



RESEARCH ARTICLE

Temperate zone coastal seascapes: seascape patterning and adjacent seagrass habitat shape the distribution of rocky reef fish assemblages

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Abstract

Context Whilst the composition and arrangement of habitats within landscape mosaics are known to be important determinants of biodiversity patterns, the influence of seascape patterning and connectivity on temperate reef fish assemblages remains largely unknown.

Objectives We examined how habitat patterns at multiple spatial scales (100–1000 m) explained the abundance and diversity of temperate reef fish in a reef-seagrass dominated seascape.

Methods Fish assemblages were surveyed using remote underwater videos deployed on 22 reefs in Jervis Bay, NSW, Australia. Using full-subset GAMMs, we investigated if habitat area, edge, structural connectivity and a metric for habitat diversity (Shannon's diversity index) of reef and seagrass

can predict variations in a temperate reef fish assemblage.

Results A key finding of the study was that temperate reefs close (< 55 m) to large (> 6.25 ha) seagrass meadows contained greater abundance and diversity of fish. A consistent negative correlation was also found between reef area (> 0.01 ha) and the fish assemblage. The influence of seascape metrics on the abundance of fishes varied with functional traits (trophic groups, mobility and habitat associations). Fish-seascape relationships occurred at a range of spatial scales with no single scale being solely important for structuring the fish assemblage.

Conclusions We demonstrate that it is important not to view reef habitats in isolation, rather consider a reefs context to adjacent seagrass when predicting the distribution of temperate reef fish. This finding improves current understanding of the multi-scale factors structuring temperate reef fish assemblages and highlights the importance of reef-seagrass connectivity for the management of temperate marine ecosystems.

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Introduction

Understanding the factors governing the distributions of organisms is fundamental in ecology (Andrewartha and Birch 1954). In terrestrial systems, landscape ecology has established that the composition (number and area) and spatial configuration of habitats within landscape mosaics (i.e. landscape structure) can profoundly affect patterns of biodiversity and ecological processes (Forman and Godron 1986; Turner 2005; Wu 2006). Although these concepts have been well documented for a range of terrestrial taxa (Turner 2005), the influence of landscape structure on marine species is less understood. The techniques and concepts developed in landscape analyses are, however, being increasingly applied in the marine environment (Grober-Dunsmore et al. 2009; Boström et al. 2011). This has led to the establishment of the burgeoning field of seascape ecology that focuses on understanding the ecological consequences of spatial patterning in seascapes across multiple spatiotemporal scales (Pittman 2017).

There is a growing appreciation that seascape structure at a range of scales influences the distribution of fishes. The characteristics of focal habitats, such as habitat area and edge environment have been highlighted as predictors for the observed variation in the structure of fish assemblages (Jackson et al. 2006; Smith et al. 2008; Boström et al. 2011). For instance, positive relationships have been reported between habitat area and fish diversity and abundance on both coral and rocky reefs (Sale and Douglas 1984; Acosta and Robertson 2002; Chittaro 2002; Parsons et al. 2016), however this relationship appears to be more ambiguous in seagrass habitats (Boström et al. 2011). Recently, the structural connectivity (i.e. the area and isolation; Calabrese and Fagan 2004) of habitats has been identified as a key predictor for fish communities in tropical seascapes (Grober-Dunsmore et al. 2008; Olds et al. 2012). For example, coral reefs in tropical seascapes with large areas of adjacent seagrass habitats at scales between 100 and 1000 m have been reported to contain a higher abundance and diversity of reef fish (Kendall et al. 2005; Grober-Dunsmore et al. 2007; Olds et al. 2012; Berkström et al. 2013). There is also evidence that the structural connectivity of reefs to seagrass may be of more importance for structuring reef fish assemblages than the area of reef habitat (Grober-Dunsmore et al. 2007).

In coastal marine ecosystems, reefs are often embedded within heterogeneous seascapes dominated by seagrass, mangrove and soft sediment habitats. Many reef fish species connect multiple habitat types as they move across the seascape to access resources throughout their life-histories (Pittman and McApine 2003; Green et al. 2015; Sambrook et al. 2019). These movements occur over a range of spatial scales, from 10 to 100's of metres for foraging, diel or tidal migrations (Beets et al. 2003; Unsworth et al. 2007; Hitt et al. 2011). Movements may also span over large scales (1–100's of kilometres) for broader-scale dispersal such as ontogenetic shifts or spawning (Gillanders et al. 2003; Nagelkerken et al. 2015). Seagrass meadows are particularly important habitats for reef fishes, with many species using them as nursery areas or foraging locations (Gillanders 2006; Heck et al. 2008; Nagelkerken 2009). Consequently, the spatial context of reefs to adjacent seagrass meadows can have a major influence on resource availability and the structure of fish assemblages (Grober-Dunsmore et al. 2009).

Research into the effect of seascape patterns on reef fish has largely been focused in tropical regions containing coral reefs, mangroves and seagrass habitats (Dorenbosch et al. 2005; Grober-Dunsmore et al. 2007; Olds et al. 2012). Despite rocky reefs and seagrass being large components of temperate seascapes, few studies have explored how reef-seagrass connectivity influences temperate reef fish distributions and ecological processes (but see Ricart et al. 2018; Rees et al. 2018; Perry et al. 2018). The temperate seascape literature has instead investigated fish-habitat relationships in predominantly reef and soft sediment seascapes (Moore et al. 2011; Schultz et al. 2012; Rees et al. 2014; Ortodossi et al. 2018) or fish assemblages in vegetated habitats (Jackson et al. 2006; Green et al. 2012; Staveley et al. 2016). Furthermore, few studies in temperate seascapes have examined how the functional roles (e.g. feeding groups) and movement capabilities of fish species affect the response of reef fish to variations in seascape patterning. This information can elucidate relationships between ecological processes and seascape patterns, such as the link between trophic dynamics and the seascape (Berkström et al. 2012; Martin et al. 2018).

An initial investigation by Rees et al. (2018) suggested the area of seagrass meadows adjacent to

reefs may be a key predictor for the distribution of demersal temperate reef fish. Research from tropical seascapes have reported that metrics other than seagrass area, such as the isolation of reefs from seagrass, reef area and edge can be useful for predicting variation in fish assemblages (Boström et al. 2011; Wedding et al. 2011). Here we sought to better understand how the distribution of temperate reef fish is associated to seascape structure and structural connectivity within a seascape dominated by seagrass (*Posidonia australis*) and rocky reefs; which are both habitats considered a high priority for management. This study builds on the work of Rees et al. (2018) but incorporates higher levels of replication and a greater number of seascape metrics. We predicted that greater abundance of reef fish, individuals in functional groups and diversity would be found on reefs with low isolation to large seagrass meadows in comparison to reefs further away. Our expectations were based on the likelihood of increased resource availability and immigration rates of recruits from nursery seagrass habitats to nearby reefs. We also predicted large reefs will contain a greater abundance and diversity of fish due to species-area relationships.

