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Diversity surrogates for estuarine fish assemblages in a temperate estuary in New South Wales, Australia

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Abstract

The efficacy of fish diversity surrogates is central to their utility in conservation planning and management. Here we examine the linkages among a range of biotic and abiotic surrogates for estuarine fish diversity within the Port Stephens estuary in NSW, Australia. We examine the effectiveness of using biotic habitats as surrogates for diversity, and examine whether this surrogacy persists through time. The study was conducted using fish assemblage data gathered across eight *a priori* identified biotic habitat types. Significant differences in fish assemblages, species richness, and functional richness were detected among 26 out of 28 biotic habitats pairs, and these differences persisted for over 1 year within key *Dendronephthya australis* (soft coral) and filter feeder habitats, demonstrating the potential for biotic habitats to be used as surrogates for estuarine fish diversity. Significant correlations between abiotic variables (i.e. depth, location, substrate type, and substrate complexity) and fish assemblages were also established. Overall, the results demonstrate that both abiotic variables and biotic habitats can be used as surrogates for fish diversity in the study estuary, and combining both these types of predictor variables can provide a high level of discrimination among estuarine fish assemblages. The use of both abiotic variables and biotic habitats in conservation planning can, therefore, improve representation of estuarine fishes within marine protected areas.

KEY WORDS: Conservation; marine protected areas; biotic habitat; Port-Stephens Great-Lakes Marine Park; Underwater Visual Census

1 Introduction

Understanding diversity, and relationships between diversity and habitats, is central to conservation planning (Margules and Pressey 2000; Tear et al. 2005), and the management of ecosystems (Grumbine 1994). Key information includes relationships between species and habitats, as well as the distributions of rare and threatened species (Margules and Pressey 2000). Regional biodiversity (Gamma diversity), is frequently partitioned into Alpha diversity, measuring the diversity of species within habitats, and Beta diversity measuring the effective number of distinct habitats occurring within regions (Whittaker 1960). This partitioning allows exploration of factors driving patterns in species assemblages both within and among habitats, and has led to the

establishment of improved understanding of the relationships between habitats and their constituent species assemblages for a wide range of phyla including; vegetation (Whittaker 1960), birds (Fretwell and Calver 1969), mammals (August 1983), and fish (Malcolm et al. 2010; Rees et al. 2014; Sheaves 2016).

Assessing relationships between fish and marine habitats is particularly challenging due to the highly variable nature of fish assemblages in space and time (Willis et al. 2000; Birt et al. 2012), and habitat shifts during the ontogeny of many species, whereby individuals occupy different habitats at different points in their life cycle (Harasti et al. 2014a; Harasti et al. 2014b). To overcome problems associated with assessing fish–habitat relationships, managers of marine ecosystems often use abiotic factors (e.g. depth, substrate type) as surrogates for fish diversity (Mumby and Harborne 1999; Malcolm et al. 2011), as they can be measured relatively inexpensively, compared with fish assemblages, using visual and acoustic technologies (Anderson et al. 2009). Nonetheless, surrogates are only useful management tools if they accurately correlate with the assemblages of interest, are independent of each other, have a wide geographic range, and are amenable to survey (Smith 2005).

Studies have shown the surrogacy potential of abiotic variables (e.g. depth, location, and substrate type (Friedlander and Parrish 1998; Rees et al. 2014)) and biogenic habitats (Mumby and Harborne 1999; Harborne et al. 2008) for fully marine fish assemblages. However, relatively few studies have examined the effectiveness of such surrogates for fish diversity in estuarine ecosystems, potentially due to variability among estuarine systems (Sheaves 2016). Establishing reliable surrogates is especially important within estuaries as they contain highly diverse ecosystems that are threatened by a range of anthropogenic stressors (Lotze et al. 2006). Thus, there is a clear need for a more detailed understanding of how abiotic variables and biogenic benthic habitats including sand, hereafter termed 'biotic habitats' perform as surrogates for fish diversity in estuarine systems.

Improved understanding of surrogates for fishes within estuaries is also needed for planning of marine protected areas (MPAs), where adequate information about species distributions is often unavailable, leading to inefficient MPA design (Ban et al. 2011; Malcolm et al. 2012). Marine protected areas are seen as key tools for protecting biodiversity (Coleman et al. 2013; Kelaher et al. 2014), as they provide areas of refuge from human impacts such as over-fishing, pollution, and coastal clearing and development (Agardy 1994; Mumby and Steneck 2011). To be effective, surrogates need to be critically evaluated (Smith 2005) and, ideally, surrogates should be assessed through time to ensure their continued effectiveness when temporal shifts in species assemblages occur (Favreau et al. 2006).

