

Habitat and seascape patterns drive spatial variability in temperate fish assemblages: implications for marine protected areas

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ABSTRACT: Habitat classes are often used as surrogates to represent or capture species assemblages in the design of spatial conservation strategies, such as multi-use marine protected areas (MPAs). Little research, however, has critically evaluated how well habitat classes can reliably predict species distributions and abundances over scales relevant to spatial planning. In this study, we used hierarchical models to quantify spatial variability in demersal and mid-water fishes at multiple scales to determine whether habitat classes are appropriate surrogates for temperate fishes. Baited remote underwater video systems (BRUVS) and mid-water BRUVS were used to sample fish assemblages in Jervis Bay, NSW, Australia, over rocky reef, seagrass *Posidonia australis* and unvegetated sediment among locations (>3 km), habitat classes (~400 m) and sites within habitats (~200 m). Each habitat class displayed a distinct assemblage of demersal fish driven by many species and families showing strong habitat associations (e.g. platycephalids and labrids). In contrast, the mid-water fish assemblage and certain demersal families, such as habitat generalists (e.g. sparids), showed no differentiation among habitat class. Considerable variation in the fish assemblage was also observed among locations. Seascape connectivity explained much of this variability, as reefs surrounded by large areas of seagrass harboured a greater abundance and diversity of fishes. Overall, we provide quantitative support for the use of habitat classes as surrogates for most temperate fishes. Spatial planners, however, need to be aware of species-specific relationships with habitat and the importance of seascape patterning when using habitat-based surrogates for MPA design.

KEY WORDS: Fish habitat relationships · Landscape ecology · Temperate fish · Surrogates · Marine protected areas · Marine reserves · BRUVS · Spatial planning · Conservation

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INTRODUCTION

Coastal marine ecosystems and the habitats within them are among the most productive and ecologically important worldwide (Costanza et al. 1997, Beck et al. 2001, Waycott et al. 2009). Increasingly,

these ecosystems and their associated biodiversity are under threat from a variety of anthropogenic activities such as overfishing, habitat degradation, pollution and urbanisation (Lotze et al. 2006, Diaz & Rosenberg 2008, Barnes et al. 2013). In the last 2 decades, no-take or partially protected marine pro-

tected areas (MPAs) have been highlighted as one management approach to mitigate some of these threats to coastal biodiversity (Halpern et al. 2010). Although many studies have demonstrated positive effects of MPA implementation on marine biodiversity, meta-analyses indicate that this is not always the case (Lester et al. 2009). MPAs not achieving conservation outcomes may be a result of poor placement and design, with ineffective MPAs therefore leading to a false sense of protection (Roberts et al. 2003).

In an attempt to better place MPAs on a cost-effective but firm ecological foundation, habitat classes (e.g. rocky reef, coral reef, seagrass, sand) are increasingly being used as a surrogate to represent species distributions and guide zoning arrangements (Ward et al. 1999, Stevens & Connolly 2004, Lindsay et al. 2008, Dalleau et al. 2010, Malcolm et al. 2012, Davis et al. 2016). The premise is that different habitat classes support different biological communities, species, age classes and functional guilds. Hence, the use of a diverse range of habitat classes as a basis to design MPAs is believed to ensure adequate representation of the total biodiversity of an area (Ward et al. 1999, Roberts et al. 2003, Mumby & Hastings 2008, Dixon-Bridges et al. 2014, Rees et al. 2014). With the growing prevalence of habitat-based surrogates in marine conservation planning, it is important that we evaluate the use of this approach and, specifically, determine whether habitat classes can reliably predict species distributions and abundances over scales relevant to spatial conservation planning. Without a quantitative and detailed understanding of these patterns, habitat surrogacy may poorly represent local biodiversity and lead to undesirable planning outcomes, such as ineffective protection of biodiversity.

In temperate coastal ecosystems, the design of MPAs is often guided by the distribution of 2 key habitat types, rocky reef and seagrass, which are embedded within an unvegetated sediment matrix (Caveen et al. 2012, Fetterplace et al. 2016). Studies on temperate fish assemblages over these broad habitats have often explored spatial variability of the assemblages within a particular habitat type (Curley et al. 2002, García-Charton et al. 2004, Whitmarsh et al. 2014) or compared structurally complex habitats (e.g. rocky reef and seagrass) to adjacent unvegetated habitats with low structural complexity (Heck et al. 1989, Ferrell & Bell 1991, Connolly 1994, Gray et al. 1998, Williams & Bax 2001). In contrast, only a small number of studies have explicitly quantified differences in temperate fish assemblages among

seagrass, rocky reef and unvegetated sediment habitats (but see Jenkins & Wheatley 1998, Guidetti 2000, La Mesa et al. 2011, Davis et al. 2016, Whitfield 2017, Perry et al. 2018). This limited amount of research may be driven by a notion that spatially consistent differences exist in fish assemblages among these habitat classes. Without quantitative evidence, however, the applicability of nearshore habitat classes as surrogates for temperate fishes and MPA planning remains poorly resolved. This is despite the approach being a central tenant in the design of many MPAs worldwide (for example, comprehensive, adequate and representative principles in Australia; ANZECC TFMPA 1998a,b).

One consideration that is often overlooked in the use of habitat classes in MPA planning is the size of habitat patches and their connectivity to one another (McNeill & Fairweather 1993, Olds et al. 2016, Weeks 2017). If organisms respond to habitat at broader spatial scales, the arrangement and size of habitat patches may be an important driver of their distribution (Wiens 1989, Dunning et al. 1992). There is growing evidence that the seascape connectivity of habitat patches within coastal ecosystems plays an important role in structuring nearshore fish assemblages (Boström et al. 2011, Pittman & Brown 2011). In tropical environments, previous research has shown positive correlations between coral reef fish assemblages and the amount of adjacent seagrass and mangrove habitat within the seascape (Grober-Dunsmore et al. 2007, Olds et al. 2012, 2013). These findings have important implications for MPA planning, as they indicate that habitat alone may not be an adequate surrogate for biodiversity and consideration may need to be given to spatial heterogeneity of the surrounding seascape (Olds et al. 2016, Weeks 2017). Despite growing evidence of the importance of seascape connectivity in driving the abundance and diversity of fishes in tropical environments, very little research has employed a seascape approach to understand spatial patterns in temperate zone fishes (but see Jones & Andrew 1993, Moore et al. 2011, Staveley et al. 2017, Ricart et al. 2018). As many temperate fishes use nearshore vegetated habitats as nurseries before undertaking ontogenetic migrations to rocky reef habitat (Curley et al. 2013), there is a high likelihood that the connectivity of these patches may influence temperate fish assemblages. In the absence of research on the seascape ecology of temperate fishes, it remains unclear whether patch size and connectivity of rocky reef and vegetated habitats need to be considered in the planning of MPAs within temperate regions.

Previous research exploring fish habitat relationships in temperate coastal ecosystems have predominantly focused on linkages between demersal fish assemblages and the physical and biogenic characteristics of seafloor habitats. This is not unexpected, as demersal fish are heavily reliant on benthic habitats for food, shelter, spawning and ontogenetic migrations (Choat 1982). In contrast, much less attention has been directed towards understanding whether relationships exist between fish that occupy mid-water environments and underlying benthic habitats in coastal regions (but see Costa et al. 2014). The paucity of research is most likely due to the general assumption that mid-water fishes or fishes which are transient between demersal and mid-water environments are unlikely to be affected by benthic habitat characteristics. No studies to our knowledge, however, have explicitly tested the importance of nearshore habitat classes in structuring temperate mid-water fish assemblages and, consequently, whether habitat is an appropriate surrogate for these taxa.