Methods

Study site

This study surveyed fish on 22 shallow-water temperate reefs in Jervis Bay, a large oceanic embayment in south eastern Australia (Fig. 1) that forms the central section of the Jervis Bay Marine Park. The Jervis Bay seascape is dominated by rocky intertidal and subtidal reefs, seagrass meadows (*Posidonia australis*) and soft sediments. These habitats are replicated across the seascape and vary spatially in their size and arrangement (Fig. 1). Therefore, Jervis Bay offers an excellent opportunity to examine how seascape patterns drive the abundance and diversity of temperate reef fishes.

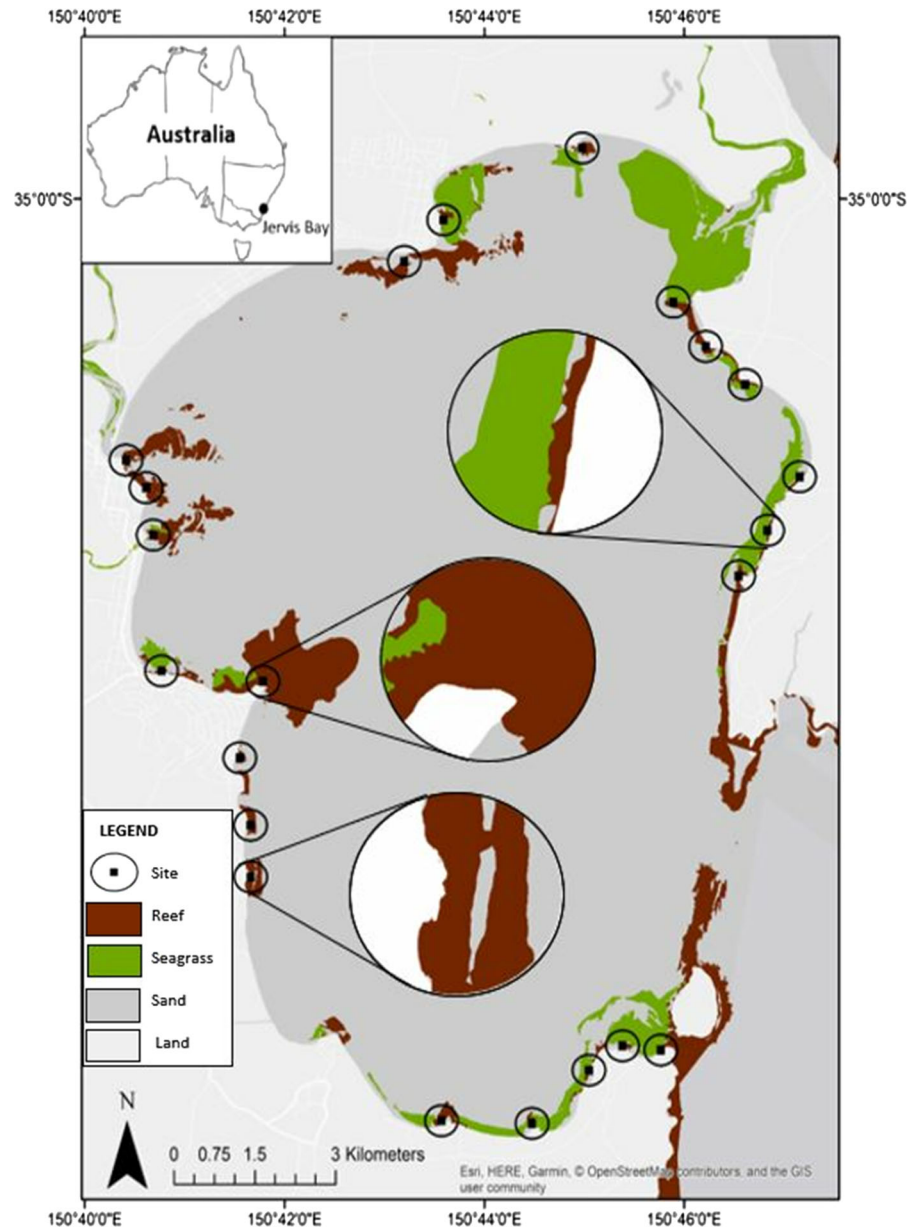
Fish surveys

Reef fish assemblages were surveyed using single camera Remote Underwater Video stations (RUVs) from March to May in 2016 within Jervis Bay (Fig. 1). RUVs consisted of a GoPro Hero 3 camera mounted to

a brick fixed onto a metal wire base (Kiggins et al. 2018). Four RUVs were deployed 60 m apart on each of the 22 reef locations (n = 88). The reef locations were separated by a minimum linear distance of 500 m which allowed us to systematically sample nearly every reef in Jervis Bay (Fig. 1). The RUVs were deployed at a depth of 2 m on subtidal reefs for a minimum of 35-min to ensure a 30-min sample of footage and a 5 min settlement period post deployment. This set time has been reported to be appropriate for both baited and unbaited underwater videos sampling fishes on temperate reefs (Bernard and Götz 2012; Harasti et al. 2015). To minimize potential spatial and temporal confounding, reefs were sampled in a haphazard order around the Bay. Sampling was conducted in daylight hours (08:00–16:00) to mitigate potential effects of crepuscular feeding behaviours (Wraith et al. 2013) and restricted to three hours either side of high tide.

Fish diversity (species richness) and abundance (MaxN) were recorded from RUV deployments. MaxN was defined as the maximum number of individuals for a given species in a single frame during the 30-min footage (Harvey et al. 2007). Total MaxN for each deployment (n = 88) was calculated by summing the MaxN values for all species. Each fish species was then placed into functional groups based on their mobility, trophic status and habitat associations. The mobility groups included three categories; (i) resident species known to be site attached to focal reefs or sedentary (10–100's of metres), (ii) mobile species which can migrate to adjacent habitat patches but show site fidelity to a focal reef or move over scales of 100's of metres to kilometres, and (iii) transient species that are highly vagile and move over the scale of 1–100's km (Grober-Dunsmore et al. 2007). If limited information was available for a species movement patterns, they were assigned a movement group based on their maximum length, as movement distances generally increase with increasing body size (Green et al. 2015). Trophic groupings were based on the predominance of prey items and included; algal invertebrate consumers, generalist carnivores, invertebrate carnivores, herbivores, macroinvertebrate carnivores and zooplanktivores (Wraith et al. 2013). Fish were also grouped on their associations to seagrass forming two categories; (1) seagrass associated taxa which have been observed on seagrass meadows as juvenile or adults, and (2) non-

