Effects of habitat on reef fishes biodiversity and composition in rocky reefs

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ABSTRACT: Reef fish are highly valuable to human society — socially, nutritionally and economically. However, they are vulnerable to both overfishing and habitat degradation. Understanding the community structure and habitat associations of reef fish is important for their management and conservation. Using a gillnet survey conducted in a subtropical rocky reef area of Ma'an Archipelago, China, we developed habitat models linking reef fish diversity and community composition with habitat factors. The parsimonious generalized additive model results showed that higher reef fish diversity was associated with southern shallower water, temperature of 25°C, lower levels of dissolved oxygen and chlorophyll *a*, and rock bottom type. The multivariate generalized linear model identified that month, depth, bottom type, and location significantly influenced the local reef fish; these habitat variables explained 18% of the variation in reef fish community composition. However, the lack of strong patterns and correlations between species derived from the joint species distribution model revealed that reefs within our study area are difficult to classify based on habitat-driven patterns in their associated reef fish assemblages. These findings enhance our understanding of the habitat effects on reef fish diversity and community composition and have relevance for the management of reef fish, including habitat zonation and deployment of artificial reefs.

KEY WORDS: Reef fishes · Rocky reefs habitat · Ma'an Archipelago · Habitat models · Gillnet survey

1. INTRODUCTION

Reef fish are socially, nutritionally, and economically valuable to human society (Sadovy 2005). However, they are vulnerable to overfishing because of their long-lived, slow-growing, and limited-dispersal characteristics (Parker et al. 2000, Love et al. 2006). Rocky reefs, the habitat of reef fish, are also under anthropogenic stress as a result of port construction, mariculture, and destructive bottom trawl fisheries (Neira & Cantera 2005). The bladder of reef fish creates a relatively narrow zone of neutral buoyancy in shallow waters which makes them easily injured by forced up-and-down movements through the water column (Parker et al. 2006); therefore, release strategies for reef fish are often ineffective (Parker et al. 2000, Yamanaka & Logan 2010). Ecosystem-based fisheries management (EBFM), the establishment of marine protected areas (MPAs), and construction of artificial reefs are approaches aimed at conserving these vulnerable fish, but their effectiveness requires a robust understanding of reef fish structure, including the effects of habitat on fish assemblages.

Physical and biological habitat variables can drive the spatial variation of populations and assemblages of various reef inhabitants (Guidetti et al. 2004, Schroeter et al. 2015). Nutrient availability and temperature influence local fish community structure

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by altering recruitment and post-recruitment processes (Connell & Jones 1991, Tupper & Boutilier 1997), prey availability (Warfe & Barmuta 2004), and interspecies interactions (Hixon & Beets 1993, Johnson 2006). The magnitude of the associations between fish assemblages and habitat variables has been a key criterion for the designation, management, and assessment of MPAs (Anderson & Millar 2004, García-Charton et al. 2004). Artificial reefs are commonly used for fishery-enhancement programs (Smith et al. 2017), but uncertainties regarding their design and site selection can influence the targeted marine communities. However, associations between fish assemblages and habitat variables have not been explicitly incorporated into the deployment of artificial reefs (Parsons et al. 2016). Recent studies of associations between species and habitat variables focused on tropical (Beger & Possingham 2008, Richardson et al. 2017) and temperate (Tuya et al. 2009, Cameron et al. 2014, Parsons et al. 2016) marine ecosystems. Thus, the effective conservation and enhancement for reef fish in subtropical rocky reefs has not been well promoted.

Habitat suitability modeling has become a common ecological tool to understand how physical and biological variables influence species distribution and assemblages (Guisan & Zimmermann 2000, Cameron et al. 2014, Nash et al. 2016, Parsons et al. 2016). Generalized additive models (GAMs) are one of the most commonly used statistical modeling techniques for habitat suitability modeling, as GAMs can explore nonlinear relationships between response (e.g. species presence or abundance) and explanatory (e.g. temperature, depth, salinity, etc.) variables. However, potential biotic interactions (e.g. species co-occurrence) are not included in GAM-based analyses. The multivariate generalized linear model (MGLM) and joint species distribution model (JSDM) have been developed for analyzing multivariate community abundance data (Hui 2016), and have improved our ability to model community-level responses to physical and biological variables, while accounting for species correlations (Warton et al. 2015). Here, we used a combination of these modeling methods to make our analysis more comprehensive and in-depth.

In Ma'an Archipelago, in the East China Sea, the rocky reefs are under high anthropogenic pressure from road/port construction and fishing (Wang et al. 2012). Based on a combination of the life-history characteristics of the reef fish and the status of their habitat in Ma'an Archipelago, there is an urgent need to conserve them. In this study, we examined the effects of habitat on reef fish diversity (using a GAM) and community composition (using a MGLM and a JSDM) in Ma'an Archipelago. The results of this study will further our understanding of the associations between habitat and reef fish in subtropical rocky reefs and provide guidance for the management of reef fish and their habitats, including habitat zonation and the deployment of artificial reefs.

2. MATERIALS AND METHODS

2.1. Study area

Ma'an Archipelago is located at the center of the Zhoushan fishing ground, where the confluence of the Yangtze River, Qiantang River, Yellow Sea cold water mass, Taiwan Warm Current surface water, and Taiwan Warm Current deep water occurs (Zhang et al. 2007). This complex hydrological environment makes Ma'an Archipelago a feeding ground for many marine organisms (Wang et al. 2012). The coast of Gouqi Island in Ma'an Archipelago is dominated by *Sargassum horneri*, which provides feeding and spawning areas as well as shelter for a variety of invertebrates and fish (Chen et al. 2015). Ma'an Archipelago is under high fishing pressure, with more than 150 000 fishermen yr^{-1} operating fishing vessels in the area (Lin 2017). In order to protect the fishery, an MPA and ongoing artificial reef program were established. The MPA has been moderately effective, although its management still needs to be improved (Sun 2018). This area is closed to fishing from 1 May to 1 September.

