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A method for selecting health index metrics in the absence of independent measures of ecological condition

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Abstract

We describe a novel, weight of evidence-based approach for selecting fish community metrics to assess estuarine health, and its application in selecting metrics for a multi-metric health index for the Swan Estuary, Western Australia. In the absence of reliable, independent measures of estuarine condition against which to test the sensitivity of candidate metrics, objective, multivariate statistical analyses and multi-model inference were employed to select metric subsets likely to be most sensitive to inter-annual changes in the health of this ecosystem. Novel pre-treatment techniques were first applied to down-weight the influence of highly erratic metrics and to minimise the effects of seasonal and spatial differences in sampling upon metric variability. A weight of evidence approach was then adopted to select those metrics which responded most consistently across multiple analyses of nearshore and offshore fish abundance data sets collected between 1976 and 2009. Sets of 11 and seven metrics were selected for assessing the health of the nearshore and offshore waters of the Swan Estuary, respectively. Selected metrics represented species composition and diversity, trophic structure, life history and habitat functions and, in the case of the nearshore index, a potential sentinel species. These metric sets are currently being used to construct a multi-metric health index for the Swan Estuary, which is the first such tool to be developed for assessing the health of estuaries in Australia. More broadly, while the methodology has in the present case been applied to the fish fauna of the Swan Estuary, it is generally applicable to any ecosystem and type of biotic community from which an ecosystem health index might be sensibly derived.

Keywords: ecological integrity, ecosystem health, fish community, guild, metric selection, sensitivity

1. Introduction

Multi-metric biotic indices integrate information from a suite of characteristics (metrics) of the biological communities upon which they are based to provide an assessment of the ecological integrity of ecosystems (Karr, 1981; Gibson et al,. 2000). These indices typically comprise metrics that measure the species composition, diversity and trophic, habitat and/or life history structure of the assemblage such that, in combination, they reflect the structure and function of the ecosystem of interest. Such indices are now a key component of national estuarine monitoring programs in the United States, South Africa and Europe (Deegan et al., 1997; Bilkovic et al., 2005; Harrison and Whitfield, 2006; Uriarte and Borja, 2009) although, to date, their application to Australian estuaries has been limited (Borja et al., 2008).

Typically, independent measures of ecosystem condition are used to test hypotheses of metric responses to changes in physical habitat quality (Deegan et al., 1997), water quality (Hughes et al., 1998) or anthropogenic degradation (Breine et al., 2007), and those metrics which are most sensitive to these types of environmental degradation are then selected as those which best reflect ecosystem health, for inclusion in a multi-metric index. However, in several cases, such independent measures of ecosystem condition are not readily available, thereby limiting any of the currently-known quantitative methods for selecting the most useful suite of metrics. The only alternative in such cases is to employ expert judgement, which not only suffers from the influence of subjectivity, but provides no sound evidence that the suite of metrics selected is the most useful.

We outline a novel, quantitative and broadly applicable approach for selecting the most responsive subset of metrics for constructing a multimetric biotic index. This approach, which can be applied to any appropriate biota in any ecosystem, employs a combination of multivariate statistical analyses to assess metric sensitivity and redundancy, thereby allowing the most useful and parsimonious subset of metrics to be selected for subsequent incorporation into a multi-metric index of ecosystem health.

To outline this approach and demonstrate its characteristics, we sought to select appropriate fish community metrics from which to construct a multi-metric, biotic health index for the permanently-open Swan Estuary, located on the lower west coast of Western Australia (WA) (32.055°S, 115.735°E; Fig. 1). Due to the lack of established national or, until recently, State strategies for monitoring and assessing estuarine health in Australia, existing schemes, which have been based largely on water quality or floral communities, have generally been limited in scope, poorly developed and/or inconsistently applied and tested (Deeley and Paling, 1998; Borja et al., 2008; Hirst, 2008). This is particularly so in WA, which suffers from a lack of existing ecological indicators or independent measures of habitat quality for systems including the Swan Estuary, against which the sensitivity of candidate fish metrics might be assessed.

2. Methods

2.1. Collation of data sets

Given a lack of knowledge of the magnitude and/or direction of change in the health of the Swan Estuary (or any such ecosystem) over time, the approach to metric selection which we describe rests on the assumption that the ecological condition of the estuary has simply varied over time, in an unquantified and non-directional manner, in response to changes in the suite of stressors acting upon it. Given this assumption, the approach to metric selection described here focused on selecting that subset of candidate metrics that most consistently exhibited inter-annual changes at the ecosystem level over periods spanning 33 years, and thus which are likely to be most sensitive to longer-term changes in ecosystem condition. This approach was applied across multiple sets of fish species abundance data collected during each season in particular regions of the Swan Estuary, both historically (1976-2007) and during the current study (2007-09; Table 1; Fig. 1). As marked seasonal and regional differences in fish community composition have been documented for the Swan Estuary (Loneragan et al., 1989; Loneragan and Potter, 1990; Kanandjembo et al., 2001; Hoeksema and Potter, 2006), which would increase metric variability and potentially obscure their responses to inter-annual changes in ecosystem condition, data sets selected for inclusion in these analyses were restricted to those that were collected at comparable locations and times of year.