Fig. 1 Location of sites within Jervis Bay and types of benthic habitats; rocky reef (brown), seagrass (green), unconsolidated soft sediment (dark grey) and land (light grey). Black circles represent the 250-m scale around each of the twenty-two reef sites where four RUVs were deployed ($n = 88$). Circular insets illustrate the variability of the seascape at the 250-m scale between three sites; from top, small reef with extensive seagrass, reef with a small seagrass meadow and reef with no seagrass present (*Note* White areas in each inset represent land)



seagrass associated taxa not known to reside on seagrass. We used information from Fish Base (Froese and Pauly 2010), the Australian Museum Fish Database (McGrourther 2001), local identification guides (Hutchins and Swainston 1986; Kuitert 1993), Bell and Westoby (1986), Ferrel et al. (1993), Hannan and Williams (1998), Jelbart et al. (2007), Curley et al. (2013), Wraith et al. (2013) and personal observations to classify species into diet or habitat association groups. In circumstances where no data were available

for a species diet or habitat associations, species were placed into the group most common for their genus. Definitions for each functional guild can be found in Online Appendix S1.

Habitat sampling

The seascape surrounding the 88 deployments were quantified from existing benthic habitat maps of Jervis Bay (source: NSW State Government, Office of

Environment and Heritage). These data were derived from swath mapping with a spatial resolution of up to two meters, Laser Airborne depth sounders (LADS) and high-resolution aerial photographs (< 1 m pixels) and ground-truthing (Williams et al. 2007; Creese et al. 2009). Seagrass was classified by its presence/absence, meaning if there was any seagrass within the seagrass polygons delineated from aerial imagery it was classified as seagrass (Williams et al. 2007; Creese et al. 2009). Habitat patterns were depicted using the patch-matrix model (Boström et al. 2011) with reef and seagrass habitats embedded in an unconsolidated sediment matrix.

Seascape patterns surrounding each deployment were quantified using spatial pattern metrics at four spatial scales; 100 m, 250 m, 500 m and 1000 m (Rees et al. 2018). Each scale was measured as radii centred over each of the 88 deployments. These scales were selected to provide sufficient data on the response of fishes to seascape patterning and incorporate the known home ranges of common reef fish in JBMP (Curley et al. 2013). Each radii or scale represented a “seascape” and each seascape (n = 88) was analysed using spatial pattern metrics quantified in ArcGIS version 10 spatial analyst extension and FRAGSTATS 4.2 spatial analysis software. The metrics selected were based on previous research showing their potential to explain variations in demersal fish assemblages and included; (1) the total area of reef and seagrass (Kendall 2005; Grober-Dunsmore et al. 2008; Rees et al. 2018), (2) the length of reef and seagrass edge (Kendall et al. 2011; Moore et al. 2011), (3) the Shannon’s diversity index, a measure of habitat diversity where 0 means only one patch is present in the seascape (no diversity) and increases with a greater number of habitat types and as the proportion of different habitat types within the seascape becomes equal (Wedding et al. 2011; Staveley et al. 2016), and (4) the edge to edge distance of focal reefs to the nearest seagrass meadow (Olds et al. 2012). This metric was calculated irrespective of spatial scale, with the distance to seagrass measured even if seagrass was not present within the 1000 m spatial scale.

Statistical analyses

Correlations between the fish assemblage and seascape metrics were examined using generalized additive mixed models (GAMMs) (Hastie and Tibshirani

1987; Hastie 2017). GAMMs account for non-linear and non-monotonic relationships between the response and explanatory variables by the addition of a smoothed function (Guisan et al. 2002). Preliminary data exploration was performed to assess for potential outliers, homogeneity and collinearity of the explanatory variables using the methods outlined in (Zuur et al. 2009). Pearson’s correlations and Variance Inflation Factor (VIF) indicated the presence of strong collinearity between explanatory variables. Spatial autocorrelation in the data was assessed using spline correlograms (Bjornstad and Falck 2001) and Morans *I*. Spatial autocorrelation was present in the raw data and was accounted for by adding ‘site’ as a random effect in the GAMM models (Online Appendix S3–S8).

To overcome issues with collinearity among explanatory variables a full subsets approach was used to construct the GAMMs (Fisher et al. 2018). The approach constructs all possible combinations of models and excludes models with collinear variables specified by a Pearson’s correlation > 0.28 (Graham 2003). This technique has great utility for ecological applications exploring the influence of environmental factors on the distribution of biota (Bond et al. 2018; Wellington et al. 2018).

The GAMMs for reef fish diversity and the abundance of macroinvertebrate consumers were fitted using a Poisson distribution. A Tweedie error distribution was fitted for all other models due to the large number of zeroes (Tweedie 1984). The maximum number of explanatory variables for each model was limited to three and all continuous variables were fitted with smoothing splines with the number of knots $k = 4$. These parameters were set to prevent overfitting and create conservative, ecologically interpretable models (Wood 2006; Fisher et al. 2018). Models were compared using Akaike information criterion corrected for small sample sizes (AICc), with the best fitting model having the lowest AICc (Burnham and Anderson 2004). When multiple candidate models occurred within ± 2 AICc of the best model, the most parsimonious model(s), that is the model(s) containing fewest predictors, was selected. The relative importance of predictor variables for the model set was determined by summing the weight of all models containing each variable (Burnham and Anderson 2004). All statistical analyses and plots were developed using the statistical computing program R

(R Core Development Team 2018) and the functions; FSSGAM 1.11 (Fisher et al. 2018), mgcv (Wood and Wood 2015), visreg (Breheny and Burchett 2013) and gamm4 (Wood and Scheipl 2014).

Results

In total, we observed 81 species comprising 40 families of fish on shallow water rocky reefs in Jervis Bay (Online Appendix S2). Reef area was the most common predictor explaining variations in the temperate reef fish assemblage (Fig. 2). Other important seascape variables included the distance to seagrass and the Shannon’s diversity index, whilst the length of seagrass edge was the poorest performing predictor (Table 1; Fig. 2). Fish responded to seascape predictors over a range of spatial scales and no specific scale appeared to be universally important (Fig. 2).

At the assemblage level, the abundance of reef fish was found to be greater on reefs close to large seagrass meadows, with declines in abundance from approximately 100 on reefs connected (i.e. 0 m) to seagrass meadows to 50 on reefs 55 m from seagrass (Table 2; Fig. 3a). Further, reef fish abundance increased from 20 to 75 as the area of seagrass adjacent reefs rose from 0 to 64 hectares (Table 2; Fig. 3a). Reef fish abundance and diversity decreased from 100 to 20 individuals and 13 to 5 species, respectively, with

increasing reef area (Table 2; Fig. 3a, b). Increases in reef fish diversity from 7 to 14 species were found as seagrass area increased from 0 to 6.25 hectares before a sharp decrease (Table 2; Fig. 3b). It is notable, that the two key predictors for reef fish diversity exhibited the strongest correlations of any response variables ($R^2 = 0.59–0.6$) (Table 2).