2.2. Survey data

This study was based on a fishery-independent multi-mesh gillnet survey conducted in Ma'an Archipelago from January to December in 2009 (Fig. 1). A total of 21 sites were sampled during the survey; details of the total sample composition and sampling months for each site can be found in Wang et al. (2012). Each site was sampled for 24 h by 2 groups of parallel gillnets. One group consisted of 4 connected gillnets with mesh sizes of 2.5, 3.4, 4.3, and 5.8 cm, each net being 1.5 m in height and 3.75 m long (= 1.5 m height × 15 m total length). The other group consisted of 4 connected gillnets with mesh sizes of 5, 6, 7, and 8 cm, each net being 2.4 m in height and 7.5 m long (= 2.4 m height × 30 m total length). Catches from the 2 gillnets were combined for further analysis. Depth (m), temperature (°C), salinity (‰), dis-
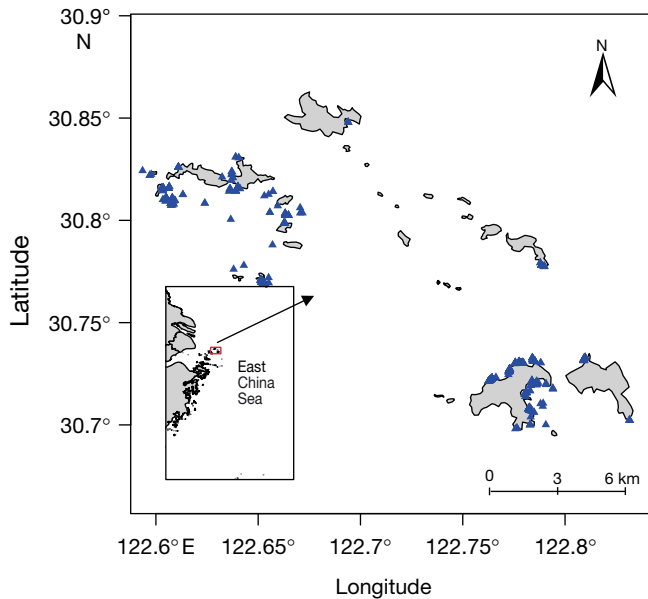
Fig. 1. Gillnet survey sites in Ma'an Archipelago; blue triangles: sampling locations

solved oxygen (DO; mg l^{-1}), chlorophyll a (chl a; mg l^{-1}), and turbidity (NTU) at each site were measured with a water quality measuring instrument (AAQ1183). Using a grab sampler at each site, mud, mixed sand, rock, and mud (srm), sand, mixed sand and rock (sr), and rock were identified.

2.3. GAM

A GAM was used to assess the effects of habitat variables on reef fish diversity. Three indices of diversity were modeled as response variables: the total number of species (S), Shannon-Wiener index (H'), and Simpson's diversity index (D). H' and D were calculated by the following formulae:

$$H' = -\sum_{i=1}^{s} P_i \mathrm{Ln} P_i \tag{1}$$

$$D = 1 - \sum_{i}^{s} P_i^2 \tag{2}$$

where i is the number of ith species and P_i is the proportion of ith species in the total number of species. Location (longitude and latitude), month, depth (m), bottom type, temperature (°C), salinity (‰), DO (mg l^{-1}), chl a (mg l^{-1}), and turbidity (NTU) were selected as explanatory variables.

To check the multicollinearity of candidate explanatory variables, Spearman's correlation and variance inflation factors (VIFs) were used. Firstly, we calculated the Spearman coefficients between vari-

ables. If the coefficient between 2 variables was >0.7 (Jaureguizar et al. 2016), a variable explaining less variation of reef fish diversity in the GAM was removed. We further detected collinearity using VIFs, where variables with VIF > 10 were removed (Borcard et al. 2011). To assess the influence of DO along the depth gradient, an interaction between DO and depth was included in the models. An interaction between longitude and latitude was also included to assess the spatial influence.

The general formulation of a GAM can be expressed as:

$$\log[E(y_i)] = \alpha + \sum_{i=1}^{p} f(x_i) + \varepsilon \tag{3}$$

where y_i is the response variable, α denotes an intercept term, f denotes the non-parametric cubic spline smooth function, x_i denotes the ith explanatory variable, and ε is the residual error term. The GAM was fitted with a Tweedie family distribution to account for large proportion of zeros within response variables (Jaureguizar et al. 2016). A Tweedie GAM parameter, p, can be a value between 1 and 3, where $p = 1$ corresponds to Poisson distribution and $p = 3$ corresponds to inverse Gaussian distribution (Tweedie 1984). The Tweedie GAM developed in our study was fitted by restricting p between 1 and 2, which defined a compound Poisson that can model positive values and zeros at once. Model selection was carried out through backwards selection based on Akaike's information criterion (Wood 2017); model assumptions were evaluated by examining the plots of residuals. The relative importance of each variable in the GAM was calculated by (1) assessing the original adjusted R^2 and smooth parameter of each variable from the best-fitting GAM; and (2) removing a variable and re-modeling the other variables with their smooth parameter derived from (1) (above) in a new GAM to get a new adjusted R^2. The relative importance of the removed variable was evaluated by the new adjusted R^2 minus the original adjusted R^2 (Wood 2005). All statistical analyses were conducted using the 'mgcv' package (Wood & Wood 2007) in R v.3.6.1 (R Development Core Team 2019).