We investigated variation in fish diversity (measured as multivariate assemblage data, species richness, and functional richness) among distinct biotic habitats within the Port Stephens estuary in NSW, Australia, testing the primary hypothesis that fish diversity differs significantly among biotic habitats, and thereby that biotic habitats provide useful surrogates for fish diversity in the study estuary. Furthermore, temporal patterns in fish diversity within key habitats were examined, to assess the temporal stability of the surrogacy. In addition, to improve understanding of the relative importance of abiotic factors (depth, substrate type, location, and substrate complexity) as surrogates, we examined the relationships between these variables and fish assemblages, testing the secondary hypothesis that abiotic variables provide effective surrogates for fish diversity in the study estuary.

2 Material and methods

2.1 Study area

The study was conducted on the southern side of the Port Stephens estuary (Figure 1) which contains a range of temperate estuarine habitats (Davis et al. 2015; Poulos et al. 2015) and a high diversity of biota (Smith et al. 2010; Poulos et al. 2013). The estuary is subject to strong tidal flows which ensure that salinity in the study area is essentially marine (i.e. 35 to 35.5 psu) (DPWS 1998). The entire Port Stephens estuary lies within the 98,000 Ha Port Stephens-Great Lakes Marine Park (PSGLMP), the largest MPA within the state waters of New South Wales (NSW) (NSWMPA 2010). Two sets of surveys were conducted. Firstly, surveys to examine the effectiveness of biotic habitats, and abiotic variables, as surrogates for fish diversity were carried out in January/February 2015 (summer 2015) within eight *a priori* defined habitat types (Davis et al. 2015) (Table 1), with 6 replicate transects sampled from randomly selected starting locations within previously mapped areas for each habitat type (Davis et al., 2015).

Secondly, surveys to examine temporal stability of habitat surrogacy were undertaken for 3 month periods (hereafter periods), from June 2014 (winter 2014) to August 2015 (winter 2015), in two *a priori* selected key habitats (i.e. the soft coral *Dendronephthya australis* and filter feeder), with 12 replicate transects sampled within previously mapped areas for each habitat type. Filter-feeder and *D. australis* were selected as key biotic habitats as the presence of large areas of these habitats within an estuarine system was thought to be relatively unique; *D. australis*, in particular, was thought to be under threat from anthropogenic impacts (Poulos et al. 2013; Harasti 2016; Smith and Edgar 2014); and previous research indicated that these habitats contain highly diverse fish assemblages and protected species (Poulos et al. 2013).

2.2 Survey methodology

Underwater visual census (UVC) surveys were conducted at slack water on high tide using the methodology developed by Smith et al. (2008). Briefly, each survey consisted of randomly positioned replicate transects within predefined areas for the specified habitat type. To ensure independence, transects were separated from each other by a distance of at least 10 m. Each transect involved counting fish in a 25 m x 5 m strip along the transect tape, to a height of 5 m above the substratum, with larger (> 50 mm) non-cryptic demersal and pelagic fish surveyed as the tape was laid, to improve counts of species that actively avoid divers (Dickens et al. 2011). Benthic and cryptic fish were surveyed by conducting a subsequent thorough search of the substrate to avoid biases in estimates of the abundance of cryptic species, which have been shown to occur in transect areas of this size (Brock 1982; Lincoln-Smith 1989). The benthic and cryptic fish search included searching through vegetation, as well as examining crevices and the underside of movable rocks, over a period not exceeding 30 min per transect. Vertical photo-quadrats (covering an area approximately 0.7 m x 0.5 m) were taken at five equally spaced points along each transect, and water depth and an assessment of substrate complexity were recorded for each point. From each photo-quadrat, the percentage cover of rock substratum was calculated, providing a quantitative assessment of the proportion of hard substrate to soft sediment on each transect. Substrate complexity was qualitatively assessed in situ as the height change of the substrate within each quadrat,

based on the method proposed by Gratwicke and Speight (2005), using a geometric scale (1 < 5 cm, 2 = 5–10 cm, 3 = 11–20 cm, 4 = 21–40 cm, 5 = 41–80 cm, 6 > 80 cm). Values of percentage rock substrate, depth, and substrate complexity were averaged for points on each transect and subsequently used for assessment of abiotic variable surrogacy. Water temperatures were continuously monitored at two locations spanning the study site using Onset Hobo U22-001 temperature loggers (www.onsetcomp.com accessed 18 August 2015) to provide data on temperature variations over time.

