

Identification of discrete and ecologically relevant types of ichthyo-habitat at two spatial scales for process-based marine planning

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ABSTRACT: One objective of marine planning is the protection of biodiversity. The majority of planning strategies are based on descriptive methodologies, i.e. detecting and managing diversity hotspots. The disadvantage of such approaches is the lack of explanatory power in elucidating what facilitates the variation in diversity. The present study proposes an alternative approach: planning based on ecological processes. Correlations between 24 variables of the biophysical habitat and 4 ecological indices of fish assemblage composition were established. Variables strongly correlated to at least 1 index (adjusted $r^2 > 0.6$) were regarded as likely drivers of variation and used as a basis for cluster analyses to classify discrete, ecologically relevant habitat types. Variables were quantified at 2 spatial scales: individual transects (at scales of 10s of meters) and whole reefs (at scales of 100s of meters to kilometers). Habitat variables at the reef scale were not strongly correlated to ecological indices as often as variables at the transect scale. Aspects of vegetation and habitat complexity correlated strongly to most indices. In all approaches, high capacity habitat, i.e. habitat containing high values of habitat variables positively correlated to diversity indices, was defined by high abundance of Phaeophyta and high structural complexity of the reef itself. High capacity habitat was spatially confined. All cluster analyses yielded similar spatial patterns of habitat types. The statistical methodology used in the present study—identifying distinct and ecologically relevant habitat types and habitat with high capacity to support high diversity—be a useful approach for identifying candidate areas for protection in marine conservation planning.

KEY WORDS: Process-based management · Diversity · Fishes · Rocky reefs · Habitat

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INTRODUCTION

Many marine conservation efforts aim to directly maintain species diversity (Norse 1993). This is based on descriptive research, which includes assessing the variation in abundance of one or many species (Edgar et al. 2008). Marine conservation based on research on the interaction of processes facilitating diversity is less common (Roff & Evans 2002). This is concerning, as the investigation of ecological processes, and consideration of such regarding marine planning, seems pertinent (Roberts et al. 2003). Such ecological processes influencing diversity are invariably ensuing between any individual and the habitat it lives in. If the ecologi-

cal processes facilitating variation in diversity, rather than only variation as such, are understood and subsequently managed, higher levels of diversity are more likely to be sustained in the long run (Anderson et al. 2009).

The physical space constituting the habitat of organisms, including fishes, can be described by a set of biophysical variables (Thiel et al. 1995). These variables are potential drivers of variation in species abundance, yet their ecological potency as drivers varies (Krumme et al. 2008). The particular habitat requirements of species in general, and fishes in particular, form a link between variation in habitat variables and variation in abundance or composition of whole assemblages

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(Anderson & Millar 2004). Habitat variables operate at different spatial scales or grain sizes (Wiens 1989, Arias-Gonzalez et al. 2008), and it can be difficult to detect their respective effect when such variables are assessed at an inappropriate grain size (Underwood & Chapman 1998). The grain size for some habitat variables is the reef itself. Such variables include the size of the reef (MacNeil et al. 2009), effects of the surrounding matrix, e.g. distance to other reefs or other distinct habitats, or the reef perimeter, potentially facilitating edge effects (Dorenbosch et al. 2005). These habitat variables can affect fish assemblages at spatial scales of kilometres (Dorenbosch et al. 2006).

Other habitat variables can be analysed at smaller grain sizes, i.e. 'patch' or 'transect' scales. Such variables, e.g. measures of structural complexity of the reef matrix (Steele 1999) or aspects of the vegetation (Bergman et al. 2001), vary substantially, on the order of metres (Flynn & Ritz 1999), and can affect abundance of fishes at similar spatial scales. Variables operating at smaller grain sizes can be upscaled, i.e. quantified at a larger grain size, and subsequently compared with variables operating at larger grain sizes. The incorporation of multiple grain sizes into a sampling regime allows for comparisons across grain sizes, e.g. it becomes possible to determine whether a variable, which is important in defining habitat at a small grain size, is equally important in defining habitat at a larger grain size (Claudet et al. 2011).

Past studies have investigated effects of the biophysical environment on a species or assemblage (Adams et al. 2004, Hauser et al. 2006, McIntyre et al. 2008) among others by generating multiple regression models, which explain the most variation in the observed fauna with a set of explanatory habitat variables (Alexander et al. 2009). However, such models have disadvantages, as the effect of individual habitat variables is not established (McArdle & Anderson 2001) because only the variable explaining the greatest amount of variation is selected out of a set of however strongly correlated parameters. This incurs the possibility that other potentially important variables are disregarded. Such models furthermore include variables that, at times, explain only a minor fraction of the variation. While this is appropriate when the aim is to maximise the explanatory power of the model, the overall importance of such variables as drivers of variation is arguable. Multiple regression models are therefore unlikely to be suitable for determining all strong drivers of variation out of a set of measured variables and subsequently classifying habitat types, i.e. discrete and distinctly different from each other, in a stringent manner based on these variables.