In this study, we tested and quantified the variation within fish assemblages among the habitats rocky reef (sandstone), seagrass *Posidonia australis* and unvegetated sediment (sand). We sought to determine how well these habitat classes act as surrogates for fish assemblages in MPA planning. To achieve this, we employed a hierarchical sampling design to explore spatial variation in nearshore fish assemblages over 3 scales: (1) among locations (3–6 km), (2) among habitats within locations (rocky reef, seagrass and unvegetated sediment [~ 400 m]), and (3) between sites within habitats (~ 200 m). We predicted that there would be consistent differences in the demersal fish assemblages among habitat classes across replicated experimental units (i.e. locations). Consequently, we predicted that habitat class would be a suitable surrogate for conservation planning of demersal fishes. In contrast, we predicted that mid-water fish assemblages would show no affinity to habitat class and, therefore, that habitat class was an inappropriate surrogate for this assemblage. Finally, we assessed the explanatory value of the seascape attributes of each rocky reef site.

MATERIALS AND METHODS

This study was done in Jervis Bay, a temperate embayment in southeastern Australia, between December 2013 and March 2014. The bay forms part of the central section of the Jervis Bay Marine Park

(JBMP) (Fig. 1) and also contains waters under Commonwealth jurisdiction (Booderee National Park). The JBMP covers an area of 215 km² comprising a network of no-take sanctuary zones, habitat protection zones and general use zones. The embayment contains 3 main benthic habitat types: rocky reef, unvegetated sediments and extensive near-pristine beds of the seagrass *Posidonia australis* (Marine Parks Authority 2008). These habitat types are replicated throughout the bay (Fig. 1); therefore, the JBMP provides an ideal system to test habitat- and seascape-related questions about conservation management.

Fish assemblages were surveyed using mid-water baited remote underwater video systems (mBRUVS) as well as demersal baited remote underwater video systems (BRUVS) positioned on the seafloor. mBRUVS were constructed following the design of Heagney et al. (2007) and Rees et al. (2015) but adapted so that the camera was positioned 0.5 m below the surface of the water. Demersal BRUVS were fitted with mats to reduce macroalgae and seagrass restricting the field of view. Mats consisted of 1.5 × 2 m plastic mesh supported on a PVC frame. Both mBRUVS and BRUVS contained Canon HG21 video cameras fitted with a 0.7× wide-angle lens within underwater camera housings constructed by SeaGIS. Fish surveys were conducted at 2 sites sepa-

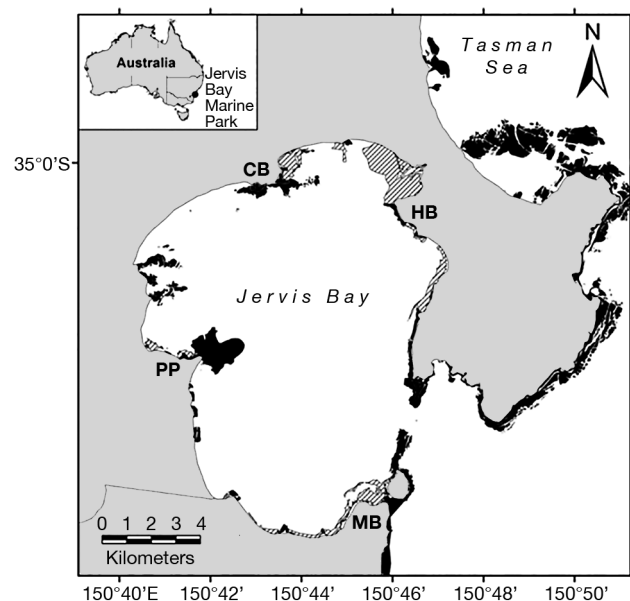


Fig. 1. Habitat map of the Jervis Bay Marine Park. Dark areas indicate rocky reef, cross-hatched areas the seagrass *Posidonia australis* and white areas unvegetated sediment. The 4 survey locations indicated are Murrays Beach (MB), Plantation Point (PP), Callala Bay (CB) and Hare Bay (HB)

rated by 400 m on each of the 3 habitat types (rocky reef, unvegetated sediment and seagrass) across 4 locations (Murrays Beach, Callala Bay, Plantation Point and Hare Bay) within the JBMP. Locations were separated by between 3 and 6 km (Fig. 1). Within each habitat at each site, 2 mBRUVS and 2 BRUVS ($n = 4$ per habitat per location) were deployed at least 200 m apart along the 5 m depth contour. Prior to deploying the systems, 500 g of crushed defrosted sardines *Sardinops sagax* were placed in each bait bag (Wraith et al. 2013). The bait was replenished prior to each redeployment. Both mBRUVS and BRUVS were deployed for 35 min to achieve a 30 min recording. Previous studies have indicated that a 30 min deployment provides a representative sample of temperate demersal fish assemblages (Harasti et al. 2015). Although untested, we assumed that a 30 min deployment would provide a representative sample of the mid-water fish assemblage. It is worth noting, however, that longer soak times may be optimal for surveying mid-water assemblages using mBRUVS (see Santana-Garcon et al. 2014)

Footage from mBRUVs and BRUVs was analysed in the laboratory using EventMeasure software (SeaGIS). For each deployment, species richness and relative abundance (MaxN) were recorded. Species richness was the number of species of fish observed during the sample. The relative abundance of fishes, MaxN, was the maximum number of individuals of 1 species viewed at any 1 time during the sample (Willis & Babcock 2000, Cappelletti et al. 2003). MaxN values for individual species were then summed to generate the overall relative abundance for each sample. Two species, *Trachurus novaezelandiae* and *Nelussetta ayraudi*, dominated both the mid-water and demersal fish assemblage. A separate response measure of total fish abundance was analysed with these species removed.

Hypotheses about multivariate fish assemblages were tested using a 3-factor PERMANOVA (PRIMER Software, Plymouth Marine Laboratories) on Bray-Curtis dissimilarity values calculated from 4th root transformed data for demersal fishes and untransformed data for mid-water fishes (Anderson 2001, Anderson et al. 2008, Clarke & Gorley 2006). A transformation was applied to the demersal fish data to reduce the influence of the numerically dominant species *T. novaezelandiae* and *N. ayraudi*. The factors were location (4 levels and random), habitat (3 levels and fixed; rocky reef, unvegetated sediment and seagrass) and site (2 levels nested within the Location \times Habitat interaction and ran-

dom). Non-metric multidimensional scaling was used to generate 2-dimensional ordinations to illustrate patterns in mid-water and demersal fish assemblages. Species richness, total abundance and the abundance of numerically dominant families as well as species from those families were analysed separately using a 3-factor ANOVA in the R statistical platform (R Core Team 2017) using the GAD package (Sandrini-Neto & Camargo 2014). Numerically dominant species and families were those that were observed in high abundance across all samples or within certain habitats (i.e. *Platycephalus* spp. on unvegetated sediment and *Hyporhamphus australis* in the mid-water environment). These analyses used the same factors as described for the multivariate analyses. Prior to analysis, data were visually assessed for normality, and Cochran's *C*-test was used to test for departures from homogeneity of variances. If significant heterogeneity was present, the natural logarithm of the data or a square root transformation was performed. Following transformation, the abundances of *Ophthalmolepis lineolatus*, *Achoerodus viridis* and *Platycephalus* spp. were still heterogeneous, but as ANOVA is robust to heterogeneity in balanced experimental designs with large numbers of samples (Underwood 1997), these analyses were still performed. Student-Newman-Keuls tests were used for post hoc comparisons. Following ANOVA, post hoc pooling of the Location \times Habitat interaction was performed if $p > 0.25$ to increase the power of the main tests (Underwood 1997). To determine whether habitat classes were adequate surrogates, final models had to fulfill one of 2 criteria: (1) the factor habitat had to be a significant main effect with consistent differences among habitats across locations (i.e. no interaction between Location \times Habitat), or (2) if there was a significant Location \times Habitat interaction, similar patterns among habitats had to be observed at most locations (e.g. the rank order of habitats was consistent across locations although the absolute differences may vary).

