63 % of the spatial variation of fish species turnover within the lagoon of the great barrier reef of Toliara was explained by the two above-mentioned key drivers (Table 5). The partial contribution plot of these out-performed predictors revealed that the species replacement rapidly increased beyond 40 % of sediment cover and within 2 km from the coast (Fig. 6). Conversely, the effect of the other features such as seagrass diversity and substrate heterogeneity on species turnover patterns were very weak. When removing the data related to mangroves, the coast distance was the main driver while the effect of the sediment cover became very weak (see supporting information S1 Table 3).

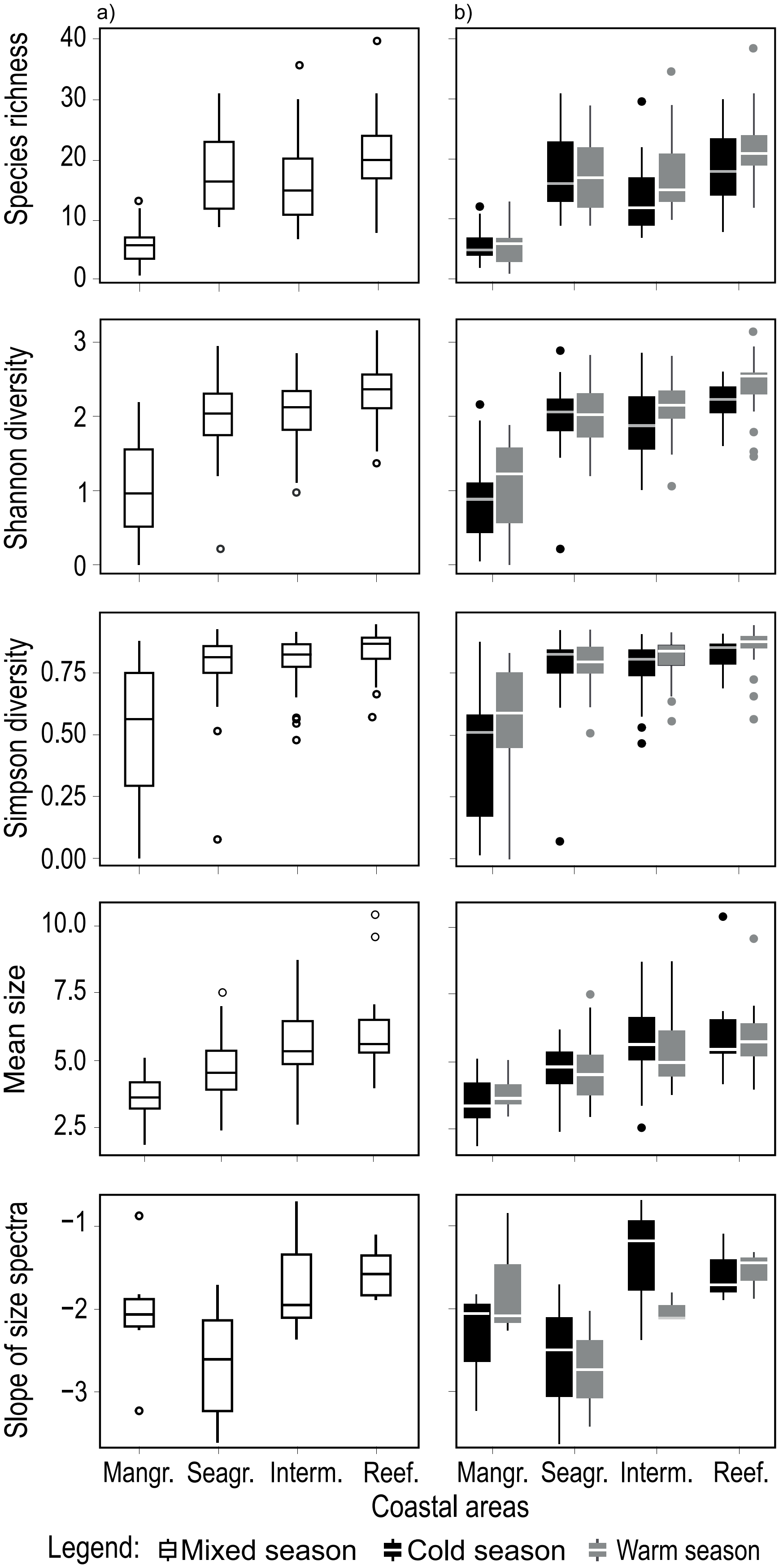
4. Discussion

This ecological study at the scale of a lagoon from an overexploited barrier reef system (Ranaivomanana et al., 2023) revealed that the distance from the shoreline and the sediment cover are dominant drivers of the diversity in fish communities. In addition to a significant variation of species richness between seasons, we showed that Shannon diversity and size spectra varied significantly across coastal areas allowing the identification of nursery zones essential for the early life stages of fish. Consistent with large-scale studies (Bevilacqua and Terlizzi, 2020; Maxwell et al., 2022), species turnover between areas was the dominant factor driving beta-diversity patterns at small-spatial scales less than 10 km. These major results were discussed in an ecological context with additional perspectives in conservation.

4.1. Temporal variation

Season may play crucial roles in shaping fish biodiversity patterns in coastal ecosystems. Our study found that the species richness of fish communities from varied lagoonal areas including seagrasses was significantly higher during the warm season. This aligns with findings from tropical seagrass beds in Indonesia, where species richness