The present study identified discrete habitat types in general, and high-capacity habitat in particular, rele-

vant to the fish fauna in Port Phillip, Australia. For the purpose of this study, capacity of habitat to facilitate diversity (hereafter simply referred to as 'capacity') was related to values of variables associated with diversity indices. High capacity entailed high values of variables positively correlated, and low values of variables negatively correlated to diversity indices. Low capacity entailed low values of variables positively correlated, or high values negatively correlated to diversity indices. In a first step the effect of 24 separate habitat variables on 4 ecological indices describing local fish assemblages was investigated. The choice of habitat variables investigated was hypothesis driven: chosen habitat variables had been previously described in the literature as drivers of variation in fish assemblages. Because drivers of variation can operate at different spatial scales (MacNeil et al. 2009), the effect of habitat variables was assessed at both the level of individual transects and whole reefs. Variables strongly correlated to indices were used in cluster analyses to identify distinct habitat types and high-capacity habitat. The objective of identifying high-capacity habitat was process-based management, i.e. protection of processes between habitat features and assemblages that facilitate high diversity.

MATERIALS AND METHODS

The study was conducted in Port Phillip, Victoria, Australia (Fig. 1). Fish abundance and habitat variables were quantified along 4 transects on each of 12 discrete rocky reefs, hereafter termed 'sites', with 3 sites located in each of 4 regions (north, west, east, heads). Sites were defined as rocky bottom habitat, and individual sites were separated from one another by >1 km of soft sediment. Within a region, sites were separated from each other by <16 km. Although areas with rocky bottom were present between sites within a region, sites from different regions were separated from each other by >24 km of soft sediment bottom (Bay of Carrum between north and east, Dromana Bay between east and heads, Werribee Bank between north and west, Great Sands/Western Channel between west and heads; Fig. 1).

The depth of reefs ranged from 3 to 6 m, and the slope was <2 m over a distance of 25 m. Fish abundance was quantified using underwater visual census (SCUBA). Starting points and orientation of 25 m transects were haphazardly chosen before the dive. After transects were laid out on the reef, divers waited 3 min before counting commenced, which was determined as the most effective method to maximise fish counts during trials. Demersal reef fishes were counted up to 2.5 m to either side of the transect belt and up to 3 m

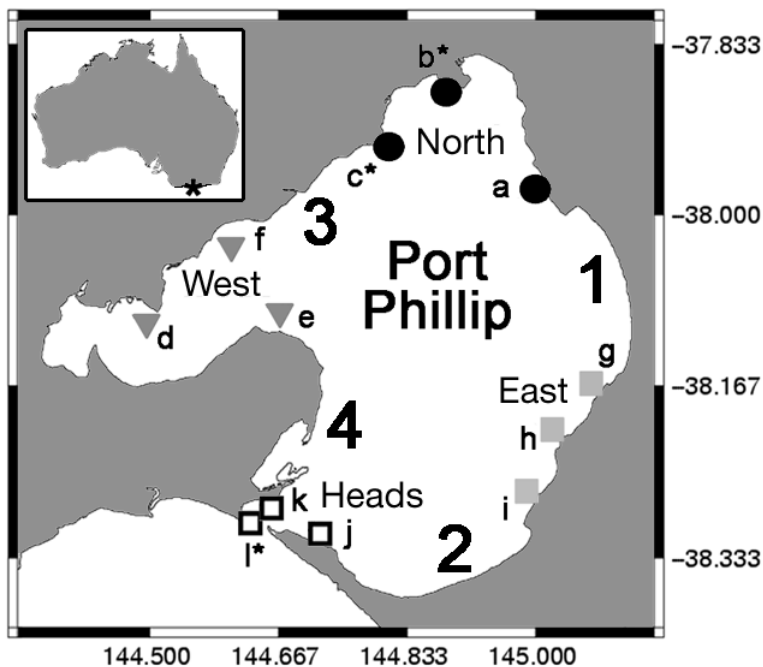


Fig. 1. Location of study system in Port Phillip, Victoria, Australia (asterisk on inset). Sampling sites in the respective regions — north (●): (a) Half Moon Bay, (b) Jawbone, (c) Point Cook; west (▼): (d) Point Wilson, (e) Steel Rock, (f) Kirk Point; east (■): (g) Mount Eliza, (h) Snapper Point, (i) Mount Martha; heads (□): (j) Point Franklin, (k) Dogbeach, (l) The Springs. No-take marine sanctuaries are indicated with asterisks. Soft-sediment areas separating regions — 1: Bay of Carrum; 2: Dromana Bay; 3: Werribee Bank; 4: Great Sands

ahead of the diver (Table 1); pelagic or cryptic species were not taken into account, due to the unsuitable sampling methodology. Two transects each were completed at respective sites on 2 separate occasions in the summers (November to March) of 2007/2008 and 2008/2009. All data were collected when only 1 diver was in the water, and the observer was the same throughout.