2.3 Statistical analysis

Data from summer 2015 was analysed to examine variation among biotic habitats for fish assemblages, species richness, and functional richness as the convex hull volume (FRic) which is calculated as the volume in functional space required to enclose the extreme values for all traits (Villéger et al. 2008). Functional richness was calculated using the functional diversity package 'FD' in R (Laliberté et al. 2014), with 9 functional traits obtained from Fishbase (**http://fishbase.org** accessed 10 August 2015) and from the global fishes trait database used by Stuart-Smith et al. (2013) (Supplementary Table S1). Non-metric multidimensional scaling (nMDS) analysis, using the PRIMER 7 software package (Clarke and Gorley 2015), was used to examine patterns in fish assemblages among biotic habitats. For all analyses similarity matrices were constructed using the Bray-Curtis index (Clarke 1993) using data that were dispersion weighted to reduce the influence of highly variable species, and then square-root transformed to reduce the influence of abundant species. Dispersion weighting down-weights species abundance counts for highly variable species (e.g. schooling fishes) that would otherwise add 'noise' to multivariate data (Clarke and Gorley 2015) and was found to provide similar results to removing schooling species from the data prior to applying transformations. Permutational multivariate analysis-of-variance (PERMANOVA) analyses were used to test for significant differences among biotic habitats. Pairwise PERMANOVA tests were conducted where significant differences were identified, with a significance level P = 0.05 used for all tests. Bonferroni corrections were not applied to account for the number of pairwise tests (28), as conclusions were not based on single pairwise test results, and the increased possibility of a Type 1 error was therefore deemed to be acceptable. Species driving similarities within biotic habitats were identified using the SIMPER routine within the PRIMER software package (Clarke and Gorley 2015),

Temporal data spanning winter 2014 to winter 2015 were analysed in PERMANOVA to test for differences between key habitats and periods, using a 2-factor design (habitat-fixed, periods-random) with pairwise PERMANOVA analyses conducted for factors where significant differences or interactions were identified. Metric multidimensional scaling (mMDS) analysis was used to examine temporal changes in fish assemblages, displaying data as mean assemblage locations with 95% confidence intervals obtained by bootstrap averaging, with replacement, across samples within each habitat/period pair (Clarke et al. 2014). The RELATE module in PRIMER was used to examine Spearman's rank correlations between assemblage patterns and modelled distance matrices representing: an annual cycle (cyclicity test); and a progressive change over time (seriation test) (Clarke et al. 2014). Species driving differences between periods were identified using the SIMPER routine, and biogeographic affinities were used to identify whether changes were driven by temperate or tropical species. Biogeographic affinities were determined from Reef Life Survey data on the thermal distribution of fish (Edgar and Stuart-Smith 2014), with species with a central tendency in thermal distributions >23.8 ºC (i.e. mean

water temperature for Port Stephens +2 S.D.) deemed to be tropical immigrants. Analysis-of-variance (ANOVA) was used to test whether, proportionally, more tropical immigrants were present when water temperatures were higher (Summer/Autumn 2015), than when water temperatures were lower (Winter/Spring 2014).

The Biota and Environment matching routine (BIOENV) within the PRIMER software package was used to determine the best match between multivariate patterns in abiotic variables, with resemblance as Euclidean distance, and summer 2015 patterns in fish assemblages (Clarke 1993). Combinations of abiotic variables (comprising: depth; location (as distance from the estuary mouth); substrate type (as percentage rock substrate); substrate complexity) were tested to identify the subset that best matched fish assemblage patterns. Abiotic variables were square-root transformed to overcome skewness, standardised, and tested for co-linearity, with variables with absolute values for correlation coefficients $|r| > 0.7$ substituted as recommended by Dormann et al. (2013). Testing for co-linearity identified that substrate type and substrate complexity were highly correlated ($|r|=0.81$), and substrate type was therefore used to represent both variables in subsequent analyses. BIOENV was also used to test for spatial autocorrelation between summer 2015 fish assemblages and distance between transects. No significant correlation was detected ($\rho_s = 0.034$, $P = 0.267$), indicating that assemblage differences among habitats were not primarily caused by distance.

3 Results

3.1 Variations in fish diversity across habitat types

A total of 17738 fish from 175 species were identified during 156 UVC transects across habitats, and periods (Supplementary Table S2). Non-metric multi-dimensional scaling (nMDS) showed clustering of fish assemblages within different habitat types (Figure 2). PERMANOVA identified significant differences among assemblages, species richness, and functional richness in different biotic habitats ($P < 0.001$, all tests). Pairwise tests identified that assemblages in 26 out of 28 habitat pairs were significantly different from each other, especially where habitats had widely differing substrates and physical structures (e.g. sand and barrens) (Table 2). Differences in fish assemblages were not detected among filter feeder and branching algae habitats ($P = 0.061$), and seagrass-dominated Z. muelleri/H. ovalis and P. australis habitats ($P = 0.051$, Table 2) where biotic habitats were on similar substrates with similar benthic growth. Pairwise tests for species richness and functional richness also identified significant differences between some biotic habitats (Table 2) with higher species richness and functional richness generally associated with more structurally complex biotic habitats (e.g. branching algae, filter feeder) or heterogeneous reef substrates (e.g. barrens) (Table 3). SIMPER analyses identified that differences between biotic habitats were primarily driven by differing abundances of commonly occurring temperate species (Table 3).