For the mobility groups, the abundance of resident taxa exhibited the strongest relationship with seascape patterns; revealing a negative relationship with reef edge until a threshold of 1500 m, where abundance gradually increased ($R^2 = 0.53$; Table 2; Fig. 3c). Mobile taxa were found to be more abundant on reefs close to seagrass, with declines from approximately 60 to 20 individuals when a reefs distance from seagrass increased from 0 to 55 m (Table 2; Fig. 3d). Transient taxa exhibited no relationship to seascape patterns (Table 2).

The abundance of trophic groups showed differing responses to seascape metrics (Table 1; Fig. 2). The abundance of zooplanktivores and invertebrate consumers showed positive relationships with the Shannon’s diversity index, increasing from approximately 0 to 50 and 2 to 8 respectively (Table 2; Fig. 4a, c). The Shannon’s diversity index was also important for the abundance of generalist carnivores exhibiting a negative relationship, declining from 4 to 1 individual as the Shannon’s diversity index reached 1 (Table 2; Fig. 4c). Both algal invertebrate and

Fig. 2 A heat-map highlighting the relative importance (calculated as the sum of the AIC weights/ number of models) for each explanatory variable (x-axis) against each of the fish assemblage variables (y-axis). The X label indicates the explanatory variable selected in the most parsimonious model(s) for the given response variable. See Table 1 for the acronyms used for each explanatory variable. Numbers next to acronyms represent the spatial scale. Sqrt and log denote the variable has either been square root or log transformed

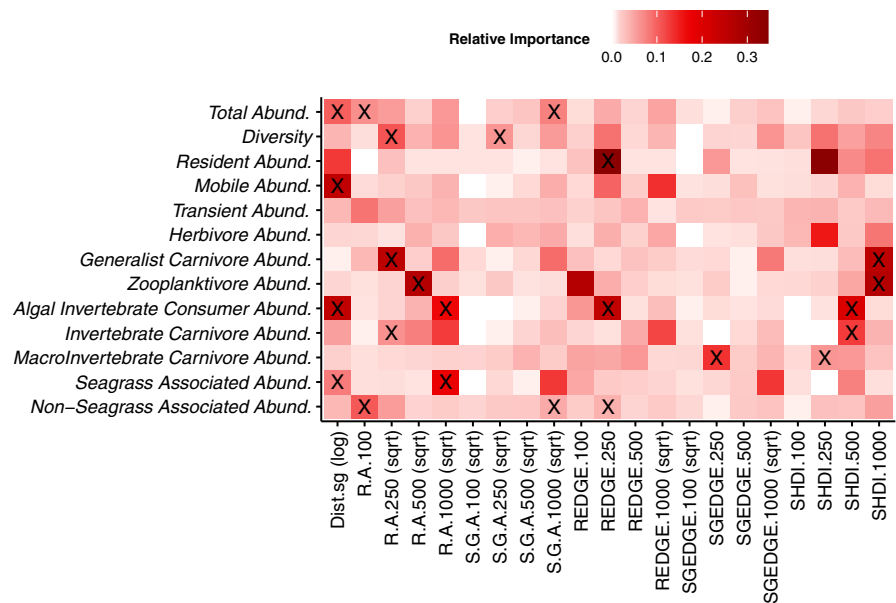


Table 1 Seascape metrics used to test for ecological patterns related to seascapes. All metrics were calculated using ArcGIS 10 and FRAGSTATS 4.2

Habitat metric	Abbreviation	Description	Spatial scale (m)	Min	Max
Distance to seagrass	Dist.sg	The edge to edge distance (metres) from the focal reef patch to the closest seagrass habitat	–	0.2	2707
Reef area	R.A	The total area (ha) of reef habitat in the seascape	100	0.0014	0.0311
			250	0.0086	0.1633
			500	0.0116	0.541
			1000	0.0176	1.41
Seagrass area	S.G.A	The total area (ha) of seagrass habitat in the seascape	100	0	1.93
			250	0	9.03
			500	0	36.48
			1000	0	74.4
Reef edge	REDGE	The sum of the perimeter (m) of all reef patches within each spatial scale	100	0	816
			250	479	2217
			500	724	5909
			1000	1774	21,424
Seagrass edge	SGEDGE	The sum of the perimeter (m) of all seagrass patches within each spatial scale	100	0	669
			250	0	1966
			500	0	4482
			1000	0	17,135
Shannon's diversity index	SHDI	An index representing the number of habitats within the seascape and their proportional distribution	100	0	1.094
			250	0.32	1.092
			500	0.332	0.979
			1000	0.232	1.079

The minimum and maximum values of each metric at the four spatial scales (radii) are also provided

macroinvertebrate carnivore abundance were found to have non-linear relationships to the Shannon's diversity index (Table 2; Figs. 4d, 5). Algal invertebrate consumer abundance increased to 18 with a Shannon's diversity index of 0.7 and then decreased (Fig. 5). Macroinvertebrate carnivore abundance decreased to 1.5 at a Shannon's diversity index of 0.6 before increasing to 2.5 individuals at an index of 0.9 and then decreasing again (Fig. 4d). The abundance of invertebrate carnivores and generalist carnivores declined from approximately 8 to 2 and 4 to 2, respectively, as reef area increased from 0.01 to 0.1225 hectares (Table 2; Fig. 4b, c). Zooplanktivore abundance had a non-linear relationship to reef area, showing an increase from approximately 10 to 30 individuals as reef size increased from 0.01 to 0.06 hectares before declining on larger reefs (Table 2; Fig. 4a). Further, algal invertebrate consumer abundance declined with reef area, with abundance decreasing from approximately 35 to 5 individuals as reef area rose from 0.04

to 1.44 hectares (Table 2; Fig. 5). The abundance of algal invertebrate consumers also declined from 50 to 20 as the distance to seagrass from reefs increased to 10 m and from 40 to 10 individuals as the length of reef edge increased from 500 to 2000 m (Table 2; Fig. 5). Lastly, macroinvertebrate consumers abundance on reefs increased from 1.5 to 3 individuals as the length of seagrass edge habitat increased from 0 to 2000 m (Table 2; Fig. 4d). There were no relationships observed between the abundance of herbivorous fishes and seascape variables (Table 2).