was also higher during the warm season than in cold and transition seasons (Du et al., 2018). Such a temporal variation could be associated with the seasonal increase in sea surface temperature, which can enhance ecosystem productivity and prey availability (Máñez-Crespo et al., 2022). For instance, warmer conditions sustain higher biomass of meiofauna within seagrass beds (Mascart et al., 2015), thereby increasing food availability for fish and other consumers. Accordingly, the recorded density of epifauna, a major food source for reef fishes (Ravelohasina et al., 2024), was slightly higher during the warm season across the lagoon (Supporting information S2 Fig. 2). While we were unable to formally test the likely impacts of food availability on fish species richness over time due to the limited seasonal replication, these patterns suggest a strong link between SST-driven productivity and fish community composition.

In addition, the seasonal dynamics of seagrass-associated fish assemblages likely reflect differences in habitat use and life-history strategies. Seagrass meadows support a mosaic of fish residency types, including permanent residents, temporary residents (seasonal visit during a part of their lifecycle), regular visitors (through diurnal



(caption on next page)

Fig. 4. Spatial distribution of species richness, Shannon diversity, Simpson diversity, mean size and slope of size spectra for all the seasons together or mixed season (a) and per season (b). The alpha-diversity and mean size were calculated for each sample. Slope was linear fitted from the size frequency data at each location. The lower and upper hinges of the boxplot correspond to the 25th and 75th percentiles; the middle line is the median. The upper whisker extends to the largest value which is within 1.5 times the interquartile range; the lower whisker extends to the smallest value within 1.5 times the interquartile range.