3.2 Temporal variability in fish diversity in key habitats

Metric multidimensional scaling (mMDS) for mean assemblages from each habitat in each season indicated that species assemblages changed through time (Figure 3). PERMANOVA analyses identified significant differences

in assemblages, species richness, and functional richness among periods, and habitats ($P < 0.016$, all tests). Significant interactions between habitats and periods were detected for assemblages ($P = 0.020$), but were not found for species richness and functional richness ($P > 0.071$, both tests). Pairwise tests between habitats, for assemblages within periods, identified that assemblages in key habitats (i.e. filter feeder, *D. australis*) were significantly different from each other in all periods ($P < 0.001$, all pairs). Pairwise tests among periods, for assemblages within habitats, identified that assemblages in *D. australis* were significantly different from each other for all periods ($P < 0.030$, all pairs), except winter and autumn 2014 ($P = 0.390$). In the filter feeder habitat, assemblages were significantly different from each other among winter 2014 and summer/autumn/winter 2015, as well as among spring 2014 and autumn/winter 2015 ($P < 0.034$, all pairs).

SIMPER analyses identified that differences in species assemblages between periods were driven by changes across a wide range of predominantly temperate species, with no single species contributing > 5% to differences among periods for the filter-feeder habitat, or > 8% to differences for *D. australis* habitat. No significant annual cycle in fish assemblages was detected in either filter-feeder habitat ($P = 0.213$, $\rho = 0.020$), or *D. australis* habitat ($P = 0.196$, $\rho = 0.025$). Testing for a progressive change in assemblages (i.e. seriation) identified a significant, albeit relatively weak (i.e. low ρ-value), relationship between changes to fish assemblages and elapsed time in both filter-feeder habitat ($P < 0.001$, $\rho = 0.145$), and *D. australis* habitat ($P < 0.001$, $\rho = 0.186$).

Significant differences among key habitats for species richness and function richness were driven by higher species richness and functional richness in the filter-feeder habitat compared to the *D. australis*, across all periods (Table 4). Significant differences in species richness and function richness between periods were influenced by higher richness in both habitats during summer/autumn 2015 when water temperatures were highest (Table 4). SIMPER analyses identified that assemblage changes over time were predominantly driven by temperate fish species. Tropical species were not highly abundant, but a significantly greater proportion ($P = 0.016$) was present during summer/autumn 2015 (3.8 ± 0.6%, mean ± S.E.) than during winter/spring 2014 (1.8 ± 0.5%).

3.3 Relationships between abiotic variables and fish assemblages

BIOENV analyses identified significant Spearman rank correlations (ρ_s) between all abiotic variables examined and summer 2015 fish assemblages ($P < 0.010$), with the highest correlation occurring for substrate type ($\rho_s = 0.614$), then substrate complexity ($\rho_s = 0.494$), then depth ($\rho_s = 0.273$), and the lowest correlation occurring for location ($\rho_s = 0.069$). Testing correlations between combinations of abiotic variables and fish assemblages identified that the greatest explanatory power was provided by a combination of substrate type and depth ($\rho_s = 0.693$), while explanatory power was reduced when substrate type, depth, and location were combined ($\rho_s = 0.614$).

4 Discussion

Abiotic and biotic surrogates are frequently used to represent differences in fish diversity among areas in conservation planning (Malcolm et al. 2011; Malcolm et al. 2012), with these surrogates needing to be easy to measure, and representative of species of interest, if they are to be effective (Smith 2005). Where significant

relationships can be established between habitats and species assemblages these provide an indication that habitats can provide highly cost-effective surrogates for biological assemblages in marine conservation planning (Ward et al. 1999). In this study, we identified significant differences in fish diversity between biotic habitats within an estuarine system, and showed that these differences persisted through time within two key habitats, thereby, demonstrating significant relationships between biotic habitats and fish diversity within the Port Stephens estuary, and indicating the potential utility of biotic habitats as surrogates for fishes in conservation planning in the estuary.

Differences in biological assemblages among biotic habitats have been linked to variations in resources, or other limiting factors (Guisan and Thuiller 2005), with increased habitat complexity linked to higher fish diversity through the provision of more diverse food resources (Ross 1986), and more varied options for sheltering from predators and environmental extremes (Anderson et al. 1989; Charbonnel et al. 2002; Friedlander et al. 2003). We found significant differences in fish assemblages among the majority of the benthic habitats examined, predominantly among habitats on differing substrates with differing levels of complexity in terms of either biotic growth or structure. In addition, both species richness and functional richness tended to be greatest in biotic habitats containing diverse benthic growth (e.g. branching algae and filter feeder) or heterogeneous reef substrates (e.g. barrens) while simpler habitats (e.g. sand and *Z. muelleri*/*H. ovalis*) had lower species and functional richness. Of particular note was the key *D. australis* habitat, which had fish assemblages that were significantly different to all other habitats examined, supporting previous work identifying *D. australis* as a unique habitat of particular importance to fish species (Poulos et al. 2013).