The abundance of both seagrass associated and non-seagrass associated taxa was found to correlate with seascape variables, although the explanatory power of models was greater for seagrass associated ($R^2 = 0.57\text{--}0.48$) than non-seagrass associated taxa ($R^2 = 0.23\text{--}0.22$) (Table 2). Reductions in the abundance of non-seagrass associated and seagrass associated taxa were found as reefs became larger, both decreasing from 40 to 10 individuals as reef size

Table 2 Candidate models correlating temperate reef fish assemblage and associated functional groups to seascape variables using full subset GAMMs

Response variable	AICc	w AIC	R ²	edf	Best model(s)
Total abundance	958.0019	0.099	0.32	12.74	Distance to seagrass (log)
	958.5831	0.074	0.31	13.57	Seagrass area 1000 m (√)
	958.8751	0.064	0.30	12.03	Reef area 100 m
Diversity	487.4258	0.107	0.59	16.90	Reef area 250 m (√)
	488.609	0.059	0.60	17.80	Seagrass area 250 m (√)
Resident taxa abundance	521.541	0.126	0.53	19.23	Reef edge 250 m
Mobile taxa abundance	840.4992	0.245	0.365	15.67	Distance to seagrass (log)
Transient taxa abundance	–	–	–	–	Null
Herbivore abundance	–	–	–	–	Null
Zooplanktivore abundance	624.4686	0.241	0.15	9.37	Reef area 500 m (√) + Shannon's diversity index 1000 m
Generalist carnivore abundance	435.8685	0.250	0.34	16.87	Reef area 250 m (√) + Shannon's diversity index 1000 m
Invertebrate carnivore abundance	481.3837	0.069	0.445	17.32	Shannon's diversity index 500 m
	481.5952	0.062	0.435	17.55	Reef area 250 m (√)
Algal invertebrate consumer abundance	637.2203	1.562	0.505	20.48	Distance to seagrass (log) + Reef edge 250 m
	637.6041	1.268	0.43	20.15	Reef edge 250 m + Shannon's diversity index 500 m
	637.9928	0	0.38	18.37	Reef area 1000 m (√) + Shannon's diversity index 500 m
Macroinvertebrate consumer abundance	288.96	0.132	0.25	6.56	Seagrass edge 250 m
	290.582	0.059	0.27	7.99	Shannon's diversity index 250 m
Seagrass associated taxa abundance	745.5288	0.175	0.48	19.14	Reef area 1000 m (√)
	747.1506	0.078	0.57	19.58	Distance to seagrass (log)
Non-seagrass associated taxa abundance	885.9278	0.104	0.215	11.17	Reef area 100 m
	887.6425	0.044	0.23	13.11	Seagrass area 1000 m (√)
	887.8791	0.039	0.23	14	Reef edge 250 m

The table includes the Akaike information criterion value for small sample sizes (AICc), AIC weights (wAIC), explained deviance (R²) and the estimated degrees of freedom (edf). All parsimonious models within ± 2 AICc of the best model are included. Square root (√) and log (log) indicate the transformation employed on the explanatory seascape variable

increased from 0.005 to 0.03 and 0.01 to 1.44 hectares respectively (Table 2; Fig. 6a, b). The abundance of non-seagrass associated taxa increased from 10 to 30 as the area of seagrass adjacent to reefs increased from 0 to 64 hectares (Table 2; Fig. 6a). Non-seagrass associated taxa also declined from 30 individuals on reefs with 500 m of reef edge to 10 on reefs with greater than 2000 m of edge environment (Table 2; Fig. 6a). Finally, the abundance of seagrass associated taxa decreased from 70 on reefs with seagrass directly adjacent to 20 on reefs 55 m from seagrass (Table 2; Fig. 6b).

Discussion

The spatial context of reefs to adjacent seagrass meadows has been reported to drive the distribution of tropical reef fish (Grober-Dunsmore et al. 2007; Olds et al. 2012; Berkström et al. 2013), but these relationships are largely unknown in temperate seascapes. A key finding from this study was that temperate reef fish assemblages had a greater (i) total abundance, (ii) abundance of mobile taxa, (iii) abundance of seagrass associated taxa, and (iv) diversity on reefs close to seagrass (< 55 m) or with large (> 6.25 ha) adjacent seagrass meadows. Additionally, reef area was found

