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# The Importance of Regional, System-Wide and Local Spatial Scales in Structuring Temperate Estuarine Fish Communities

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## Abstract

An extensive literature base worldwide demonstrates how spatial differences in estuarine fish assemblages are related to those in the environment at (bio)regional, estuary-wide or local (within-estuary) scales. Few studies, however, have examined all three scales, and those including more than one have often focused at the level of individual environmental variables rather than scales as a whole. This study has identified those spatial scales of environmental differences, across regional, estuary-wide and local levels, that are most important in structuring ichthyofaunal composition throughout south-western Australian estuaries. It is the first to adopt this approach for temperate microtidal waters. To achieve this, we have employed a novel approach to the BIOENV routine in PRIMER v6 and a modified global BEST test in an alpha version of PRIMER v7. A combination of all three scales best matched the pattern of ichthyofaunal differences across the study area ( $\rho = 0.59$ ;  $P = 0.001$ ), with estuary-wide and regional scales accounting for about twice the variability of local scales. A shade plot analysis showed these broader-scale ichthyofaunal differences were driven by a greater diversity of marine and estuarine species in the permanently-open west coast estuaries and higher numbers of several small estuarine species in the periodically-open south coast

estuaries. When interaction effects were explored, strong but contrasting influences of local environmental scales were revealed within each region and estuary type. A quantitative decision tree for predicting the fish fauna at any nearshore estuarine site in south-western Australia has also been produced. The estuarine management implications of the above findings are highlighted.

Keywords: Estuaries, Spatial scale, Fish assemblages, BIOENV, Faunal prediction

## **Introduction**

Many studies throughout the world have examined how the structure of estuarine fish communities is influenced by environmental differences at regional scales (hundreds to thousands of kilometers; e.g. Harrison 2002, 2004; Harrison and Whitfield 2006a, b, 2008), estuary-wide scales (tens to hundreds of kilometers; e.g. Edgar et al. 1999; Saintilan 2004; Harrison and Whitfield 2008) or local scales (habitats or ecounits, 0.1–1 km; e.g. Valesini et al. 1997; Nobriga et al. 2005; Ramos et al. 2006).

Within this large body of work, it is generally perceived that broader-scale regional differences act as the primary influence on these faunal assemblages (i.e. given the potential for shifts in biogeography and/or climate) and that, within regions, estuary-scale differences such as estuarine morphology and bar type exert a major influence. The more detailed, site-specific differences in estuarine fish faunas are typically considered to be related to local-scale factors, such as salinity, substrate composition and the type of any submerged vegetation present (e.g. Whitfield 1999). Metacommunity theory further proposes that the influence of processes at nested spatial scales are interconnected, in that communities at local scales are influenced not only by site-specific processes, but also by those operating at broader scales (e.g. Leibold et al. 2004; Sanvicente-Añorve et al. 2011). The validity of this concept is clearly demonstrated by Witman et al. (2004) in their global study of marine epifaunal diversity at regional and local scales.

It is rarely the case, however, that environmental factors ranging across all three of the above spatial scales are tested, in combination, to quantify their relative importance in ‘explaining’ spatial differences among estuarine fish faunas. Moreover, when factors across multiple scales are examined, they are typically tested at the level of individual environmental variables rather than as a collective group representing a scale as a whole. For example, in an extensive study of the fish assemblages in 190 estuaries throughout South Africa, Harrison and Whitfield (2006a) demonstrated that species composition differed significantly between most estuarine types (i.e. permanently-open, small normally-closed and moderate to large normally-closed estuaries) within each of the three bioregions along the coast. They also showed that the pattern of those differences was largely consistent among bioregions. However, that study did not compare the relative importance of bioregions vs estuarine types in structuring estuarine fish faunas—the latter was simply, and intuitively, tested within the former. While later analyses of these data did include tests for differences in fish guild contributions between estuary types within each bioregion and vice versa (Harrison and Whitfield 2008), focus was again not placed on an explicit comparison of the importance of each spatial scale. Moreover, whereas Edgar et al. (1999) and Nicolas et al. (2010) both rigorously identified the combination of individual environmental variables at a system-wide and, to a lesser extent, regional scale<sup>1</sup> that best reflected spatial differences in the fish faunas across many estuaries throughout Tasmania (71) and Europe (135), respectively, they also did not aim to quantify the relative importance of those scales or include local-scale factors. While Sanvicente-Añorve et al. (2011) did test how spatial scales, as a whole, differ in their ability to explain differences in estuarine fish faunas along the Mexican Atlantic coast, they included only inter-estuary and, to a lesser extent, regional scales in their study. Several other studies, such as that of Ley (2005), have also examined linkages between estuarine fish faunas and environmental factors at different spatial scales, but are lacking in one or more of the above criteria.

One study that has focused on testing how collective environmental differences at local, inter-estuary, regional and also climatic scales each differ in their ability to explain spatial variation in estuarine fish faunas, is that undertaken by Sheaves and Johnston (2009) across 21 meso- to macro-tidal estuaries in tropical north-eastern Australia. These workers demonstrated that estuary-scale differences were far

more important in structuring estuarine fish assemblages than other scales, and particularly the broader regional and climatic levels. By correlating spatial differences in the environment with those in faunal assemblages at the scale level rather than individual variables, these authors were able to make reliable generalisations about the level at which the majority of faunal variability is occurring, and logically refine which environmental processes are key from a conservation standpoint.

The aim of this study was to quantify the relative importance of collective environmental differences at regional, estuary-wide and site-specific scales (subsequently referred to as ‘environmental layers’) in structuring the composition of nearshore fish assemblages in five divergent estuaries throughout south-western Australia. It is the first study to examine statistically how environmental attributes across all three of the above spatial scales influence the distribution of estuarine fish assemblages in a temperate microtidal area, with a focus on quantifying the relative effect of each scale rather than their representative variables.

## **Methods**

### **Study Area**

The south-western coast of Australia experiences a Mediterranean climate, comprising cool wet winters and hot dry summers (Gentilli 1971) with 60–80 % of rainfall occurring between May and September (Table 1; Hodgkin and Hesp 1998). It has predominantly diurnal tides with a spring range of only ~0.6–0.8 m (Ranasinghe and Pattiaratchi 1999; Department of Defence 2011), and is thus classified as microtidal (Davies 1964). The total offshore wave climate is characterised by mean significant wave heights of 1.8 m in summer and 2.8 m in winter (Masselink and Pattiaratchi 2001). The energy of offshore waves approaching the lower west coast is attenuated by an average of ~60 % due to an extensive chain of limestone reefs that runs parallel to the shoreline and other nearshore features such as sand banks, islands and headlands (Sanderson and Eliot 1996; Masselink and Pattiaratchi 2001). Although localised aspects of the coastal bathymetry and morphology partially

attenuate offshore waves approaching the south coast of Western Australia, this is typically far less than along the lower west coast.

An atypical eastern boundary current, the Leeuwin Current, flows poleward along the continental shelf of Western Australia (Batteen and Miller 2009) and carries warm, low salinity surface waters from the tropical north of the state. This results in the southward extension of many tropical marine fish species with pelagic life cycle phases into the temperate waters of south-western Australia, some of which may use estuaries as juveniles or infrequently as adults (Hutchins and Pearce 1994; Beckley et al. 2009).

The five estuaries in this study were distributed throughout south-western Australia and differed markedly in their physical characteristics (Table 1, Fig. 1). They can be broadly characterised by (1) whether they are located on the lower west coast (Swan–Canning and Peel–Harvey estuaries) or south coast (Broke Inlet, Wilson Inlet and Wellstead Estuary) of Western Australia and (2) the frequency with which their mouths are open to the sea, i.e. permanently-open (Swan–Canning and Peel–Harvey estuaries), seasonally-open (Broke and Wilson inlets) or normally-closed (Wellstead Estuary). These broad differences have led to wide variations in a range of local-scale or site-specific factors within these estuaries and, in particular, (1) the relative extent to which sites are predisposed to receiving marine vs fresh waters, (2) exposure to wave activity generated by local winds and (3) the composition of the substrate and any submerged vegetation. A large number of nearshore sites (where a site is defined as all waters within a 100 m radius of a central point on the shoreline) were thus initially chosen throughout each estuary to adequately represent the full range of environmental diversity across these three local-scale layers, i.e. 101 sites in the Swan–Canning Estuary, 102 sites in the Peel–Harvey Estuary, 104 sites in Broke Inlet, 60 sites in Wilson Inlet and 34 sites in the Wellstead Estuary. These sites, which were spaced 400–2,500 m apart depending on the degree of environmental heterogeneity, were chosen through visual assessment of high-resolution remotely sensed images of each system (1 pixel = 0.4–2.4 m) and several field reconnaissance trips.

## **Data for Environmental Layers**

The environmental layers considered in this study ranged in spatial scale from regional (coast type, i.e. west or south) to estuary-wide (bar type, i.e. permanently-open, seasonally-open or normally-closed) to local (potential influence of marine vs fresh waters, potential exposure to wave activity and substrate/submerged vegetation type). The regional and estuary-wide environmental layers were clearly categorical. As such, sampling sites were coded as “1” if a category was applicable and “0” if it was not. However, the three local-scale layers, which were represented by a suite of enduring environmental features to ensure their applicability at any temporal scale and facilitate easy and accurate measurement from readily available mapped data (e.g. remotely sensed images or bathymetric charts), required fully quantitative measurement.

The full details of the methods for measuring each of the representative variables in the ‘potential exposure to wave activity’ and ‘substrate/submerged vegetation type’ local-scale layers are given in Valesini et al. (2010). The wave exposure layer comprised measurements for modified effective fetch in each cardinal direction (north, south, east and west fetch) and that along the bearing perpendicular to the beach aspect (direct fetch), distance to the wave shoaling margin (1–2 m depth contour) and slope of the substrate. The benthic habitat layer comprised the percentage cover at each site of bare unconsolidated substrate, submerged aquatic vegetation (seagrass and macroalgae combined; see Table 1 for species names), rock, submerged fallen tree branches (snags), submerged artificial structures such as jetty pylons, beds of large dead bivalve shells and littoral vegetation extending into the shallows (reeds and samphire; see Table 1 for species names).