Habitat variables were quantified at both transect and reef scale. At the scale of transects, 15 habitat variables were quantified after each fish count (Table 2). These variables were quantified at stations located every 2 m along the transect belt and 2 m to each side, starting at 1 m. This resulted in a 24×4 m grid of 39 stations. Each station covered an area of 20×20 cm. Variables included bottom type (rock platform Δ height < 10 cm within 1 station; boulder Δ height > 10 cm within 1 station; soft sediment); abundance of invertebrates (abundance of Echinoidea, abundance of Gastropoda, abundance of Bivalvia, combined abundance of all macroinvertebrates); vegetation (percentage vegetation cover, abundance of Chlorophyta, abundance of Phaeophyta, abundance of seagrass); and structural complexity (number of refuges $> 10 \times 10 \times 10$ cm in volume; total volume of refuges $> 10 \times 10 \times 10$ cm in size; average volume per refuge; relief height). The dimensions for refuges were based on personal observations of refuge space utiliza-

tion by demersal reef fishes *in situ* and comprised overhangs and caves. Values for number of refuges and volume of refuges were attained for the space located beneath each station. Relief height was calculated from Δ depth between stations, measured with Suunto depth gauges. Volume per refuge and relief height were collinear (linear regression, adjusted $r^2 > 0.8$), and, thus, only relief height was included in the analysis due to its importance in other studies (McCormick 1994). Only the value of the most common type was noted for bottom type, invertebrate class and vegetation phylum, if > 1 type was present. Vegetation cover was estimated by eye in 10% steps at each station. Sufficient reliability of estimates was confirmed by comparing visual estimates with photo measurements in the laboratory during a pilot study. Total abundance of invertebrates also included separate colonies/individuals from the taxa Porifera, Ascidiacea, Hydrozoa (phylum Cnidaria) and Asterozoa (phylum Echinodermata), which were encountered at $< 5\%$ of stations and thus were not separately quantified. Values from all stations were averaged to attain 1 measure per transect per variable. Habitat variables quantified at the transect level were

also averaged at the reef level when used in analyses at the reef scale. Underwater cameras were present on all dives, and photos of specimens (fishes, invertebrates, algae) with uncertain identity were taken and later identified in the laboratory.

Nine habitat variables were quantified at the reef scale (Table 3). Variables included reef area, reef perimeter, distance to nearest reef, area of nearest reef, distance to nearest seagrass bed, area of nearest seagrass bed and distance to 10, 15 and 20 m water depth. The latter 3 variables were collinear to each other (linear regression, adjusted $r^2 > 0.8$); thus, only distance to 20 m water depth was included in the analysis, to maximise the variation in this parameter among reefs. All values for geographical features were extracted from Blake & Ball (2001).

Simple linear regression was used to determine the strength of the relationships between habitat variables and the 4 ecological indices of fish assemblage composition, at 2 separate levels of spatial resolution — reef level and transect level. Subsequently, all transects at respective sites ($n = 4$) were pooled for analysis on the reef level, and all transects at respective sites in respective regions ($n = 12$) were pooled for analysis on the regional level. The ecological indices calculated from the fish abundance data were: (1) species richness, (2)

Table 1. Average densities per 250 m² of the 5 most abundant species at respective sites

