Structural complexity of seagrass and environmental variables as a determinant of fish larvae assemblages in tropical coastal waters: Implications for seagrass management and conservation

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Abstract

Anthropogenic activities including climate change affect the development of structural complexity in seagrass and the state of environmental variables. It remains unclear whether these variables, alone or in combination, have an important influence on fish larvae assemblages. This study examined the influence of the structural complexity of seagrass meadows and various environmental variables on fish larvae assemblages in tropical coastal waters of Tanga, Tanzania. The study was conducted in four *Thalassia hemprichii* dominated seagrass meadows from June 2019 to January 2021. Multiple regression analysis indicated that the structural complexity of seagrass (canopy height, seagrass cover, and shoot density) and environmental variables (dissolved oxygen, temperature and salinity) were the foremost predictors for fish larvae assemblages; abundance and richness (R^2 = 0.75, p = 0.0185, R^2 = 0.54, p = 0.0396, respectively). Based on these findings, the structural complexity of seagrass and environmental variables are both important determinants of fish larvae assemblages in tropical coastal waters. The findings suggest that reducing anthropogenic activities that affect the development of structural complexity of seagrass and negatively impact environmental variables in seagrass meadows through more effective governance would result in increased production of fish larvae in meadows and, as a result, increased fish recruitment in tropical coastal waters.

Keywords: seagrass, fish larvae, assemblages, coastal waters, anthropogenic stress

Introduction

Anthropogenic activities, including climate change, are increasingly affecting the health and function of seagrass meadows (Dunic *et al.,* 2021), with significant impacts on the recruitment of fish stocks (Waycott *et al.*, 2009; Brodie and De Ramon N'Yeurt, 2018; Hedberg *et al.,* 2019). Threats directly affecting the health and functions of seagrass meadows include destructive fishing methods such as drag-net fishing, the use of beach seines, ring nets, gleaning, trampling, pulling or pushing boats towards deeper waters, surface rain runoff, and excessive nutrient and sediment fluxes from activities related to agriculture (Gullström *et al.,* 2008; Erzad *et al.,* 2020). Also, increased populations of grazers, such as sea urchins, can cause local overgrazing of seagrasses. Increases in grazers are associated with overfishing of predatory fish that feed on sea urchins (Eklöf *et al.,* 2008). These threats underscore the need for effective conservation and governance to address the pressures that impact the ecosystem function of seagrass meadows in coastal waters.

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Seagrass meadows are important fishing and nursery grounds for a variety of fish species (Nagelkerken *et al.,* 2000; Gullström *et al.,* 2008; Unsworth *et al.*, 2019). They are distinguished by an abundance and diversity of fish larvae, which play an important role in recruitment of fish stocks in coastal waters (Cullen-Unsworth and Unsworth, 2016; Unsworth *et al.,* 2019). While relatively high abundance of fish larvae in seagrass meadows is often attributed to the availability of prey (Vonk *et al.,* 2010), the structural components of seagrass meadows could diminish predator foraging efficiency (Lugendo *et al.,* 2007; Muhando and Rumisha 2008; Hedberg *et al.,* 2019) and be important in attracting fish larvae seeking refuge (Gillanders, 2006; Lugendo *et al.,* 2007; Gullström *et al.,* 2008; Jones *et al.,* 2021; Tarimo *et al.,* 2022). The degree of structural complexity in seagrass meadows is influenced by the local environment (Huwer *et al.,* 2016), which also has an impact on the fish larvae assemblages. Furthermore, seagrass plays a crucial role in combatting climate change (Uku *et al.,* 2022), ensuring food security, protecting coastlines, and biodiversity enhancement (Nordlund *et al.,* 2016; Brodie and De Ramon N'Yeurt, 2018).

Seagrass cover, shoot density, canopy height, length and width of leaves, and number of leaves per shoot are used as a structural complexity measure or indicators, and have been shown to decrease with disturbance in previous studies (Hedberg *et al.,* 2019; Jones *et al.,* 2021; Mwaluma *et al.,* 2021). Research on how the complexity of seagrass structures affect fish larvae assemblages is lacking. A few studies in the Western Indian Ocean (WIO) region have examined the impact of seagrass complexity on juvenile, sub-adult, and adult fishes but not on fish larvae (Gullström *et al.,* 2006; Palmqvist *et al.,* 2013; Hedberg *et al.,* 2019; Jones *et al.,* 2021). Other studies focused on seasonal patterns of fish larvae in mangrove creeks, and inshore seagrass meadows (located adjacent to mangroves) (Lugendo *et al.,* 2007; Tarimo *et al.,* 2022). In other geographical areas, studies focused on the complexity of vegetated areas on fish larvae distribution and variability (Rappe *et al.,* 2013; Erzad *et al.,* 2020). Despite these studies, there is limited information on the impact of tropical seagrass structural complexity alone or in conjunction with environmental variables on fish larvae assemblages, making it difficult to determine which characteristics are crucial for setting management priorities (Molina *et al.,* 2020). The present study was designed to examine the relative importance of seagrass structural complexity and environmental variables on fish larvae assemblages (abundance and family richness) in tropical coastal waters. The explicit hypotheses was tested that abundance and family richness of fish larvae are determined by (1) seagrass structural complexity (seagrass percentage cover, shoot density, and canopy height), and (2) environmental variables (temperature, dissolved oxygen, pH, salinity, and water depth).

Methodology

Study site description

The study was conducted in Kitanga (ST1), Fungu ya Kaangoni (ST2), Nyonza (ST3), and Mwamba Karange (ST4), situated on the north coast of Tanzania (Fig. 1). The selection of sites was based on the presence of seagrass meadows influenced by varying degrees of anthropogenic disturbance, affecting the development of seagrass structural complexity. In general, seven seagrass species were present in the surveyed areas of which *Thalassia hemprichii* was dominant. The data collected were for the single species *Thalassia hemprichii,* based on the finding of Jones *et al.,* (2021) that seagrass diversity (both functional and species) had minimal effect on fish assemblages. Therefore, in this study it was decided to concentrate on the single dominant species.

These sites experience varying degrees of anthropogenic disturbances that impact on the development of seagrass structural complexity. Fungu ya Kaangoni (ST2) and Mwamba Karange (ST4) were characterized by reduced intensity and frequency of fishing, and anthropogenic activities that impact on seagrass beds, as well as natural factors like the influence of seasonal streams inflow, which brings sediments from land sources, as these sites are comparatively far from the coastline (about 10 km away from the coast). Kitanga (ST1) and Nyonza (ST3) are located nearshore, where the majority of damaging fishing practices (e.g., drag nets) are carried out and streams flow directly into these sites, bringing sediments and wastes from agricultural and industrial activities and contribute to impacts on these sites. While Nyonza (ST3) is influenced by the Kisare stream, Kitanga (ST1) is influenced by the Koreni stream. These streams transport domestic waste, sediment from land-based operations, nutrients, or fertilizers from sisal estates during the rainy season. Furthermore, these sites are impacted by fishing activities (the use of ring nets, gleaning, beach seines and other fishing methods), trampling, and pulling or pushing boats towards deeper waters.