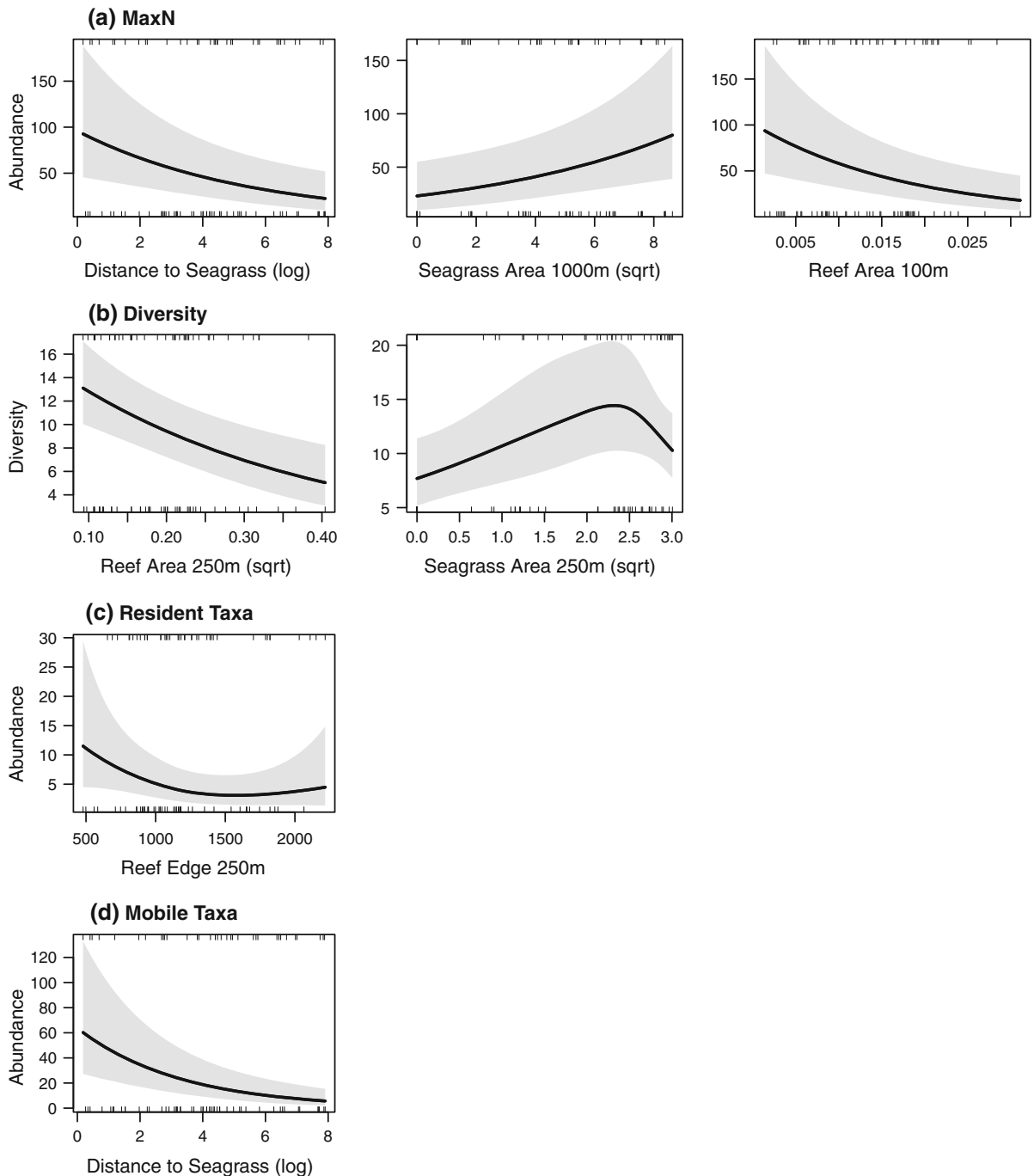


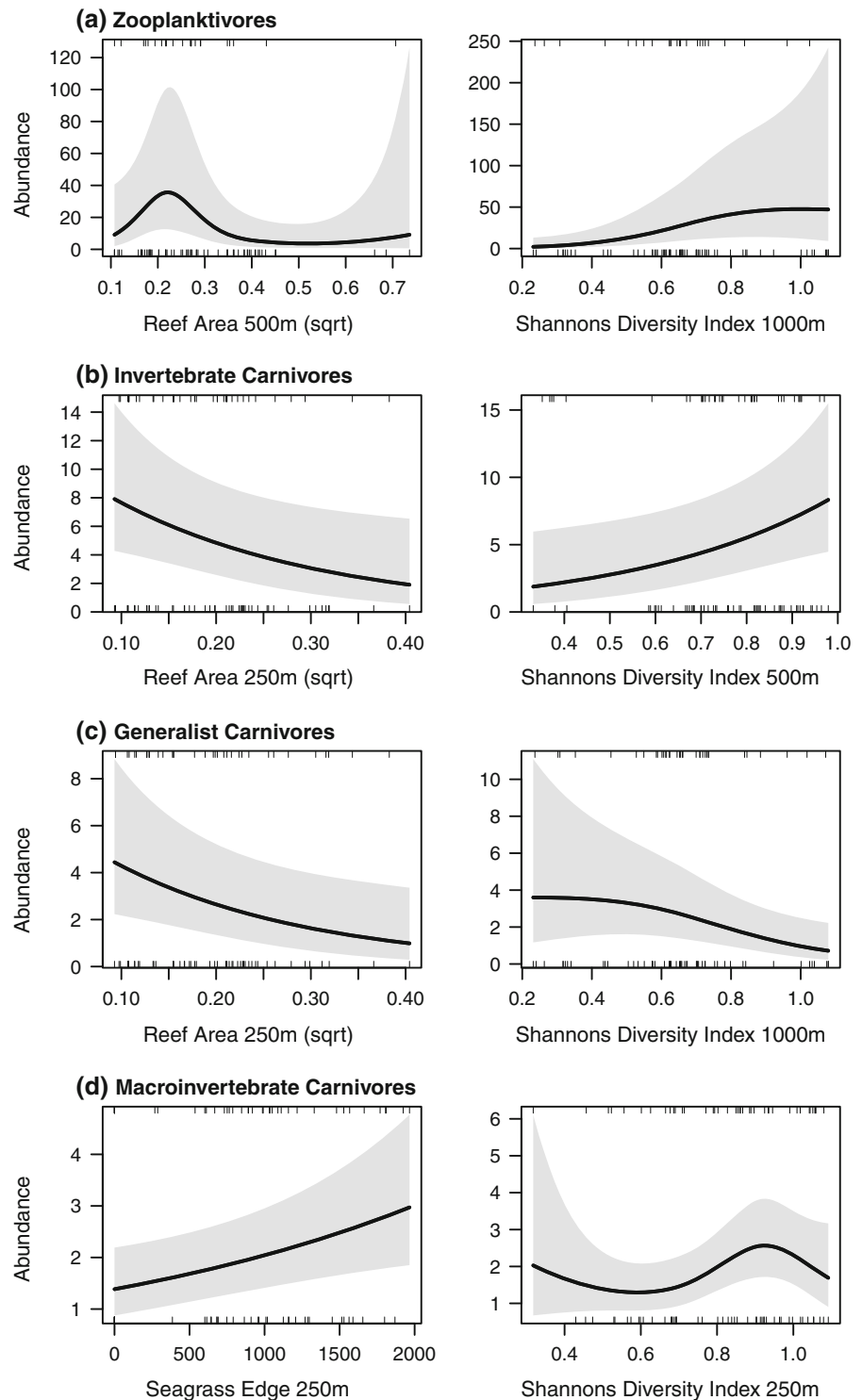
Fig. 3 Relationships for the most parsimonious models found to predict **a** reef fish abundance (MaxN), **b** species diversity, **c** abundance of resident taxa and **d** abundance of mobile taxa. Solid lines illustrate the predictions of the model and shaded

areas define the 95% confidence intervals around the fitted values. The summary of each model is provided in Table 2. Sqrt and log denote the variable has either been square root or log transformed

to have a consistent negative relationship with reef fish abundance, diversity and the abundance of several functional guilds. The importance of adjacent seagrass

meadows structuring temperate reef fish assemblages found in the current study provides robust support for the findings of Rees et al. (2018) and the notion that