In contrast, differences in fish assemblages were not detected where biotic habitats were on similar substrates with similar benthic growth (e.g. filter feeder and branching algae), with the inability to detect significant differences between some habitat types indicating that they could possibly be grouped in future local conservation planning, where protection of fish diversity is the primary objective. This could potentially simplify planning and management, especially where the spatial distributions of these habitats are contiguous. It should be noted however that differences in fish assemblages between seagrass-dominated *Z. muelleri/H. ovalis* and *P. australis* habitats, that were not detected in our study, were found by Middleton et al. (1984) using a combination of methods (i.e. poisoning, beam trawling, and gill netting), suggesting that increased replication within habitats in the study period may have improved the ability to detect differences among fish assemblages in some habitats in our study.

Another factor contributing to differences in fish assemblages among habitats was temporal variation, which has been shown to occur in many regions due to fluctuations in water temperatures and seasonal breeding cycles (Booth et al. 2007), as well as seasonal changes in food availability (Edgar and Shaw 1995). It was, therefore, anticipated that fish assemblages in this study would exhibit annual cyclic variations, and that species richness and functional richness would be higher when average water temperatures were at their greatest, due to the recruitment of tropical larvae (Booth et al. 2007). Species richness and functional richness were found to be greatest in the warmer months and, as anticipated, the proportion of tropical species was also greater during warmer months. However, despite the observed increased prevalence of tropical species over summer/autumn, the anticipated annual cycle in fish assemblages was not detected, with fish assemblages in winter 2014 and winter 2015 strongly differing in both habitats. Instead, fish assemblages exhibited a temporal drift in

composition, with an inter-annual change in assemblages greater than any change between adjacent periods. This long-term shift in assemblages resulted from changes in abundances of large numbers of predominantly temperate species over time, outweighing the impact of immigrant tropical species. The lack of an apparent seasonal effect on fish assemblages was not entirely unexpected because there are often no clear seasonal changes in demersal fish assemblages along the NSW coast (Gray and Otway 1994). Despite this, there were significant differences in fish diversity among the key biotic habitats across all periods of sampling, indicating that temporal shifts in fish assemblages do not dilute the surrogacy value of habitat types for the key habitats in this study. Results from previous research indicates that temporal differences also persist between fish assemblages in *Z. muelleri* and *P. australis* (Middleton et al. 1984) and between *Z. muelleri* and sand (Gray et al. 1996), indicating that temporal persistence in fish assemblage patterns also occurs among other habitats. However, further work is required to determine whether differences detected in this study persist for all habitats within the study locality.

Examination of correlations between fish assemblages and abiotic variables highlighted that variations in fish assemblages were closely correlated with substrate type and substrate complexity, moderately correlated with depth, and weakly associated with location. Substrate type and substrate complexity were found to be strongly correlated with each other, with substrate complexity increasing with the percentage of rocky substrate: these variables were therefore assessed as being interchangeable in their ability to act as surrogates for fish assemblages. However, substrate type would be the logical choice to use as a surrogate given the relative ease with which it can be measured using modern acoustics techniques (Jordan et al. 2010) and the importance of substrate type in determining the structure of fish assemblages (Malcolm et al. 2012; Morton and Gladstone 2014). The ability of abiotic variables to act as surrogates for fish assemblages was further improved when depth was considered, supporting the secondary hypothesis that abiotic variables can provide effective surrogates for fish assemblages. It should be noted however that using abiotic surrogates increases the risk of errors associated with distinguishing between sites which have similar abiotic conditions but dissimilar habitats (false homogeneity), and sites with dissimilar abiotic conditions but similar habitats (false heterogeneity - Stevens and Connolly 2004). In the study area, abiotic surrogates would not provide an effective mechanism for distinguishing between barrens and filter feeder or branching algae habitats, a false homogeneity error, with these habitats all occurring on hard substratum at similar depths. In addition abiotic surrogates would not adequately distinguish between sand, *P. australis*, and *Z. muelleri* with these habitats occurring on soft sediment at similar depths.

The results of this study demonstrate that both biotic habitats and abiotic variables are effective surrogates for fish diversity, a conclusion that is supported by previous work in Western Australian estuaries, where fish community structure is correlated with the type of substrate and benthic vegetation (Valesini et al. 2014), and in central NSW where combining abiotic and biotic factors was shown to provide improved effectiveness in conservation planning for temperate reefs (Lindsay et al. 2008; Malcolm et al. 2012). Identifying the relative importance of the biotic and abiotic surrogates for fishes was complicated by relationships that exist between these surrogates within the estuary (Davis et al. 2015). It should be noted, however, that assessment of biotic habitats currently requires costly visual surveys, due to limitations in the ability of acoustic survey techniques to distinguish between different types of biogenic habitats (Jordan et al. 2010). It could therefore be argued that abiotic variables provide a more cost-effective surrogate for fish diversity, especially in situations where

resources are constrained, as abiotic variables (e.g. depth, location, substrate type) are amenable to measurement using acoustic techniques (Jordan et al. 2010), however care is required to address false homogeneity and false heterogeneity where abiotic surrogates are used in isolation (Stevens and Connolly 2004). Where data for both abiotic variables and biotic habitats are available, our study results suggest that combining these data will provide a higher level of discrimination between distinct fish assemblages, than using either type of surrogate in isolation, thereby ensuring improved representation of fish species distributions in conservation planning and fisheries management. Additionally, it was demonstrated that diverse biotic habitats warrant increased levels of protection in conservation planning, as these habitats generally contain functionally diverse fish assemblages with a correspondingly high importance to ecosystem function (Poulos et al. 2013; Farré et al. 2015).