Site	Species and densities	Scobinichthys granulatus	Neodax balteatus	Upeneichthys vlamingii	Parma victoricae
Half Moon Bay	<i>Trachinops caudimaculatus</i> 240	4	2.5	1.5	1
Jawbone	<i>Girella zebra</i> 47.5	<i>Trachinops caudimaculatus</i> 14.5	<i>Meuschenia hippocrepis</i> 1.5	<i>Parma victoricae</i> 1	<i>Scobinichthys granulatus</i> 1
Point Cook	<i>Trachinops caudimaculatus</i> 38.5	<i>Girella zebra</i> 15	<i>Dactylophora nigricans</i> 2	<i>Tilodon sexfasciatus</i> 2	<i>Upeneichthys vlamingii</i> 1
Point Wilson	<i>Girella zebra</i> 45	<i>Trachinops caudimaculatus</i> 16.5	<i>Tilodon sexfasciatus</i> 8.5	<i>Parma victoricae</i> 2.5	<i>Siphemia cephalotes</i> 1.5
Steel Rock	<i>Trachinops caudimaculatus</i> 93.5	<i>Siphemia cephalotes</i> 16.5	<i>Neodax balteatus</i> 13.5	<i>Vincentia conspersa</i> 2	<i>Diodon nichthemerus</i> 1.5
Kirk Point	<i>Trachinops caudimaculatus</i> 165	<i>Neodax balteatus</i> 8	<i>Siphemia cephalotes</i> 7	<i>Brachaluteres jacksonianus</i> 2.5	<i>Notolabrus tetricus</i> 1
Mount Eliza	<i>Trachinops caudimaculatus</i> 687.5	<i>Siphemia cephalotes</i> 44	<i>Meuschenia hippocrepis</i> 21.5	<i>Neodax balteatus</i> 17	<i>Girella zebra</i> 14.5
Mount Martha	<i>Trachinops caudimaculatus</i> 310	<i>Scobinichthys granulatus</i> 50.5	<i>Siphemia cephalotes</i> 12.5	<i>Enoplosus armatus</i> 12	<i>Neodax balteatus</i> 8
Snapper Point	<i>Trachinops caudimaculatus</i> 1975	<i>Neodax balteatus</i> 12.5	<i>Tilodon sexfasciatus</i> 8	<i>Scobinichthys granulatus</i> 6	<i>Upeneichthys vlamingii</i> 5.5
Point Franklin	<i>Notolabrus tetricus</i> 15	<i>Upeneichthys vlamingii</i> 7	<i>Scobinichthys granulatus</i> 6.5	<i>Siphemia cephalotes</i> 4	<i>Neodax balteatus</i> 3
Dogbeach	<i>Notolabrus tetricus</i> 5.5	<i>Scobinichthys granulatus</i> 3.5	<i>Upeneichthys vlamingii</i> 3.5	<i>Parma victoricae</i> 2	<i>Notolabrus fucicola</i> 1
The Springs	<i>Notolabrus tetricus</i> 36.5	<i>Parma victoricae</i> 9.5	<i>Meuschenia hippocrepis</i> 4	<i>Pempheris multiradiata</i> 3	<i>Girella zebra</i> 3

total abundance of fishes, (3) Shannon's H and (4) Simpson's λ (Legendre & Legendre 1998). The goal of these analyses was parameter selection, i.e. to identify the likely potent drivers of variation in assemblage composition; thus, only habitat variables with adjusted $r^2 > 0.6$ were included in subsequent cluster analyses.

To classify habitat types at the reef and transect scales, 4 separate cluster analyses were conducted. Cluster analysis mitigates effects of collinearity of variables, because contributions to among-group differences of variables decrease with increasing collinearity. Unweighted arithmetic average clustering (UAAC) was used because it is hierarchical and does not misclassify objects (Legendre & Legendre 1998). In UAAC, clusters are based on calculation of the average similarity of the individual nodes for every new node, and numbers of clusters are determined by the dissimilarity of data and not by prior definition of cluster number. UAAC results in an intermediate model between the inclusive (great distance between few clusters) and exclusive (little distance between many clusters) extremes. Four cluster analyses were conducted based on: (1) all variables at the reef scale that correlated with at least 1 ecological index (Model 1), (2) all variables at the reef scale that correlated with at least 3 ecological indices (Model 2), (3) all variables at the transect scale that correlated with at least 1 ecological index (Model 3) and (4) all variables at the transect scale that correlated with at least 3 ecological indices (Model 4). Multiple models were created to validate potential spatial patterns and thus enhance confidence in interpretation of results.

Because different cluster analyses result in a different numbers of clusters, and, consequently, not all clusters are necessarily significantly different from each other in a statistical manner, cluster identities were used as a fixed factor in a 1-factor permutational multivariate ANOVA (PERMANOVA), to confirm differences among present UAAC clusters ($p < 0.05$). PERMANOVA included the same variables used in the cluster analyses. Bonferroni adjusted post hoc tests were used to control for multiple testing. Principal components ordination of the first 2 axes was used to determine which habitat variables were most important in separating clusters.

Table 2. Environmental variables quantified at the scale of individual transects. Variables that were removed from the analysis due to collinearity with another variable are underlined. Variables with a correlation >0.6 with any ecological index are in **bold**

Transect variable	Ecological importance	Predicted relationship to indices	Source
Percentage rock platform	Decreased structural complexity	–	Almany (2004)
Percentage boulder	Microhabitat type, increased structural complexity	+	Almany (2004)
Percentage soft sediment	Decreased structural complexity	–	Almany (2004)
Abundance Echinoidea	Habitat alteration, i.e. removal of macroalgae	–	Baxter et al. (2005)
Abundance Gastropoda	Competition for resources, food item	+	Baxter et al. (2005)
Abundance Bivalvia	Competition for resources, food item	+	Baxter et al. (2005)
Abundance invertebrates	Competition for resources, food item	–	Baxter et al. (2005)
Percentage vegetation cover	Structural complexity, microhabitat type, food item	+	Bergman et al. (2001)
Abundance Chlorophyta	Structural complexity, microhabitat type, food item	+	Bergman et al. (2001)
Abundance Phaeophyta	Structural complexity, microhabitat type, food item	+	Bergman et al. (2001)
Abundance seagrass	Structural complexity, microhabitat type, food item	+	Bergman et al. (2001)
Number of refuges	Structural complexity, microhabitat type	+	García-Charton & Perez-Ruzafa (2001)
Volume of refuges	Structural complexity	+	García-Charton & Perez-Ruzafa (2001)
<u>Average volume per refuge</u>	Structural complexity	+	García-Charton & Perez-Ruzafa (2001)
Relief height	Structural complexity	+	García-Charton & Perez-Ruzafa (2001)