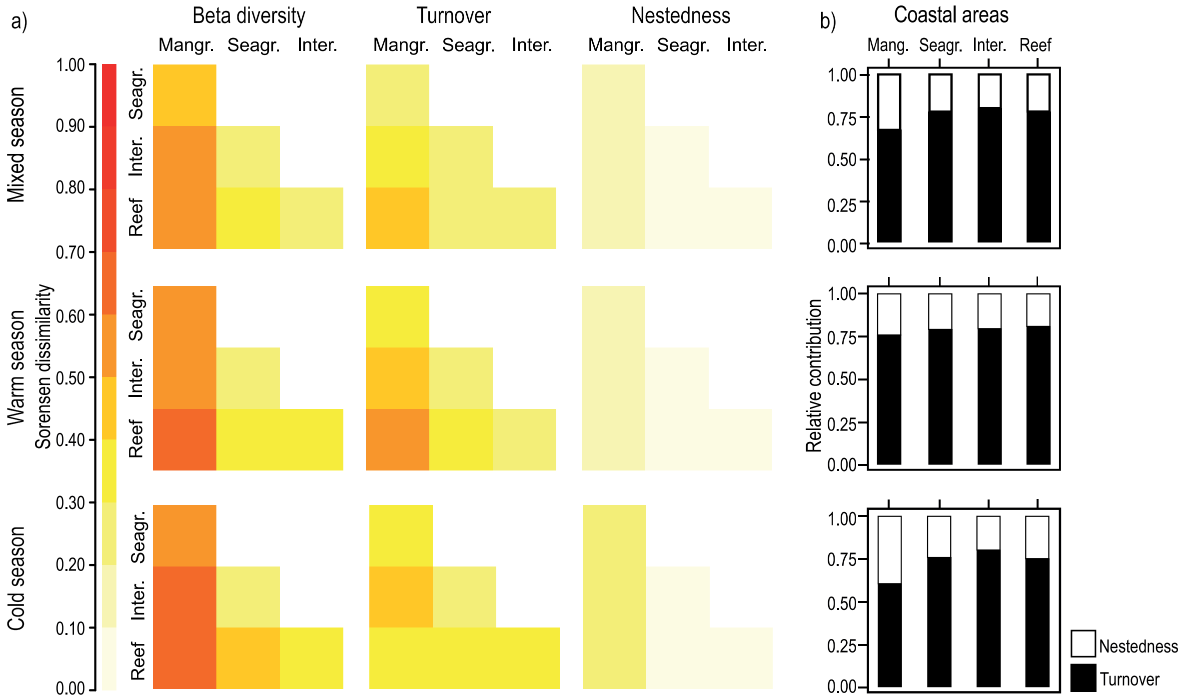


Fig. 5. Change in beta diversity, turnover and nestedness between areas and seasons using sørensen index (a) and relative contribution of turnover and nestedness component to beta diversity obtained after averaging pairwise dissimilarities between areas (b). "Mangr." for mangrove area, "Seagr." for seagrass area, "Inter." for intermediate area, and "Reef "for reef area.

Table 4

Percentage of species shared by areas across seasons and for all seasons together.

Combinations	Overlap species in %		
	Warm season	Cold season	Mixed season
All areas	15	11	18
Mangrove area – Reef area	28	23	32
Seagrass area – Reef area	64	53	65
Intermediate area – Reef area	63	60	66

migration) and occasional residents (Hemminga and Duarte, 2000). The temporary residents reflect the function of seagrass meadows operating as a nursery grounds for some fish species (Parrish, 1989). The significantly higher Shannon diversity index observed during the warm season may therefore result from the increased recruitment and ontogenetic influx, as fish post-larvae settle and grow in shallow and sheltered environments (Gray and Miskiewicz, 2000). For instance, in estuaries, seasonal shifts in fish assemblages have been mainly contributed by recruitment, growth and subsequent ontogenetic habitat shift (Sheaves et al., 2010), suggesting a similar mechanism occurring in seagrass habitats. This hypothesis is further supported by our finding of a more negative size spectra slope in the seagrass area during warm season, indicating a dominance of smaller size classes, consistent with juvenile-dominated assemblages (Graham et al., 2007). Moreover, the higher fish diversity during warm season could also be linked to the abundance of juvenile fishes that might sustain a more diversified and more intense ecological networks made of multiple consumers from different trophic levels, as commonly observed in the estuaries (Figueiredo and Pessanha, 2016). Altogether, these fundings reinforce the functional importance of seagrass beds and highlight the need for seasonally resolved assessments when investigating coastal fish biodiversity and ecosystem functioning.

4.2. Spatial variation

Based on the concept of ecological niches, areas with higher diversity of resources are expected to host more fish species as they provide shelters (Willis and Anderson, 2003) and increase food availability (Letourneur et al., 2003). Accordingly, reef fish diversity has often been found to be strongly associated with habitat heterogeneity reflecting the availability of shelters in structurally complex ecosystems such as coral reefs and seagrass beds (Komyakova et al., 2013). Conversely to our expectations, models revealed that the spatial patterns of fish diversity in the lagoon of the great barrier reef of Toliara were mainly explained by the distance from the shoreline, while resource-based predictors such as epifauna density (a proxy for food availability) and habitat heterogeneity had lower explanatory power. We hypothesized that the factor "shoreline distance" acts as a proxy for multiple ecological components. First, spatial proximity with barrier reef systems may facilitate the exchange of individuals across habitats, enhancing species richness and functional group representation in surrounding areas. This pattern aligns with previous observations in Indonesia, where fish communities in seagrass beds directly connected to the reef exhibited higher diversity than those closed to the mangroves (Irawan and Hutabarat, 2019). Our findings similarly showed elevated fish diversity in areas close to the barrier reef, likely due to the presence of all seagrass-associated fish guilds, including permanent residents, temporary residents, regular visitors and occasional residents (Hemminga and Duarte, 2000). Conversely, large distances from the barrier reef certainly limit an easy access by regular visitors, such as diurnal predatory fish visiting