With estuaries facing an increased range of anthropogenic threats it is essential that effective conservation strategies are in place (Lotze et al. 2006). Conservation planning for marine ecosystems is challenging, especially when knowledge about the distribution of species is lacking, and suitable diversity surrogates have not been established. Our study demonstrates that both biotic habitats and abiotic variables have the potential to act as effective surrogates for temperate estuarine fish diversity in Port Stephens. The use of these surrogates in conservation planning will allow efficient and cost-effective determination of MPA boundaries where protection of fish diversity is a primary objective.

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Table 1: Sub-tidal habitat types within the Port Stephens estuary examined in the study of biotic habitat surrogacy for fish diversity. Habitat type classified by dominant biotic cover where biotic cover >10% or by substrate type where biotic cover <10%, as defined by Davis et al. (2015)

Habitat type	Description
P. australis	Areas dominated by the seagrass *Posidonia australis* occurring on soft substratum
Z. muelleri /*H. ovalis*	Areas dominated by intermingled seagrasses *Zostera muelleri* subsp. *Capricorni* and/or *Halophila ovalis* occurring on soft substratum
E. radiata	Areas dominated by the macroalgae *Ecklonia radiata* (i.e. kelp) occurring on hard substratum
Branching algae	Areas dominated by mixed branching and filamentous macroalgal species, with filter feeders present in lower abundance, predominantly occurring on hard substratum
Filter feeder	Areas dominated by filter feeders (i.e. sponges, ascidians, hydroids, bryozoans, and corals) with macroalgae present in lower abundance, predominantly occurring on hard substratum
D. australis	Areas dominated by the soft coral *Dendronephthya australis*, with other filter feeders and macroalgae present in lower abundance, predominantly occurring on soft substratum
Barrens	Areas with rocky substrate dominated by encrusting coralline algae, with high abundances of the urchin *Centrostephanus rodgersii*
Sand	Sand substrate with minimal biotic cover (i.e. <10%)

Table 2: PERMANOVA pair-wise tests for differences between habitat types (*P*-values) for fish assemblages (A), fish species richness (S), and fish functional richness (F). Significant values ($P < 0.05$) in bold

		D. australis	Branching algae	*Z. muelleri* / *H. ovalis*	Sand	*P. australis*	Barrens	*E. radiata*
Filter feeder	A S F	**0.005,** **0.004,** **0.007**	0.061, 0.573, 0.180	**0.002,** **0.009,** **0.026**	**0.003,** **0.003,** **0.004**	**0.003,** **0.008,** **0.004**	**0.004,** 0.484, 0.395	**0.005,** 0.271, 0.087
D. australis	A S F	-	**0.002,** **0.006,** **0.004**	**0.005,** 0.651, 0.269	**0.001,** **0.005,** **0.005**	**0.004,** 0.449, 0.155	**0.003,** **0.010,** 0.290	**0.002,** **0.012,** 0.985
Branching algae	A S F	-	-	**0.005,** **0.005,** **0.009**	**0.001,** **0.002,** **0.002**	**0.002,** **0.005,** **0.006**	**0.001,** 0.222, 0.098	**0.004,** 0.095, **0.012**
Z. muelleri / *H. ovalis*	A S F	-	-	-	**0.008,** **0.023,** 0.054	0.051, 0.913, 0.980	**0.002,** **0.014,** 0.135	**0.003,** **0.023,** 0.375
Sand	A S F	-	-	-	-	**0.001,** 0.068, 0.051	**0.004,** **0.002,** **0.001**	**0.003,** **0.005,** **0.004**
P. australis	A S F	-	-	-	-	-	**0.004,** **0.006,** 0.079	**0.001,** **0.014,** 0.282
Barrens	A S F	-	-	-	-	-	-	**0.004,** 0.586, 0.440

Table 3: Species richness per transect, functional richness per transect (as convex hull volume for traits as per Table S1) (mean ± S.E., n = 6), and dominant species, for fish assemblages by habitat type