2.4. MGLM

A MGLM was used to model the relationship between the habitat variables and reef fish community composition. A MGLM fits a separate GLM for each species; resampling-based hypothesis testing is then used to find predictors that influence multivariate abundances (Yi et al. 2012). The MGLM in our

study was fitted with a negative binomial error distribution. Variation in species composition explained by predictors was calculated by the 'anova.manyglm' function in packaqge 'mvabund' (Yi et al. 2012).

2.5. JSDM

We used a JSDM to further explore our multi-species data set. A JSDM incorporates the impact of habitat predictors and interspecific interactions in a single model (Hui 2016). Two latent variables were included in our JSDM to create an unconstrained ordination to visualize the main trends between reef sites based on their species composition. Latent variables account for unknown or unmeasured variables, and enable an unconstrained ordination for visualizing site and species patterns by inducing correlations between taxa (Warton et al. 2015). There was no row effect in our JSDM, which means that the ordination patterns were driven by differences in both abundance and species composition between sites. The residual correlation matrices were also evaluated to explore correlations between species (i.e. co-occurrence) due to habitat factors and unmeasured variables. The JSDM was built using the R package 'boral' (Hui 2016).

3. RESULTS

3.1. Observed species composition

A total of 12 species of reef fish were identified from the gillnet survey in 2009 (Table 1). The most frequently observed species were *Sebastiscus marmoratus*, *Hexagrammos agrammus*, and *Hexagrammos otakii* representing 63.6, 20.3, and 7.3% of the total abundance, respectively.

3.2. Effects of habitat on reef fish diversity

Turbidity and chl *a* were highly correlated (correlation: 0.71, p < 0.01) (Fig. 2). Turbidity was removed from the candidate variables, as the GAM including turbidity explained less variation in reef fish diversity than the GAM including chl *a*. The rest of the candidate variables were included in our models because their VIF values were less than 10 (Table 2).

The best-fitting Tweedie-GAM identified that *S* in Ma'an Archipelago was significantly influenced by chl *a*, temperature, DO, month, bottom type, the interaction of latitude and longitude, and the interaction of DO and depth (Table 3). These predictors explained 77.5% of variation in *S*. The most important predictor for *S* was the interaction between DO and depth (Table 3). The chl *a* response curve from the best-fitting model showed higher *S* at 50, 250, and >450 mg l^{-1} (Fig. 3). The temperature response curve showed the highest *S* at 25°C (Fig. 3). The DO response curve showed *S* decreased with DO (Fig. 3). Higher *S* was found in May and November (Fig. 3), and the highest *S* occurred in rock bottom type (Fig. 3). The interaction of depth and DO response map showed higher *S* associated with 5–15 m depth and DO < 4 mg l^{-1} (Fig. 3).

H' and *D* were significantly influenced by month, bottom type, chl *a*, and temperature (Table 3). These variables explained 42.5% and 37.5% of variation in *H'* and *D*, respectively. The most significant factor for *H'* and *D* was chl *a* (Table 3). Higher values of *H'* and

Table 1. Total number of individuals of each species collected in 2009 in Ma'an Archipelago; common names were derived from FishBase (Froese & Pauly 2019)

Species	Common name	Abundance (ind. yr^{-1})
Sebastiscus marmoratus	False kelpfish	1671
Hexagrammos agrammus	Spotty-bellied greenling	532
Hexagrammos otakii	Fat greenling	193
Microcanthus strigatus	Stripey	65
Parajulis poecilepterus	Multicolorfin rainbowfish	60
Pagrosomus major	Red seabream	40
Acanthopagrus schlegelii	Blackhead seabream	34
Apogon semilineatus	Half-lined cardinal	24
Epinephelus akaara	Spinycheek grouper	4
Oplegnathus fasciatus	Barred knifejaw	2
Goniistius zonatus	Spottedtail morwong	1
Enedrias nebulosus	Tidepool gunnel	1

Table 2. Candidate explanatory variables used in this study. VIF: variance inflation factor; n/a: not assessed