The study sites are influenced by southeast and northeast monsoon winds (Peter *et al.,* 2021), which affects water temperature, wind, rainfall, water circulation, wave action, and biological processes. The southeast monsoon season (SEM), from May to September, is characterized by strong winds (blowing relatively strongly from the southeast towards the northwest, at a speed of about 9 ms^{-1}), heavy rains, and low air temperatures. The northeast monsoon season (NEM), from November to March (Peter *et al.,* 2018), is characterized by steady winds (blowing from the northeast towards the southwest at about 5 ms^{-1}), short rainy periods, and high air temperature (Peter *et al.,* 2021). Field surveys in seagrass meadows were conducted during spring low tides while fish larvae sampling was conducted over the seagrass meadows during the corresponding high tides. During the SEM, sampling was conducted for four months; June and August (2019) as well as July and September (2020). During the NEM season, sampling was also conducted for four months; December (2019), February and November (2020) as well as January (2021).

Field sampling and laboratory procedures

Environmental variables, including temperature, salinity, pH, dissolved oxygen, and water depth were measured directly in the field. Temperature and dissolved oxygen (DO) were measured using a thermometer with a temperature sensor and a DO meter (ECOSENSE DO 200A), respectively. Salinity was measured using a refractometer (RS 20). The pH was recorded using a pH meter (HANNA S8128) and water depth was recorded using an echo sounder (speed tech instrument 4308055). All equipment used were handheld.

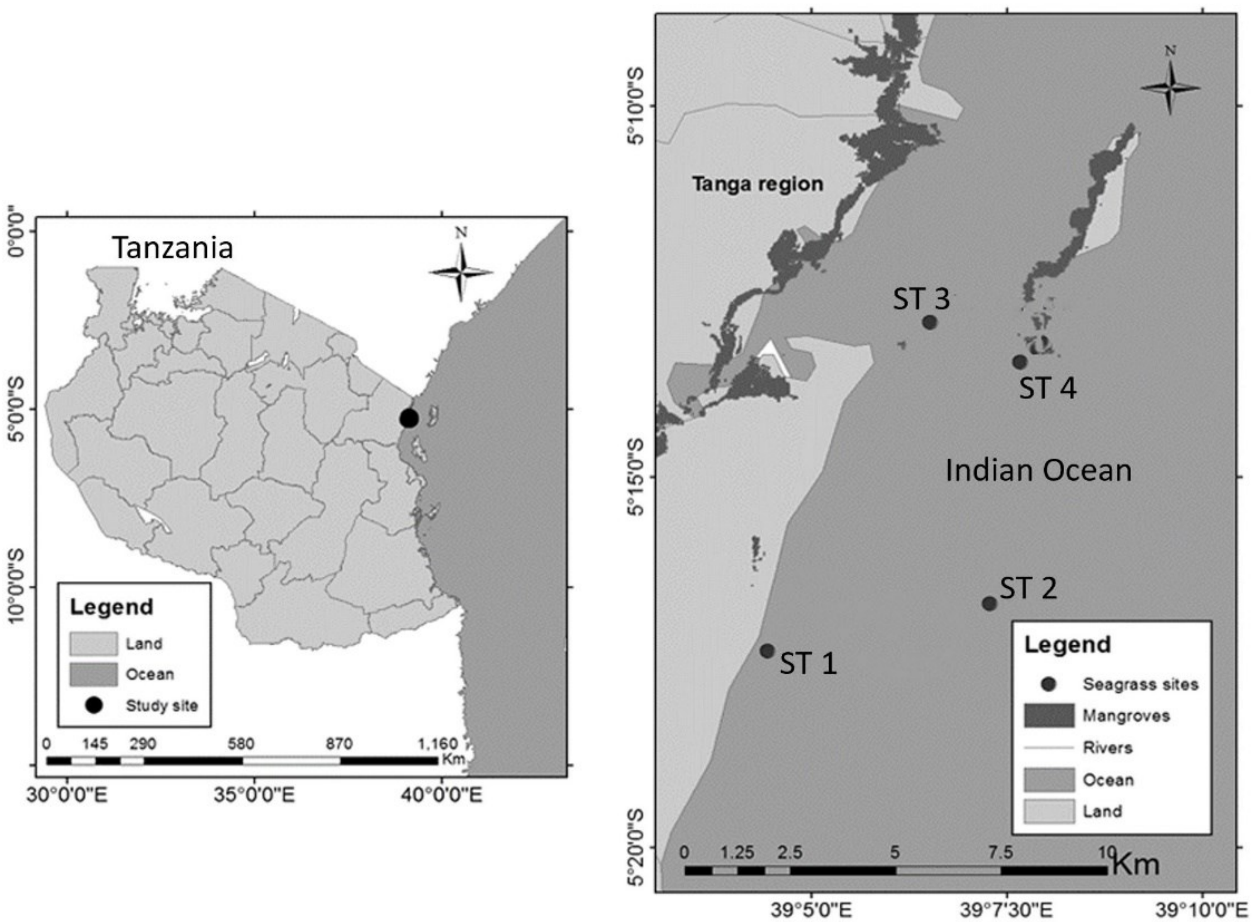

Figure 1. Map showing the study sites: the black dot on the map of Tanzania shows the general location of the sampled area, which is then expanded on the map on the right-hand side, giving the exact locations of the four sites. Where ST1 - Kitanga, ST2 - Fungu ya Kaangoni, ST3 – Nyonza, ST4 - Mwamba Karange.

At each seagrass meadow site, two transects were established perpendicular to the shoreline covering upper, middle, and lower zones. These transects were set 100 m apart to capture site representation. On each transect, three plots in each zone were randomly selected using a 0.25 x 0.25 m quadrat, for nine plots in total. In each quadrat, data for seagrass cover, canopy height, and shoot density were recorded. Seagrass species were identified *in situ* using field manuals appropriate for the region (Richmond, 2002). Shoots of the dominant seagrass species, *Thalassia hemprichii,* were counted and then used to estimate shoot density. Seagrass shoot density was determined as the number of individual seagrasses in a quadrat, which was expressed in a square meter area (m^2) (Erzad *et al.,* 2020). Seagrass percentage cover of *T. hemprichii* was determined by visual estimate using 0.25 x 0.25 m quadrats (Saito and Atobe, 1970). Within the quadrat, canopy height of *T. hemprichii* was measured using a ruler (30 cm).

Fish larvae samples were collected by towing an ichthyoplankton net (mesh size of 500 µm, mouth diameter of 0.5 m and a total length of 2.5 m) fitted with a hydro-bios mechanical flow meter to calculate the volume of water passing through the net. The net was towed behind the boat over seagrass meadows dominated by *T. hemprichii* as close to the canopy as possible, ranging between 0.75 and 6 m depth and maintained in surface waters at approximately 1 meter per second current speed for 15 minutes to concentrate fish larvae samples. After each tow, the fish larvae samples were decanted into 200 mL plastic bottles then immediately fixed with 75% ethanol solution and transported to the laboratory for further analysis. In the laboratory, fish larvae samples were drained and a fresh 75% ethanol solution was added. The separation of fish larvae from the entire sample was carried out under a stereomicroscope. Using the available taxonomic guides of Mwaluma *et al.* (2014) and Leis and Carson-Ewart (2000), each fish larvae specimen was identified to family level.