Details of the sampling regimes and methods used historically to collect fish community data throughout the Swan Estuary can be found in the published accounts of those studies, listed in Table 1. Sampling during the current study was performed throughout the estuary during the middle month of each season from winter 2007 to autumn 2009. Both 21.5 and 41.5 m-long seine nets were employed in the nearshore waters (<2 m deep) and multi-mesh gill nets were used in the offshore waters (>2 m deep); the dimensions and mesh sizes of these nets being consistent with those of similar nets employed historically (Table 1). Fish collected were immediately placed in an ice slurry and taken to the laboratory for processing. All fish were identified to species and the total number of individuals belonging to each species in each sample was recorded. The total length of each fish was measured to the nearest 1 mm, except when a large number of individuals of any one species was encountered in a sample, in which case the lengths of a representative subsample of 50 individuals were measured.

2.2. Allocation of fish to ecological guilds

All fish species encountered in the Swan Estuary during studies of this system were first allocated to functional ecological guilds (Potter and Hyndes, 1999; Elliott et al., 2007;

Franco et al., 2008) to enable the calculation of various candidate metrics (see Appendix A for a full list of these guilds). Three categories of guilds were employed, namely (i) ‘Habitat’, which reflects the relative size and preferred position within the water column of each species, (ii) ‘Estuarine Use’, which reflects the proportion of their life cycle that each species spends in the estuary and their main activities in that environment, i.e. life history, and (iii) ‘Feeding Mode’, which reflects the diet of the adults of each species (Noble et al., 2007). Guild allocation was undertaken on the basis of information contained within the Codes for Australian Aquatic Biota (Rees et al., 1999), published literature and FishBase (Froese and Pauly, 2007).

2.3. Candidate fish metrics

A list of candidate fish metrics was compiled from an extensive review of existing fish-based indices for estuaries throughout the world and using expert knowledge of the fish fauna of the Swan Estuary. These candidate metrics represented a range of fish community characteristics, including measures of species composition and diversity, trophic structure, life history and habitat functions, and also included a potential ‘sentinel’ species (Noble et al., 2007), the Blue-spot, or Swan River Goby, *Pseudogobius olorum* (Table 2). This species has various adaptations that make it well-suited to survival in degraded environments, including its tolerance of hypoxic conditions (H. Gill, Murdoch University, personal communication), which reflects its ability to use atmospheric oxygen via aquatic surface respiration (Gee and Gee, 1991), its ‘preference’ for silty substrates (Gill and Potter, 1993) and its omnivorous feeding mode. Where appropriate, two potential variants of each fish metric were calculated and assessed, namely ‘number of taxa’ and ‘proportion of total individuals’, as recommended by Noble et al. (2007).

Prior to selecting those fish metrics that exhibited the most consistent inter-annual differences and thus could be considered to be the most sensitive to temporal shifts in ecosystem health, several candidate metrics were eliminated from further consideration on the basis of their ambiguous nature (total fish density), high correlation with other metrics (various trophic structure metrics, including the contributions of piscivores, carnivores, omnivores and opportunistic species) or a lack of information (Pielou's evenness index [which is undefined for zero catches], the contribution of introduced species and its complement, the contribution of native species). Elimination of these metrics generated a refined list of candidate metrics to be tested for inclusion in the index of estuarine health (Table 3).

Data derived from samples collected during all studies using each of the four sampling methods listed in Table 1 (i.e. the 21.5, 41.5 and 102-133 m seine nets in the nearshore waters and the gill net in the offshore waters) were analysed separately to overcome the effects of gear-induced biases. Values for each of the candidate metrics in the refined list (Table 3) were calculated for each replicate sample in each data set, and the resultant data were then subjected to the following statistical analyses in the PRIMER v6 multivariate statistics package (Clarke and Gorley, 2006) with the PERMANOVA+ for PRIMER add-on module (Anderson et al., 2008), to identify that subset of metrics that most consistently exhibited inter-annual differences between 1976 and 2009 in both the nearshore and offshore waters of the Swan Estuary.