To examine the relationship between seascape connectivity of seagrass and rocky reef habitats on nearshore reef fish assemblages, the area of seagrass around each rocky reef site was estimated from habitat maps using Focal Statistics in ArcGIS version 10. Habitat maps of the JBMP's subtidal features were derived from swath bathymetry, a laser airborne depth sounder and a Leica ADS40 aerial digital sensor (Williams et al. 2007, Creese et al. 2009). Seagrass area was quantified at each rocky reef BRUV deployment at a variety of scales: 200, 500, 1000 and 1500 m

radii. To determine the most appropriate spatial scale for each response variable, a series of simple linear regressions was constructed. Response variables included the abundance and cumulative richness (total number of species observed among replicates within a site and habitat) of demersal and mid-water fishes recorded on rocky reef. We also examined the relationship between the abundance of sparids and surrounding seagrass area. As the abundance of mid-water fishes did not conform to normality, generalised linear models with a negative binomial error structure were used over simple linear regressions. All analyses were done in R (R Core Team 2017). The MASS package (Venables & Ripley 2002) was used for generalised linear models. Models were ranked using Akaike's information criterion corrected for small sample sizes (AICc) and AICc weights (Table S1 in the Supplement at www.int-res.com/articles/suppl/m607p171_supp.pdf) using the MuMIn package (Bartoń 2015). Models with the lowest AICc were considered to best explain the variation for each response variable (Burnham & Anderson 2002), Wagenmakers & Farrell 2004). There were occasions when the best-fitting model was within 2 AICc points of another, indicating a plausible alternative scale of seagrass area (Table S1). As all models within 2 AICc points displayed similar positive relationships between response measures and seagrass area (Fig. S1 in the Supplement), we chose to present models with the lowest AICc.

RESULTS

A total of 8900 fish, comprising 71 species from 41 families, were observed during the 96 video deployments. Of the total number of individuals recorded, 50% were observed over rocky reef, 29% over seagrass and 21% over unvegetated sediment. Of the total number of species recorded, 57 species were observed over rocky reef habitat, 37 species over seagrass and 21 species on unvegetated sediment. Only 2 species, *Hyporhamphus australis* and *Seriola rivoliana*, were recorded exclusively in the mid-water environment.

Habitat associations of demersal fishes

Habitat class had a clear effect on the demersal fish assemblage, with a distinct fish assemblage for each habitat (Fig. 2a, Table 1). Differences in the diversity of demersal fishes were observed among habitat classes, but patterns were dependent on location (Table 2a). With the exception of Callala Bay, all locations displayed a higher diversity of demersal fishes on rocky reef, with no difference between seagrass and unvegetated sediment (Fig. 3a; Table 2a). The diversity of demersal fishes recorded on rocky reef also varied among locations, with Murrays Beach and Hare Bay recording a greater diversity compared to Callala Bay and Plantation Point (Fig. 3a). Rocky reef and sea-

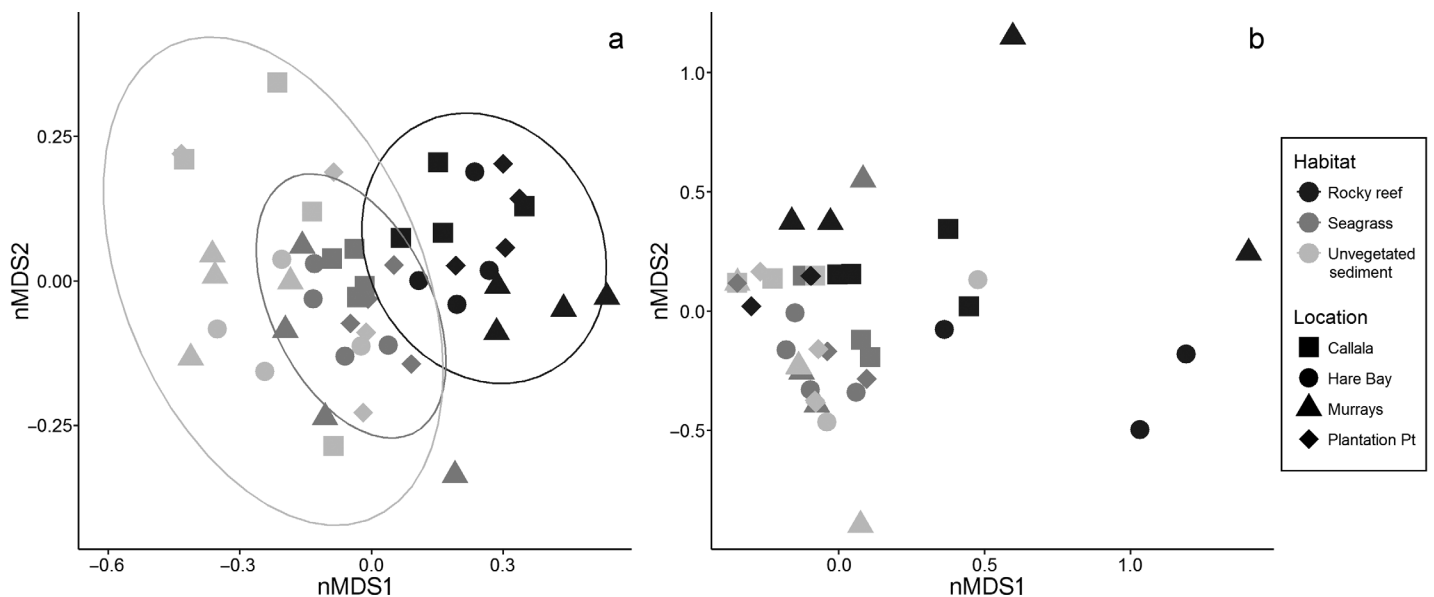


Fig. 2. Non-metric multidimensional scaling (nMDS) ordinations comparing (a) demersal and (b) mid-water fish assemblages among habitats and locations. Points closer together in ordination space represent replicates with more similar species compositions. Pt: Point

Table 1. Permutational MANOVA of fish assemblages among habitat classes and locations. Habitat (H) is a fixed factor with 3 levels: rocky reef (RR), seagrass (SG) and unvegetated sediment (US). Location (L) is a random factor with 4 levels: Callala Bay, Hare Bay, Murrays Beach and Plantation Point. Site (Si) is a random factor nested within the H × L interaction. Demersal fish data were 4th root transformed, while mid-water fish data were untransformed. Values in **bold** indicate statistical significance at $\alpha = 0.05$

| Source | df | MS | Pseudo- <i>F</i> | p (perm) |
|--------------------------------------|----|---------|------------------|--------------|
| (a) Demersal | | | | |
| H | 2 | 20342.1 | 10.12 | 0.001 |
| L | 3 | 4028.8 | 2.425 | 0.002 |
| H × L | 6 | 2009.2 | 1.209 | 0.205 |
| Si(H × L) | 12 | 1661.3 | 1.366 | 0.032 |
| Residual | 24 | 1216.4 | | |
| Pairwise comparison: RR ≠ SG ≠ US | | | | |
| (b) Mid-water | | | | |
| H | 2 | 7529.6 | 1.89 | 0.085 |
| L | 3 | 6968.2 | 2.10 | 0.029 |
| H × L | 6 | 4002.9 | 1.22 | 0.243 |
| Si(H × L) | 9 | 3207.1 | 1.39 | 0.065 |
| Residual | 16 | 2311.2 | | |

grass habitat displayed a greater abundance of demersal fishes compared to unvegetated sediment (Fig. 3c, Table 2b). This result, however, was driven by 2 numerically dominant species, *Trachurus novaezelandiae* and *Nelusetta ayraudi*. Excluding these species from the analysis, the abundance of demersal fishes was greatest on rocky reef, with no difference between seagrass and unvegetated sediment (Fig. 3e, Table 2c). There were clear differences in the abundance of demersal fishes observed on rocky reef habitat among locations (Fig. 3e). Rocky reef at Murrays Beach displayed the greatest abundance of demersal fishes followed by Hare Bay, Callala Bay, then Plantation Point (Fig. 3e).