Data analysis

Before statistical analyses, the assumption of homogeneity of variance was checked by using Shapiro-Wilk's test at the significance level of $p < 0.05$. Fish larvae abundance and environmental variable data were $\log_{10}(x+1)$ transformed when necessary based on the values of skewness. This was carried out using R statistical programming version 4.1.2 software. When the data remained heteroscedastic despite transformations, hypotheses were rejected at alpha levels lower than the *p*-values of the Shapiro-Wilk's test. Data of seagrass structural complexity measurements (i.e., percentage cover, shoot density, and canopy height) and fish larvae abundance were analyzed using Analysis of Variance (ANOVA) to compare the means and state significant differences, followed by Tukey's *post hoc* test in the four sites. A two sample t-test was used to test the seasonal difference between the SEM and the NEM seasons. Multiple linear regression analysis was used to explore the relative importance of various continuous variables: seagrass structural complexity (percentage cover, shoot density, and canopy height); and environmental variables (temperature, dissolved oxygen, pH, salinity, and water depth) on fish larvae assemblages. Moreover, before the analysis, all predictor variables were checked for collinearity. The data for testing the response of fish larvae abundance and fish family richness were grouped into two distinct groups: (1) seagrass structural complexity; and (2) environmental variables. Given that multiple variables were included within the two categories, Principle Component Analysis (PCA) was performed using the prcomp() function in R and the values for PC1 were extracted and exported to create a single variable accounting for the majority of the variance. Afterwards, PCA values accounting for the majority of variance to do multiple linear regression were used to evaluate the influence of seagrass structural complexity and environmental variables on fish larvae assemblages. The approach constructed a linear model from the analyses of the principal component instead of the original values of the predictors to avoid the redundancy and multicollinearity between them.

Linear mixed-effects were used to explore the relative importance of three seagrass structural complexity variables and five environmental variables on two fish response variables; fish larvae abundance and fish family richness. Multivariate analysis of the fish larvae assemblage was performed using PRIMER ver. 6.1.2 software (Plymouth Routines in Multivariate Ecological Research) (Clarke and Warwick, 2001). Two-way crossed analysis of similarities (ANOSIM) was used to test for differences in fish larvae assemblages among sites. Patterns of similarities were visualized using non-parametric multidimensional scaling (nMDS) based on the Bray-Curtis similarities measure (a well-suited similarities index since it does not require exclusion of rare species or family), calculated by means of square root-transformed data. The similarity of percentages (SIMPER) procedure was carried out to determine which fish larvae family contributed most to dissimilarities among the different study sites. To determine the degree of correlation between 2 independent distance (dissimilarity or similarity) matrices, the Mantel test was applied whereby a randomization technique to test whether dissimilarity matrices of fish assemblages and habitat variables (i.e., seagrass structural complexity, environmental

Table 1. Average values (± SE) of environmental variables in the study sites and season. Where, ST1 - Kitanga, ST2 - Fungu ya Kaangoni, ST3 – Nyonza, and ST4 - Mwamba Karange. SEM - southeast monsoon, and NEM - northeast monsoon seasons.

Sites/Season	Environmental variables				
	Temperature (°C)	DO (mg/L)	pH	Salinity (psu)	Depth (m)
ST1	27.69 ± 0.39	6.5 ± 0.36	8.60 ± 0.12	35.30 ± 0.24	3.80 ± 0.32
ST2	27.50 ± 0.38	7.39 ± 0.36	8.61 ± 0.15	35.88 ± 0.35	3.23 ± 0.42
ST3	27.65 ± 0.38	6.115 ± 0.38	8.58 ± 0.11	35.0 ± 0.30	3.19 ± 0.26
ST4	27.76 ± 0.39	6.70 ± 0.42	8.68 ± 0.11	35.95 ± 0.39	3.24 ± 0.60
p value	$p = 0.29$	$p = 0.06$	$p = 0.19$	$p = 0.23$	$p = 0.27$
SEM	26.59 ± 0.20	7.78 ± 0.30	8.56 ± 0.05	36.02 ± 0.28	3.18 ± 0.25
NEM	28.65 ± 0.27	6.77 ± 0.30	8.63 ± 0.03	35.19 ± 0.16	3.21 ± 0.25
p value	6.4e-06***	0.00186**	0.0207*	0.00426*	$p = 0.12$

variables) showed association among sites (Mantel, 1967). Distance matrices based on $X^{0.25}$ transformed fish larvae data (abundance and family richness) were calculated based on Bray-Curtis similarities, whereas distance matrices of *z* transformed habitat and environmental variables were made on Euclidean similarities measures.

Results

General description of environmental variables, fish larvae assemblages and seagrass structures

Variations in environmental variables in the different seagrass meadow sites and seasons are presented in Table 1. There were no statistically significant differences in environmental variables among sites ($p > 0.05$). However, a two-sample t-test revealed a significant seasonal difference in environmental variables ($p < 0.05$), except for the depth, as presented in Table 1. During the SEM season, dissolved oxygen, and salinity levels were higher than during the NEM season. Temperature and pH, on the other hand, were significantly higher in the NEM season than in the SEM season. In the present study, there were no significant seasonal differences in fish larvae assemblage and seagrass structures between SEM and the NEM ($p > 0.05$) (Table 2).

Seagrass habitat structure varied among *T. hemprichii*-dominated seagrass meadows (Fig. 2). For structural complexity variables (mean seagrass percentage cover, and canopy height), there was a significant difference among seagrass meadow surveyed sites ($p = 0.000$, $p = 0.022$ respectively). In contrast, estimates of the mean shoot density were comparable with no significant differences among sites ($p = 0.16$). There was significantly higher seagrass cover at sites ST2 and ST4 than ST1 and ST3, while canopy height was significantly higher at sites ST1 and ST3 than at ST2 and ST4.

A total of thirty-eight (38) fish larvae families were identified (Fig. 3). One-way ANOVA showed a significant difference ($p = 0.013$) in fish larvae abundance (number of individual families per m^3) among study sites (Fig. 4). The Tukey's *post hoc* test revealed highest values at ST1, ST2 and ST4, while lowest values were recorded at ST3. There was no significant difference in fish larvae abundance at seagrass sites ST1 and ST4 ($p = 0.14$). Statistically, fish larvae abundance at seagrass sites ST3 and ST2 were significantly different from each other ($p = 0.041$). Also, the two sample t-test revealed no significant difference in fish larvae abundance and fish family richness between SEM and NEM seasons ($p = 0.31$,

Table 2. Average values (± SE) of fish larvae assemblages and seagrass structures between southeast monsoon (SEM) and the northeast monsoon (NEM) seasons.