Table 3. Environmental variables quantified at the scale of individual reefs. Variables that were removed from the analysis due to collinearity with another variable are underlined. Variables with a correlation >0.6 with any ecological index are in **bold**

Reef variable	Ecological importance	Predicted relationship to indices	Source
Reef area	Number of microhabitat types	+	MacNeil et al. (2009)
Reef perimeter	Edge effect	+	Dorenbosch et al. (2005)
Distance to nearest reef	Connectivity of subpopulations	+	Dorenbosch et al. (2006)
Area of nearest reef	Connectivity of subpopulations	+	Dorenbosch et al. (2006)
Distance to nearest seagrass bed	Connectivity of subpopulations, microhabitat type, nursing ground	+	Jenkins & Wheatley (1998), Dorenbosch et al. (2006)
Area of nearest seagrass bed	Connectivity of subpopulations, microhabitat type, nursing ground	+	Jenkins & Wheatley (1998), Dorenbosch et al. (2006)
<u>Distance to 10 m water depth</u>	Food and larval supply, connectivity of subpopulations, microhabitat type	+	Hamer & Jenkins (2004)
<u>Distance to 15 m water depth</u>	Food and larval supply, connectivity of subpopulations, microhabitat type	+	Hamer & Jenkins (2004)
Distance to 20 m water depth	Food and larval supply, connectivity of subpopulations, microhabitat type	+	Hamer & Jenkins (2004)

All abundance data were 4th root transformed, and all environmental data were normalised following Quinn & Keough (2002). All mathematical distances given are based on Euclidian distances. All statistical analyses were performed with SYSTAT12 and PRIMER6 + PERMANOVA.

RESULTS

At the transect scale, 5 variables were strongly correlated to at least 1 index (Table 4): percentage vegetation cover, abundance of Phaeophyta, number of refuges, volume of refuges and relief height. Abun-

dance of Phaeophyta and relief height were both strongly correlated to 3 or more indices. At the reef scale, 9 variables correlated strongly to at least 1 index: distance to nearest seagrass bed, distance to 20 m water depth, abundance of Echinoidea, abundance of Gastropoda, percentage vegetation cover, abundance of Phaeophyta, number of refuges, volume of refuges and relief height. All but abundance of Echinoidea and Gastropoda were strongly correlated to 3 or more ecological indices (Table 4). At both the transect and reef scales, several variables were not strongly correlated to any indices ($n = 7$ and 5 , respectively), thus being unlikely strong drivers of variation in the fish assemblage. At the transect scale, these variables were: per-

Table 4. Adjusted r^2 values from linear regressions between ecological indices and all habitat variables at both the reef and transect levels. Only habitat variables correlating to ≥ 1 ecological index are given. Variables correlating with ≥ 3 ecological indices are in **bold**

Variables	Species richness	Total abundance	Shannon's H	Simpson's λ
Reef level				
Distance to nearest seagrass	0.798	0.888	0.670	<0.6
Distance to 20 m water depth	-0.662	<0.6	-0.732	-0.706
Abundance Echinoidea	<0.6	<0.6	-0.73	-0.857
Abundance Gastropoda	0.631	0.631	<0.6	<0.6
Percentage vegetation cover	0.645	<0.6	0.755	0.785
Abundance Phaeophyta	0.901	0.829	0.907	0.826
Number of refuges	0.810	0.790	0.745	0.605
Volume of refuges	0.796	0.758	0.744	0.628
Relief height	0.867	0.838	0.801	0.655
Transect level				
Percentage vegetation cover	<0.6	<0.6	0.606	<0.6
Abundance Phaeophyta	0.692	0.674	0.667	<0.6
Number of refuges	<0.6	0.615	<0.6	<0.6
Volume of refuges	0.601	0.610	<0.6	<0.6
Relief height	0.706	0.709	0.645	<0.6

centage of rock platform, boulders or soft sediment as bottom type, abundance of Bivalvia, combined abundance of all invertebrates, abundance of Chlorophyta and abundance of seagrass. At the reef scale, they were: reef area, reef perimeter, area of and distance to nearest reef and area of nearest seagrass bed.

Two variables, abundance of Phaeophyta and relief height, correlated with 3 or more ecological indices at both spatial scales. For both variables, the correlations were positive. Overall, the percentage of strong correlations (>3 indices) between habitat variables and ecological indices was higher at the reef than at the transect scale (30 vs. 13%). However, out of 9 variables correlating with indices at the reef scale, only 2 were reef-scale variables, while 7 were transect-scale variables (Table 4).