Many species contributed to the differences in the fish assemblage and total abundance among habitats. Scorpidids and labrids were clearly reef associated, as they were observed solely on rocky reef habitat at each location (Figs. 4e & 5b, Tables 3c & 4b). Two common labrids, *Achoerodus viridis* and *Ophthalmolepis lineolatus*, had greater abundances on rocky reef compared to other habitats at all locations (Fig. 5c,d, Table 4c,d). Similarly, the abundance of *T. novaezelandiae* in the demersal environment was greater on rocky reef and seagrass compared to unvegetated sediment (Fig. 4c, Table 3b). In contrast, individuals from the genus *Platycephalus* were only observed on unvegetated sediment (Fig. 5e, Table 4e). The eastern fiddler ray *Trygonorrhina fas-*

ciata was equally abundant on seagrass and unvegetated sediment but displayed much lower abundances on rocky reef (Fig. 5f, Table 4f). The numerically dominant *N. ayraudi* displayed considerable variability among habitats, indicating no preference for any habitat class (Fig. 4a, Table 3a). Similarly, the abundance of individuals from the commercially important Sparidae showed no clear pattern with habitat class; however, there were differences observed at some locations (Fig. 5a, Table 4a). Despite substantial variability in the abundance of sparids between seagrass and unvegetated sediment across locations, sparids were consistently recorded over rocky reef habitat. Their abundance on rocky reef clearly varied among locations, however, with greater abundances observed at Murrays Beach and Hare Bay compared to Callala Bay and Plantation Point (Fig. 5a).

Habitat associations of mid-water fishes

Unlike demersal fishes, habitat class did not influence the diversity or assemblage structure of mid-water fishes (Figs. 2b & 3b, Tables 1b & 2a). Habitat class also had no effect on the total abundance of mid-water fishes. This outcome was independent of whether the numerically dominant *T. novaezelandiae* and *N. ayraudi* were included or excluded from the data set (Fig. 3d,f, Table 2b,c). Reflecting patterns observed in the demersal fish assemblage, the abundance and diversity of mid-water fishes recorded on rocky reef were greatest at Murrays Beach and Hare Bay compared to Callala Bay and Plantation Point (Fig. 3b,f). The abundance of *T. novaezelandiae* was highly variable and showed no clear pattern with habitat. Low abundances of this schooling species were recorded at all locations except Callala Bay, where there was a substantially higher abundance recorded on rocky reef compared to the other habitats (Fig. 4d, Table 3b). Habitat had no effect on the abundance of *H. australis*, a species which was only recorded in the mid-water environment (Fig. 4f, Table 3d).

Seascape effects

The abundance and diversity of fish observed on rocky reef habitat displayed substantial variability among locations (Fig. 3). This suggested that broader-scale habitat patterns within the seascape may be influencing the spatial variability of fishes on

Table 2. ANOVA of demersal and mid-water fish assemblages among habitat classes and locations. Habitat (H) is a fixed factor with 3 levels: rocky reef (RR), seagrass (SG) and unvegetated sediment (US). Location (L) is a random factor with 4 levels: Callala Bay (CB), Hare Bay (HB), Murrays Beach (MB) and Plantation Point (PP). Site (Si) is a random factor nested within the H × L interaction. Values in **bold** indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to as 1-pooled data and 2-pooled data. NS: not significant. Results of Student-Newman-Keuls tests are presented below analyses

| | Demersal | | | | Mid-water | | | |
|--|--|--------|-------|------------------|---|----------|------|-------|
| | df | MS | F | p | df | MS | F | p |
| (a) Species richness | | | | | | | | |
| H | 2 | 441.75 | 16.45 | 0.004 | 2 | 0.49 | 1.97 | 0.22 |
| L | 3 | 21.47 | 3.13 | 0.037 | 3 | 0.05 | 0.18 | 0.90 |
| H × L | 6 | 26.86 | 3.92 | 0.004 | 6 | 0.25 | 0.79 | 0.60 |
| Si(H × L) | 12 | 7.44 | 1.09 | 0.401 | 12 | 0.31 | 1.61 | 0.16 |
| Residual | 24 | 6.56 | | | 24 | 0.20 | | |
| Total | 47 | | | | 47 | | | |
| 1-pooled data | 36 | 6.85 | | | | | | |
| Pairwise comparison: | CB: US < SG = RR, HB: US = SG < RR, MB: US = SG < RR, PP: US < SG < RR Cochran's C (NS): 0.26 | | | | Cochran's C (NS): 0.34, ln(x + 1) | | | |
| (b) Total abundance | | | | | | | | |
| H | 2 | 13.06 | 10.43 | 0.011 | 2 | 49582.31 | 2.06 | 0.21 |
| L | 3 | 0.54 | 0.69 | 0.561 | 3 | 9178.41 | 0.38 | 0.77 |
| H × L | 6 | 1.25 | 1.62 | 0.170 | 6 | 24046.70 | 1.72 | 0.15 |
| Si(H × L) | 12 | 0.44 | 0.57 | 0.853 | 12 | 4120.31 | 0.29 | 0.99 |
| Residual | 24 | 0.94 | | | 24 | 18960.19 | | |
| Total | 47 | | | | 47 | | | |
| Pairwise comparison: | US < SG = RR Cochran's C (NS) 0.27, ln(x) | | | | Cochran's C (NS): 0.27 | | | |
| (c) Total abundance minus dominant taxa | | | | | | | | |
| H | 2 | 10.54 | 29.70 | <0.001 | 2 | 4.38 | 1.84 | 0.238 |
| L | 3 | 1.26 | 3.17 | 0.034 | 3 | 6.04 | 2.54 | 0.153 |
| H × L | 6 | 0.40 | 1.13 | 0.363 | 6 | 2.38 | 2.17 | 0.069 |
| Si(H × L) | 12 | 0.31 | 0.88 | 0.576 | 12 | 1.03 | 0.94 | 0.520 |
| Residual | 24 | | | | 24 | 1.13 | | |
| Total | 47 | | | | 47 | | | |
| 1-pooled data | 36 | 0.35 | | | 36 | 1.10 | | |
| 2-pooled data | 42 | 0.35 | | | | | | |
| Pairwise comparison: | US = SG < RR Cochran's C (NS): 0.25, ln(x + 1) | | | | Cochran's C (p < 0.01): 0.44, ln(x + 1) | | | |

this habitat type. Quantifying the seascape composition of each rocky reef site at multiple spatial scales, best-fitting models confirmed clear positive relationships between response measures and the surrounding area of seagrass habitat (Table 5, Table S1). The area of seagrass within 500 m of each reef was the best predictor of the abundance of demersal fishes ($R^2 = 0.67$) and their cumulative richness ($R^2 = 0.29$), although the latter relationship was not statistically significant (Fig. 6, Table 5). The abundance of mid-water fishes was best explained by the area of seagrass within 1000 m ($R^2 = 0.91$), while their cumulative diversity was best explained by the area of seagrass within 1500 m of each site ($R^2 = 0.66$) (Fig. 6, Table 5). The abundance of sparids was best explained by the area of seagrass within 1500 m of each rocky reef site ($R^2 = 0.45$) (Fig. 6, Table 5).

DISCUSSION

Habitat classes (e.g. rocky reef, seagrass, mangroves, unvegetated sediments) are increasingly used as surrogates of biodiversity, thereby guiding the design of MPAs (Jordan et al. 2005, Dalleau et al. 2010, Malcolm et al. 2012). This approach is based on the notion that different habitat classes support different biological communities, species, age classes and functional guilds. By representing habitat diversity within a protected area, it is assumed that biodiversity and ecological processes will also be captured. Our study provided support for this notion, with evidence that mapped habitat classes strongly influence demersal fish assemblages and thus may act as simple surrogates for capturing the diversity and abundance of demersal fishes. There were some