Variables	Season		
	SEM	NEM	*p value*
Seagrass % cover	39.47 ± 0.39	40.83 ± 0.40	0.34
Shoot density	396.59 ± 1.24	455.85 ± 1.33	0.12
Canopy height	5.55 ± 0.15	5.67 ± 0.15	0.42
Fish larvae abundance (Ind/ 100m³)	5.06 ± 0.14	3.68 ± 0.11	0.31
Family richness	4.93 ± 0.13	3.68 ± 0.11	*0.199*

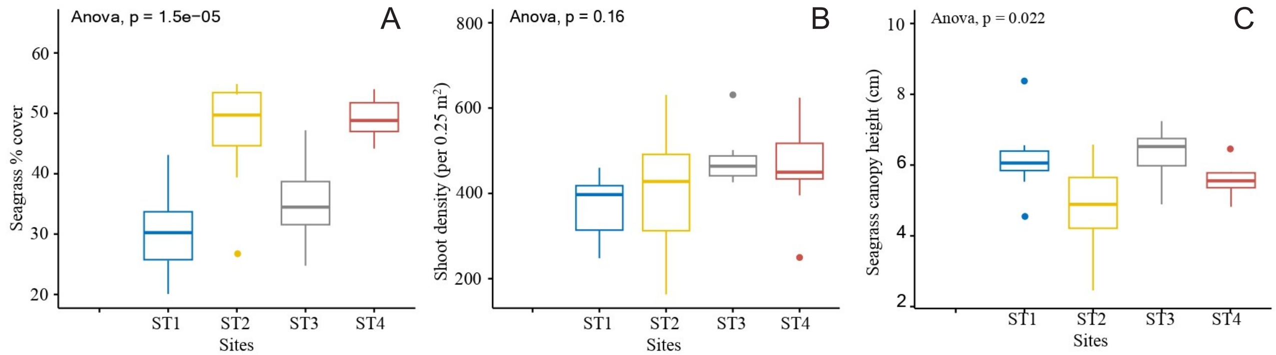

Figure 2. Boxplot showing seagrass habitat structure among the study sites. ST1 - Kitanga, ST2 - Fungu ya Kaangoni, ST3 – Nyonza, ST4 - Mwamba Karange.

p = 0.199 respectively) (Table 2). There was a significant variation in fish larvae family richness among the study sites (p = 0.031). Tukey's *post hoc* test revealed the highest and the lowest values at sites ST1 and ST4 (p = 0.034). While lower values were observed at seagrass sites ST2 and ST3 (p = 0.45), high family richness was observed at ST4 and ST1. The dominant fish larvae families identified throughout the study were Scaridae, Syngnathidae, Labridae, Sphyraenidae, Belonidae, Clupeidae, Carangidae, and Bleeniidae.

The influence of seagrass structural complexity and environmental variables on fish larvae assemblages

Principle Component Analysis (PCA) was performed to extract variables accounting for the majority of the variance (Fig. 5). In the PCA of seagrass structural complexity, PC1 accounted for 52.9% of the variation while PC2 accounted for 32%. All seagrass variables contributed to PC1 which was positively correlated with canopy height and shoot density, and were negatively correlated with seagrass percentage cover. For environmental variables, PC1 accounted for 39.8% while PC2 accounted for 23.6% of the variation and each had substantial factor loadings on PC1. For environmental variables, dissolved oxygen and depth were positively correlated while temperature, salinity, and pH were negatively correlated on PC1. From the multiple linear regression analyses, combined seagrass structural complexity variables (seagrass percentage cover, canopy height, and shoot density) and environmental variables (temperature, dissolved oxygen, pH, salinity, and depth) significantly predicted fish larvae abundance (R^2 = 0.756, p = 0.0185; Table 3). Also, the same result was observed on fish family richness whereby all predictors statistically significantly predicted fish larvae families (R^2 = 0.54, p = 0.0396; Table 3).

Using individual variables in one model, multiple linear regression analyses of seagrass percentage cover, canopy height, and shoot density variables statistically, they significantly predicted fish larvae abundance

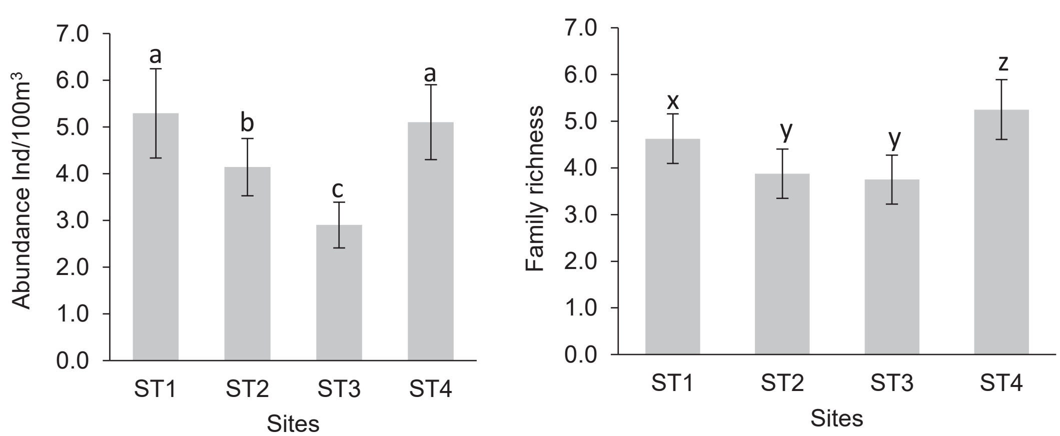

Figure 3. Fish larvae abundance and family richness among meadows at the four sites (Where, ST1 - Kitanga, ST2 - Fungu ya Kaangoni, ST3 - Nyonza, and ST4 - Mwamba Karange). Note that bars with the same letters (a, b, c, x, y, z) indicate values which are not statistically different at $p < 0.05$ within the same group.