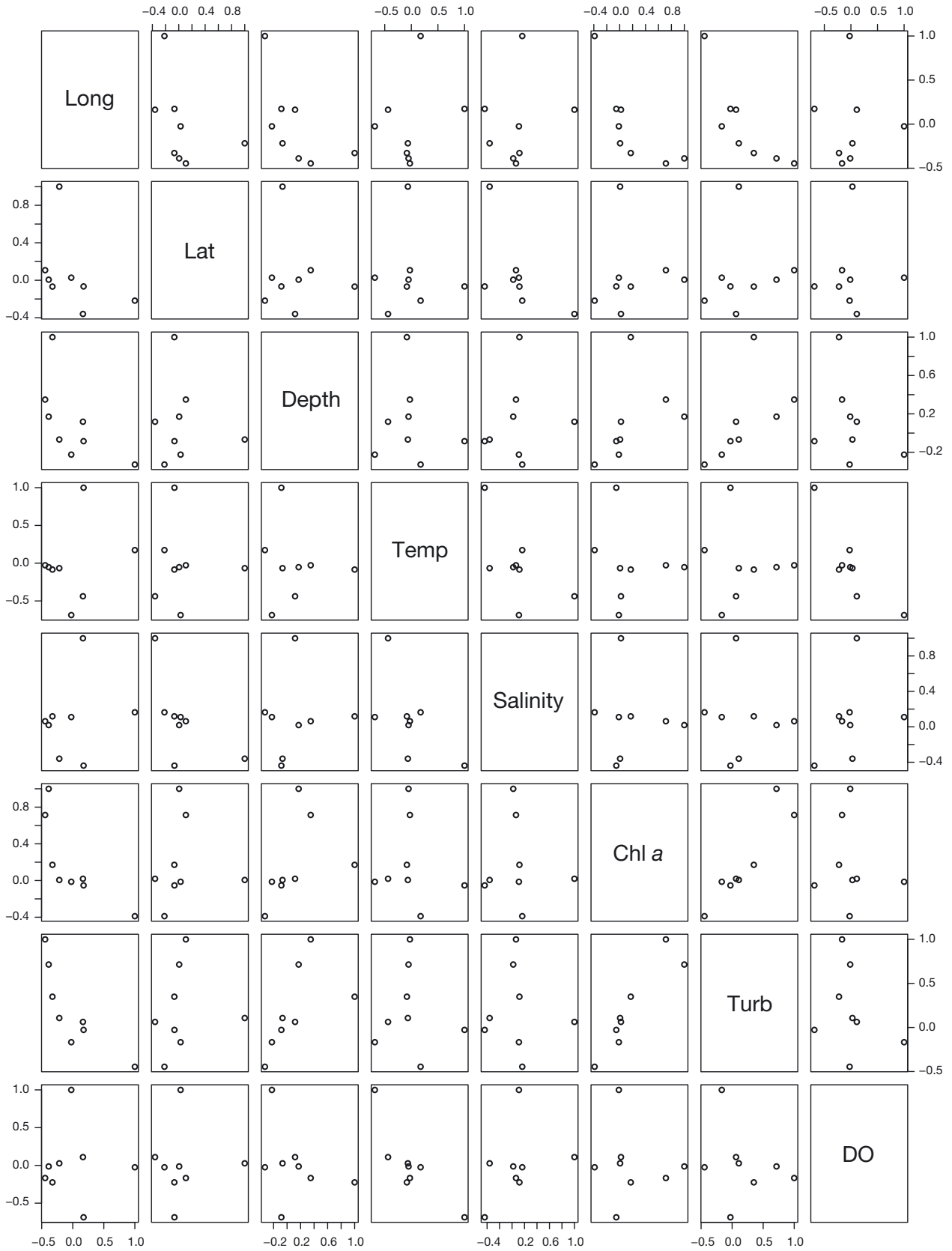| Variable	Type	VIF
Longitude (°)	Spatial	6.70
Latitude (°)	Spatial	5.58
Bottom type	Abiotic	n/a
Month	Temporal	n/a
Depth (m)	Abiotic	1.59
Temperature (°C)	Abiotic	3.94
Salinity (‰)	Abiotic	1.36
Dissolved oxygen (mg l^{-1})	Abiotic	3.51
Chlorophyll *a* (mg l^{-1})	Abiotic	1.19

Fig. 2. Spearman correlations between candidate habitat variables (categorical variables were not included). Long: longitude, Lat: latitude, Temp: temperature, Turb: turbidity

Table 3. Full and best fitting generalized additive models for the total number of reef fish, Shannon-Wiener index, and Simpson's diversity index. Relative importance of predictors for the best fitting model are listed in the last column. edf: estimated degree of freedom; AIC: Akaike's information criterion