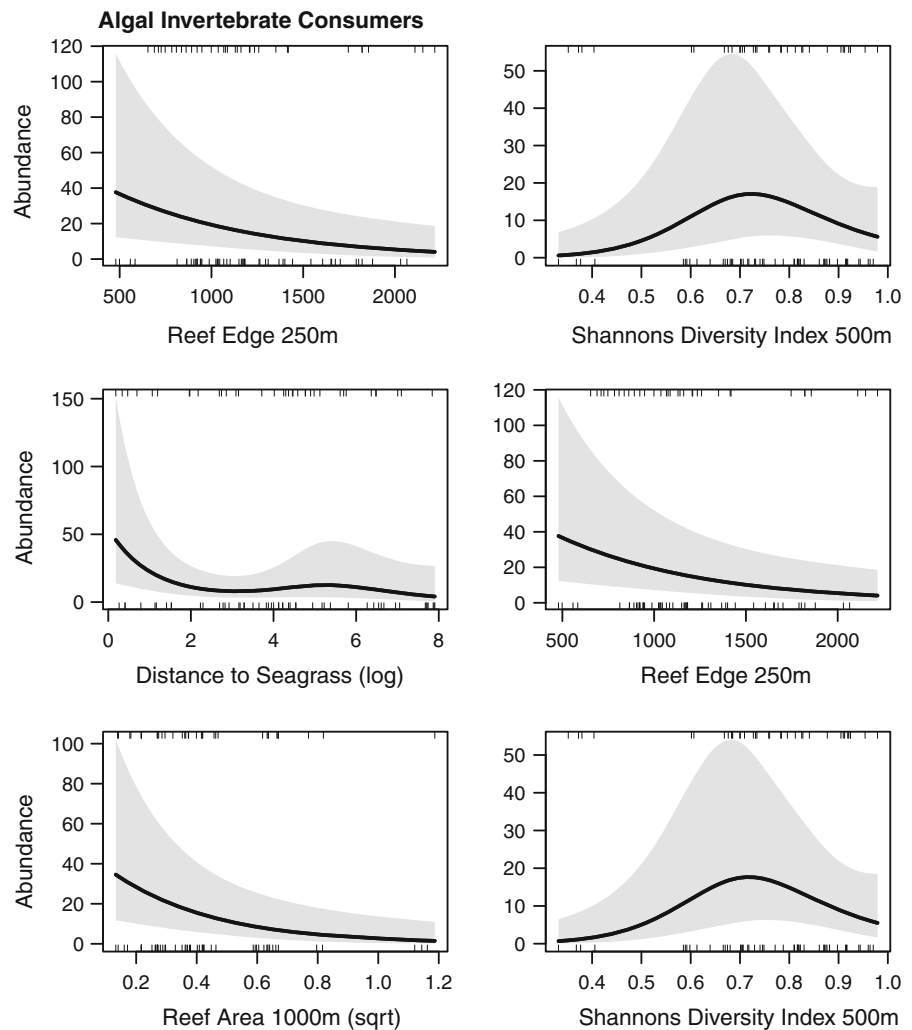
Fig. 4 Relationships for the most parsimonious models found to predict the abundance of **a** zooplanktivores, **b** invertebrate carnivores, **c** generalist carnivores and **d** macroinvertebrate carnivores. Solid lines illustrate the predictions of the model and shaded areas define the 95% confidence intervals around the fitted. The summary of each model is provided in Table 2. Sqrt and log denote the variable has been either square root or log transformed



temperate systems act in parallel fashion to seascape patterns as tropical systems (Kendall 2005; Grober-Dunsmore et al. 2007; Olds et al. 2012). Therefore, we

suggest that generalities exist for the response of reef fish to the seascape between tropical and temperate systems and that seascape patterning should be

Fig. 5 Relationships for the most parsimonious models found to predict the abundance of algal invertebrate consumers. Solid lines illustrate the predictions of the model and shaded areas define the 95% confidence intervals around the fitted values. The summary of each model is provided in Table 2. Sqrt and log denote the variable has either been square root or log transformed



considered more integral to the ecology of temperate marine systems.

The size of habitats has been commonly regarded as a key predictor for species diversity and abundance in a range of taxa, including reef fish (MacArthur and Wilson 1967; Simberloff 1976; Boström et al. 2011). The findings of the present study contradict studies exploring species-area relationships in both temperate (Parsons et al. 2016) and tropical marine biomes (Sale and Douglas 1984; Acosta and Robertson 2002; Chittaro 2002) with smaller reefs observed to have greater reef fish abundance, diversity and the abundance of several functional groups. The increased biodiversity observed on small reefs may be attributed to the smaller reefs in this study having large seagrass meadows in close proximity in comparison to the

larger reefs which were surrounded by smaller areas of seagrass. Conversely, increased biodiversity on small reefs could be driven by edge effects, as smaller habitats contain large edge to area ratios (Smith et al. 2008). There have been contradictory findings for the response of reef fish assemblages to reef edge environments with both increases and decreases in abundance and diversity reported (Acosta and Robertson 2002; Moore et al. 2011; Rees et al. 2014). Importantly, these studies were conducted on reefs with soft sediment boundaries whereas reefs in this study often bordered seagrass habitats. In comparison to a boundary between reef and unconsolidated sediment, the reef-seagrass interface offers greater structural complexity and provide extra refugial opportunities for reef fish (Heck Jnr et al. 2003;

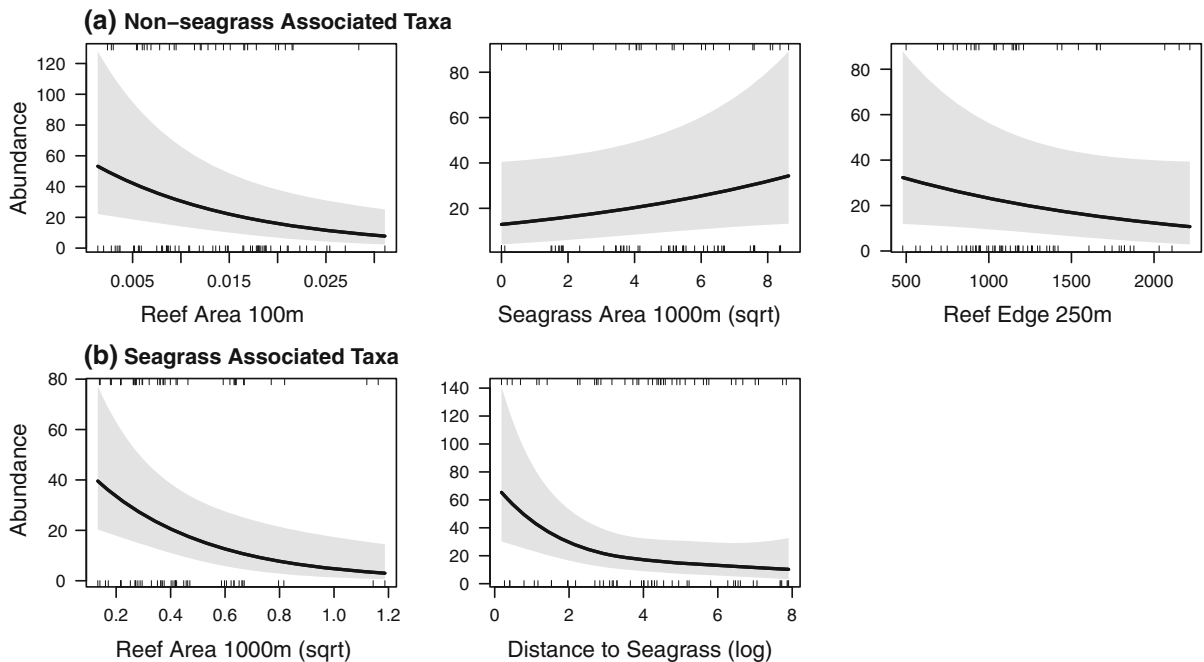


Fig. 6 Relationships for the most parsimonious models found to predict the abundance of **a** non-seagrass associated taxa and **b** seagrass associated taxa. Solid lines illustrate the predictions of the model and shaded areas define the 95% confidence

intervals around the fitted values. The summary of each model is provided in Table 2. Sqrt and log denote the variable has either been square root or log transformed

Dorenbosch et al. 2005). Further, the reef-seagrass interface may promote greater abundance and diversity because seagrass meadows may subsidize nutrients to adjacent reefs leading to a higher holding capacity (Parrish 1989; Dorenbosch et al. 2005; Valentine et al. 2007; Heck Jr et al. 2008).