Table 5

Outputs of the fitted models analyzing and predicting the Species richness, Shannon diversity, Simpson diversity, and fish size with Random Forests algorithm, and the species turnover with GDM. *Pseudo-R^2* and R^2 indicate the explained deviance by the models and the coefficient of determination for the model performance. RF-overall relates the contribution importance of each predictor to RF models, while the Coefficient to the partial contribution of the predictor to GDM models.

Algorithms	Responses	Model outputs		Important predictors	RF-Overall/ Coefficient
		pseudo-R^2	R^2		
Random forests (RF)	Species richness	0.64	0.65	Coast distance	28.29
				Sediment cover	26.83
				Seagrass cover	23.58
				Seagrass diversity	16.30
				Heterogeneity index	14.11
				SST	12.89
				Live coral	4.38
	Shannon diversity	0.58	0.70	Coast distance	21.17
				Sediment cover	15.96
				Seagrass diversity	12.50
				Seagrass cover	11.91
				Epifauna density	9.57
				Heterogeneity index	8.72
				Live coral	6.49
	Simpson diversity	0.52	0.52	Coast distance	13.59
				Sediment cover	11.17
				Seagrass cover	8.76
				SST	8.32
				Epifauna density	8.12
				Seagrass diversity	8.07
				Heterogeneity index	7.06
	Fish size	0.50	0.54	Coast distance	35.14
				Sediment cover	20.81
				Seagrass cover	16.10
				Debris cover	15.44
				Seagrass diversity	14.80
				Heterogeneity index	13.84
Generalized Dissimilarity Modeling (gdm)	Species turnover	0.62	0.63	Sediment cover	0.342
				Coast distance	0.114
				Seagrass diversity	0.050
				Heterogeneity index	0.023

adjacent areas to forage. Secondly, shoreline distance might reflect a gradient of fishing pressure, which is particularly intense in inshore, soft-bottom habitats close to mangroves. In the lagoon of the great barrier reef of Toliara, mosquito net trawling is concentrated in these areas close to mangroves, whereas offshore zones near the barrier reef are predominantly fished with larger-mesh gillnets, due to the presence of dead and living coral that inhibits mosquito net trawl deployment (R. M. Randiantsara, unpubl.). This spatial variation in gear selectivity and fishing effort, driven by substrate type and accessibility, likely contributes to the observed pattern of fish diversity. Human-impacted sites were reported to exhibit fish communities that are less structured by habitat features and more influenced by exploitation intensity (Jones et al., 2021). Furthermore, while we included a wide array of environmental variables known to affect fish communities in coastal ecosystems, such as sea surface temperature, salinity, seagrass diversity, and habitat heterogeneity, their influence on alpha diversity was limited in our models. This differs from results in other coastal systems, where these variables strongly shaped both taxonomic and functional diversity of fish (Barrilli and Branco, 2024). In the context of Toliara reef, the overriding role of shoreline distance suggests that spatial access and anthropogenic disturbance may outweigh the effects of habitat composition or environmental gradients. This is further supported by the species turnover results: community composition changed sharply within 2 km from the coast and above 40 % sediment cover, indicating distinct nearshore and offshore assemblages. These differences may reflect community filtering under fishing pressure, with inshore habitats hosting more tolerant or opportunistic species.