The UAAC revealed variation in cluster number (Table 5). In Model 1 (Fig. 2), the 12 reefs were grouped into 3 clusters, with capacity decreasing from Cluster A to C. Abundance of Echinoidea, percentage vegetation cover and volume of refuges were the most important drivers of separation among clusters. In Model 2 (Fig. 3) reefs were grouped into 4 clusters, with capacity decreasing from Cluster A to D to C to B. Distance to 20 m water depth, percentage vegetation cover and volume of refuges were the most important drivers of separation among clusters. In

Model 3 (Fig. 4), the 48 transects grouped into 5 clusters, with diversity decreasing from Cluster D to E to C to A/B. Although Clusters A and B were distinct, differences in variables were inconsistent; thus, no cluster ranked higher in capacity. The most important drivers of separation among clusters in this model were percentage vegetation cover and number of refuges. Model 4 (Fig. 5) revealed 2 clusters, with Cluster A having a higher capacity than Cluster B. In this model, the abundance of Phaeophyta was the most important driver of separation between clusters.

When cluster identities were used as factors in PERMANOVAs, only 1 cluster comparison in Model 3 (comparison between Clusters B and D) was marginally non-significant (Table 6). This was likely an effect of low power, as the pairwise comparison comprised only 3 transects overall.

Analysis of cluster identities revealed several spatial patterns. Regardless of the analysis, 3 reefs grouped as having low-capacity habitats (regions N, W, E and H: north, west, east and heads, respectively; see Fig. 1): Jawbone (N), Point Wilson (W) and Kirk Point (W). An analysis with higher spatial resolution demonstrated that these reefs were uniformly comprised of low-capacity habitat (Table 5; Models 3 and 4). Five reefs could be classified as having intermediate-capacity habitat. Although some of these reefs clustered together with the aforementioned low-capacity reefs when analysed at the reef scale (Table 5; Models 1 and 2), increased spatial resolution of the analysis revealed that they contained areas

Table 5. Respective cluster identities (A to E) from the 4 separate analyses—Model 1: reef level, all variables correlating to ≥ 1 ecological index; Model 2: reef level, all variables correlating to ≥ 3 ecological indices; Model 3: transect level, all variables correlating to ≥ 1 ecological index; Model 4: transect level, all variables correlating to ≥ 3 ecological indices. See Fig. 1 for site locations

Region	Site	Model 1	Model 2	Model 3	Model 4
North	Half Moon Bay	C	C	C, C, A, A	B, B, B, B
	Jawbone	C	B	A, A, A, A	B, B, B, B
	Point Cook	C	C	A, C, C, C	B, B, B, B
West	Point Wilson	C	B	A, A, A, A	B, B, B, B
	Steel Rock	C	C	C, C, A, A	A, A, B, B
	Kirk Point	C	B	A, A, A, A	B, B, B, B
East	Mount Eliza	A	A	E, E, C, C	A, A, A, A
	Mount Martha	A	A	E, E, C, C	A, A, A, A
	Snapper Point	A	A	E, E, E, E	A, A, A, A
Heads	Point Franklin	B	D	C, C, C, C	B, A, A, A
	Dogbeach	B	D	B, B, C, C	B, B, A, A
	The Springs	A	A	E, D, C, C	A, A, A, A

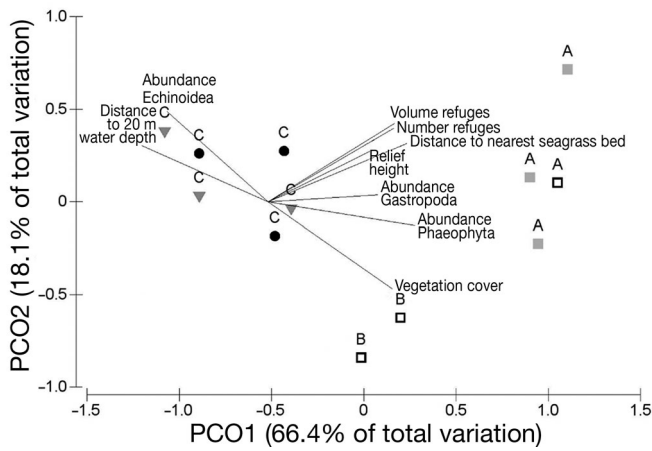


Fig. 2. Principal component ordination (PCO) of Model 1, including the separating variables between significantly different clusters, A to C ($F_{2,9} = 12.871$, $p = 0.001$). Letters indicate significant among-group differences for reefs in the north (●), west (▼), east (■) and heads (□) regions