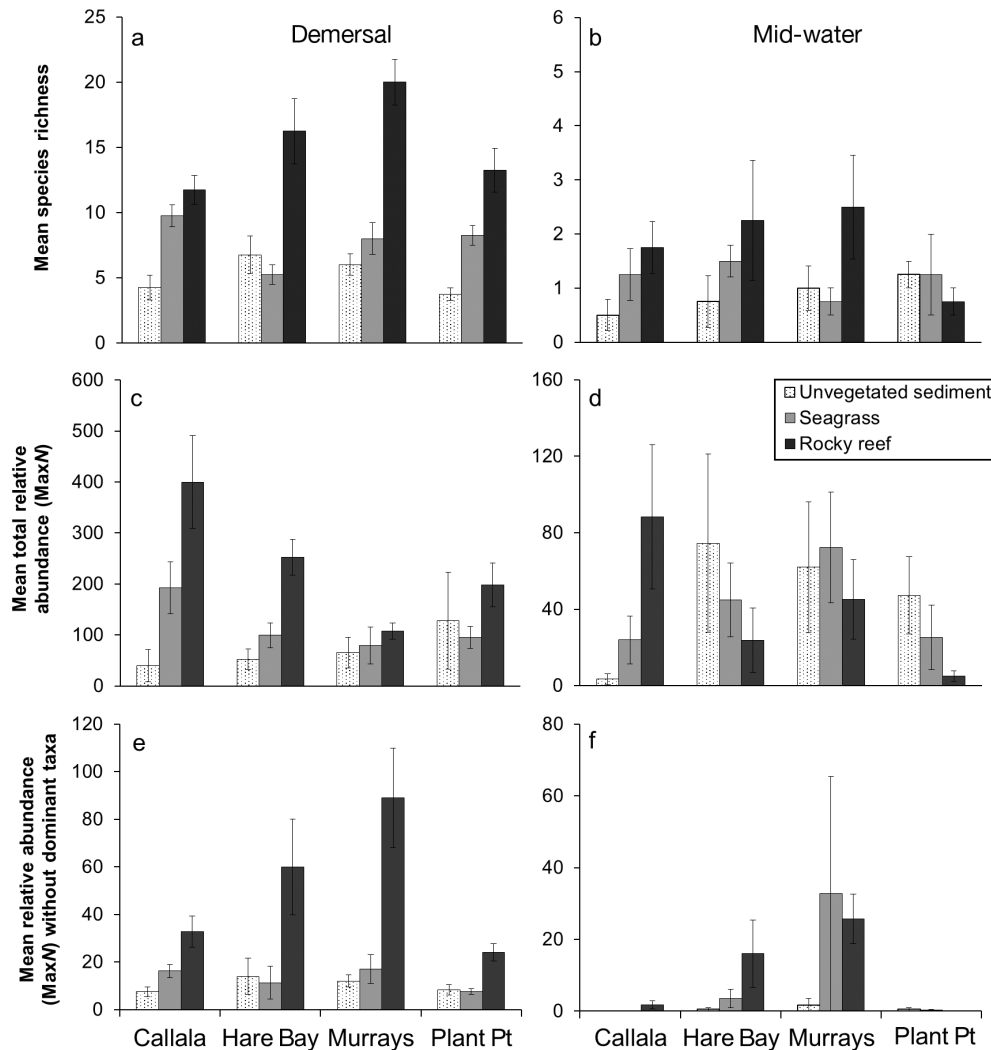


Fig. 3. Patterns in mean (a) species richness, (b) total abundance and (c) total abundance excluding dominant taxa among habitats and locations in demersal and mid-water environments ($n = 4$ per habitat). Plots in left column are from the demersal environment, while plots in right column are from the mid-water environment. Plant Pt: Plantation Point. Error bars are \pm SE

important exceptions, however, as mid-water assemblages and the abundance of certain demersal families and species were not influenced by habitat class. Furthermore, assemblages observed on rocky reef displayed considerable variability among locations, which was attributed to the surrounding area of seagrass habitat. We consider these caveats in detail in the following paragraphs, as they have important implications for MPA design.

As we predicted, habitat class was generally a consistent predictor of spatial variability for most species of demersal fish, with each habitat represented by a distinct assemblage. These findings support previous research in temperate systems that has observed different demersal fish assemblages between rocky

reef, seagrass and unvegetated sediment (Jenkins & Wheatley 1998, Guidetti 2000, La Mesa et al. 2011, Davis et al. 2016). Distinct assemblages of demersal fish among habitat classes were driven by rocky reef harbouring a greater diversity and total abundance of fish compared to seagrass and unvegetated sediment. Similarly, differences in the abundance of species and families among habitats also contributed to the multivariate patterns observed, with a number of taxa displaying strong habitat preferences. Labrids and 2 species within this family in particular, *Achoerodus viridis* and *Ophthalmolepis lineolatus*, as well as individuals from the Scorpididae were almost exclusively recorded over rocky reef habitat. Meanwhile, individuals from the genus *Platycephalus*

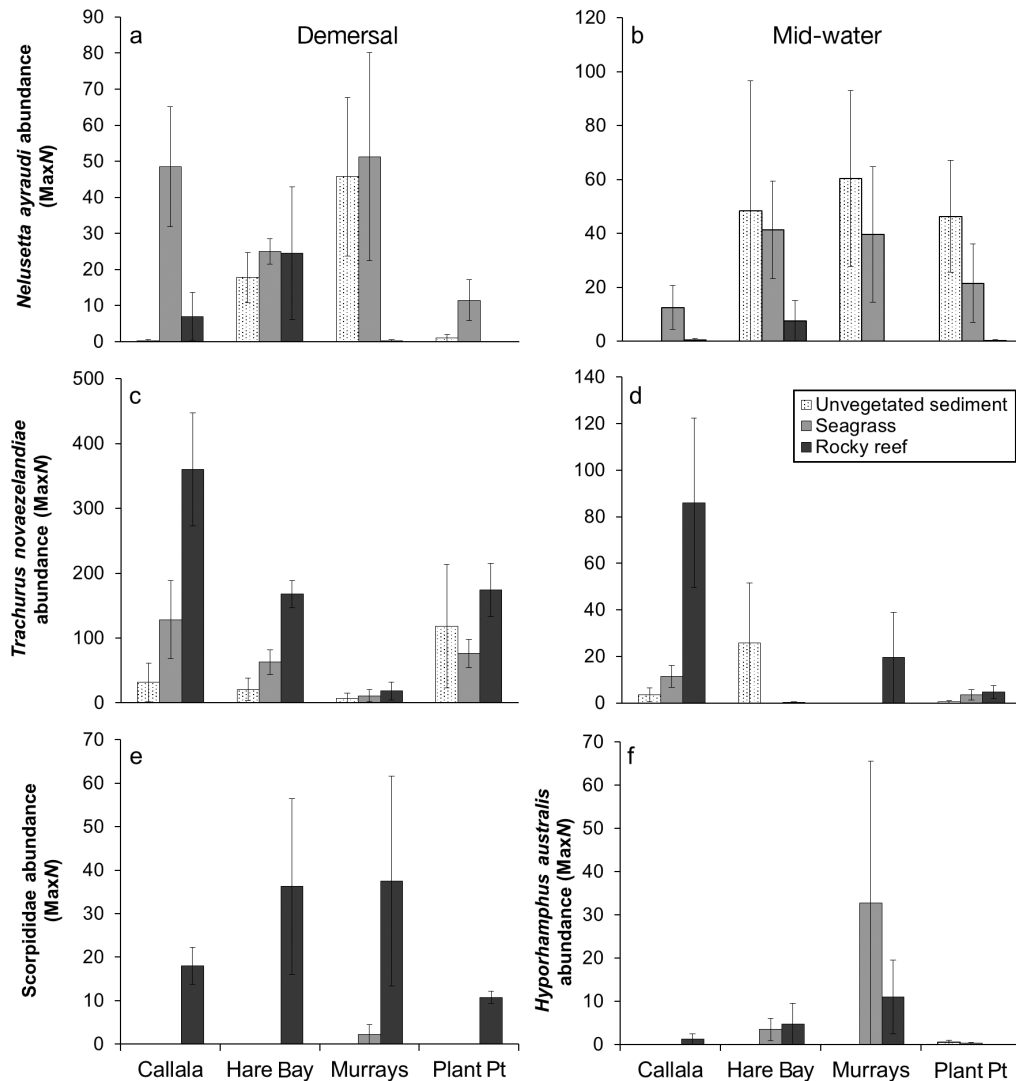


Fig. 4. Patterns in the abundance of common demersal and mid-water species/families among habitats and locations ($n = 4$ per habitat). Plots in left column are from the demersal environment, while plots in right column are from the mid-water environment. Plant Pt: Plantation Point. Error bars are \pm SE

were only observed on unvegetated sediments. In contrast, certain species clearly preferred more than 1 habitat type. For example, *Trygonorrhina fasciata* were equally abundant on seagrass and unvegetated sediment but displayed much lower abundances on rocky reef. Meanwhile, *Trachurus novaezelandiae* were more abundant over seagrass and rocky reef compared to unvegetated sediment. Clear differences in the abundance of demersal fishes among habitat classes are not unexpected, as many species are specialists in foraging, seeking shelter and spawning in particular benthic habitats (Choat 1982). For example, *T. fasciata* and *Platycephalus* spp. display depressiform body types clearly specialised for foraging on unconsolidated sediments. Strong, spa-

tially consistent patterns also provide compelling evidence that the habitat classes investigated in this study may be appropriate surrogates in MPA planning for certain demersal fishes. As preferential habitats varied among taxa, our findings highlight the importance of capturing a mix of habitats within MPA boundaries to cover a wide or representative group of species, as 1 habitat will not support all species (Ward et al. 1999, Dalleau et al. 2010, Rees et al. 2018).