| Response variable	Model	Formula	edf	Deviance explained (%)	AIC	Predictor's importance
Total number of reef fish (S)	Full	s(Latitude,longitude) + month + bottom + s(chl a) + s(temperature) + s(DO,depth) + s(salinity) + s(depth) + s(DO)	17.75, 2.76, 4.02, 12.04, 2.91, 1.00, 4.48	82.50	907.49	
	Best-fitting	s(Latitude,longitude) + month + bottom+ s(chl a) + s(temperature) + s(DO,depth) + s(DO)	4.09, 7.10, 5.85, 18.88, 5.41	77.50	905	0.035, 0.146, 0.001, 0.029, 0.035, 0.102, 0.012
Shannon-Wiener index (H′)	Full	s(Latitude,longitude) + month + bottom + s(depth,DO) + s(salinity) + s(DO) + s(chl a) + s(depth) + s(temperature)	2.88, 5.72, 2.14, 1.00, 3.98, 1.21, 1.00	49.50	351	
	Best-fitting	Month + bottom + s(chl a) + s(temperature)	4.68, 1.00	42.50	300.22	0.06, 0.073, 0.087, 0.086
Simpson's diversity index (D)	Full	s(Latitude, longitude) + month + bottom +s(depth, DO) + s(salinity) + s(DO) + s(chl a) + s(depth) + s(temperature)	2.88, 8.92, 1.55, 1.00, 4.87, 1.00, 1.00	46.30	113.5	
	Best-fitting	Month + bottom + s(chl a) + s(temperature)	4.84, 1.00	37.50	61.44	0.05, 0.056, 0.092, 0.074
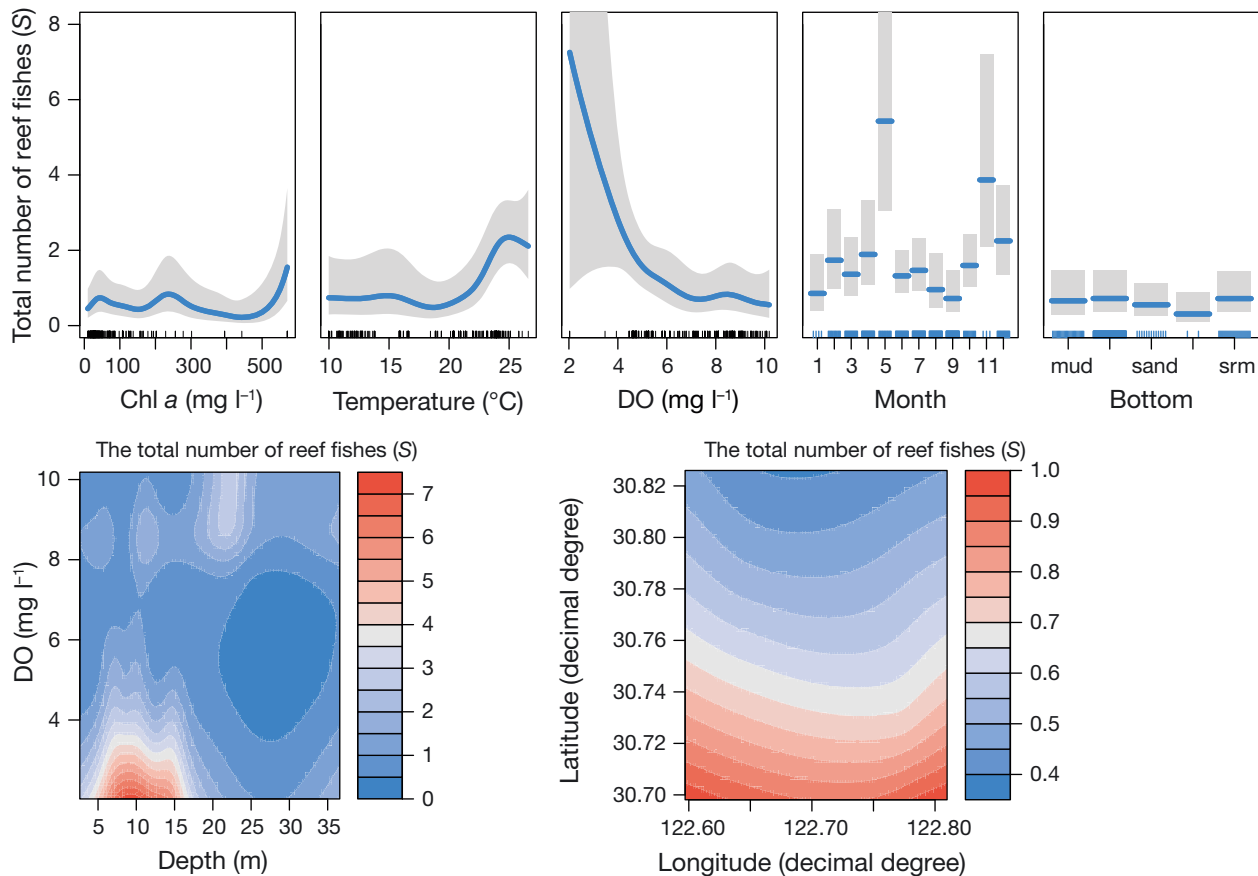
Fig. 3. Fitted back-transformed smoothing curves for significant univariate explanatory variables in the best-fitting generalized additive model explaining the total number of reef fish species. Tick marks on x-axis: relative density of observation; gray shading: 95% CIs
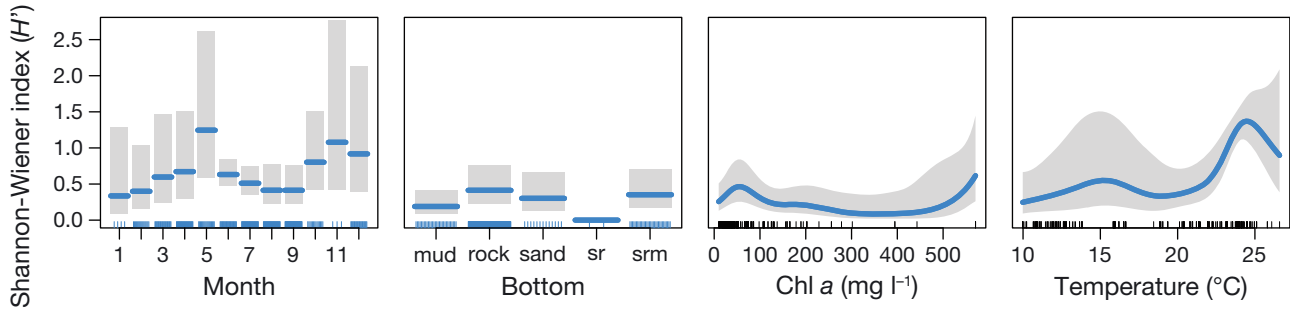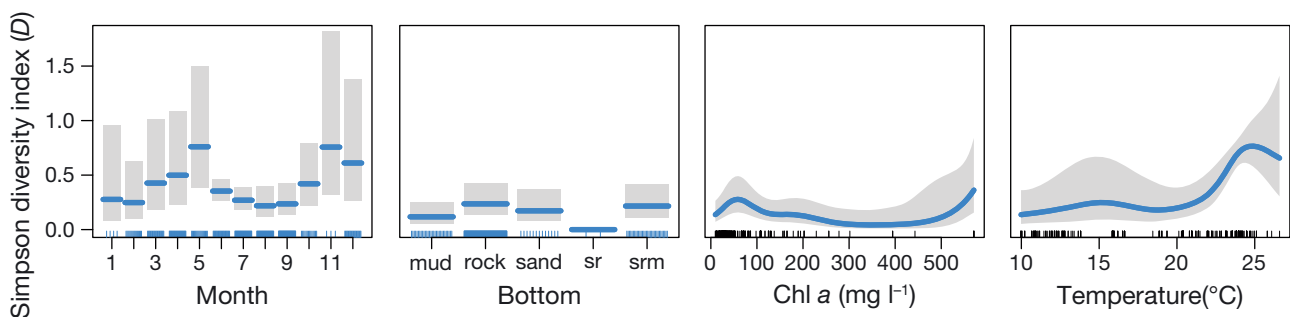
Fig. 4. Fitted back-transformed smoothing curves for significant univariate explanatory variables in the best-fitting generalized additive model explaining the Shannon-Wiener index. Tick marks on *x*-axis: relative density of observation; gray shading: 95% CIs