The remaining local-scale layer, namely the ‘potential influence of marine vs fresh waters’ (hereafter, the ‘marine/freshwater ratio’), was considered a surrogate for the numerous water quality parameters that typically change spatially throughout an estuary due to differences in the proportion of tidal to riverine input (e.g. salinity, temperature, dissolved oxygen concentration, water colour etc.). This layer was represented by a single variable scaled between 0 (marine) and 1 (freshwater). The method for quantifying this layer was modified from that in Valesini et al. (2010) to better standardise the measurements between those estuaries with essentially linear morphologies (i.e. the Swan–Canning

and Wellstead estuaries, where the marine and fresh water sources are located at opposite ends of the system), and those with non-linear morphologies (i.e. the Peel–Harvey Estuary and the Broke and Wilson inlets). Thus, in each estuary, a line was drawn down the middle longitudinal axis of the system from the mouth(s) to the limit of tidal influence in the river(s), and the marine/freshwater ratio calculated by dividing a sites' distance to the ocean, as measured along that line, by the length of the full line. Note that where there were multiple longitudinal lines within a system, the ratio for any given site was calculated using the line which extended from the nearest river/mouth.

### **Fish Faunal Sampling**

Samples of the fish in nearshore shallow waters ( $\leq 1.5$  m deep) were collected throughout each of the five estuaries at a representative subset of those sites at which the above local-scale environmental layers were measured, i.e. 23 sites in the Swan–Canning Estuary, 24 sites in the Peel–Harvey Estuary, 47 sites in Broke Inlet, 16 sites in Wilson Inlet and 12 sites in the Wellstead Estuary. In each system, the selected sites were spread throughout the estuary from its mouth to the upstream extent of tidal influence (Fig. 1). Fish were sampled during the day in the last month of six to eight seasons, at least four of which were consecutive, over 2 years between the Austral autumn of 2005 and Austral spring of 2009. Four randomly located replicate samples were collected from each site in each sampling season, except in Broke Inlet, where two replicate samples were taken from each site. Collection of the replicates in each estuary was staggered over 1–3 weeks in each sampling season to obtain a better representation of intra-seasonal variability and reduce the influence of any atypical catches on the resultant dataset.

Fish were collected using a 21.5 m long and 1.5 m high seine net, comprising 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m long central bunt (3 mm mesh), which swept an area of 116 m<sup>2</sup>. Whenever a large number of a species was collected in a replicate sample, a random subsample of 50–100 individuals were retained and the remainder counted and returned live to the water. All retained fish were immediately euthanised, stored in an ice slurry and then frozen.



In the laboratory, the total number of individuals of each fish species in each replicate sample was recorded. Each species was also assigned to an estuarine usage functional guild using the classification of Potter et al. (2013).

### **Data Analyses**

All of the following analyses were carried out using the PRIMER v6 multivariate statistics package (Clarke and Gorley 2006) with the exception indicated in the 'Statistical analyses' subsection.

### **Data Pre-treatment**

The number of individuals of each fish species in each sample was first subjected to dispersion weighting (Clarke et al. 2006). This procedure divides the counts for each species by their index of dispersion  $D^-$  (variance to mean ratio, or a 'clumping' measure) to differentially downweight the contributions of those species that exhibit pronounced replicate-to-replicate variability, such as highly-schooling species. In order to focus only on any spatial differences in the fish fauna, the dispersion-weighted data were then averaged for each site across the various seasons and years.

The local-scale enduring environmental data at each site was firstly used to construct scatterplots (draftsman plots) between each pair of environmental variables to provide (1) a visual basis for assessing whether the data distribution for any variable was notably skewed and thus for selecting an appropriate transformation to ameliorate any such effect and (2) calculations of the correlation between each pair of variables. The percentage contribution of bare sand was highly correlated with that of several other substrate/submerged vegetation variables, and was thus excluded from subsequent analyses. All remaining local-scale variables required a  $\log_e(N + 1)$  transformation, except for the marine/freshwater ratio which was square-root transformed. Note that the regional and estuary-wide data were not included in the draftsman plots because they were categorical rather than quantitative.

All environmental data for each sampling site across the regional, estuary-wide and local scales were then compiled and subjected to normalisation to place each variable on the same (dimensionless)

scale. Each variable was then weighted using the methods described in Valesini et al. (2010) to ensure that each environmental layer had equal opportunity to contribute to the subsequent analyses.

## Statistical Analyses

The main steps in the statistical approach to address the study aim were as follows.

1. Identify the natural and significantly different ‘breaks’ (groups) in the composition of the fish fauna across the whole study area in order to define a pattern of their spatial differences that provides a reliable reference base for exploring fish–environmental scale relationships.
2. Identify which fish species best characterise each significantly different group of fish fauna.
3. Determine which combination of environmental scales (layers) are best correlated with the full spatial pattern of ichthyofaunal differences across the study area, and ascertain the relative importance of each selected scale.
4. Explore whether any fish–environmental scale correlations, which may not be readily apparent across the full pattern of ichthyofaunal differences explored in (3) above, are more evident when localised to just particular subsets of the data.

To address the first of these steps, the dispersion-weighted fish species abundance data, averaged for each site, was initially used to construct a Bray–Curtis resemblance matrix defining site-to-site similarities (Bray and Curtis 1957). This matrix was then subjected to group-average hierarchical agglomerative clustering (CLUSTER) and an associated Similarity Profiles (SIMPROF) permutation test (Clarke et al. 2008). This combination of routines provides a sound statistical basis for identifying those points in the clustering procedure at which further subdivision of samples is unwarranted and thus, in this case, a completely objective approach for determining (1) those groups of sites with homogeneous fish faunal compositions (hereafter referred to as ‘fish groups’) and (2) the full spatial pattern of ichthyofaunal differences across the study area. The null hypothesis that there were no significant differences in ichthyofaunal composition among groups of sites was rejected if the significance level ( $P$ ) was  $<0.05$ . Fish groups represented by only one site were considered to be outliers and thus removed from further analyses. The pre-treated fish data were then averaged for each

remaining fish group and used to create another Bray–Curtis similarity matrix, which was then subjected to non-metric multidimensional scaling (nMDS) ordination to produce a plot illustrating the spatial pattern of differences among fish groups.

The second step was addressed by subjecting the above pre-treated fish data, averaged for each fish group, to a ‘shade plot’ analysis (Clarke et al. 2013). This routine, which was carried out using an alpha test version of the PRIMER v7 software, produces a visual display of the abundance matrix of variables (the dispersion-weighted fish species counts in this case) against samples (here, the averaged fish groups), where the intensity of grey-scale shading is proportional to abundance. The variables were ordered according to the results of a group-average hierarchical agglomerative cluster analysis that was applied to a resemblance matrix defined *between variables* as Whittaker’s index of association (Legendre and Legendre 1998). Species exhibiting similar patterns of abundance across fish groups were thus clustered together on the resultant dendrogram, which was displayed on the y axis of the shade plot. The samples (displayed on the x axis) were ordered by region and, within each region, by their Bray–Curtis similarities. Only those fish species accounting for >5 % of the pre-treated and averaged abundances in at least one of the fish groups were included in these analyses. Lastly, to ensure no influential species were overlooked by this summary analysis carried out at a relatively coarse level of spatial resolution, the results were verified against those from a Similarity Percentages analysis (SIMPER; Clarke 1993) undertaken on the pre-treated fish data averaged for each site and using the fish groups as the grouping framework (data not shown). While this categorical procedure, which is based on ‘between-sample’ relationships (defined here using Bray–Curtis similarity), provides a more comprehensive analysis for identifying those species that best typify and/or distinguish a priori groups of samples, the extensive tabulated output is less readily interpretable, particularly in cases such as this where there are a large number of groups.

Step 3 above, namely to identify which environmental layer, or combination of layers, provided the best correlation with the overall spatial pattern of differences among fish groups, was explored using the Biota and Environment matching routine (BIOENV; Clarke and Ainsworth 1993; Clarke et al. 2008). To achieve this, all possible one, two, three, four and five environmental layer combinations

were individually examined by forcing the inclusion of all variables representing a selected layer (or combination of layers) while simultaneously forcing the exclusion of all others. In this suite of analyses, the above Bray–Curtis matrix constructed from the pre-treated and averaged fish group data was used as the reference, while the pre-treated environmental data, also averaged for each fish group, was used as the secondary or explanatory data matrix from which Manhattan distances (Legendre and Legendre 1998) were calculated. The relative extent of the correlation between the complementary data sets was determined by the magnitude of the ‘matching’ statistic Spearman’s rank correlation coefficient ( $\rho$ ), i.e. values close to 0 indicate little correlation in rank order pattern between matrices, while those close to +1 indicate a near perfect agreement. Thus, the environmental layer or combination of layers that produced the highest  $\rho$  value was considered to provide the best match with the spatial differences among fish groups.

A novel application of the global BEST test (Clarke et al. 2008) was then used to test the statistical significance of the optimum layer(s). The null hypothesis of no similarities in rank order pattern between the fish and environmental resemblance matrices could be rejected by a single 0.05 level significance test if, under 999 random permutations of the biotic sample designations in relation to their environmental counterparts, a search over all possible combinations of layers produced an optimal  $\rho$  statistic greater than or equal to the observed  $\rho$  statistic for no more than 5 % of the 1,000 permutations (i.e. the 999 random ones plus the real match of fish to environmental layers). This is precisely the test of Clarke et al. (2008), but applied only to selecting and dropping all *layers* in combination rather than the much larger number of possibilities when selecting and dropping all *variables* in combination. This refinement of the global BEST test was again carried out using the above alpha test version of the PRIMER v7 software.

To illustrate the relationships between the spatial trends in the fish groups and those in each composite environmental layer selected by BIOENV, the data for each such layer were subjected to a principal components analysis (PCA) and the sample scores for principal component (PC) 1 and, where necessary, 2 (i.e. to capture at least 80 % of the variation within the layer of interest) were then overlaid as circles of proportionate sizes on the nMDS ordination plot of the fish group data. This

allowed the collective spatial trends within an environmental layer to be summarised as a whole and compared visually with those in the fish fauna, rather than displaying the trends for each component environmental variable. Interpretation of the specific environmental causes of differences in circle (PC score) size was aided by examining the eigenvectors for each PCA plot.

The fourth and final main step of the statistical approach accounted for the fact that, while the above BIOENV analyses identified those environmental layers that were best correlated with the full spatial distribution of fish groups, they did not provide a means for determining whether significant correlations might be localised to just particular groups of samples, i.e. so-called ‘interaction effects’. Investigation of the latter was explored using LINKTREE, a linkage tree approach that identifies how samples from a reference resemblance matrix are best split into groups, by successive binary division, based on threshold values of explanatory variables in a complementary dataset (Clarke et al. 2008). The Bray–Curtis similarity matrix constructed from the pre-treated and averaged fish group data was used as the reference, while the environmental data provided the explanatory information. The resultant linkage tree thus comprised terminal nodes represented by fish groups, with each branch of the tree annotated by those environmental variable(s), and their quantitative thresholds, that best “mirrored” that split. Note that for ease of interpretation of those thresholds, the environmental data were not subjected to prior transformation or normalisation, since this does not affect the LINKTREE outcome (Clarke et al. 2008). The notation associated with the environmental thresholds (e.g. variable  $A < x$  [ $>y$ ], where  $x$  and  $y$  are quantitative values of environmental variable  $A$ ), indicates whether a left ( $<x$ ) or right path ( $[>y]$ ) should be followed at each branching node.