The spatial distribution of fish diversity also indicates some area-specific ecological importance. The low level of alpha-diversity observed in the seagrass beds connected to the mangroves suggests the significant dominance of few species over others. In addition, the spatial pattern of fish size spectra showed that these nearshore areas harbored an important proportion of small-sized juvenile fish in comparison with the seagrass beds connected to the barrier reef. The dominance of small-sized fish (Supporting information S1 Table 2) indicates that these zones provide a settlement area and nursery ground for the early life stages of some fish species (Guerreiro et al., 2021). Our data from the GRT are in agreement with other studies (e.g. Romero-Berny et al. (2020) (Gairin et al., 2023; Whitfield, 2017);) showing that seagrass beds and mangroves operate as major nursery areas for reef fishes. The selection of these precise locations in the nearshore areas but not closed to the barrier reef should have ecological explanations which may differ among species. For the early life stage of some species including gobies, the selection of the nearshore areas has been known to be linked to food availability, the sediment particle size, sandy bottoms, and high turbidity (Whitfield, 1998; Nodo et al., 2017). Some works provided also evidence that small-sized fish and juveniles tends to recruit in shallow waters (Beckley, 1986; Loyola Da Cruz et al., 2024). Models also showed that the spectra size distribution that permitted to discover the likely nursery areas was strongly driven by the shoreline distance. The large proportion of small-sized fish recruits in the seagrass beds closed to the shoreline rather than in areas connected to reef is likely explained by a strategy of predatory avoidance (Seitz et al., 2020). The coral reefs are known to be an important habitat for predatory reef fish (Osuka et al., 2022), the juveniles therefore tends to recruit far from the reef to maximize their survival (Almany and Webster, 2006).

It is generally expected that adjacent areas should show higher similarity in their fish assemblages than spatially segregated areas (Medina et al., 2007). However, in the present study, species turnover appeared to be the major driver of variation in beta-diversity patterns across coastal areas, suggesting strong dissimilarity among fish assemblages. Interestingly, this spatial variation in fish community composition through species replacement was significantly linked to sediment cover in the lagoon of Toliara, but not related to habitat features such as species diversity, seagrass cover or habitat heterogeneity. These results contrast with patterns observed on coral reefs, where habitat features and depth like the coral assemblages generally drove species turnover (Costa Barrilli et al., 2024; González-Barrios et al., 2025). In the lagoon of the great barrier reef of Toliara, the sediment cover appears to work not simply as a habitat type but as an indicator of environmental degradation, particularly in areas close to the coast. While seagrasses naturally grow in soft sediments, excessive sediment accumulation can smother vegetation, reduce light availability, and alter fish habitat structure (Dennison et al., 1993). Thus, the observed relationship between sediment cover and species turnover may reflect both a decline in habitat quality and shift in fish assemblages toward more disturbance-tolerant species. This increase on sediment could stem from anthropogenic-induced erosion on land (Payet et al., 2012) or from mechanical disturbance by fishing gears such as mosquito net trawls,