Not all demersal fish taxa showed consistent differences in their patterns of abundance among habitat types. Most notable was the high variability in the abundance of the commercially and recreationally important Sparidae among habitats and locations.

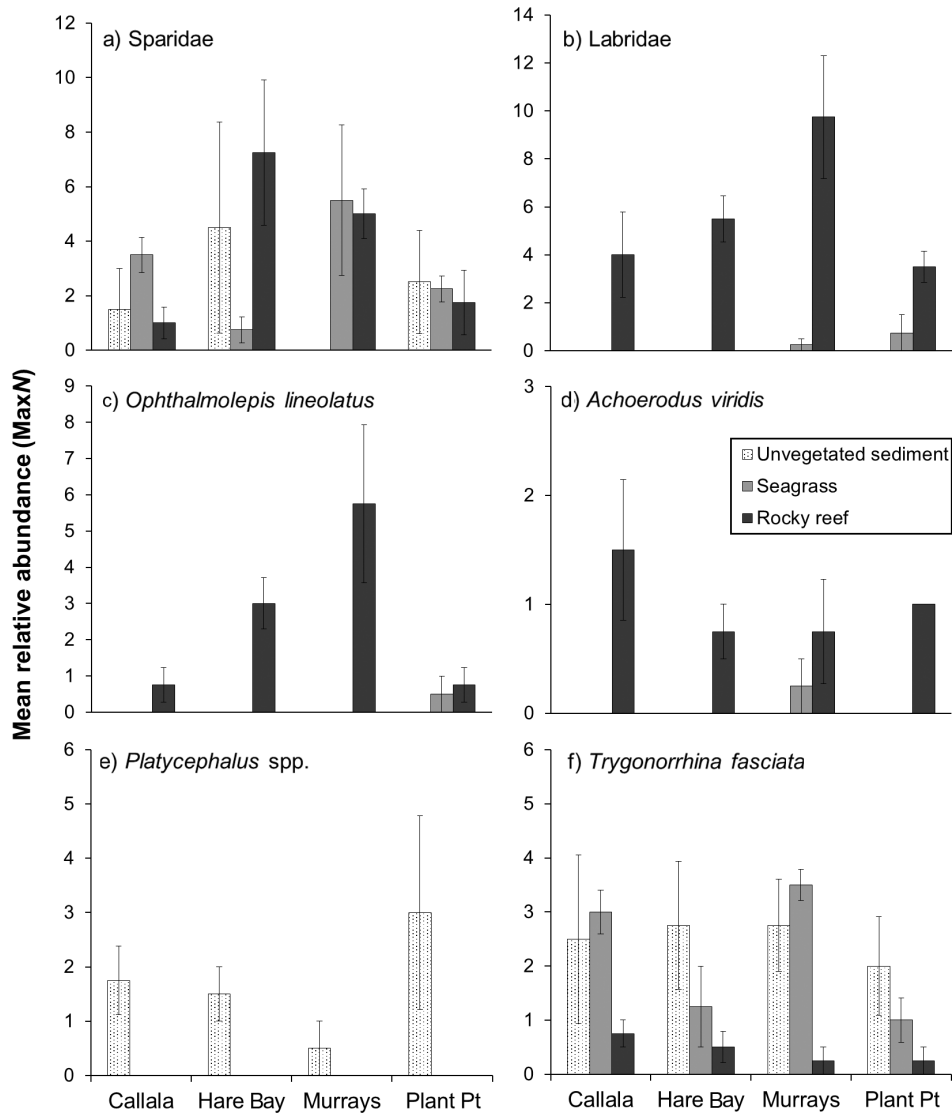


Fig. 5. Patterns in the abundance of common demersal species/families among habitats and locations (n = 4 per habitat). Plant Pt: Plantation Point. Error bars are \pm SE

This outcome was consistent with members of the family being habitat generalists or using specific habitats at different life stages. The latter is likely for snapper *Chrysophrys auratus*, as they are known to undertake ontogenetic migrations between near-shore habitats by first recruiting to seagrass and unvegetated sediments before taking up residence on rocky reefs as adults (Hamer et al. 2006, Parsons et al. 2014). Our findings, therefore, suggest that a combination of habitats needs to be represented in MPAs to capture the variability in sparid habitat use. Measuring sparid length, perhaps through use of stereo BRUVS, would provide an opportunity to determine whether rocky reef, seagrass and un-

vegetated sediments support different age classes of fishes and better guide MPA zoning (see Galaiduk et al. 2017). For example, if rocky reef supports higher abundances of adults, this habitat type could be prioritised in MPA planning regarding impacts of fishing. Other fisheries management strategies such as size limits may already be protecting juveniles on other habitat types, assuming low mortality associated with fishing bycatch.

Mid-water fishes displayed no affinity for particular habitats, confirming the limited explanatory value of habitat classes for mid-water fishes. For this assemblage, we observed inconsistent and highly variable patterns in assemblage structure, abun-

Table 3. ANOVA of the abundance of numerically dominant species and families recorded in the demersal and mid-water environment among habitats and locations. Habitat (H) is a fixed factor with 3 levels: rocky reef (RR), seagrass (SG) and unvegetated sediment (US). Location (L) is a random factor with 4 levels: Callala Bay (CB), Hare Bay (HB), Murrays Beach (MB) and Plantation Point (PP). Site (Si) is a random factor nested within the H × L interaction. Values in **bold** indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to as 1-pooled data and 2-pooled data. NS: not significant; sqrt: square root. Results of Student-Newman-Keuls tests are presented below analyses