Fig. 5. Fitted back-transformed smoothing curves for significant univariate explanatory variables in the best-fitting generalized additive model explaining Simpson' diversity index. Tick marks on *x*-axis: relative density of observation; gray shading: 95% CIs

D were found in May and November (Figs. 4 & 5), and the highest *H*′ and *D* occurred in the rock bottom type (Figs. 4 & 5). The chl *a* response curves showed *H*′ and *D* increased with chl *a* between 0–50 and >450 mg l^{-1} and decreased with chl *a* between 50 and 450 mg l^{-1} (Figs. 4 & 5). The temperature response curves showed the highest *H*′ and *D* at 25°C (Figs. 4 & 5).

3.3. Effects of habitat variables on species composition

The MGLM results showed month, depth, rock and srm bottom type, and the interaction of longitude and latitude significantly influenced reef fish composition (Table 4). All these variables explained 18% variation in the reef fish community among our survey sites.

The biplot of residual ordination from the JSDM distinguished no obvious clusters of sites based on species composition (Fig. 6). The residual correlations (Fig. 7) showed that *H. agrammus* was positively correlated with *Pagrosomus major*; *Apogon semilineatus* was positively correlated with *S. marmoratus* and *Microcanthus strigatus*; and *S. marmoratus* was positively correlated with *M. strigatus*.

Table 4. Results of the multivariate generalized linear model. Significant variables (p < 0.05) are in **bold**. DO: dissolved oxygen; sr: sand and rock; srm: sand, rock, and mud

|	Wald value	p
(Intercept)	**4.94**	**0.01**
February	0.99	0.54
March	1.79	0.15
April	**2.36**	**0.04**
May	**2.93**	**0.02**
June	**2.94**	**0.02**
July	2.32	0.11
August	2.19	0.13
September	2.31	0.1
October	1.18	0.37
November	1.49	0.26
December	0.61	0.76
Depth	**4.71**	**0.02**
Salinity	2.95	0.53
DO	3.88	0.14
Temperature	4.1	0.08
Rock	**5.66**	**0**
Sand	2.64	0.1
sr	0.67	0.45
srm	3.62	**0.03**
Chl *a*	2.85	0.58
Longitude × Latitude	**5.03**	**0.02**
Depth × DO	4.09	0.08

Biplot of latent variable posterior medians
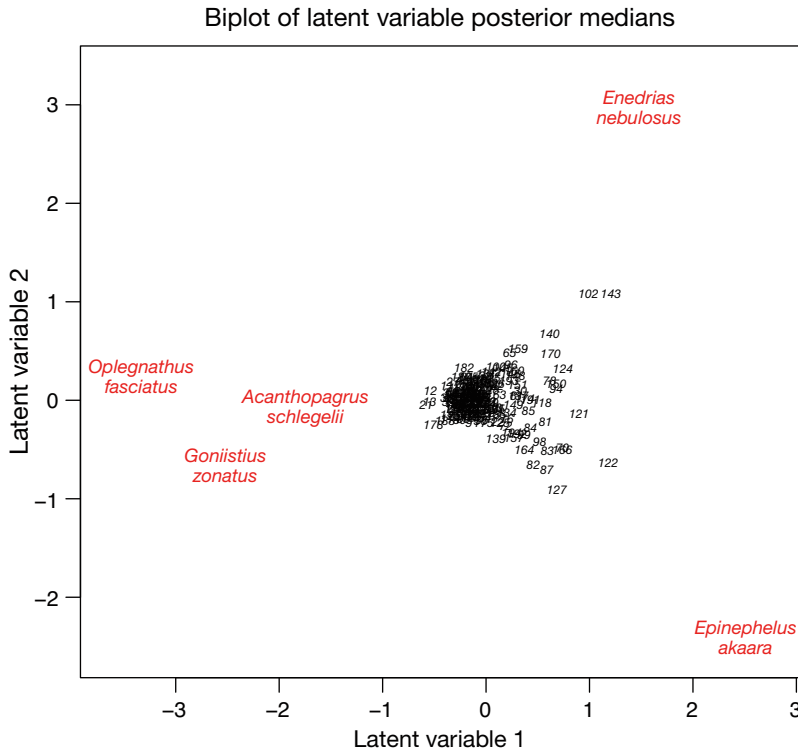
Fig. 6. Unconstrained ordination of sites and species coefficients. Sites are numbered. Only the 5 most important species are plotted (i.e. those with the strongest response to the latent variables). Species in the same direction and far from the origin are more correlated
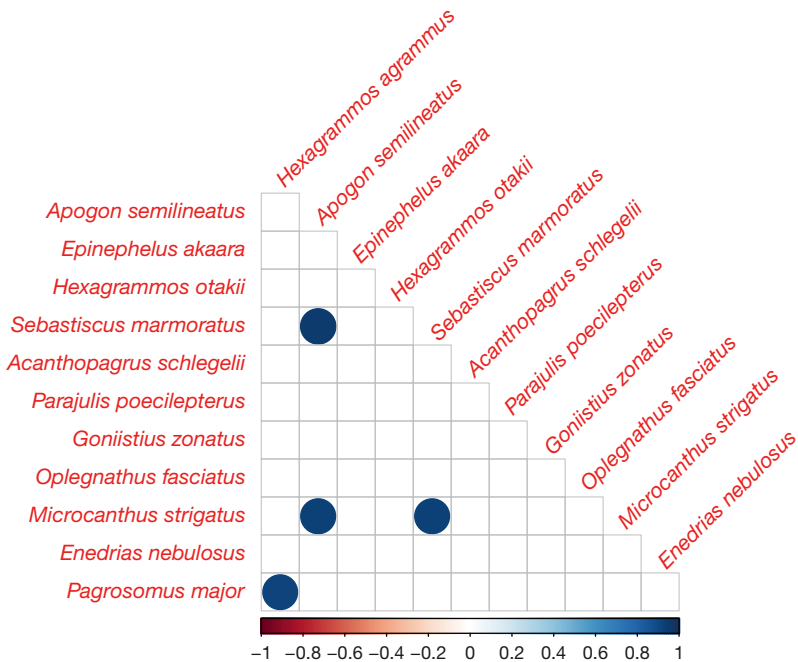