## **Results**

### **Identification of Significantly Different Groups of Fish Fauna**

The CLUSTER and SIMPROF procedures, carried out using the pre-treated average abundance of each fish species at each of the 119 sampling sites, demonstrated that 23 significantly different groups of sites (‘fish groups’, labelled B to AB) could be identified across the five estuaries throughout

south-western Australia, after five outliers represented by individual sites (A, C, K, N and V) had been excluded (Fig. 2). The pattern of differences among the various fish groups is more clearly illustrated by the nMDS ordination plot shown in Fig. 3, which has been derived from the group averages. The fish groups with the most distinct compositions (i.e. those occupying the extremes of each quadrant of the plot) included J/H in the top left (comprising sites from the entrance channels of the Swan–Canning and Peel–Harvey Estuary, respectively), E in the bottom left (sites from the upper Swan–Canning Estuary), B in the top right (sites from the very shallow basin areas of Broke Inlet) and W/X in the bottom right (sites from the lower Wellstead Estuary). The gradational patterns between these extremes, and the species most responsible for causing those trends, are explored further in the following subsection.

The original (untreated) mean densities of the full suite of species recorded in each fish group, which collectively represented 83 species, 36 families and eight estuarine usage functional guilds, are given in Appendix Table 2. The most speciose fish groups were G, H, J, L and M (40–47 species), all of which contained sites from the two permanently-open estuaries on the west coast, while the least speciose were B, O, Q, R, S, W and X (5–12 species), all of which comprised sites from periodically-open systems on the south coast. In contrast, by far the greatest overall mean densities were recorded in the latter two fish groups (1,535–1,994 fish 100 m<sup>-2</sup>), both of which comprised sites in the normally-closed Wellstead Estuary. However, several other fish groups with low numbers of species were also among those with the lowest overall mean densities, i.e. B, O and Q (13–57 fish 100 m<sup>-2</sup>). The most abundant and consistently-occurring species belonged to the family Atherinidae, with the solely estuarine *Atherinosoma elongata* being by far the most abundant and occurring in every fish group, followed by the estuarine and freshwater *Leptatherina wallacei* then the estuarine and marine *Leptatherina presbyteroides*, which were found in nearly all fish groups. While still relatively abundant, the remaining species in this family were more restricted in their distributions, occurring in about half of the fish groups (Appendix Table 2). Other relatively abundant and consistently-occurring species included the gobiids *Favonigobius lateralis* and *Pseudogobius olorum*, both able to reproduce in estuaries and found in all fish groups except B in the case of the latter species. The

marine estuarine-opportunists *Hyperlophus vittatus* and *Torquigener pleurogramma* were also relatively abundant, but were restricted to fish groups from the west coast estuaries and, particularly in the case of the latter species, exhibited notable variability in occurrence.

### **Spatial Relationships Between Fish Groups and Environmental Layers**

BIOENV demonstrated that the combination of environmental layers whose overall pattern of spatial differences was best correlated with that among the 23 fish groups was (1) coast type, (2) estuary bar type, (3) site proximity to marine vs fresh water sources and (4) site composition of substrate/submerged vegetation type. This combination of layers, which included regional, estuary-wide and local scales, produced a Spearman rank correlation value of 0.59 which was significant in the modified global BEST test ( $P = 0.001$ ), indicating that the spatial distinctions in estuarine ichthyofaunas across south-western Australia are relatively well matched with those in the above environmental subset. When each of the selected layers were correlated individually with the fish group matrix, the extent of the match was approximately two times greater for the coast and bar type layers ( $\rho = 0.42$  and  $0.50$ , respectively) than for the two local-scale layers ( $\rho = 0.24$  and  $0.25$  for marine/freshwater ratio and substrate/submerged vegetation type, respectively). Each of these matches were again shown by the global BEST test to be significant ( $P = 0.001-0.02$ ).

The plots shown in Fig. 4a-f provide a visual comparison of the pattern of differences among fish groups (i.e. Fig. 3) and those in each of the selected environmental layers (summarised by their PC1 and/or PC2 scores and overlaid as circles of proportionate sizes). The only exception is Fig. 4d, in which the selected layer (marine/freshwater ratio) was represented by a single variable, thereby precluding the need for PCA and allowing the environmental data itself to be overlaid. Figure 4a, with the PC1 scores for coast type overlaid (capturing 100 % of sample variation), clearly illustrates that all fish groups on the left half of the plot (D, E, F, G, H, I, J, L, M, Y, AB) comprised sites from the west coast region (represented by small circles), while all of those to the right (B, O, P, Q, R, S, T, U, W, X, Z, AA) comprised sites from the south coast region (represented by larger circles). Spatial differences in the composition of the estuarine fish fauna across south-western Australia are thus closely related to the coast type, or region, in which estuaries are located. The shade plot shown in

Fig. 5, in which the fish groups have also been ordered by region, clearly indicates that while the faunas of the west coast systems were characterised by a relatively wide range of species spanning various families and guilds in the estuarine and marine categories, those of the south coast systems were largely dominated by small estuarine species from the families Atherinidae and Gobiidae.

Not surprisingly, a similar clear-cut relationship was also observed when the PC1 scores for estuary type (capturing nearly 58 % of sample variation) were overlaid on the distribution of fish groups (Fig. 4b), with all groups to the left of the plot comprising sites from the permanently-open estuaries (represented by larger circles) and those to right comprising sites from the periodically-open estuaries (small circles). However, the PC2 scores for this environmental layer (which captured 42 % of the remaining sample variation) further demonstrated that within the latter set of fish groups, a clear distinction could also be made between those from seasonally-open (smaller circles at the top right of the plot) and normally-closed systems (larger circles at the bottom right; Fig. 4c). This trend reflected clear differences in the faunas of those estuary types. Thus, fish groups mainly from the seasonally-open estuaries (i.e. B, O, P, Q, R, S, T, U) were dominated by a spectrum of faunas, ranging from those that were highly depauperate (i.e. fish group B in the top right corner of Fig. 4c, comprising very shallow basin sites in Broke Inlet) to those that were relatively diverse and abundant (i.e. fish group T in the mid-right region of Fig. 4c, containing sites from the entrance channel of Broke Inlet that were characterised mainly by *L. presbyteroides*, *L. wallacei*, *Afurcagobius suppositus*, *A. elongata*, *F. lateralis* and, uniquely, the marine straggler *Notolabrus parilus*; Fig. 5). In contrast, fish groups entirely from the normally-closed Wellstead Estuary (i.e. W and X located at the bottom right of Fig. 4c) were largely characterised by very high densities of *A. elongata* as well as *F. lateralis* in the case of the former group and *L. wallacei* in the case of the latter (Fig. 5).

Unlike the above two environmental layers, the relationships between the full distribution of fish groups and the selected local-scale layers were not as clear cut. Thus, there were no distinct overall trends when the data for the marine/freshwater ratio was overlaid on the fish groups (Fig. 4d). While the PC1 scores for the substrate/submerged vegetation layer showed clearer overall relationships with the fish groups (explaining ~ 55 % of sample variation, with larger circles in one corner of the plot



representing dense samphire and reeds; Fig. 4e), those for PC2 (capturing 28 % of sample variation) did not show any such trend (Fig. 4f).

Clear relationships between the fish groups and the above local-scale environmental layers were evident, however, when the same data were explored using LINKTREE (Fig. 6). While this analysis also showed that the broader-scale coast and estuary-type layers explained the major distinction among fish groups (i.e. the primary division at node *a* [ $B = 83\%$ ], which partitioned all fish groups from periodically-open estuaries on the south coast to the left side of the linkage tree and all of those in the permanently-open estuaries on the west coast to the right side), it demonstrated that the marine/freshwater ratio and substrate/submerged vegetation variables were clearly important in distinguishing fish groups within particular subsets of the data. Thus, along with estuary-scale variables separating seasonally-open and normally-closed systems, local-scale substrate/submerged vegetation variables helped explain the division of fish groups at node *b* in the upper branches of the linkage tree ( $B = 77\%$ , left side of the plot). Moreover, the marine/freshwater ratio was very important in explaining a major separation of fish groups in the permanently-open estuaries on the right of the tree (node *f*;  $B = 65\%$ ), splitting E, D, Y and AB (comprising sites in the upper Swan–Canning and Peel–Harvey estuaries) away from G, F, J, H, L, M, I (comprising sites in the middle and lower reaches of those systems). The shade plot in Fig. 5 shows that the former set of fish groups contained notably greater abundances of several solely estuarine/estuarine and freshwater species than the latter (e.g. *Acanthopagrus butcheri*, *Favonigobius punctatus*, *Amniataba caudavittata*, *P. olorum*, *L. wallacei* and *A. suppositus*), while the reverse was true for various marine-affiliated species (e.g. *T. pleurogramma*, *F. lateralis* and *L. presbyteroides*). The importance of the marine/freshwater ratio in the permanently-open systems contrasted with the situation in the periodically-open systems, where it was selected only at a very low level of sample division (node *e*;  $B = 27.1\%$ ; Fig. 6).

## **Discussion**

This study has developed a unique and fully objective approach for identifying and ranking the spatial scales of environmental differences across regional, estuary-wide and local levels that are most influential in structuring the species composition of estuarine fish assemblages across south-western Australia. It has also produced a quantitative framework for predicting, on the basis of environmental attributes across the above three scales, the types of fish communities that would be expected to occur at any nearshore estuarine site throughout the study area. The approaches developed in this study could readily be applied to estuaries in any other area of the world.

## **Data and Statistical Methods**

Comparisons of the ecological importance of environmental scale that have been drawn in this study were greatly enhanced by (1) the availability of comprehensive data for both ichthyofaunal and environmental characteristics at the local, site-specific scale in each estuary and (2) the consistent sampling methodologies used throughout. Rigorous and comparable data recorded at this level are often lacking in studies of ecological shifts across spatial scales, and is commonly cited as a limiting factor (e.g. Edgar et al. 1999; Nicolas et al. 2010). It is recognised that such detailed collection of data at the local scale generally compromises more extensive sampling at broader scales, with the number of estuaries sampled in this study (5) being far lower than, for example, the 190 examined by Harrison and Whitfield (2008) in their study of ichthyofaunas across estuary types and bioregions in South Africa. Given the highly diverse and dynamic nature of estuarine environments, however, it is argued that adequately capturing the spatial and temporal heterogeneity within these systems is imperative for making reliable comparisons of their ecology at broader inter-estuary and regional scales.