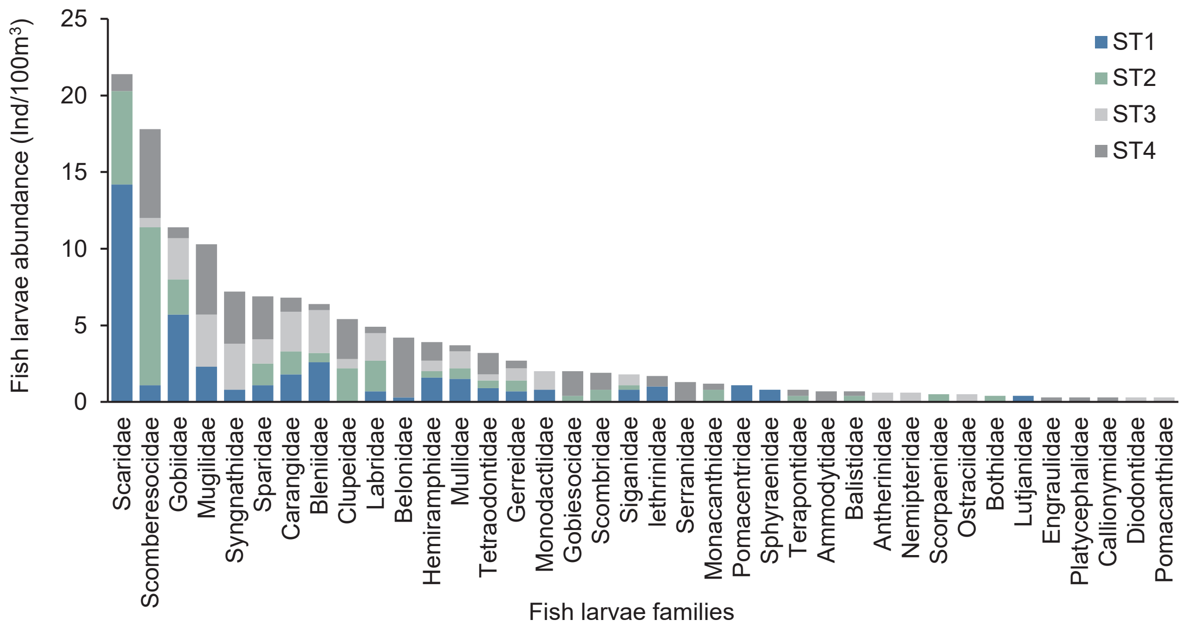

Figure 4. Dominant fish larvae family abundance among sites (Where, ST1 - Kitanga, ST2 - Fungu ya Kaangoni, ST3 - Nyonza, and ST4 - Mwamba Karange).

(R^2 = 0.72, p = 0.011). Canopy height and shoot density positively predicted fish larvae abundance and it was significant (p = 0.03, p = 0.045; Table 4). Likewise, a significant negative prediction by seagrass percentage cover on fish larvae abundance was observed (p = 0.005; Table 4). In terms of fish family richness, only canopy height was a significant positive predictor of fish family richness (p = 0.012), while shoot density and seagrass percentage cover showed a positive prediction on family richness but were not statistically significant (p = 0.15, p = 0.95, respectively).

Environmental variables showed a statistically significant prediction on fish larvae abundance (R^2 = 0.54, p = 0.032). Temperature and dissolved oxygen were significant predictors of fish larvae abundance (p = 0.04, p = 0.026, respectively). Furthermore, pH was shown to be a positive predictor of fish larvae abundance (p = 0.88), and a negative predictor of fish richness (p = 0.75), but not significantly. Other predictor variables such as salinity and depth negatively predicted fish larvae abundance, however, they were not statistically significant (p > 0.05). Multiple linear regression analyses of seagrass structural complexity significantly predicted fish larvae family richness (R^2 = 0.65, p = 0.0124). Predictor variable canopy height had a significant prediction of fish larvae family richness (p = 0.012) while shoot density and seagrass cover

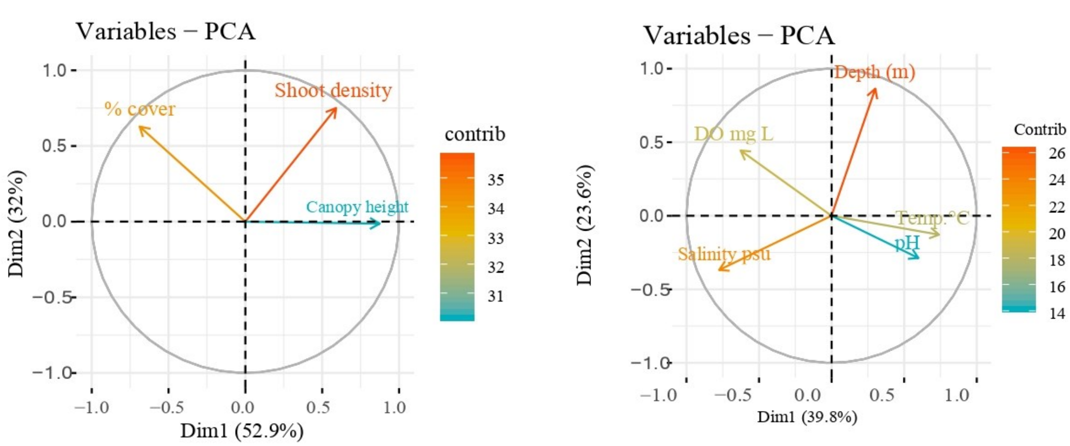

Figure 5. Principle Component Analysis (PCA) plots showing the variation in seagrass structural complexity and environmental variables on fish larvae assemblages.

Table 3. Results of multiple linear regression analysis showing combined seagrass structural complexity and environmental variables extracted from PCA accounting for the majority of variance for predicting fish larvae assemblages.

Dependent variable	Predictor variables	Estimate	Std. Error	t value	Pr(>|t|)	R^2	p- value (overall model)
Fish larvae abundance	Intercept	1.40811	0.68	2.060	0.0485 *		
	Seagrass structural complexity	0.7689	0.081	9.426	0.00 *	0.756	0.0185 *
	Environmental variables	0.140	0.122	2.6244	0.062.		
Family richness	Intercept	0.674	2.815	5.337	0.00 *		
	Seagrass structural complexity	0.484	0.805	2.288	0.0296 *	0.54	0.0396 *
	Environmental variables	0.228	0.121	1.19	0.09851.		

Table 4. Results of multiple linear regression analysis showing variables significantly predicting fish larvae abundance and family richness.

Dependent variable	Predictor variables	Estimate	Std. Error	t value	Pr(>|t|)	R^2	p- value (overall model)
Fish larvae abundance	Intercept	4.31	1.98	2.17	0.051.		
	Seagrass % cover	-0.14	0.041	3.43	0.005*		
	Shoot density	0.17	0.030	2.16	0.045.	0.72	0.011*
	Canopy height	0.61	0.90	0.67	0.03*		
Fish larvae abundance	Intercept	84.19	75.36	1.12	0.27		
	Temp (°C)	-1.03	0.90	-1.15	0.026*		
	DO (mg/L)	1.62	0.81	1.99	0.04*	0.54	0.032 *
	pH	1.17	7.41	0.16	0.88		
	Salinity (psu)	-1.98	1.26	-1.57	0.13		
	Depth (m)	-0.50	0.60	-0.83	0.41		
Family richness	Intercept	4.17	3.92	1.06	0.30		
	Seagrass cover	0.20	0.5	0.02	0.98		
	Shoot density	0.046	0.030	1.510	0.159	0.65	0.0124*
	Canopy height	0.41	0.13	2.99	0.012*		
Family richness	Intercept	78.30	45.05	1.738	0.116		
	Temp (°C)	-1.08	0.46	-2.37	0.03*		
	DO (mg/L)	0.38	0.41	0.93	0.36		
	pH	-1.20	3.76	-0.32	0.75	0.73	0.013*
	Salinity (psu)	-1.27	0.64	-2.00	0.04*		
	Depth (m)	-0.26	0.30	-0.85	0.40		

NB: Significance difference at: $p < 0.05$ *

Table 5. Fish families contributing (by > 5%) to dissimilarities (cumulative limit of 68%) among sampling sites (legend described in Fig. 1) in the SIMPER analysis on fish larvae abundance.