Fig. 7. Residual correlation matrix from the joint species distribution model showing significant correlations between reef fish due to their shared response to habitat variables

4. DISCUSSION

4.1. Habitat effects on reef fish diversity in Ma'an Archipelago

The reef fish diversity along the coast of Ma'an Archipelago was significantly influenced by habitat variables. Chl a, temperature, DO, month, bottom type, the interaction of longitude and latitude, and the interaction of depth and DO had significant effects on S, while month, bottom type, chl a, and temperature significantly influenced H' and D.

In general, the number of fish species increases with chl a since higher levels of chl a support more zooplankton, on which of the fish rely for food (Badsi et al. 2010). However, our GAM results showed that S decreased with chl a levels between 50–200 and 250–450 mg l^{-1}; H' and D also decreased with chl a between 50 and 450 mg l^{-1} (Figs. 3–5). Zhao et al. (2013) also found that fish diversity decreased as chl a increased in Ma'an Archipelago. The negative relationship between chl a and reef fish diversity found in this study might be influenced by $S.$ $marmoratus$, the most abundant species collected by the gillnet survey, which had a significant effect on the biodiversity indices of reef fish. Zeng et al. (2016) found that $S.$ $marmoratus$ was negatively influenced by chl a at levels >50 mg l^{-1}. All these negative correlations between chl a and fish diversity were likely the result of a lack of food for the fishes, because Ma'an Archipelago is located in an upwelling core area in an environment where zooplankton are not abundant even though the chl a is high (He et al. 1984). The highest levels of S, H', and D at 25°C were expected, since the preferred temperature of these warm water fish is higher than 20°C.

Reef fish diversity (including S, H' and D) varied among months and bottom types. Higher diversity was found in May and November along the coast of Ma'an Archipelago. This may be a re-

sult of the inshore–offshore movement of reef fish during different life stages, such as the movement of adult *S. marmoratus* to offshore areas for foraging and gestation during spring, fall, and winter; this species would not be caught by the gillnet survey conducted in the inshore areas during these times (Massutí et al. 2001, Mitamura et al. 2009, Wu et al. 2012). The higher reef fish diversity in November was likely due to the inshore movement of reef fish for recruitment, as the average total length of fish caught during November was 3.1 cm (much smaller than their mature length) (Wu et al. 2012, Ji 2014). Bottom type also significantly influenced *S*; rock bottoms were associated with the highest *S*, as reef fish prefer rocky habitats (Aburto-Oropeza & Balart 2001, Barros 2005). Kelp also provides feeding and spawning ground for most species of reef fish that inhabit rocky reefs (Zhao et al. 2013).

The interaction between depth and DO was the most important habitat variable for *S* (Table 3). The highest *S* occurred in areas with shallower depths and lower DO. A decrease in reef fish density and richness with increasing depth was also found in Kimbe Bay, Papua New Guinea (MacDonald et al. 2016). This depth-related decline was expected because the biological coverage (e.g. kelp) decreased with depth in Ma'an Archipelago (Bi et al. 2013), and shallow reef areas can act as fish nurseries (Parsons et al. 2016). The negative correlation between DO and fish diversity identified in our study was consistent with a previous study in Ma'an Archipelago (Zhao et al. 2013). These negative correlations may be caused by the large number of mussel farms operating along the coast of Ma'an Archipelago. The aquaculture infrastructure leads to lower DO in the water, but can also provide shelter for reef fish (Zhao et al. 2013).

The higher *S* observed in the southern Ma'an Archipelago was also consistent with a previous study (Zhao et al. 2013). This association was likely due to the higher kelp coverage in the southern part of the study area (Zhang et al. 2008), which provides a feeding ground for reef fish (Wang et al. 2013). A positive correlation between reef fish and macroalgae has been acknowledged in temperate rocky reefs (Parsons et al. 2016). Therefore, the kelp coverage may be a potential contributor to the southern concentration of reef fish in Ma'an Archipelago.

4.2. Habitat effects on reef fish community composition

Effects of habitat variables on species composition are important for diverse fish assemblages when multiple species respond to these factors. In this study, the JSDM indicated that there was a minor shared response to habitat variables (Fig. 7), with multiple species responding to month, depth, bottom type, and location (interaction of longitude and latitude) (Table 4). These habitat factors explained only 18% of the variation in species composition among survey sites, which indicates that the reef fish composition was weakly influenced by our candidate habitat variables. This result, combined with the residual correlation between species derived from the JSDM, suggests that the reef fish community may be influenced by other habitat factors such as habitat complexity (which can influence the habitat use of reef fish; Bassett et al. 2018, Higgins & Mehta 2018) or species interactions (which can also have an effect on community structure; Collie & DeLong 1999, Shin & Cury 2001, Collie et al. 2008). Thus, future studies examining the effects of habitat on reef fish composition should consider habitat complexity and species interactions. Additionally, the small sample size in this study may not have encompassed the entire distribution of reef fish, which resulted in no shared environmental responses. Our results suggest that the spatial scale of the reef sites examined here can be considered as one type of reef, with insufficient patterns in reef fish composition to distinguish clear reef 'zones' based on their habitat characteristics.