Several aspects of the statistical methodology adopted in this study are noteworthy. Firstly, the SIMPROF test used in conjunction with CLUSTER provided a robust, fully objective way of optimally separating the fish faunal data into significantly different groups (e.g. Tweedley et al. 2013). This was an imperative step in ensuring a reliable reference base for exploring meaningful spatial relationships between the fish and environmental matrices. This approach represents a

considerable advance on others for determining biotic groupings in situations where there is no valid a priori grouping hypothesis, and particularly where subjective decision frameworks have been introduced, e.g. arbitrarily choosing a level of resemblance as a ‘cut-off’ point in a hierarchical cluster analysis (e.g. Barinova et al. 2011; Bedoya et al. 2011). Moreover, given that SIMPROF performs a test at each branching node of the cluster dendrogram, it provides an alternative and arguably more comprehensive method than several others aimed at optimising group selection in classification trees, which typically apply a consistent partitioning level across the whole tree (e.g. Guidi et al. 2008; Reygondeau et al. 2012).

A second important aspect of our statistical approach was that it enabled whole spatial scales (‘environmental layers’) to be tested for correlations with the fish fauna, rather than simply testing at the level of their representative environmental variables. This approach thus facilitated reliable generalisations regarding which spatial scale, or combination of scales, best explained the overall pattern of ichthyofaunal differences throughout south-western Australian estuaries. Importantly, it also allowed their relative importance to be quantified. Moreover, the use of a modified form of the global BEST test enabled a single, study-wide hypothesis test of whether the optimum combination of environmental layers had justifiable statistical support.

Thirdly, a novel shade plot analysis supplemented by an inverse (r-mode) hierarchical cluster analysis provided a further useful approach for understanding and readily visualising how key species contributed to the ichthyofaunal differences among fish groups. This procedure, which is covered in detail in Clarke et al. (2013), provided a simple, easily-interpretable summary of how the abundances of the most influential species changed among fish groups, and identification of those groups of species which displayed common trends. Providing the appropriate checks are made to ensure no loss of important detail when averaging over within-group variability, as in the current case, the shade plot approach represents a highly useful alternative to other categorical, similarity-based approaches such as SIMPER (Clarke 1993) which, while comprehensive, result in an extensive tabulated output that can be unwieldy to interpret, particularly in situations with many groups.

Lastly, and as discussed further in the subsection entitled ‘Faunal prediction’, the use of LINKTREE has produced a quantitative framework for predicting the fish fauna likely to occur at any nearshore site in south-western Australian estuaries, accounting for any interactions between explanatory environmental variables.

### **Importance of Spatial Scale in Explaining Differences Among Fish Assemblages**

A combination of regional (coast type), estuary-wide (bar type) and local-scale (site proximity to marine vs fresh water sources and substrate/submerged vegetation type) environmental layers provided the best statistical match with the overall spatial differences in the nearshore fish faunas throughout south-western Australian estuaries. The extent of that correlation was moderately high ( $\rho = 0.59$ ;  $P = 0.001$ ), indicating that a considerable amount of variability among fish groups was associated, either directly or indirectly, with conditions represented by those environmental layers.

Estuary bar type followed by coast type were by far the most important of the selected layers, with each explaining about twice the variability among fish groups than each of the two local-scale layers. Whilst few studies have quantified the relative importance of all three of the above spatial scales in structuring estuarine fish assemblages, this order largely concurs with that often perceived or assumed, with the exception that regional differences are generally considered more influential than estuary-wide factors (e.g. Whitfield 1999; Harrison and Whitfield 2006a). Indeed, while not the main focus of their study, Harrison and Whitfield (2008) demonstrated the latter to be true for fish guild compositions in three estuary types and bioregions across South Africa. Sanvicente-Añorve et al. (2011) also showed that environmental differences at regional rather than intra-regional scales had a greater influence on the composition of larval fish assemblages in estuaries along the Mexican Atlantic coast, as did Jackson and Harvey (1989), albeit for lake systems in Canada. While the difference in the correlation values for estuary-wide and regional scales was not large in the current study (i.e.  $\rho = 0.50$  vs  $0.42$ ), it is possible that their order may switch as greater numbers of south-western Australian estuaries are examined (see ‘Future work’ section). Nevertheless, as demonstrated in this study and supported by others (e.g. Edgar et al. 1999; Harrison and Whitfield 2006a), estuarine

type and, in particular bar-state, is a major driver in structuring spatial differences in estuarine fish communities in temperate, microtidal waters.

The bar-state of an estuary can influence its fish fauna in several ways. Firstly, the degree of connection between estuaries and adjacent coastal waters obviously affects the ability of marine fish species to migrate or be transported into estuarine systems, with the permanently-open estuaries in this study containing a far greater proportion of marine estuarine-opportunists and stragglers than those that are periodically-open, i.e. 30–40 vs <0.5 %. This also largely accounts for the far higher species richness in the former than latter systems, i.e. 61–66 vs 18–26 fish species. Even when the mouths of the Broke and Wilson inlets and especially the Wellstead Estuary are open to the sea, their typically narrow and shallow entrances, combined with the microtidal conditions of the study area, further limits the entry of marine species. Secondly, seasonally-open and particularly normally-closed estuaries can experience far greater extremes in water quality conditions (e.g. salinity, temperature and dissolved oxygen concentration) than permanently-open systems (e.g. Hoeksema et al. 2006; Perissinotto et al. 2010; Potter et al. 2010). Most of the dominant fish species in the periodically-open estuaries in this study have characteristics that probably reflect evolutionary adaptations to being disconnected from the sea and its moderating influences (e.g. Potter et al. 1990). For example, 99.5–99.9 % of the fish fauna recorded in those systems comprised highly euryhaline atherinid and goby species, with some such as the very abundant *A. elongata* (50–80 % of the catch in the south coast estuaries) being particularly tolerant of variable and extreme salinities. This was exemplified by the findings of Young and Potter (2002), who recorded substantial numbers of *A. elongata* in the normally-closed Wellstead Estuary in the mid-late 1990s when salinities in that system rose above 120 psu. Other species, such as the goby *P. olorum*, can obtain oxygen by ventilating their gills in the oxygen-rich zone just under the water surface, and are thus particularly well adapted for dealing with low dissolved oxygen concentrations (Gee and Gee 1991).

The strong regional shift in fish faunal composition between estuaries on the lower west and south coasts of Western Australia was driven largely by (1) the far greater number of species characterising the faunas of the former systems, which represented various guilds across the marine and estuarine

categories and included several species that were not even recorded in the south coast systems, e.g. *A. caudavittata* and *F. punctatus* (solely estuarine), *Ostorhinchus rueppellii* (estuarine and marine) and *Stigmatopora argus* (marine straggler), and (2) the greater abundance and dominance in the latter systems of several atherinid and gobiid species that are able to reproduce in estuaries, and particularly the solely estuarine/estuarine and freshwater *A. elongata*, *L. wallacei*, *P. olorum* and *A. suppositus*. These clear regional distinctions match those identified for marine waters in south-western Australia by the Interim Marine and Coastal Regionalisation of Australia on the basis of demersal fishes, marine plants, invertebrates and various physical and oceanographic data (i.e. the Leeuwin-Naturaliste and WA South Coast meso-scale marine bioregions <http://data.gov.au/132>; accessed October 2012), and Fox and Beckley (2005) using neritic fish assemblages.

The ichthyofaunal differences between west and south coast estuaries reflect, in part, regional changes in a range of coastal geomorphology features, oceanographic processes and/or climatic conditions. Firstly, the sheltering effects of the offshore reefs and islands along the lower west coast (see ‘Study area’ subsection of the Methods) have led to more complex and diverse nearshore habitats (e.g. seagrass beds, tombolos and highly sheltered beaches) than on the more exposed south coast. It is thus relevant that several of the marine-affiliated species that were more prevalent in west than south coast estuaries (e.g. *F. lateralis*, *O. rueppellii*, *S. argus* and *Gymnapistes marmoratus*) are typically associated with sheltered coastal habitats and/or submerged vegetation (e.g. Gill and Potter 1993; Ayvazian and Hyndes 1995; Valesini et al. 2004). Secondly, while not presented in our results, the pronounced regionality in the estuarine fish faunas was very closely associated with spatial differences in local-scale water temperature (Fig. 7). Thus, all of the fish groups from the west coast region were coupled with higher water temperatures than those from the south coast, i.e. 19.7–21.7 vs 17.2–19.3 °C. No such relationship was detected with either local-scale salinity or dissolved oxygen concentration. This shift in water temperature reflects, at least in part, the warmer climate on the west than south coast, with annual mean air temperatures over the last 30 years at Perth and Albany airports, respectively, having maxima of 24.8 and 20.2 °C and minima of 12.4 and 10.6 °C ([http://www.bom.gov.au/climate/averages/tables/ca\\_wa\\_names.shtml](http://www.bom.gov.au/climate/averages/tables/ca_wa_names.shtml); accessed October 2012). The

extent to which the regional correlation between fish faunal and water temperature differences actually reflects a causal relationship is unknown, but it may be relevant that several of the species found only in west coast systems are known not to extend southwards beyond the tip of south-western Australia (e.g. Potter et al. 1990). There is little evidence to suggest, however, that the Leeuwin Current, which flows poleward along the continental shelf of Western Australia and transports pelagic marine larvae from more northerly tropical waters (see 'Study area' subsection of the Methods), has contributed markedly to the regional ichthyofaunal differences found in this study. Thus, all of the marine species that were important in distinguishing the fish faunas of the west and south coast estuaries are widely distributed and spawn throughout the nearshore coastal waters of the temperate lower west coast of Australia (e.g. Gomon et al. 2008; Beckley et al. 2009; [www.fishbase.org](http://www.fishbase.org); accessed October 2012). Moreover, some are brooders (e.g. *S. argus* and *O. rueppellii*) or produce demersal eggs (e.g. *T. pleurogramma*) ([www.fishbase.org](http://www.fishbase.org); accessed October 2012).

Clearly, in this study, the potential effects of environmental differences at the regional scale are largely confounded by those at the estuary-wide scale, given that the two permanently-open estuaries are located on the west coast and the three periodically-open systems are on the south coast. Such confounding is slightly ameliorated by the fact that two estuary types, namely seasonally-open and normally-closed systems, are present in the latter region, and could be further improved, again to a small extent, with more resources and further research (see 'Future work' subsection). However, to a large extent, the sampling design of this study reflects the uneven distribution of estuary types around the coastline of south-western Australia, which in turn reflects regional differences in oceanographic and hydrological processes (Potter and Hyndes 1999). Edgar et al. (1999) noted a similar situation for estuaries along the coast of Tasmania.