S/N	Fish larvae families	% contribution to dissimilarities
1	Scaridae	14.2
2	Syngnathidae	10.8
3	Labridae	10.0
4	Sphyraenidae	8.2
5	Belonidae	7.3
6	Clupeidae	6.9
7	Carangidae	5.6
8	Bleeniidae	5.5

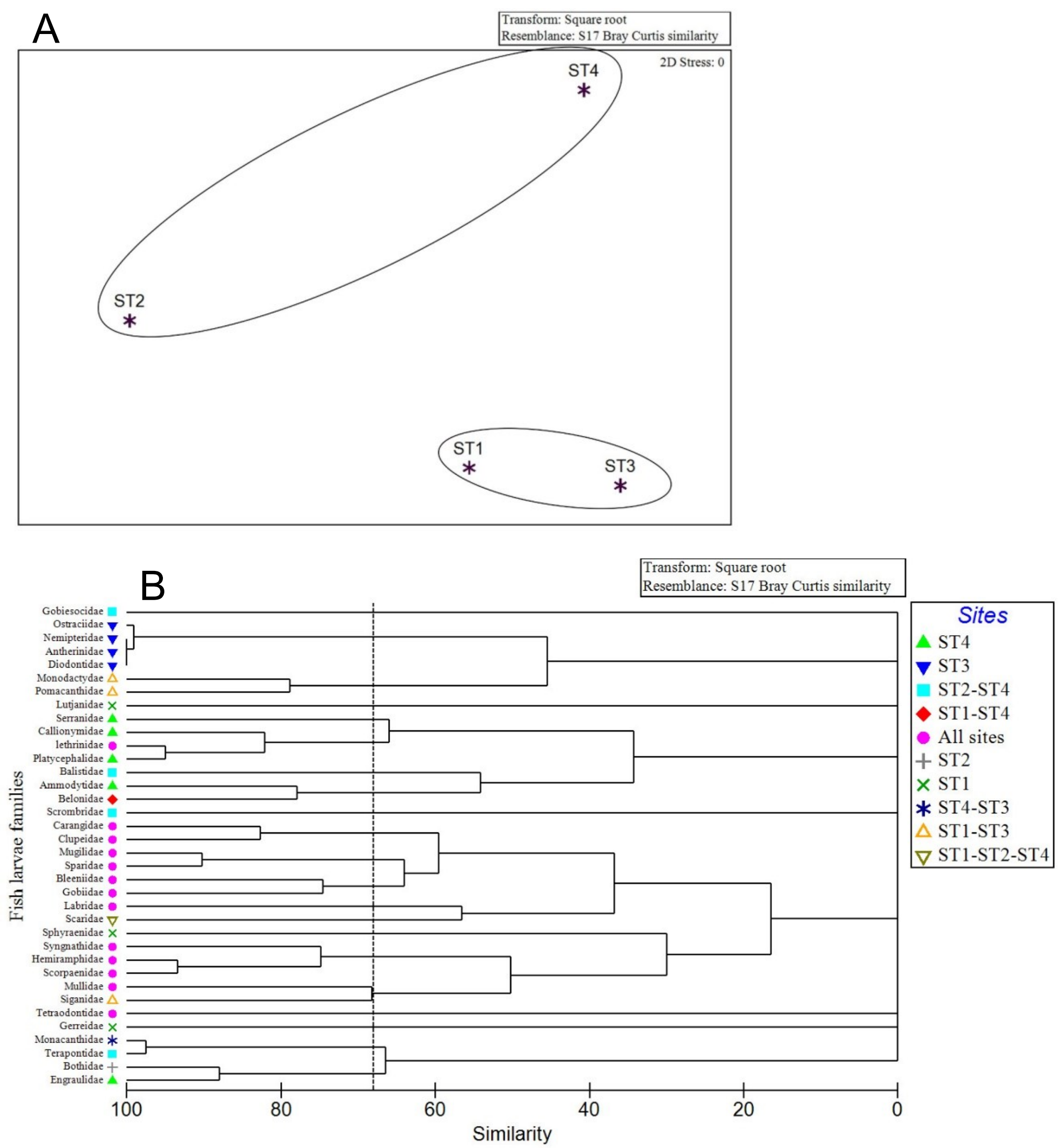

Figure 6. (a) Non-parametric multidimensional scaling (nMDS) ordinations of fish larvae assemblage structure, separated into sites (Abbreviations are as in Fig, 1.); and (b) Dendrogram plot showing similarity for fish larvae families/sites.

showed a positive prediction of fish larvae family richness, but they were not statistically significant ($p > 0.05$). On the other hand, environmental variables significantly predicted fish larvae family ($R^2 = 0.73$, $p = 0.013$). Temperature and salinity were found to be negatively correlated with fish larvae family richness ($p = 0.03$ and $p = 0.04$, respectively). Dissolved oxygen positively correlated with fish larvae family richness while pH and depth gave a negative correlation, but all were not statistically significant ($p > 0.05$; Table 4).

Multivariate patterns of fish larvae assemblages

Two-way crossed ANOSIM analyzing fish larvae assemblage structure revealed significant separation among sites (global R = 0.80, $p = 0.001$) and support the patterns in the non-multidimensional scaling (NMDS) ordination plots (Figs. 5a and 5b). Pairwise (between habitat) site comparisons showed that two sites, ST1 and ST4, were significantly different from each other ($p < 0.05$). SIMPER analyses showed that the most abundant fish larvae families were Scaridae, Sphyraenidae, Gobiidae, Sparidae, Labridae, Clupeidae, Carangidae, Belonidae, and Syngnathidae, which are all seagrass residents. These were also the families that contributed most to dissimilarities in the fish larvae assemblage structure among study meadow sites (Table 5). The study was further confirmed by nMDS analysis that reflected the analogous pattern of grouping among the sites as observed in the cluster analysis (Figs. 6a and b). The group average similarity between sampling sites ST1 and ST3 showed a similar pattern, comprising 80% similarity (Fig. 6a). Furthermore, sites ST2 and ST4 formed a separate group of less than 50% as shown in Figure 6 (a and b). The stress value was less than 0.1, which is a good ordinance pattern and a perfect description of the observed data for distances between sample sites. Both plots are based on the Bray-Curtis similarities index using square-root-transformed fish larvae abundance data.