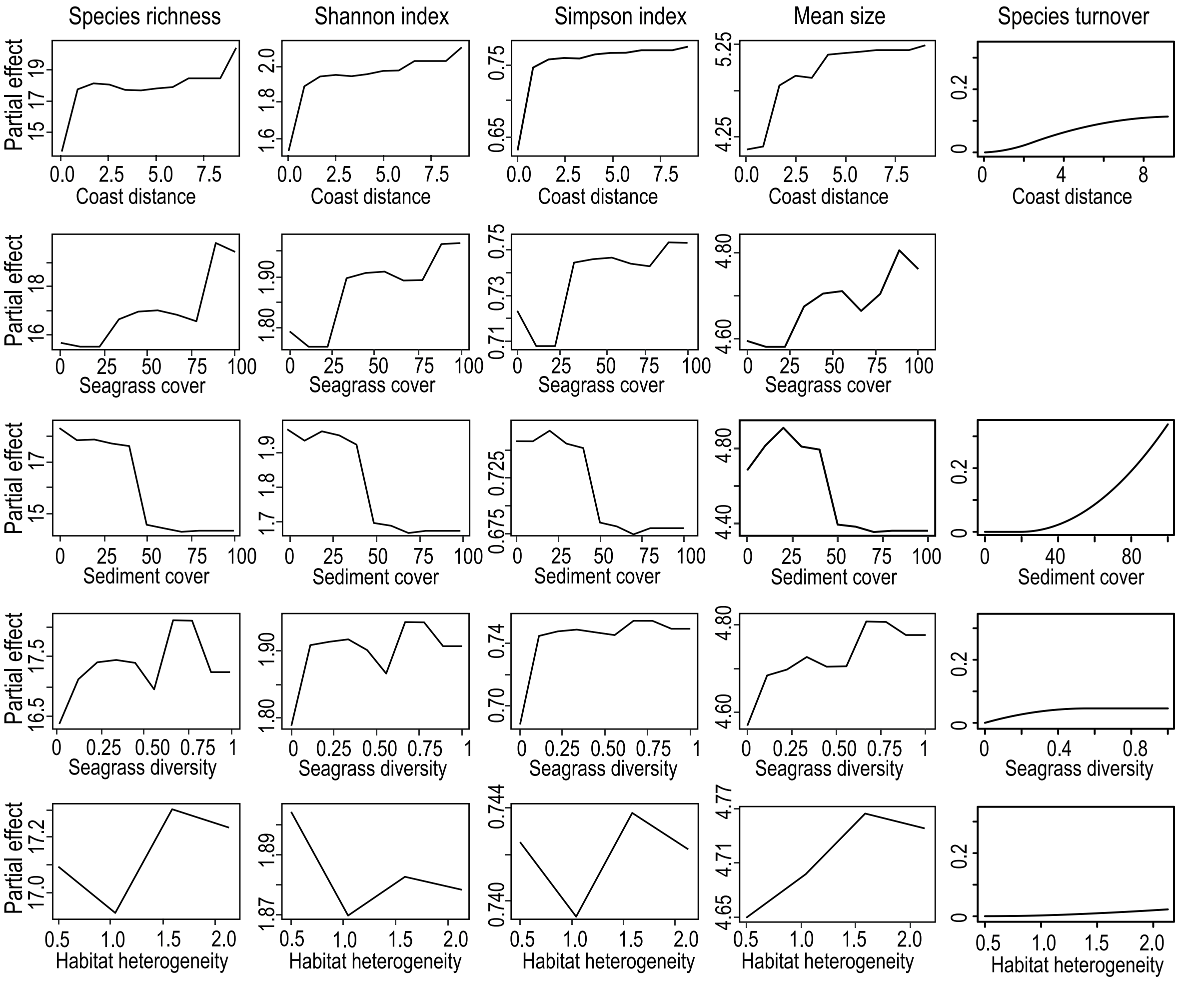


Fig. 6. Partial contribution of the most important predictors on RF models for the species richness, Shannon index, Simpson index, and mean size, and on GDM model for the species turnover. Each partial dependence plot shows how the average prediction of each of the above-mentioned response variable changes along a predictor variance gradient.

which are widespread in nearshore areas (Irawan and Hutabarat, 2019). For instance, in Kenya, a single mosquito net trawl caused an 8.3 % reduction in seagrass cover within the swept area (Mwikamba et al., 2024), illustrating the acute damage that such gears can cause to coastal vegetation. Although our findings suggest a human influence on sediment dynamics, the data do not allow us to clearly disentangle the respective contributions of terrestrial runoff versus fishing-induced disturbance. However, the lack of strong correlation between sediment and seagrass cover in our dataset implies that sediment is not merely a proxy for seagrass loss. Some benthic-foraging species such as emperor fish and goatfish may benefit from increased sediment cover, potentially contributing to community shifts (Borland et al., 2023). Future studies incorporating sediment grain size, turbidity, and spatial mapping of fishing intensity and watershed inputs would be valuable to determine causality. Further analyses should certainly be conducted to identify fish taxa mainly affected by increased proportion of sediment cover. Nevertheless, our results strengthen our knowledge about the negative effect of sedimentation on coral reef-associated communities (Rogers, 1990).

4.3. Limitations of our study and perspectives

Some research limits have been encountered for this study. Due to a limited number of observations needed for fitting models, we did not evaluate the drivers of seasonal variation in fish assemblages even we provided some hypotheses regarding potential factors driving this variation (Hu et al., 2018). This type of work needs to be repeated through long-term monitoring with at least two times for each season at the same study location for having sufficient data to deal with seasonal effects and to have a broader view of factors driving the diversity of fish communities at the scale of one barrier reef system. Such a monitoring will also inform conservation scientists if the diversity is still maintained, increased or being decreased. Additionally, our study could not document which species depend on each habitat for recruitment. While seasonal differences in diversity and size spectra suggest the effects of fish recruitment, future fine-scale studies should include surveys on the identification of habitats used by juveniles during recruitment periods. We also acknowledge a lack of quantitative data on spatial and seasonal distribution of fishing effort across the lagoon of Toliara reef when fishing effort index could be included as a potential driver of fish assemblages' variation in a small-scale area. We certainly suggest recording fishing effort information across the studied coastal areas for the future work.