The two local environmental layers selected as part of the optimal combination of scales in this study have been shown by many workers worldwide to be associated with spatial changes in the within-estuary structure of fish assemblages (e.g. Potter and Hyndes 1999; Elliott and Hemingway 2002; Sheppard et al. 2011). This was reinforced in the current study, with these layers being highly important at the within-estuary scale, but relatively unimportant in explaining broader spatial

divisions in the estuarine ichthyofauna across temperate south-western Australia. In addition, the extent of their influence was shown to be dependent on estuary type. For example, whereas the marine/freshwater ratio was linked with major ichthyofaunal divisions within the permanently-open estuaries, this was not the case in the periodically-open systems, most likely reflecting the adaptations of dominant fish species in the latter to being sporadically disconnected from the sea. Moreover, while certain substrate/submerged vegetation variables were important in both broad estuary types, this was particularly so in periodically-open systems, where they were of equal importance as the estuary-scale variables that distinguished seasonally-open from normally-closed systems. It may be the case that the latter findings are simply an artefact of only one normally-closed system being included in this study, but it is relevant that the top five fish species and their order of abundance in the Wellstead Estuary were the same as, or very similar to, those recorded by Hoeksema et al. (2006) in other normally-closed estuaries along the south coast of Western Australia.

Lastly, an interesting contrast is revealed when our findings are compared with those of Sheaves and Johnston (2009), the only other study that has quantified the relative importance of regional, estuary-wide and local-scale environmental differences in structuring estuarine fish communities. Thus, while those workers, who studied 21 estuaries in the tropical meso- to macro-tidal zones of north-eastern Australia, also demonstrated that estuary-scale differences best explained spatial variability in estuarine fish faunas, they found the influence of broader-scale regions or climatic zones to be negligible. Indeed, closely following differences at the estuary-scale, those at the level of estuarine reach (i.e. upstream, middle or downstream estuary) were the next most important. Moreover, the estuary-scale variables that provided the best explanatory power did not include, as in the current case, those related to the degree of connection between the estuary and ocean, but instead were represented by intertidal vegetation (mangrove) area and sediment composition. Sheaves and Johnston (2009) attributed the lack of influence of climatic zone (i.e. wet/dry) to the euryhaline nature of the fish faunas, and that of estuary bar-state to the large tides overcoming any physical barrier to marine fish migrations. However, they struggled to explain the lack of regional influences on the fish communities.



## **Faunal Prediction**

The linkage tree produced in this study (i.e. Fig. 6) has two important outcomes. First, it illustrates and quantifies how environmental differences across regional, estuary-wide and local spatial scales are collectively implicated in shaping the distribution of estuarine fish faunas throughout south-western Australia and, importantly, allows any interaction effects to be identified (see preceding subsection). Secondly, it provides, in principle, a quantitative pathway for predicting the type of fish fauna likely to occur at any site in a south-western Australian estuary on the basis of its environmental characteristics across the above three scales. Thus, by following the environmental thresholds at each node of the tree, any local-scale estuarine site can be allocated to its appropriate fish group and its typical fish fauna readily identified through using the accompanying list of characteristic species given in Fig. 5. Obtaining the requisite measurements for any new site of interest is greatly facilitated by the fact that all of the environmental variables employed in this study are either categorical or can be easily measured from mapped sources. Clearly, the reliability of this predictive approach will increase as more complementary environmental and fish faunal data are collected at local scales across a greater number of estuaries throughout south-western Australia, and the predictions validated with field data.

Predictive approaches such as these have a raft of applications across the science and management sectors, including exploration of ecological theory, setting quantitative benchmarks for assessing faunal change, and conservation planning and reserve design.

## **Management Implications**

From an estuarine management viewpoint, the findings of this study reiterate the importance of conserving samples of each estuary type in each bioregion to ensure representativeness in any proposed network of estuarine reserves throughout south-western Australia. At a finer scale, our results also provide quantitative reinforcement of the need to protect hydrological flows and substrate/submerged vegetation types within estuaries, given their demonstrated role in structuring discrete fish assemblages.

## **Future Work**

Expansion of the current approaches over a greater number of estuaries in south-western Australia, and ultimately throughout Western Australia, is an obvious future extension of the work presented here. This would both increase the reliability of the predictive framework produced in this study and, by extending into northern Western Australia, encompass estuarine types and fish faunas that are not present in the south. Secondly, future extensions of this work should include a greater number of variables at the system-wide level (e.g. those capturing other aspects of estuarine and also catchment morphology) to improve the definition of that spatial scale. Lastly, adapting the current study to suit different types of estuarine fauna, such as benthic invertebrates or birds, would provide estuarine ecologists and managers with a more comprehensive basis for understanding common spatial trends among these biota and their driving environmental processes.

## **Footnotes**

1 While both of these studies did include measurements for the latitude and/or longitude of each estuary to capture their geographical differences, these data were continuous rather than categorical and thus did not reflect a regional-scale classification, e.g. a grouping of estuaries according to bioregion.

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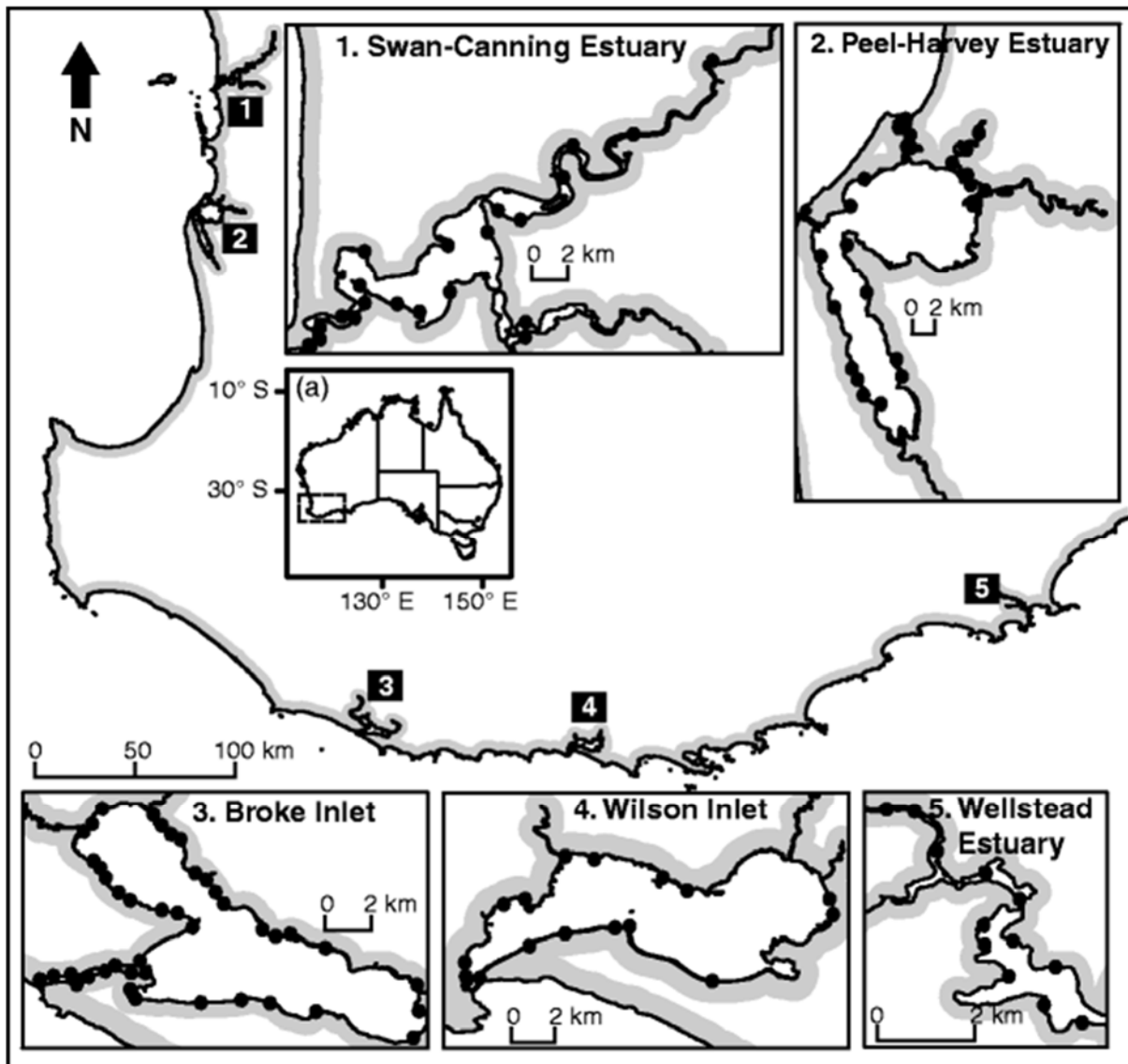
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Table 1. Physical characteristics of each of the five study estuaries in south-western Australia