Discussion

Environmental variables

Distribution of fish larvae within seagrass nursery areas differ between families and species, and depend on environmental variables (Palmqvist *et al.,* 2013). Environmental variables play an important role in fish larvae assemblage structure (Molina *et al.,* 2020). Fish larvae are distributed across a wide range of environmental conditions, yet the presence or abundance of some families or species is limited by factors such as dissolved oxygen, pH, temperature, salinity, and water depth (Gullström *et al.,* 2008). The variation in environmental variables is influenced by a range of factors including climatic, hydrological, geological, and anthropogenic stress (Hedberg *et al.,* 2019). From the present study there was no differences in the water temperature, dissolved oxygen, pH, and salinity among the sites; this lack of variation may have been caused by constant water mixing, and the patterns of the current within the relatively shallow tropical seagrass habitat (Perez-dominguez *et al.,* 2006). The seasonal difference in environmental variables are commonly related to seasonal monsoonal weather (most pronounced in the upper layer of the water column) and oceanographic conditions (McClanahan, 1988). The average water temperature in this study was higher during the NEM season due to longer exposure to sunlight radiation (McClanahan, 1988).

Additionally, in the SEM, lower temperatures are caused by strong winds that cause deep mixing, thereby bringing colder waters to the surface (Peter *et al.,* 2021). There was a significant seasonal variation in dissolved oxygen, and pH was higher during the SEM than the NEM season. Similarly, salinity was slightly higher during the SEM than during the NEM season, probably due to surface runoff caused by the rains during the NEM, which is supported by the work of Giering *et al.,* (2019) and Peter *et al.,* (2021). During the NEM season, however, pH was slightly higher than during the SEM season, presumably due to runoff from nearby agricultural areas carrying organic wastes (Levinton, 2001; Dhanam *et al.,* 2016).

Effect of seagrass structural complexity on fish larvae assemblages

Previous studies have identified that individual factors, such as the characteristics of seagrass meadows (Palmqvist *et al.,* 2013; Zerrato and Giraldo, 2018; Jones *et al.,* 2021; Mwaluma *et al.,* 2021) and environmental variables (Reynalte-tataje *et al.,* 2012; Molina *et al.,* 2020), affect the spatial patterns and variability in seagrass fish larvae assemblages. The present study showed that, when looking at abundance and richness, a number of predictor variables affect fish larvae assemblages in tropical coastal waters. In terms of seagrass structural complexity, it was discovered that seagrass cover, shoot density and canopy height all have a significant impact on fish larvae abundance, while canopy height has a significant impact on family richness. These findings concur with those of Gullstrom *et al.,* (2008) and Jones *et al.,* (2021), who observed that the seagrass cover and canopy height, which served as a measure of the complexity of the seagrass, had an impact on fish abundance and richness in coastal waters. The abundance of fish larvae and family richness were found to be strongly related to the canopy height of the seagrass meadows. One explanation for the strong positive relationship between canopy height and fish larvae abundance and family richness is that a higher seagrass canopy provides shelter, which leads to a higher survival rate by providing protection from predators (Unsworth *et al.,* 2019; Tarimo *et al.,* 2022). Furthermore, a higher seagrass canopy height supports a variety of fish larvae species because of reduced currents which favor organic matter deposition that support high primary productivity and enhance food availability (Arshad *et al.,* 2012).

Hedberg *et al.,* (2019) found that fish larvae assemblages increased with seagrass canopy height. Similar results were also reported by Palmqvist *et al.* (2013) and Jones *et al.* (2021), attributing the increased fish abundance to their ecological function as nurseries and shelter. Similarly, Erzad *et al.* (2020) noted the abundance of fish larvae in seagrass ecosystems is influenced by shelter availability. This supports the current findings that high canopy height provides shelter and food availability (Gullstrom *et al.,* 2008). It has been reported that greater fish abundance was observed in seagrass species with lower shoot density (Jones *et al.,* 2021), which contrasts with the current findings that an increase in seagrass shoot density could result in an increased fish abundance; however, the Jones *et al.* (2021) study was based on juveniles and adult fishes, whereas the current findings are based on fish larvae.

Seagrass cover had a positive relationship with family richness but a negative relationship with fish larvae abundance. Such a negative relationship might be due to other factors such as reproduction patterns and fish species preferences (Tarimo *et al.,* 2022), which were not investigated in the current study. This is in contrast to previous studies, which discovered that seagrass cover is an important factor in determining fish assemblages regardless of fish larvae stage (Arshad *et al.,* 2012; Erzad *et al.,* 2020). However, Rappe *et al.* (2013) reported that the validation of such a relationship is only possible in areas with high seagrass species richness and fish assemblages. Additionally, in contrast to earlier studies by Gullstrom *et al.,* (2008), Rappe *et al.,* (2013) and Jones *et al.,* (2021), the relative significance of seagrass habitat structure that was dominated by *T. hemprichii* was apparent in in the present study.

This implies that high seagrass percentage cover, shoot density, and canopy height attract more fish larvae families to occupy an area. These findings are similar to that of Jones *et al.* (2021) who reported that the complexity of seagrass with extensive coverage, and high leaf canopy provide strong shelter capacity and a variety of food resources. Moreover, high seagrass cover attracts various fish species because of the avoidance of predators and wide space for forage. These results are supported by Gullström *et al.* (2006) and Jones *et al.* (2021), who also found that high cover and canopy height is a harbour for a variety of faunal assemblages and support greater fish diversity and richness. Therefore, seagrass cover, shoot density and canopy height influence fish larvae richness. Overall, a complex canopy structure (high canopy height, long and more numerous leaves, but moderate shoot density) had greater fish richness as observed, and shoot density predicted fish larvae families richness, similar to what was reported previously (Rappe *et al.,* 2013; Erzad *et al.,* 2020; Jones *et al.,* 2021). Generally, seagrass structural complexity provides a favorable environment for fish larvae survival and recruitment (Gullström *et al.,* 2008; Ramli *et al.,* 2013).

Effects of environmental variables on fish larvae assemblages

Regression analysis revealed that environmental variables influence fish larvae abundance and family richness. When combined and using PCA values however, there was no significant influence on fish larvae assemblages, but when treated separately there was an influence. This means that the fish larvae abundance and family richness can be determined by the environmental variables. However, other factors need to be taken into account. Average water temperature was negatively correlated with the abundance of fish larvae and family richness. This could imply that an increase in temperature affects the fish larvae assemblage, abundance and family richness (Zerrato and Giraldo, 2018). Temperature influences the physiological processes in seagrass and fish larvae growth (Nordlund *et al.,* 2016; Mwaluma *et al.,* 2021). The average water temperature in the seagrass ecosystem in the study sites was around 27.15 °C, which is deemed ideal for fish larvae growth and survival and for the photosynthesis process of seagrass (Erzad *et al.,* 2020). The DO was found to positively predict fish larvae assemblages. According to Perez-dominguez *et al.,* (2006), DO is positively correlated with fish assemblages because a seagrass meadow provides oxygen and contributes to fish larvae survival and recruitment in the habitat. Similar findings were reported by Unsworth *et al.,* (2019).

pH had a negative correlation with family richness, but a positive correlation with fish larvae abundance. According to Molina *et* al. (2020) this could be due to differences in sensitivity and responses among fish families. Moreover, a small shift in pH can have significant impacts on fish larvae assemblages. The negative relationship between fish larvae assemblages and salinity could imply that fish larvae cannot tolerate a wide range of salinity (Arshad *et al.,* 2012). Similar results were reported by Zerrato and Giraldo (2018). Another predictor variable, depth, was negatively correlated with fish larvae abundance and family richness. The most likely explanation for this is that the majority of the fish larvae reside in nearshore habitats in shallow waters. This is in contrast with previous findings which show juvenile, subadult, and adult individual fish to be positively correlating with water depth (Jones *et al.,* 2021). This is due to fact that the occurrence of post larvae fish primarily depends on the tidal regime and species-specific mobility (Tarimo *et al.,* 2022). Large fish have a preference for slightly deeper subtidal seagrass habitats which provide a suitable environment for foraging and increased space for protection against predators (Gullström *et al.,* 2008; Jones *et al.,* 2021). This disparity could be explained by the fact that the current investigation was based on fish larvae, which are small and with limited mobility. Additionally, it is necessary to carry out an extensive comparable study that would include all fish life histories in the seagrass ecosystem in order to assess and contrast their diversity and abundance under various tidal regimes.