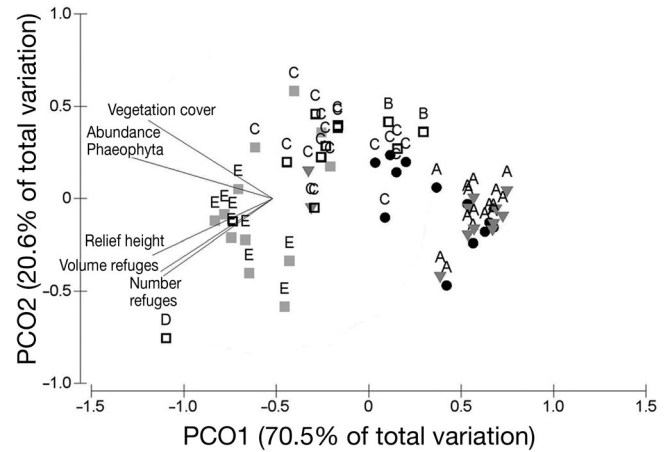


Fig. 4. Principal component ordination (PCO) of Model 3, including the separating variables between significantly different clusters, A to E ($F_{4,43} = 44.447$, $p = 0.001$). Letters indicate significant among-group differences for reefs in the north (●), west (▼), east (■) and heads (□) regions

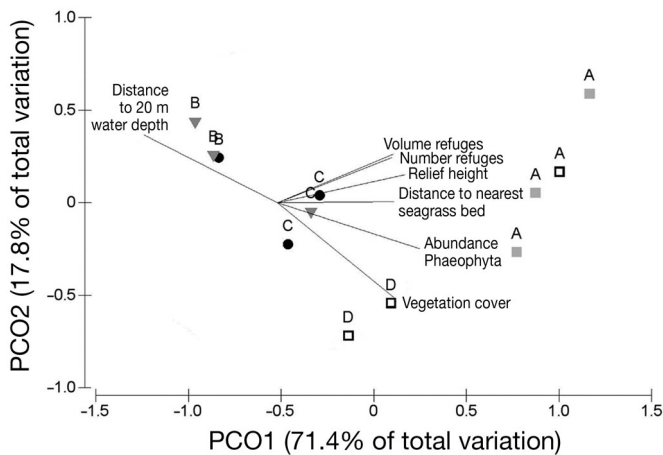


Fig. 3. Principal component ordination (PCO) of Model 2, including the separating variables between significantly different clusters, A to D ($F_{3,8} = 13.682$, $p = 0.001$). Letters indicate significant among-group differences for reefs in the north (●), west (▼), east (■) and heads (□) regions

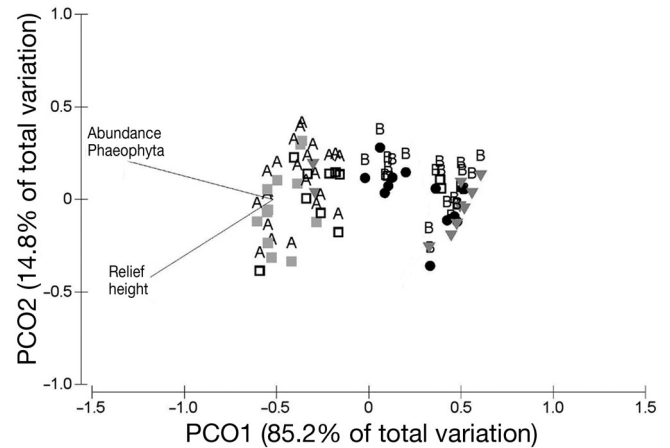


Fig. 5. Principal component ordination (PCO) of Model 4, including the separating variables between significantly different clusters, A and B ($F_{1,46} = 116.560$, $p = 0.001$). Letters indicate significant among-group differences for reefs in the north (●), west (▼), east (■) and heads (□) regions

of both low- and high-capacity habitat (Table 4; Model 3). Reefs belonging to this group were Half Moon Bay (N), Point Cook (N), Steel Rock (W), Point Franklin (H) and Dogbeach (H). Only 4 reefs comprised high-capacity habitat. However, 3 of these reefs included patches of intermediate-capacity habitat (Table 5; Model 3). These sites were Mount Eliza (E), Mount Martha (E) and The Springs (H). Only 1 site, Snapper Point (E), uniformly consisted of high-capacity habitat in all analyses, even at the transect level, with consistently high numbers of refuge spaces, large refuges, great relief height, high vegetation cover, low abundance of Echinoidea and a short distance to deeper water.