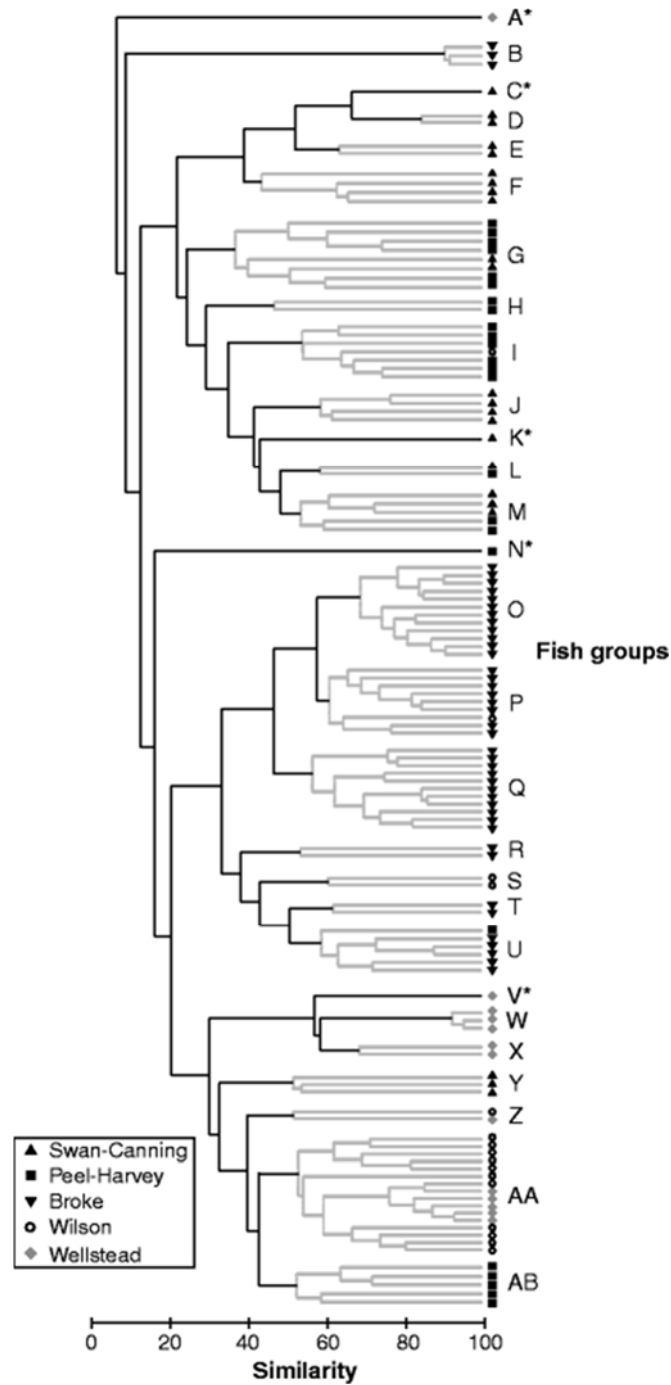
	Swan–Canning Estuary	Peel–Harvey Estuary	Broke Inlet	Wilson Inlet	Wellstead Estuary
Location	32.055°S, 115.735°E	32.526°S, 115.710°E	34.937°S, 116.373°E	35.026°S, 117.333°E	34.392°S, 119.399°E
Coast type	West	West	South	South	South
Estuary bar type	Permanently-open	Permanently-open	Seasonally-open (open Aug–Jan in study period)	Seasonally-open (open Oct/Nov in study period)	Normally-closed (closed during study; last open Jun 2005–Apr 2006)
Morphological type	Drowned river valley	Inter-barrier and basin estuary	Basin estuary	Basin estuary	Drowned river valley
Catchment area (km <sup>2</sup> )	126,000	12,000	930	2,300	720
Mean annual rainfall (mm)	800	800	1,300	1,000	600
Estuary area (km <sup>2</sup> )	55	130	48	48	2.5
Main tributaries	Swan and Canning rivers	Murray, Serpentine and Harvey rivers	Shannon, Forth and Inlet rivers	Denmark, Hay and Sleeman rivers	Bremer River
Depth (m)	Typically ≤5 m	Typically ≤2 m	Typically ≤2 m	Typically ≤2 m	Typically ≤1 m
Substrate type	Coarse–fine sands and some limestone outcrops in the channel and basins, with silt in the deeper waters. Silt, mud and river gravels in the upper reaches.	Coarse–fine sands in the channel and basins with silt in the deeper waters. Silt and soft mud in the upper reaches.	Coarse–fine sands in the channel and basin with silt in the deeper waters. Some granite outcrops.	Coarse–fine sands in the channel and basin with silt in the deeper waters. Some granite outcrops.	Coarse–fine sands in the lower reaches and mud in the middle to upper reaches.
Submerged (including littoral) vegetation	Seagrass (mainly <i>Halophila ovalis</i> , some <i>Heterozostera</i> sp. or <i>Ruppia megacarpa</i> ) and varied macroalgae (e.g. <i>Gracilaria comosa</i> , <i>Chaetomorpha linum</i> ) in the lower to middle estuary. Rushes (e.g. <i>Typha</i> sp.) in the littoral zones of the upper estuary.	Seagrass (mainly <i>H. ovalis</i> , some <i>Heterozostera</i> sp. or <i>R. megacarpa</i> ) and varied macroalgae (e.g. <i>Chaetomorpha</i> sp.) in the basins and channel. Samphire ( <i>Sarcocornia</i> sp. or <i>Halosarcia</i> sp.) and rushes ( <i>Juncus kraussii</i> ) in the littoral zones of the basins/ivers.	Sparse beds of <i>R. megacarpa</i> and the stonewort <i>Lamprothamnium papulosum</i> in the basin and channel.	Dense beds of <i>R. megacarpa</i> throughout the basin.	Dense beds of <i>R. megacarpa</i> in the lower to middle estuary. Dense samphire (mainly <i>Sarcocornia</i> sp.) in the littoral zones of the middle to upper estuary.

**Fig. 1** Map showing the location of the five estuaries studied in south-western Australia (1 Swan-Canning Estuary, 2 Peel-Harvey Estuary, 3 Broke Inlet, 4 Wilson Inlet, 5 Wellstead Estuary) and the sites (black circles) at which fish and environmental data were recorded. Insert *a* shows the location of the study area within Australia

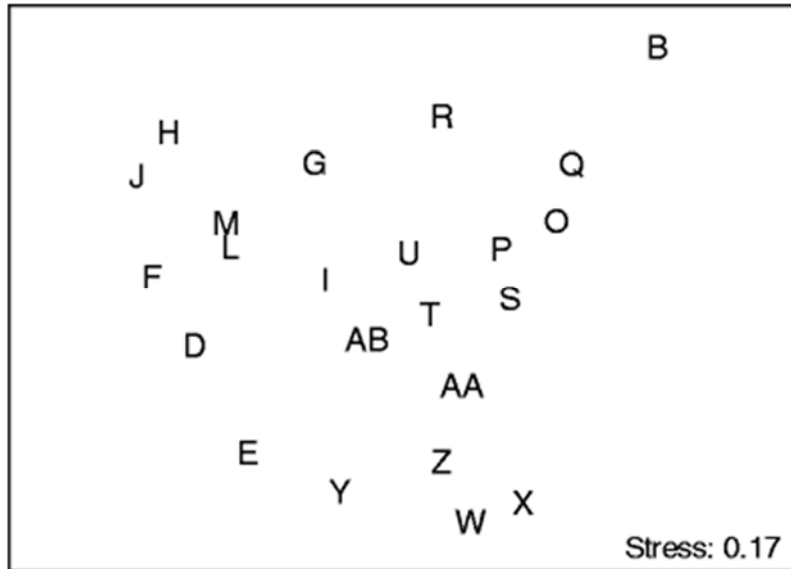




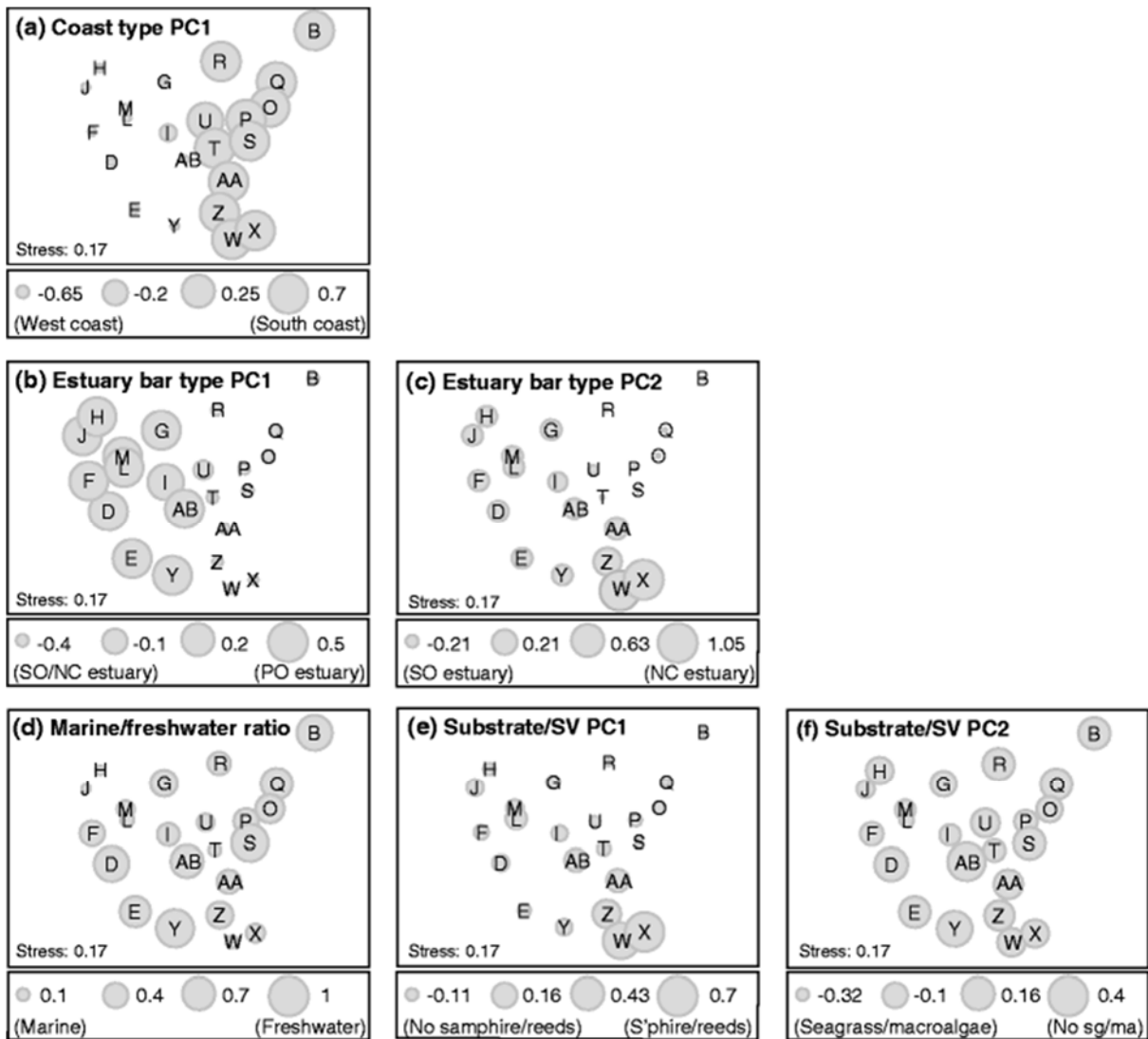
**Fig. 2** Dendrogram derived from subjecting the dispersion-weighted fish species abundances averaged for each estuarine site to CLUSTER and SIMPROF using Bray–Curtis similarities. Groups of samples marked by *light grey lines* are those which do not contain significant internal structure and thus represent fish groups. *Asterisks* denote single sites considered to be outliers