Habitat type	Species richness	Functional richness ($\times 10^{-3}$)	Dominant species (% contribution to assemblage similarities)
Branching algae	30.5 ± 3.5	136 ± 12	*Hypoplectrodes maccullochi* (13%) *Ophthalmolepis lineolatus* (8%)
Filter feeder	27.8 ± 3.1	112 ± 10	*Hypoplectrodes maccullochi* (18%) *Pseudolabrus guentheri* (9%)
Barrens	24.8 ± 2.3	94 ± 19	*Hypoplectrodes maccullochi* (26%) *Parma microlepis* (10%)
Ecklonia radiata	22.7 ± 2.6	74 ± 16	*Pictilabrus laticlavius* (15%) *Notolabrus gymnogenis* (12%)
Dendronephthya australis	14.3 ± 1.0	74 ± 4	*Upeneichthys lineatus* (19%) *Brachaluteres jacksonianus* (13%)
Zostera muelleri / *Halophila ovalis*	12.8 ± 2.4	50 ± 21	*Bathygobius krefftii* (30%) *Favonigobius lateralis* (26%)
Posidonia australis	12.3 ± 2.2	50 ± 14	*Bathygobius krefftii* (33%) *Centropogon australis* (19%)
Sand	8.0 ± 0.4	12 ± 2	*Hypoplectrodes maccullochi* (27%) *Trygonoptera testacea* (18%)

Table 4: Seasonal Alpha diversity in key habitat types (Filter feeder, *Dendronphthya australis*) calculated as species richness per transect and functional richness per 25 m x 5 m transect (mean ± S.E., n = 12). Seasonal water temperature averaged across days and sites (mean ± S.E., n = 90–92)

Season	Species richness (Filter feeder)	Species richness (*D. australis*)	Functional richness (Filter feeder) ($\times 10^{-3}$)	Functional richness (*D. australis*) ($\times 10^{-3}$)	Seasonal water temperature (ºC)
Winter 2014	20.1 ± 1.7	11.1 ± 1.1	69 ± 11	51 ± 11	16.90 ± 0.09
Spring 2014	18.7 ± 1.7	11.8 ± 1.0	72 ± 9	58 ± 10	20.14 ± 0.15
Summer 2015	26.6 ± 1.7	14.3 ± 1.1	114 ± 9	72 ± 8	22.74 ± 0.20
Autumn 2015	27.6 ± 2.6	14.6 ± 1.6	116 ± 11	54 ± 10	20.39 ± 0.13
Winter 2015	21.4 ± 1.9	11.2 ± 0.8	88 ± 16	34 ± 4	16.94 ± 0.07

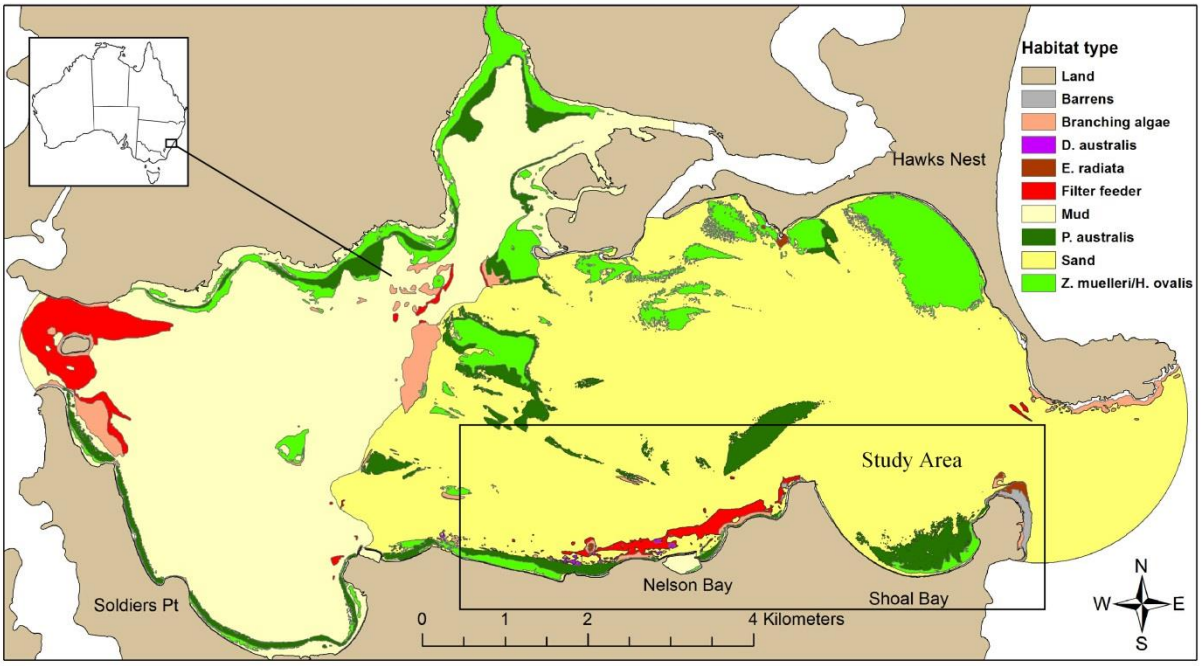

Figure 1. Study area in the Port Stephens estuary. Colours indicate habitat types.