| | Demersal | | | | Mid-water | | | |
|--|--|-------|-------|------------------|--|-------|------|--------------|
| | df | MS | F | p | df | MS | F | p |
| (a) <i>Nelusetta ayraudi</i> | | | | | | | | |
| H | 2 | 18.91 | 4.79 | 0.057 | 2 | 16.08 | 4.14 | 0.074 |
| L | 3 | 7.78 | 5.22 | 0.004 | 3 | 3.83 | 0.99 | 0.460 |
| H × L | 6 | 3.95 | 2.65 | 0.031 | 6 | 3.89 | 0.90 | 0.525 |
| Si(H × L) | 12 | 1.46 | 0.98 | 0.487 | 12 | 4.32 | 1.87 | 0.094 |
| Residual | 24 | 1.51 | | | 24 | 2.31 | | |
| Total | 47 | | | | 47 | | | |
| 1-pooled data | 36 | 1.49 | | | | | | |
| Pairwise comparison: | CB: US = RR < SG, HB: US = SG = RR, MB: US = SG > RR, PP: US = SG = RR | | | | Cochran's C (NS): 0.25, ln(x + 1) | | | |
| (b) <i>Trachurus novaezelandiae</i> | | | | | | | | |
| H | 2 | 27.46 | 14.74 | 0.005 | 2 | 19.42 | 1.28 | 0.344 |
| L | 3 | 19.91 | 6.72 | 0.007 | 3 | 24.34 | 1.60 | 0.285 |
| H × L | 6 | 1.86 | 0.63 | 0.705 | 6 | 15.17 | 3.04 | 0.017 |
| Si(H × L) | 12 | 2.96 | 1.61 | 0.155 | 12 | 4.10 | 0.82 | 0.628 |
| Residual | 24 | 1.84 | | | 24 | 5.44 | | |
| Total | 47 | | | | 47 | | | |
| 1-pooled data | 36 | 4.99 | | | | | | |
| Pairwise comparison: | US < SG = RR | | | | CB: US = SG < RR, HB: US = SG = RR, MB: US = SG = RR, PP: US = SG = RR | | | |
| | Cochran's C (NS): 0.26, ln(x + 1) | | | | Cochran's C (NS): 0.32, sqrt(x + 1) | | | |
| (c) <i>Scorpidid</i> | | | | | | | | |
| H | 2 | 64.41 | 28.24 | <0.001 | (d) <i>Hyporhamphus australis</i> | | | |
| L | 3 | 1.56 | 0.69 | 0.564 | 2 | 1.68 | 1.52 | 0.230 |
| H × L | 6 | 0.94 | 0.41 | 0.867 | 3 | 1.56 | 1.41 | 0.252 |
| Si(H × L) | 12 | 1.10 | 0.48 | 0.915 | 6 | 0.71 | 0.64 | 0.695 |
| Residual | 24 | 3.21 | | | 12 | 1.14 | 1.03 | 0.438 |
| Total | 47 | | | | 24 | 1.18 | | |
| 1-pooled data | 36 | 2.50 | | | 47 | | | |
| 2-pooled data | 42 | 2.28 | | | 36 | 1.17 | | |
| Pairwise comparison: | US = SG < RR | | | | Cochran's C (NS): 0.42, ln(x + 1) | | | |
| | Cochran's C (NS): 0.33, sqrt(x + 1) | | | | | | | |

dance and diversity among habitat classes. For example, the eastern sea garfish *Hyporhamphus australis*, a species observed exclusively in the mid-water environment, displayed no preference for habitat type. Similarly, *T. novaezelandiae* and *Nelusetta ayraudi*, which appear transient in their use of the demersal and mid-water environment, showed no clear differences among habitats. The 3 most abundant species in the mid-water assemblage, *T. novaezelandiae*, *N. ayraudi* and *H. australis*, accounted for 54, 30 and 10% of the total number of individuals, respectively. Hence, our findings demonstrate a clear decoupling of the mid-water fish assemblage from the underlying habitat class as well

as demersal fish assemblage, despite mBRUVS being positioned only approximately 4.5 m above the seafloor. Therefore, we conclude that habitat classes would not be an effective surrogate for nearshore mid-water fish assemblages. More appropriate predictors, and therefore surrogates for mid-water fishes and nearshore pelagic fishes, could be hydrographic variables such as current, sea surface temperature and ocean productivity (Hidalgo et al. 2016, Sayre et al. 2017).

Another key finding from our study was the explanatory value of the seascape surrounding rocky reef habitat. We observed substantial spatial variation in the abundance and diversity of fishes

Table 4. ANOVA of the abundance of common species and families recorded in the demersal environment among habitats and locations. Habitat (H) is a fixed factor with 3 levels: rocky reef (RR), seagrass (SG) and unvegetated sediment (US). Location (L) is a random factor with 4 levels: Callala Bay (CB), Hare Bay (HB), Murrays Beach (MB) and Plantation Point (PP). Site (Si) is a random factor nested within the H × L interaction. Values in **bold** indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to as 1-pooled data and 2-pooled data. NS: not significant; sqrt: square root. Results of Student-Newman-Keuls tests are presented below analyses

| | df | MS | F | p | | df | MS | F | p |
|---|---|------|-------|------------------|--|----|-------|-------|------------------|
| (a) Sparid | | | | | (b) Labrid | | | | |
| H | 2 | 1.99 | 1.18 | 0.369 | H | 2 | 11.11 | 28.10 | 0.001 |
| L | 3 | 0.21 | 0.32 | 0.809 | L | 3 | 0.37 | 1.38 | 0.296 |
| H × L | 6 | 1.68 | 2.62 | 0.033 | H × L | 6 | 0.40 | 1.48 | 0.265 |
| Si(H × L) | 12 | 0.68 | 1.06 | 0.422 | Si(H × L) | 12 | 0.27 | 2.54 | 0.025 |
| Residual | 24 | 0.62 | | | Residual | 24 | 0.11 | | |
| Total | 47 | | | | Total | 47 | | | |
| 1-pooled data | 36 | 0.64 | | | 1-pooled data | 36 | | | |
| Pairwise comparison: | CB: US = SG = RR, HB: US = SG, US = RR, SG < RR, MB: US < SG = RR, PP: US = SG = RR | | | | US = SG < RR | | | | |
| | Cochran's C (NS): 0.32, ln(x + 1) | | | | Cochran's C (NS): 0.31, sqrt(x + 1) | | | | |
| (c) <i>Ophthalmolepis lineolatus</i> | | | | | (d) <i>Achoerodus viridis</i> | | | | |
| H | 2 | 3.01 | 18.05 | <0.001 | H | 2 | 1.88 | 26.05 | <0.001 |
| L | 3 | 0.14 | 0.82 | 0.449 | L | 3 | 0.02 | 0.25 | 0.862 |
| H × L | 6 | 0.14 | 0.82 | 0.559 | H × L | 6 | 0.05 | 0.78 | 0.551 |
| Si(H × L) | 12 | 0.05 | 0.30 | 0.985 | Si(H × L) | 12 | 0.09 | 1.25 | 0.282 |
| Residual | 24 | 0.23 | | | Residual | 24 | 0.07 | | |
| Total | 47 | | | | Total | 47 | | | |
| 1-pooled data | 36 | 0.17 | | | 1-pooled data | 36 | 0.07 | | |
| 2-pooled data | 42 | 0.17 | | | 2-pooled data | 42 | 0.07 | | |
| Pairwise comparison: | US = SG < RR | | | | US = SG < RR | | | | |
| | Cochran's C (p < 0.05): 0.39, ln(x + 1) | | | | Cochran's C (p < 0.05): 0.38, ln(x + 1) | | | | |
| (e) <i>Platycephalus</i> spp. | | | | | (f) <i>Trygonorrhina fasciata</i> | | | | |
| H | 2 | 3.01 | 18.05 | <0.001 | H | 2 | 3.01 | 9.19 | 0.015 |
| L | 3 | 0.14 | 0.82 | 0.489 | L | 3 | 0.45 | 1.36 | 0.340 |
| H × L | 6 | 0.14 | 0.82 | 0.559 | H × L | 6 | 0.33 | 0.89 | 0.533 |
| Si(H × L) | 12 | 0.05 | 0.30 | 0.985 | Si(H × L) | 12 | 0.37 | 1.73 | 0.124 |
| Residual | 24 | 0.23 | | | Residual | 24 | 0.21 | | |
| Total | 47 | | | | Total | 47 | | | |
| 1-pooled data | 36 | 0.17 | | | 1-pooled data | 36 | | | |
| 2-pooled data | 42 | 0.17 | | | 2-pooled data | 42 | | | |
| Pairwise comparison: | US > SG = RR | | | | US = SG > RR | | | | |
| | Cochran's C (p < 0.05): 0.39, ln(x + 1) | | | | Cochran's C (NS): 0.19, ln(x + 1) | | | | |