Relative importance of seagrass structural complexity and environmental variables

Seagrass structural complexity and environmental variables influence the fish larvae assemblage abundance and richness. Multiple regression analysis indicated that seagrass structural complexity (canopy height, seagrass cover, and shoot density) was the foremost predictor of fish larvae assemblages in tropical coastal waters. This was followed by variables related to the environment (temperature, dissolved oxygen, and salinity). The current study found that both seagrass structural complexity and environmental variables are important for fish larvae assemblages in coastal waters, and that conservation efforts should take both into account.

Cluster analysis and general patterns of fish larvae assemblage among sites

The hierarchical cluster analysis showed variation in fish larvae assemblages among study sites. The distribution of fish larvae families was closely associated with the environmental variables and seagrass structure (Mwaluma *et al.,* 2021). A similar pattern of grouping among the sites in hierarchical cluster analysis and nMDS in the present study is in line with Arumugum *et al*., (2016). In their observations, these authors stated that the nMDS plot revealed the same groups as a cluster, which was again demonstrating the variations in different sampling sites. In contrast to ST3 and ST4, where there was unequal dispersion, the group average similarity across sampling sites ST1 and ST3 showed a comparable pattern, suggesting that most fish larvae families are the same and were distributed equally in the two sites. This might be due to tidal and water current fluctuation differences for distributing fish larvae in different areas as reported by Erzad *et al.,* (2020).

This study showed that the structure of fish larvae assemblages varied spatially among seagrass meadows dominated by *T. hemprichii,* displaying high fish larvae abundance and family richness at ST2 and ST4 sites. These sites are relatively far from the coast (about 10 km) experiencing lower intensity of degradation. This is in contrast to ST1 and ST3, which were near the coast and experience high intensity of degradation from fishing activities, such as the use of beach seines, ring nets and boat anchorage over seagrass beds. Similar results were reported by Palmqvist *et al.* (2013) where fish assemblages varied with seagrass localities and were primarily driven by the large differences in numbers of juvenile seagrass residents and coral-seagrass associated fish of all life stages. Given that the area with the highest severity of degradation also had the fewest fishes, it may be connected to the present findings. Within the group of fish larvae families identified, most individuals were herbivores, in particular the seagrass-grazing parrotfish, these provide an important trophic link within the seagrass food web and the reason why spawning occurs in habitats with extensive coverage of seagrass. This implies that trophic interactions affect fish larvae abundance in a complicated way, with parent fish preferences for food and shelter, species and life stage-specific interactions, and coastal habitat connectivity, all playing a role (Hedberg *et al.,* 2019; Jones *et al.,* 2021).

Implications for management and governance

The findings presented here will be of broad interest to fisheries managers, researchers, and other relevant stakeholders, including responsible authorities to ensure effective management and conservation of seagrass and adjacent coastal ecosystems. It has been observed and reported that one of the most direct adverse effects on seagrass beds is the damage caused by fishing or recreational boat activities (e.g., the use of beach seines, cutting by propellers, propeller wash, anchor and mooring damage, and boat groundings), which could result in significant localized impacts on the physical integrity of seagrasses (Turner and Schwarz, 2006; Jones *et al.,* 2021). Propeller scarring, for example, can result in a continuous line of seagrass damage, fragmenting the seagrass bed and increasing the vulnerable bed edge to erosion, thereby leading to more scouring and deepening of the scoured area. As a consequence of increased seagrass bed fragmentation, fish larvae and associated animal communities are increasingly affected. The potential long-term negative impact of destructive fishing practices and boat activities on seagrass meadows has long been known, and the cumulative effects of such events can result in large-scale loss of seagrass beds in nearshore coastal areas. However, these activities have been largely overlooked by researchers and little is known about the extent to which anthropogenic activities affect most seagrass structural complexity.

This study was carried out in a Marine Protected Area (MPA), where the current fishing management measures are insufficient and only cover a small area close to Tanga Coelacanth Marine Park (TACMP), leaving a large portion of the "protected area" unprotected, with limited monitoring, control, and surveillance of fishing vessels. The current management strategy is to reduce the fishing pressure. But, from field observations, there were many anthropogenic threats to seagrass meadows in the study area, which are overlooked and sometimes are not well managed, especially in the nearshore habitats. These include the use of ring nets, gleaning, beach seines, trampling, and pulling or pushing boats towards deeper areas at low tide via the seagrass beds. Anchoring activities in the study area both negatively influences seagrass health and reduces complexity, and in turn affects fish dispersal and recruitment which then impacts fisheries productivity (Hedberg *et al.,* 2019). These anthropogenic stresses are frequently overlooked but impact the ecological functioning of seagrass coastal habitats. This study provides important baseline observations which can guide the development of fisheries management plans and governance strategies for activities in marine protected and adjacent areas. The study indicated the importance of seagrass complexity and environmental variables in ensuring fish larvae growth and survival and contribution to overall fish recruitment. This suggests the need for greater seagrass protection and emphasizes the importance of conservation efforts within the MPAs. Moreover, there is a need for improved knowledge on the impact of anthropogenic stresses on coastal habitats to inform management and conservation development planning and governance (Mwaluma *et al.,* 2021). Nevertheless, in the WIO region, climate change is another threat to habitats and it is necessary to improve understanding of the present coastal habitats how climate change will impact fisheries productivity alongside efforts to prepare adaptation for those future changes (Jacobs *et al.,* 2020; Sekadende *et al.,* 2020; Mwaluma *et al.,* 2021).

Conclusions and recommendations

The structural complexity of seagrass beds and environmental variables are determinants of fish larvae assemblages in these coastal habitats. The abundance and diversity of fish larvae are determined by seagrass structural complexity, (canopy height, shoot density, and seagrass cover), and environmental variables (temperature, dissolved oxygen, pH, and salinity) which influence fish larvae assemblage in tropical coastal waters. The study recommends that shallow coastal habitats, including seagrass meadows, should be prioritized for conservation and governance efforts in order to protect critical habitats for fish larvae, which help to maintain robust coastal fish stocks and viable coastal fisheries, which is the main occupation of the coastal communities.

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