Functional diversity metrics represent an important additional dimension to investigate in the lagoon of the Great Barrier Reef of Toliara. Indices such as functional richness, evenness, and redundancy have been shown to effectively identify ecosystem vulnerability to anthropogenic stressors (Mouillot et al., 2013). In the context of Toliara reef, functional diversity could help determine whether the observed shifts in species composition and size spectra reflect functional homogenization, a loss of specialized ecological roles, or true turnover in functional traits. Future research should build upon our findings by incorporating trait-based analyses to explore how habitat structure and human pressures influence not only species identity but also the ecological functions provided by fish assemblages across coastal gradients.

4.4. Conservation applications

Our findings are not only supporting the fact that the lagoon of the GRT provides nursery grounds for reef fishes, but they also highlighted precise locations of nursery areas. The identification of nursery areas should help to find out sustainable solutions facing the socio-economic and ecological status of these coastal areas. For example, identifying nurseries grounds may support the designation of no-take marine temporary protected areas (Colloca et al., 2015). Their implementation were well-known to positively impact reef fish communities (Félix-Hackradt et al., 2018; Lima et al., 2023), by improving recruits survival (Cheminée et al., 2016). Therefore, the critical areas with high ecological importance as nursery ground could be well-managed and protected to benefit biodiversity conservation (Fontoura et al., 2022).

Our results dealing with beta-diversity could also help for management decisions (Koivunen et al., 2025). Our data revealed that the pattern of beta-diversity was mainly explained by species turnover (Fig. 5). According to Socolar et al., 2016 and Bevilacqua and Terlizzi (2020), when the turnover facet of beta-diversity prevails the conservation action should be carried out at multiple areas or habitats to maintain biodiversity, but not at only one habitat. These complementary results suggest that protection measures should be performed not only in the precise nurseries grounds, but also the adjacent and connected areas.

The lagoon of the GRT serves as an active fishing ground for small-scale fishermen, with a significant use of destructive fishing gear, including mosquito seine nets (Ranaivomanana et al., 2023). The cumulative negative effects of the use of destructive fishing gears on benthic substrates are well-known as they led to habitat loss, resulting in fewer small-sized fish (juvenile), reducing populations of large-sized fish (Wilson et al., 2010) and changing the diversity of fish (Pratchett et al., 2014). In addition, our study emphasized the role of the sediment cover in shaping the structure of coastal fish through species replacement. The fishing practices with net trawls have cascading effect leading to the loss of seagrass beds and to an increase of the importance of sandy bottom in terms of coverage, which also be amplified by the coastal erosion and the flooding from the rivers (Dunaev et al., 2024). The conservation of the coastal areas needs therefore broader scale actions from upstream to downstream to well-manage the dynamic of sand in the coastal areas. This necessitates an interdisciplinary and integrated approach requiring close collaboration with researchers and stakeholders from different disciplines.

To conclude, this study provides novel information on fish biodiversity components and dynamic of reef fish assemblages in the lagoon of the GRT. Our study highlighted the spatial patterns of alpha-diversity and fish size spectra in a restricted areas across the seasons, leading to the identification of the areas frequented by the juvenile fishes. Species turnover has been found as the main driver of beta-diversity across the lagoon. The distance from the shoreline and the sediment cover drove the pattern of fish size and diversity reflecting the influence of the human activities associated to the small-scale fishing effort across the lagoon. These important findings will serve as reference baseline to assess any potential changes in the structure of fish communities in the future.

CRediT authorship contribution statement

Henitsoa Jaonalison: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marilaure Grégoire:** Writing – review & editing, Formal analysis. **Jamal Mahafina:** Writing – review & editing, Project administration, Investigation, Funding acquisition. **James Mwaluma:** Writing – review & editing, Project administration, Funding acquisition. **Helga Berjulie Ravelohasina:** Writing – review & editing, Investigation. **Aina Le Don Nomenisoa:** Writing – review & editing, Visualization, Investigation. **Toky Justino Mory:** Writing – review & editing, Investigation. **Lantoasinoro Ranivoarivelo:** Writing – review & editing, Investigation. **Dominique Ponton:** Writing – review & editing, Resources, Conceptualization. **Bruno Frédérich:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Data availability statement

Data will be available on request until publishing the data paper for public use.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107330.

Data availability

Data will be made available on request.

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