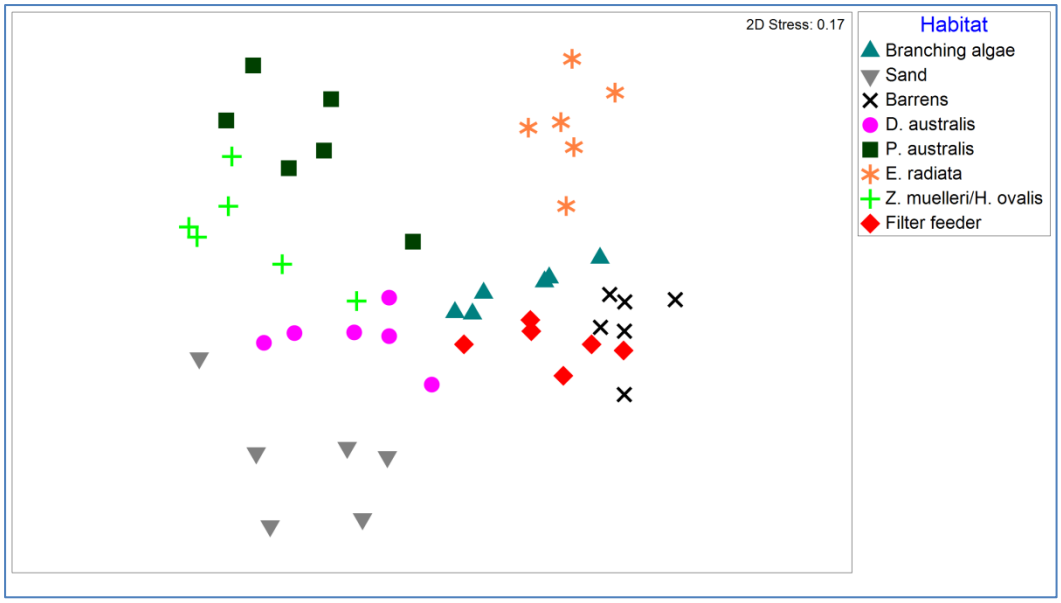

Figure 2: Non-metric Multi-Dimensional Scaling plot showing similarity of fish assemblages within biotic habitat types for the Port Stephens estuary.

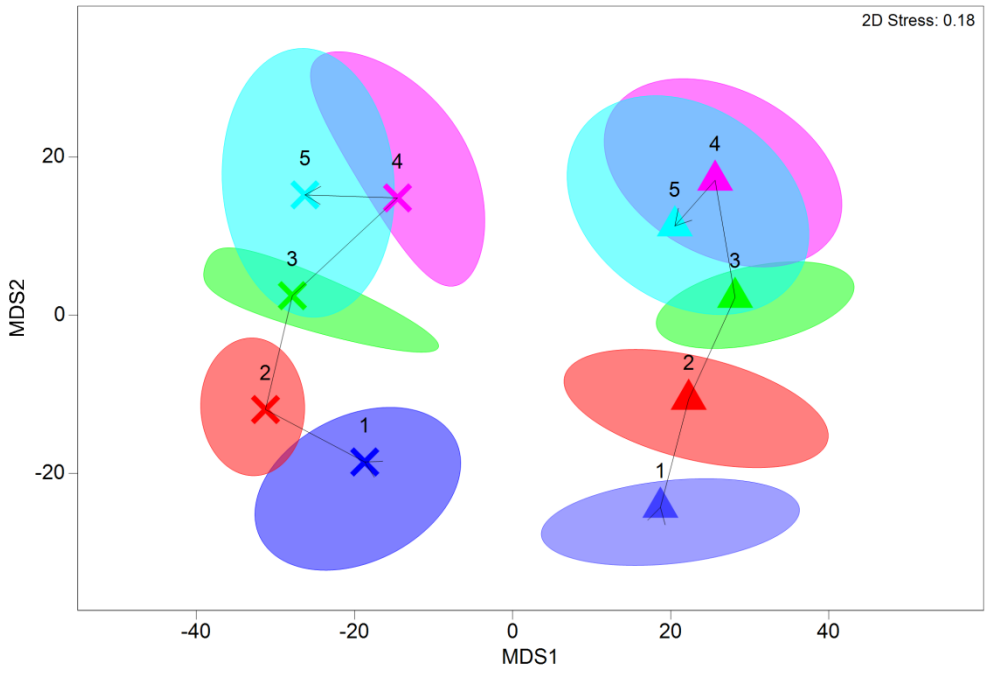

Figure 3: Metric multi-dimensional scaling plot showing similarity of mean fish assemblages within habitat types across time in the Port Stephens estuary. (Triangles = filter feeder habitat, Crosses = *D. australis* habitat, 1 = winter 2014, 2 = spring 2014, 3 = summer 2015, 4 = autumn 2015, and 5 = winter 2015). Ellipses show approximate 95% confidence boundaries for mean position calculated by bootstrap averaging across transects with replacement. Lines with arrows indicate progression in assemblages from winter 2014 to winter 2015.