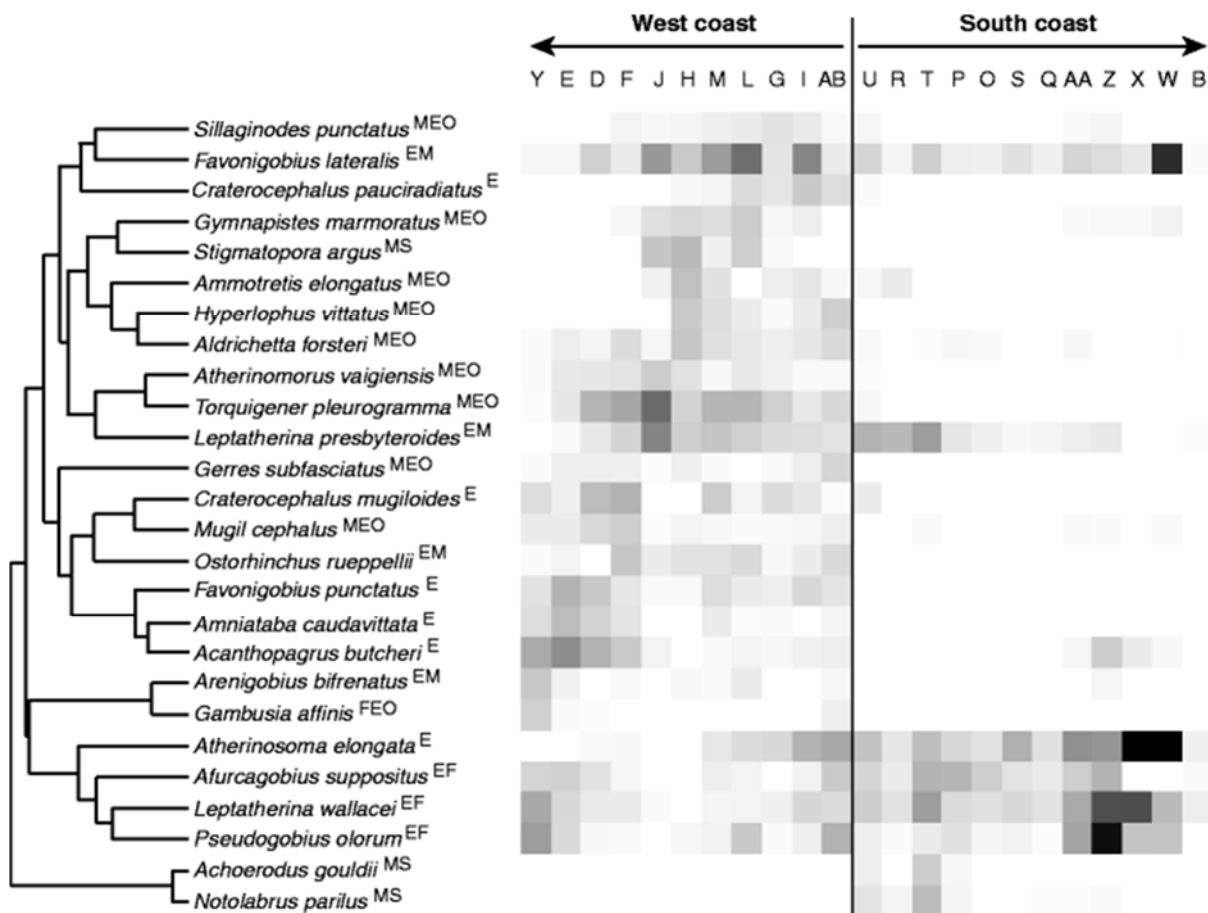
**Fig. 3** nMDS ordination plot derived from the dispersion-weighted fish species abundances averaged for each fish group identified in Fig. 2



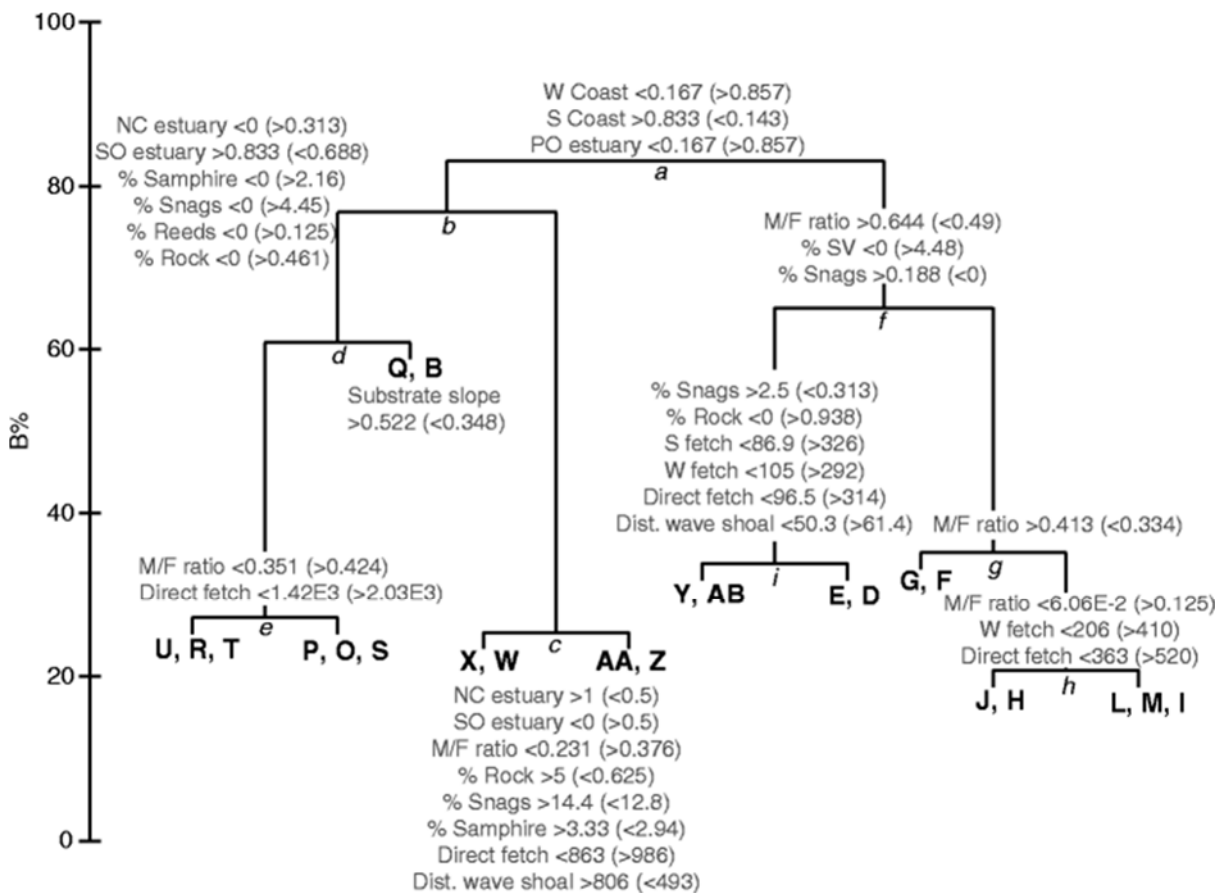
**Fig. 4** nMDS ordination plot derived from the dispersion-weighted fish species abundances averaged for each fish group, with the sample scores for principal components (PC) 1 and/or 2 (derived from a PCA of an environmental layer of interest) overlaid as *circles* of proportionate sizes. The only exception is **d**, in which the *circles* represent the original data for the marine/freshwater ratio. *PO* permanently-open, *SO* seasonally-open, *NC* normally-closed, *SV* submerged vegetation, *S'phire* samphire, *sg* seagrass, *ma* macroalgae



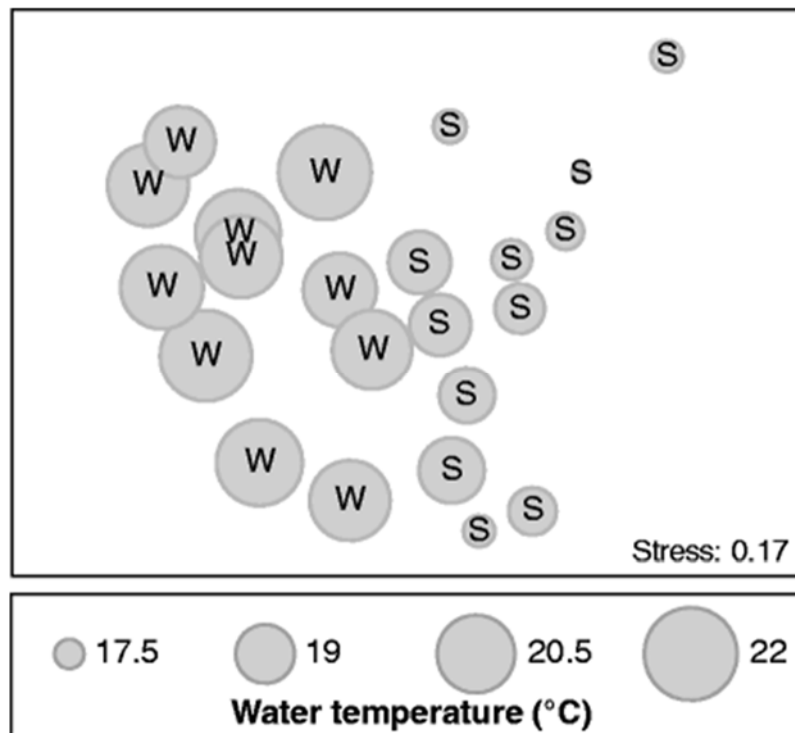
**Fig. 5** Shade plot illustrating the dispersion-weighted abundances of the most prevalent fish species in each fish group (i.e. those species accounting for >5 % of the average abundance in at least one group) with shading intensity being proportional to abundance. Fish groups are ordered by region (and, within each region by their Bray–Curtis similarity) and species are ordered by a hierarchical cluster analysis of their mutual associations across fish groups. The estuarine usage functional guild for each species (*sensu* Potter et al. 2013) is given in superscript text (*MS* marine straggler, *MEO* marine estuarine-opportunist, *E* solely estuarine, *EM* estuarine and marine, *EF* estuarine and freshwater, *FEO* freshwater estuarine-opportunist)



**Fig. 6** Linkage tree constructed using the dispersion-weighted and averaged fish species abundances in each fish group as the reference, and the measurements for environmental attributes across all scales as the explanatory data. The path to any fish group (terminal nodes of the tree) is determined by the environmental thresholds given at each branching node, with unbracketed and bracketed thresholds indicating a left and right path, respectively (*N.B.* threshold values have not been subjected to any data pre-treatment). The units of measurement for each environmental attribute are given in the ‘Data for environmental layers’ subsection of the Methods and their abbreviations are as follows: *W* west, *S* south, *PO* permanently-open, *NC* normally-closed, *SO* seasonally-open, *M/F* ratio marine/freshwater ratio, *Dist. wave shoal* distance to wave shoaling margin, *SV* submerged vegetation. *E* refers to exponential and *B %* reflects the magnitude of fish group differences as a proportion of the maximum (measured by rank dissimilarities) at the initial division



**Fig. 7** nMDS ordination plot derived from the dispersion-weighted fish species abundances averaged for each fish group, where the samples have been coded for region (*W* west coast, *S* south coast) and complementary local-scale water temperature data overlaid as circles of proportionate sizes