4.3. Management implications

One goal of EBFM is to enhance fish diversity and richness by conserving their potential habitats and other ecosystem factors (Link 2002). EBFM requires a robust understanding of community structure and the habitat associations of targeted fish species. Our habitat models identified the most significant habitat variables driving reef fish diversity and community composition, and also identified the most suitable environment for them. Although the data were based on historical sampling (in 2009), our results revealed insights into patterns of species' interactions and spatial distributions. The absence of data concerning reef fish has motivated a recent interest in examination of the historical record (Hilary 2013) because it can be useful for guiding future management decisions (Bennion et al. 2004, Stoddard et al. 2006).

MPAs are a conservation tool used worldwide, and evidence has shown that zoning has a significant influence on their effectiveness (Ban et al. 2017,
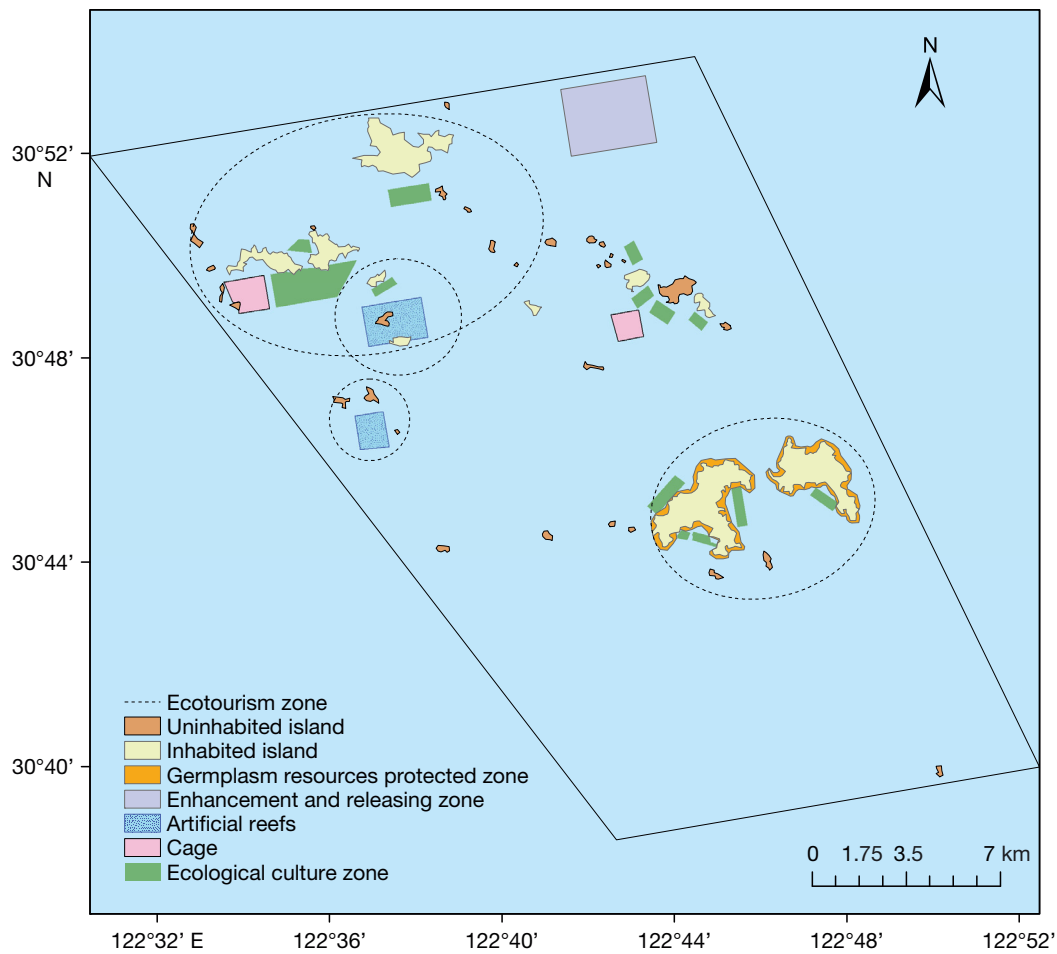
Fig. 8. Zoning of Ma'an Archipelago marine protected area

Hargreaves-Allen et al. 2017). MPA zoning is based on habitat characteristics, the distribution of the targeted species, and conservation objectives (La Mesa et al. 2010). Associations between species and habitats will provide information about the essential habitat of targeted species, which is vital for MPA zoning. There is no specific zone for reef fish in the Ma'an Archipelago MPA, as their protection was not a primary objective of this MPA (Fig. 8). Given the environmental pressures and commercial value of reef fish, conservation is needed for these species. The southern study area can be given priority as a conservation zone for reef fish because reef fish aggregate in this area (Fig. 3). In Ma'an Archipelago, the fishing season is closed from 1 May to 1 September. According to our study, to protect reef fish, fishing activities should also be restricted in November. Our findings are also valuable for artificial reef research. Artificial reefs were deployed in Ma'an Archipelago as a part of a fisheries enhancement program. However, there is considerable uncertainty about how their design and location will influence the associated fish assemblage. Our results suggest that the increased ability to host kelp and the shallow depth of artificial reefs will increase the total number of associated reef fish.

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