DISCUSSION

The present study revealed strong positive effects of small-scale habitat features. Structural complexity was likely a strong driver of diversity variation in the observed ichthyofauna. This is in line with previous studies from a variety of systems. Structural complexity of the habitat has been shown to improve measures of fish assemblages in rivers (Brooks et al. 2004), coral reefs (Almany 2004) and temperate rocky reefs (García-Charton & Perez-Ruzafa 2001), likely by increasing the provision of shelter from physical stressors (Steele 1999) or predation (Stunz & Minello 2001) or by increa-

Table 6. PERMANOVA results for differences between cluster identities

Model	Source	df	SS	F	p	Groups	t	p
Model 1	Cluster identity	2	8.249	12.871	0.001	C, A	4.437	0.001
	Error	9	2.884			C, B	2.913	0.008
Model 2	Cluster identity	3	7.682	13.871	0.001	A, B	2.435	0.013
	Error	8	1.477	C, B	3.438	0.007		
				C, A	3.520	0.005		
				C, D	3.169	0.016		
				B, A	4.725	0.001		
B, D	5.206	0.002						
A, D	2.585	0.028						
Model 3	Cluster identity	4	14.827	44.447	0.001	C, A	8.829	0.001
	Error	43	3.586			C, E	5.139	0.001
Model 4	Cluster identity	1	6.629	116.560	0.001	C, B	2.663	0.001
						C, D	4.084	0.001
						A, E	11.94	0.001
						A, B	4.789	0.001
						A, D	7.929	0.001
						E, B	4.895	0.001
						E, D	2.239	0.009
						B, D	6.240	0.070
Error	46	2.616			B, A	10.796	0.001	

sing the number of microhabitat types (Green 1996). The importance of structural complexity as a driver of variation is underscored by the fact that all 3 different measures of complexity—the number and volume of refuges, and relief height as a proxy for vertical structure—correlated to multiple ecological indices. Relief height was 1 of only 2 habitat variables that correlated to 3 or more ecological indices at both spatial scales, further underpinning its likely importance in affecting fish assemblages.

The present study found that vegetation cover and abundance of Phaeophyta algae was strongly and positively correlated to indices of the ichthyofauna. This also corroborates previous studies (Priyadarshana et al. 2001). Among the benefits of high macroalgal cover are provision of structural complexity (Diehl 1992), which, in turn, can affect fish abundance and diversity (Bergman et al. 2001), microhabitat types (Adams et al. 2004) and positive effects on predator–prey interactions (Flynn & Ritz 1999). The percentage of vegetation cover was correlated to indices at both levels of spatial resolution, whereas the abundance of Phaeophyta was strongly correlated to 3 or more indices on both spatial levels, highlighting both the importance of vegetation in general, but, in particular, the strong positive effects of canopy-forming macroalgae (Fernandez et al. 2009) in providing tertiary structure. Decreasing water quality, often associated with anthropogenic effects, may lead to declines in or disappearance of such assemblages (Shepherd et al. 2009). Consequently, conservation efforts that focus on protecting areas with high

Phaeophyta abundance (Shears & Babcock 2003) may be more effective at conserving fish assemblages than the protection of areas with beneficial, but static, habitat features, such as the structural complexity of the reef matrix. Such considerations are often not part of decision-making processes currently using software applications to design marine reserves.

The overall importance of habitat variables operating at a small spatial scale, e.g. structural complexity or abundance of Phaeophyta, is further underscored by the fact that variables quantified at the transect level and subsequently pooled correlated proportionally more often than variables quantified only at the reef level. Moreover, the variables correlating with 3 or more ecological indices at both levels of spatial resolution—abundance of Phaeophyta and relief height—were variables operating at the spatial scale of a transect.

This suggests that some habitat variables that exhibit variation at small spatial scales are likely important drivers of variation in fish assemblages (Ohman & Rajasuriya 1998) at various spatial scales and hence important defining properties of habitat types.

The present study demonstrates a statistically rigorous and ecologically meaningful multi-step approach for the classification of habitat types and high-capacity habitat. This approach has the overall advantage that discrete and, importantly, ecologically relevant habitat types, in this case relevant to the ichthyofauna on rocky reefs, can be established. Naturally, the definition of high-capacity habitat is relative and dependent on the spatial extent and target taxa of the study. Ultimately, this demonstrates the flexibility of the described method, as it can be applied to a multitude of systems. Habitat types can be substantiated at small spatial scales, i.e. 10s of meters. This is important because space designated for protection is often limited. As habitat types can be determined at a sub-reef scale, candidate areas for management can be determined at a spatial scale smaller than whole reefs. The method allows not only the location of particular types of habitat, but also the identification of high-capacity habitat based on defensible ecological criteria, and it discloses what properties high-capacity habitats have.

Scientifically sound approaches to identify priority areas for conservation based solely on species distribution have been proposed and executed (Edgar et al. 2008). However, process-based planning, primarily not elucidating the distribution of species, but establishing

which underlying processes facilitate variation in diversity and subsequently focussing on protecting these, is less common (Roberts et al. 2003). The present study demonstrates how knowledge of ecological processes can inform management decisions. Protection of high-capacity reefs or reef patches, containing perishable properties, i.e. abundant macroalgae, might be preferable over protection of areas with unchanging properties, i.e. high complexity. Such management is superior to measures based on descriptive research, i.e. simple diversity assessment, as it takes the underlying ecological processes facilitating the observed variation of diversity into consideration, thus enabling a protection of these and sustaining high levels of diversity.

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