Reef fish were found to be more abundant on reefs close to large seagrass meadows, highlighting the importance of structural connectivity for the composition of reef fish assemblages. Increased structural connectivity improves the ability of fishes to move between habitats and access resources causing increased diversity and abundance (i.e. landscape complementation and supplementation; Dunning et al. 1992). For instance, tracking data has revealed routine movements of temperate reef fish, such as the generalist carnivore *Acanthopagrus australis*, to adjacent seagrass meadows presumably for foraging (Taylor et al. 2018). Additionally, many of the species observed in this study are known to recruit to seagrass as juveniles and perform ontogenetic migrations to reefs once a certain age or size class is reached (Gray et al. 1996; Smith and Sinerchia 2004; Curley et al. 2013). Increased structural connectivity between reefs

and seagrass meadows likely enhances the number of recruits performing ontogenetic migrations. This is supported by research comparing the spatial partitioning of size classes in fish assemblages between habitats in tropical seascape (Dorenbosch et al. 2005, Nagelkerken et al. 2017). For example, Nagelkerken et al. (2017) reported the biomass and density of reef fish that use seagrass meadows as nurseries declined once reefs were within 4 km from seagrass and were close to zero at a distance of 14 km. Overall, our findings suggest not all reefs are equal and it is important not to view reef habitats in isolation; rather the context of a reef within the seascape must be considered when predicting the abundance and diversity of temperate reef fish.

Mobility has been suggested to be an important functional trait determining how variation in the abundances of fishes relate to seascape patterning and our findings support this notion (Caldwell and Gergel 2013). Resident fishes were more abundant on reefs with low amounts of edge environments, that is those which contain greater core reef habitat. Resident taxa have limited mobility and small home ranges and have been reported to interact with the within-patch

features of a reef (Hixon and Beets 1989; Sale 1998). Movement data of a resident species commonly observed in this study, the Eastern Blue Groper (*Achoerodus viridis*) supports our findings, with individuals avoiding the reef boundary in their daily home ranges (Lee et al. 2015). In contrast, mobile taxa were found to be more abundant on reefs close to seagrass, a pattern observed on coral reefs (Grober-Dunsmore et al. 2007). Mobile species migrating between seagrass and reefs have been reported to play an important role in transferring nutrients (Davis et al. 2014). Although speculative, the transfer of nutrients between habitats may be an indirect mechanism causing increased abundance of non-seagrass associated taxa on small reefs and reefs with large adjacent seagrass meadows. In contrast, the abundance of transient taxa was not influenced by seascape variables, a finding consistent with previous research (Grober-Dunsmore et al. 2007). Transient species, such as *Pseudocaranx georgianus* and *Pomatomus saltatrix* have large home ranges and are less likely to be associated with seascape patterns (Young et al. 1999; Fowler et al. 2018). Alternatively, it is possible that transient fish interact with seascape patterning at scales greater than those investigated in this study.

Seascape features were an important driver for the abundance of all trophic guilds excluding herbivores. Generally, fish consuming any invertebrates in their diets were more abundant in heterogeneous seascapes or on reefs close to seagrass. These fish likely forage on the substantial epibenthic and infaunal invertebrate assemblages found within seagrass meadows (Edgar and Shaw 1995; Bologna and Heck 2002; Bloomfield and Gillanders 2005). Generalist carnivores were found to be more abundant on small reefs in seascapes with less habitat diversity. This group consisted of larger, more transient species which can migrate between small habitat patches in lower diversity seascapes, comprised largely of sand. Zooplanktivores showed a small increase in abundance with reef size before decreasing in numbers on medium to large (> 0.063 hectares) reefs. Research has suggested that although smaller reefs deliver better access to zooplankton rich currents, they also have reduced refuge volumes and higher predation risk. Therefore, causing reduced numbers of zooplanktivores on both small and large reefs (Champion et al. 2015).

Our findings highlight the importance of employing a multi-scale design and considering the ecological

traits of organisms to account for how fishes respond to seascape patterning at a hierarchy of scales (Kendall et al. 2011; Ricart et al. 2018). No distinct scale appeared to be universally important, although the 250 m spatial scale had the most explanatory value. Further, the abundance and diversity of reef fish was found to be greater on reefs within 55 m of seagrass. These scales are smaller than those from studies in tropical seascapes, where positive correlations between reef fish abundance and diversity with seagrass area peak at scales between 500 and 1000 m (Grober-Dunsmore et al. 2007; Kendall et al. 2011; Berkström et al. 2012). Different species will respond to similar seascapes in different ways due to variations in life-history traits. Therefore, future studies should investigate the influence of the seascape on temperate reef fish at the species level as this information can contribute to the management of harvested species or managing multi-species assemblages across a range of scales (Grober-Dunsmore et al. 2009). In addition, future research should examine how temperate reef fish respond to both within-habitat condition (e.g. structural complexity, canopy structure) and broad-scale seascape patterns (e.g. van Lier et al. 2018).

In conclusion, this research has established that seascape patterns, especially the context of reefs to adjacent seagrass greatly influence temperate reef fish assemblages. These findings have important implications for the management of temperate coastal seascapes, such as the design of marine reserves (Pittman 2017). Specifically, the placement of reserves in areas with high structural connectivity between reef and seagrass may ensure the protection of increased levels of reef fish abundance and diversity, which is often a goal of management. Further, the global decline of seagrass meadows may not only influence seagrass fishes but also have flow on effects for the abundance and diversity of adjacent reef fish communities (Waycott et al. 2009; Nakamura 2010). The challenge for future research is testing the actual mechanisms underpinning the patterns observed in this study. This can be achieved using a variety of techniques such as telemetry, genetics and diet analyses and will allow for seascape patterning and connectivity to be better integrated into spatial conservation and management (Pittman 2017).

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