	West coast											South coast												
	Y	E	D	F	J	H	M	L	G	I	AB	U	R	T	P	O	S	Q	AA	Z	X	W	B	
<i>Pseudogobius olorum</i> EF	37.50 <sup>23.46</sup>	6.90 <sup>5.49</sup>	0.22 <sup>0.25</sup>	0.16 <sup>0.16</sup>	0.01 <sup>0.02</sup>	0.29 <sup>0.41</sup>	0.85 <sup>0.66</sup>	14.40 <sup>20.37</sup>	0.09 <sup>0.10</sup>	1.51 <sup>1.79</sup>	26.79 <sup>10.71</sup>	1.52 <sup>1.41</sup>	0.08 <sup>0.05</sup>	2.25 <sup>0.97</sup>	4.55 <sup>4.77</sup>	0.44 <sup>0.52</sup>	0.86 <sup>0.51</sup>	0.05 <sup>0.06</sup>	33.55 <sup>17.00</sup>	139.28 <sup>43.25</sup>	16.13 <sup>8.38</sup>	15.78 <sup>6.00</sup>		
<b>Gonorynchidae</b>																								
<i>Gonorynchus greyi</i> MS						0.02 <sup>0.03</sup>																		
<b>Hemiramphidae</b>																								
<i>Hyporhamphus melanochir</i> EM								0.27 <sup>0.78</sup>				0.12 <sup>0.23</sup>	0.05 <sup>0.08</sup>	0.30 <sup>0.18</sup>	0.26 <sup>0.71</sup>	0.02 <sup>0.04</sup>	0.13 <sup>0.03</sup>	<0.01 <sup>0.02</sup>	0.31 <sup>0.68</sup>	0.05 <sup>0.08</sup>				
<i>Hyporhamphus regularis</i> E					0.03 <sup>0.06</sup>		0.04 <sup>0.10</sup>	0.11 <sup>0.15</sup>	0.11 <sup>0.20</sup>		0.02 <sup>0.04</sup>													
<b>Kyphosidae</b>																								
<i>Girella zebra</i> MS												0.01 <sup>0.04</sup>												
<i>Microcanthus strigatus</i> MS							0.02 <sup>0.05</sup>	0.07 <sup>0.10</sup>																
<i>Scorpiis georgiana</i> MS						0.02 <sup>0.03</sup>																		
<b>Labridae</b>																								
<i>Achoerodus gouldii</i> MS												0.12 <sup>0.21</sup>	1.12 <sup>0.06</sup>	0.04 <sup>0.08</sup>										
<i>Dotalabrus alleni</i> MS							0.01 <sup>0.02</sup>																	
<i>Halichoeres brownfieldi</i> MS						0.02 <sup>0.03</sup>																		
<i>Notolabrus parilus</i> MS												0.33 <sup>0.50</sup>	0.04 <sup>0.06</sup>	1.82 <sup>1.47</sup>	0.05 <sup>0.11</sup>			<0.01 <sup>0.02</sup>	<0.01 <sup>0.01</sup>	0.02 <sup>0.03</sup>				
<b>Leptoscopidae</b>																								
<i>Lesueurina platycephala</i> MS						0.06 <sup>0.03</sup>	0.01 <sup>0.02</sup>																	
<b>Monacanthidae</b>																								
<i>Acanthaluteres brownii</i> MS					0.04 <sup>0.09</sup>				<0.01 <sup>0.01</sup>															
<i>Acanthaluteres spilomelanurus</i> MS					0.15 <sup>0.03</sup>	0.02 <sup>0.03</sup>	0.01 <sup>0.02</sup>	0.11 <sup>0.10</sup>																
<i>Acanthaluteres vittiger</i> MS						0.02 <sup>0.03</sup>																		
<i>Brachaluteres jacksonianus</i> MS						0.04 <sup>0.05</sup>																		
<i>Meuschenia freycineti</i> MS					0.14 <sup>0.08</sup>			0.13 <sup>0.13</sup>																
<i>Monacanthus chinensis</i> MS					0.05 <sup>0.05</sup>	0.02 <sup>0.03</sup>		0.02 <sup>0.03</sup>																
<i>Scobinichthys granulatus</i> MS					0.10 <sup>0.06</sup>	0.02 <sup>0.03</sup>		0.16 <sup>0.08</sup>																
<b>Mugilidae</b>																								
<i>Aldrichetta forsteri</i> MEO	0.04 <sup>0.04</sup>	0.99 <sup>1.09</sup>	0.29 <sup>0.10</sup>	3.82 <sup>3.91</sup>	0.25 <sup>0.46</sup>	9.12 <sup>8.44</sup>	3.01 <sup>1.91</sup>	1.69 <sup>2.39</sup>	0.77 <sup>0.67</sup>	1.88 <sup>2.84</sup>	4.59 <sup>4.59</sup>	0.12 <sup>0.15</sup>	0.03 <sup>0.04</sup>	0.16 <sup>0.45</sup>	0.07 <sup>0.23</sup>				0.13 <sup>0.37</sup>	0.02 <sup>0.03</sup>	0.02 <sup>0.03</sup>	0.01 <sup>0.02</sup>		
<i>Mugil cephalus</i> MEO	1.52 <sup>0.42</sup>	1.33 <sup>1.32</sup>	5.62 <sup>2.97</sup>	8.97 <sup>9.55</sup>	0.03 <sup>0.06</sup>	0.43 <sup>0.51</sup>	0.19 <sup>0.39</sup>	0.05 <sup>0.03</sup>	0.09 <sup>0.21</sup>	0.26 <sup>0.39</sup>	1.07 <sup>0.69</sup>	0.02 <sup>0.03</sup>	0.07 <sup>0.02</sup>						0.15 <sup>0.44</sup>	0.07 <sup>0.10</sup>		0.14 <sup>0.25</sup>		



	West coast											South coast												
	Y	E	D	F	J	H	M	L	G	I	AB	U	R	T	P	O	S	Q	AA	Z	X	W	B	
<i>Acanthopagrus butcheri</i> E	14.47 <sup>4.43</sup>	23.42 <sup>4.32</sup>	12.25 <sup>1.22</sup>	6.49 <sup>5.18</sup>	0.31 <sup>0.63</sup>		0.06 <sup>0.02</sup>	0.29 <sup>0.36</sup>	0.16 <sup>0.36</sup>	0.44 <sup>0.63</sup>	0.64 <sup>0.43</sup>								0.21 <sup>0.62</sup>	5.89 <sup>8.33</sup>	0.81 <sup>0.94</sup>	0.12 <sup>0.11</sup>		
<i>Rhabdosargus sarba</i> MEO		0.02 <sup>0.03</sup>					0.06 <sup>0.13</sup>	0.11 <sup>0.05</sup>		0.04 <sup>0.08</sup>	0.21 <sup>0.37</sup>	0.09 <sup>0.19</sup>		0.02 <sup>0.03</sup>										
<b>Syngnathidae</b>																								
<i>Filicampus tigris</i> MS					0.01 <sup>0.02</sup>	0.02 <sup>0.03</sup>																		
<i>Pugnaso curtirostris</i> MS					0.08 <sup>0.10</sup>												0.02 <sup>0.03</sup>		0.06 <sup>0.11</sup>	0.02 <sup>0.03</sup>				
<i>Stigmatopora argus</i> MS					2.68 <sup>1.05</sup>	3.64 <sup>4.04</sup>	0.19 <sup>0.37</sup>	2.05 <sup>0.25</sup>	0.03 <sup>0.08</sup>															
<i>Urocampus carinirostris</i> EM				0.03 <sup>0.03</sup>	0.04 <sup>0.07</sup>	0.02 <sup>0.03</sup>	0.02 <sup>0.03</sup>	0.40 <sup>0.41</sup>	0.02 <sup>0.04</sup>	0.09 <sup>0.13</sup>	0.03 <sup>0.02</sup>				0.01 <sup>0.02</sup>		0.05 <sup>0.08</sup>		0.15 <sup>0.27</sup>	0.13 <sup>0.18</sup>				
<b>Terapontidae</b>																								
<i>Amniataba caudavittata</i> E	3.14 <sup>2.45</sup>	10.63 <sup>2.69</sup>	5.24 <sup>0.05</sup>	1.94 <sup>1.19</sup>			0.90 <sup>1.27</sup>	0.02 <sup>0.03</sup>	0.04 <sup>0.09</sup>	0.01 <sup>0.02</sup>	0.25 <sup>0.32</sup>													
<i>Pelates octolineatus</i> MEO		2.28 <sup>1.09</sup>	0.05 <sup>0.08</sup>	0.31 <sup>0.30</sup>	1.81 <sup>2.60</sup>	0.45 <sup>0.32</sup>	6.38 <sup>10.49</sup>	9.21 <sup>0.28</sup>	0.44 <sup>0.85</sup>	0.55 <sup>0.87</sup>	2.89 <sup>4.63</sup>									0.02 <sup>0.03</sup>				
<b>Tetraodontidae</b>																								
<i>Contusus brevicaudus</i> MS						0.05 <sup>0.02</sup>	0.04 <sup>0.06</sup>	0.05 <sup>0.08</sup>	0.01 <sup>0.02</sup>	0.02 <sup>0.03</sup>	0.01 <sup>0.02</sup>													
<i>Polyspina piosae</i> MS					0.48 <sup>0.97</sup>																			
<i>Torquigener pleurogramma</i> MEO	0.03 <sup>0.05</sup>	2.68 <sup>3.73</sup>	20.22 <sup>0.86</sup>	27.50 <sup>10.69</sup>	61.24 <sup>20.65</sup>	8.63 <sup>3.11</sup>	19.47 <sup>6.13</sup>	20.99 <sup>1.75</sup>	9.18 <sup>4.22</sup>	2.42 <sup>2.57</sup>	6.46 <sup>4.78</sup>	0.27 <sup>0.67</sup>												
<b>Tetrarogidae</b>																								
<i>Gymnapistes marmoratus</i> MEO				0.03 <sup>0.03</sup>	0.44 <sup>0.29</sup>	0.64 <sup>0.05</sup>	0.53 <sup>0.95</sup>	1.11 <sup>1.12</sup>	0.03 <sup>0.06</sup>	0.13 <sup>0.21</sup>									0.01 <sup>0.02</sup>	0.02 <sup>0.03</sup>	0.02 <sup>0.03</sup>	0.07 <sup>0.10</sup>		
<b>Number of species</b>	22	25	21	29	47	46	45	47	40	36	34	28	11	16	16	12	10	10	20	21	8	10	5	
<b>Total mean density</b>	201	113	127	170	325	375	269	233	118	350	584	257	104	404	103	57	232	52	492	795	1,535	1,994	13	