Table 5. Simple linear regressions and a generalised linear model with a negative binomial error structure (see 'Materials and methods' for details) for various fish response measures recorded on rocky reef habitat with the areal coverage of seagrass within 500, 1000 or 1500 m of each survey site. Values in **bold** indicate statistical significance at $\alpha = 0.05$. -: not applicable. Best-fitting models were determined using an Akaike's information criterion approach (Table S1 in the Supplement)

| Dependent variable | Independent variable | F-ratio | z-value | R ² | Pseudo-R ² | p-value |
|---|----------------------|---------|---------|----------------|-----------------------|------------------|
| (a) Demersal fish cumulative diversity | Seagrass 500 m | 3.70 | – | 0.29 | – | 0.10 |
| (b) Mid-water fish cumulative diversity | Seagrass 1500 m | 14.50 | – | 0.66 | – | 0.009 |
| (c) Demersal fish abundance | Seagrass 500 m | 15.48 | – | 0.67 | – | 0.008 |
| (d) Mid-water fish abundance | Seagrass 1000 m | – | 4.62 | – | 0.91 | <0.001 |
| (e) Sparid abundance | Seagrass 1500 m | 6.67 | – | 0.45 | – | 0.042 |

observed on rocky reef across locations. This variation is intriguing, as it suggests that certain patches of habitat (i.e. rocky reef) differ across locations, and so it appears that not all reef is equivalent. Our find-

ings highlight the overwhelming significance of the area of adjacent seagrass. In all cases, response measures were positively correlated with increasing seagrass area including mid-water fish abundance,

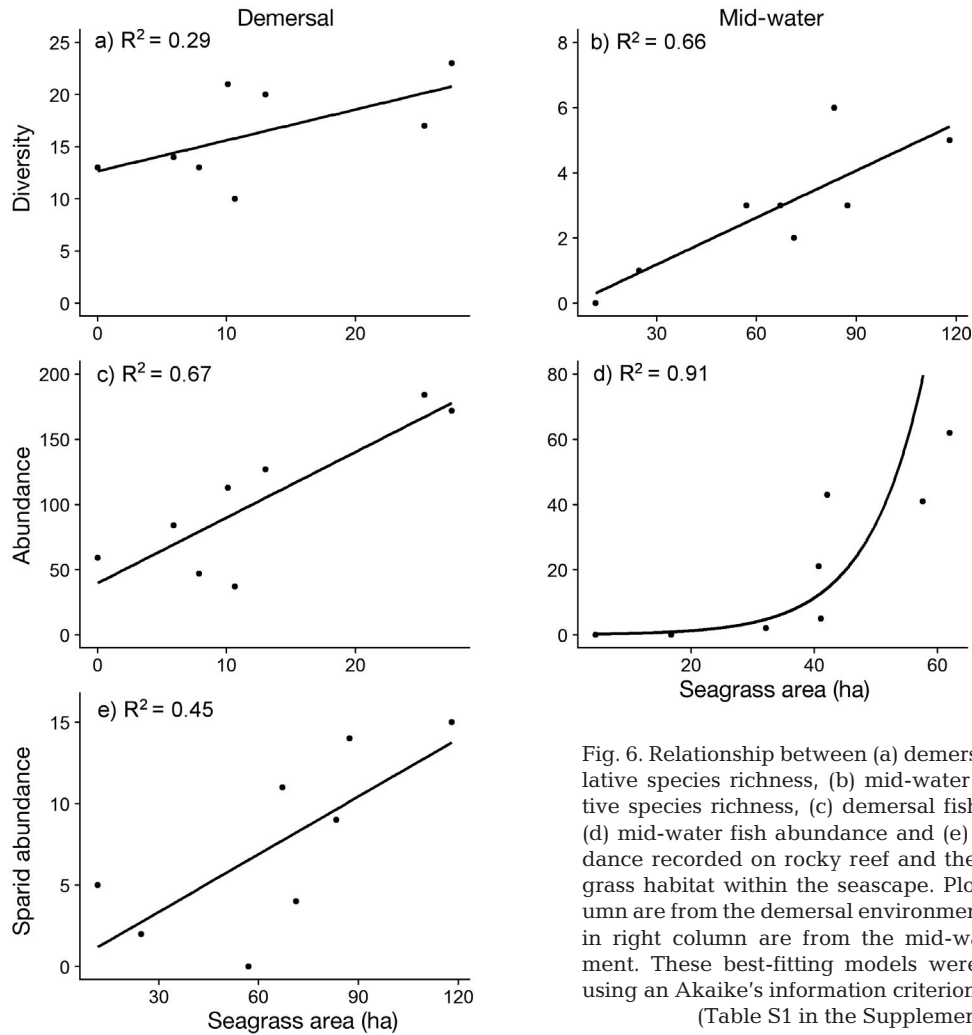


Fig. 6. Relationship between (a) demersal fish cumulative species richness, (b) mid-water fish cumulative species richness, (c) demersal fish abundance, (d) mid-water fish abundance and (e) sparid abundance recorded on rocky reef and the area of seagrass habitat within the seascape. Plots in left column are from the demersal environment, while plots in right column are from the mid-water environment. These best-fitting models were determined using an Akaike's information criterion approach (Table S1 in the Supplement)

diversity, demersal fish abundance and the abundance of sparids on rocky reef habitat. Although not statistically significant at $\alpha = 0.05$, there was also a positive trend between demersal fish diversity and seagrass area. Strong relationships between seagrass area and mid-water fishes were unexpected, considering they displayed no affinity to differences in underlying habitat classes. This discrepancy suggests that mid-water fishes may be responding to patterns of habitat patches at broader spatial scales within coastal seascapes.

Elevated abundance and richness of fishes found on reefs adjacent to seagrass are not unexpected, considering many species from families observed in this study (for e.g. labrids, girellids and sparids) recruit into seagrass habitats before undertaking ontogenetic migrations to other habitat types (Curley et al. 2013). Temperate species may also undertake diel migrations between different habitat patches to seek refuge or for habitat-associated foraging. As an

example, snapper *C. auratus* (Sparidae) are known to prefer areas of greater patch diversity and complexity (coralline turf, mussel beds, sponge gardens, pits and burrows) (Kingett & Choat 1981, Parsons et al. 2014). Therefore, seascapes that display a high diversity of habitat patches are likely to facilitate a number of ecological processes and promote local biodiversity (Dunning et al. 1992). Our findings also support those from tropical environments which have highlighted the positive effect of connectivity between vegetated habitats such as seagrass and mangroves with coral reef habitat (Mumby 2006, Grober-Dunsmore et al. 2007, Nagelkerken et al. 2012). This suggests that there may be generalities in the importance of seascape connectivity between reef and vegetated habitats in temperate and tropical regions.

Given that reefs adjacent to large beds of seagrass contained disproportionately high levels of fish biodiversity, our results suggest that habitat class sur-

rogates may be too simplistic, highlighting the need to incorporate seascape features in temperate MPA planning (Olds et al. 2016, Weeks 2017). As greater seagrass coverage adjacent to reef habitat is likely to facilitate ecological processes such as ontogenetic migrations, foraging behaviour and diel movements (Pittman & Olds 2015), areas that display these seascape attributes should be prioritised in MPAs. A significant concern is the loss and degradation of seagrass habitat worldwide (Waycott et al. 2009). Nevertheless, if the conservation objectives of MPAs are to protect ecological processes and biodiversity, as is the case in Australia and worldwide, the inclusion of seagrass–rocky reef connectivity should be a priority (Wescott & Fitzsimons 2016). Further research establishing links between quantifiable seascape metrics and temperate marine biodiversity will better facilitate the representation of ecological processes and biodiversity in MPA design.

Amid growing concerns over the health and functioning of coastal marine ecosystems, it is critical that conservation strategies such as MPAs are effective in reaching conservation goals. Mapped habitat classes have become a popular method to represent and protect marine biodiversity within MPA boundaries. Our study demonstrates that habitat classes are appropriate surrogates at the simplest level for the abundance and diversity of demersal fish in coastal environments. There were, however, a number of caveats that conservation managers and planners need to be aware of when using this approach. First, habitat class did not influence the spatial variability observed in certain demersal fish families and species. Nor were habitat classes effective for mid-water fishes. Consequently, habitat class is unlikely to be an effective surrogate for all taxa. This finding is important especially if the exceptions are exploited and ecologically important species, as was the case here. Second, substantial variability among similar habitat types (i.e. rocky reef) across locations indicates that certain habitat patches have greater biological value than others. We demonstrate that this variation was explained by the connectivity and size of habitat patches, highlighting the need to capture seascape patterning in MPA design. Increasing our understanding of how habitat influences coastal fish assemblages at a variety of spatial scales will improve the use of habitat-based surrogates in MPA planning.

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