2.4. Data pre-treatment

The 21.5, 41.5 and 102-133 m seine net metric data sets (hereafter '21 m data set', '41 m data set' and '102-133 m data set', respectively) were each used, in combination, to select the most informative subset of metrics for incorporation into an index of health for the nearshore waters of the Swan Estuary, and the gill net data set was used to select metrics for incorporation into a similar index for the offshore waters of the Swan Estuary. Prior to analysis, each metric in each data set was transformed, where necessary, to stabilise its variance across different region*season*year combinations, so that standard general linear models could be fitted to the data. The most appropriate transformation in each case was determined by ascertaining the slope of the relationship between $\log_e(mean)$ and $\log_e(SD)$ for the various groups of replicate samples, i.e. each of the above combinations (Clarke and Warwick, 2001). Depending on the extent of this slope, transformations selected from the set of none, $x^{0.5}$, $x^{0.25}$, $\log_e(c_1 + x)$ were applied to either the x value or its complement, $c_2 - x$, where c_1 is typically 0.01 and c_2 is typically 1 for proportions. For each of these data sets, the draftsmans plot routine was used to ascertain the degree to which each pair of metrics was highly correlated (i.e. Pearson's correlation coefficient [r] ≥ 0.95), and thus the extent of redundancy among metrics. The metrics *Prop trop gen*, *No detr, No est res* and *Prop est res* (see Table 3 for metric codes) were found to be highly correlated with other metrics in each nearshore and offshore data set, and were thus eliminated from further analyses. In addition, the metrics *Prop P. olorum* and *Tot no P. olorum* were also eliminated from the latter data set, as the small goby species *Pseudogobius olorum* is not captured by the gill nets employed to sample offshore waters.

As the values of the fish metrics for each data set exhibited marked differences in their relative variability within groups of replicate samples, even after transformation, each was then divided by its average standard deviation (calculated as the mean of the standard deviations for each group of region*season*year replicates) to weight it by its inherent variability. This novel pre-treatment step thus relatively down-weighted the influence of highly erratic, 'noisy' metrics whilst relatively up-weighting the influence of those metrics with comparatively consistent values across replicate samples.

In order to focus on the inter-annual differences in fish metric composition in each of the data sets, the confounding effects that differences among regions and seasons and their interactions are known to have on the composition of fish communities in the Swan Estuary were removed in the standard way for a general linear model by moving all samples to a common centroid in Euclidean space. This was achieved for each pre-treated metric in each data set by initially calculating the mean of all samples (across all years) in each region*season group, then subtracting the relevant region*season mean from each sample value. The resultant data for each metric thus comprised the main inter-annual effects and residual differences under the reduced model (but note, also included the effects of any interactions between years and regions or seasons).

2.5. Model matrix construction

For each of the data sets, a Euclidean distance matrix containing all pairs of sampling years between 1976 and 2009 was then constructed from the reduced metric residuals. This matrix was also used to create a ‘model resemblance matrix’, whereby samples from the same year had a distance of 0 and samples from different years had a distance of 1. This model resemblance matrix, in conjunction with the data matrix of reduced metric residuals, was subsequently used in the following two approaches to identify those metrics which exhibited the most consistent inter-annual differences.

2.6. Modelling and weight of evidence

Firstly, distance-based linear modelling (DISTLM; McArdle and Anderson, 2001) was used in a novel way to determine the subset of ‘predictor’ variables (fish metrics) which best modelled the ‘response’ data cloud (the 0-1 model matrix), and thus whose values were relatively constant within any year, yet differed consistently between years.

The proportion of explained variation (r^2) was calculated for each model (i.e. combination of predictor variables), although the value of this selection criterion always increases with the number of predictor variables and thus does not provide a good basis for the selection of parsimonious metric sets. Therefore, the selection criterion employed in this analysis was a modified version of the information criterion (AIC) described by Akaike (1973), namely AIC_c, which was developed for application in situations like that of the current study, where the number of samples (n) relative to predictor variables (q) is small, i.e. n / q <40 (Burnham and Anderson, 2002). The selection procedure used was the 'Best' procedure, which calculates AIC_c for all possible models and identifies that with the lowest AIC_c value ($AIC_{c(min)}$) as the estimated 'best' of the candidate models.

It is important to note that, according to information theory, competing models with AIC_c values within 2 units of $AIC_{c(min)}$ are also substantially supported by the evidence and are useful in estimating the uncertainty associated with any likely 'best' model for the data set (Burnham and Anderson, 2002). Thus, by analogy, we propose that AIC_c differences (Δ_i) can be calculated for each competing model (i) according to the equation $\Delta_i = AIC_{c(i)} - AIC_{c(min)}$, to allow comparison and ranking of those models. For each of the data sets, the subset of models with $\Delta_i \leq 2$ were identified and the relative log-likelihoods of each of these models were calculated as being equal to $\exp(-0.5*\Delta_i)$. To better interpret the strength of evidence supporting each of the models in the subset, these log-likelihoods were then normalized to produce a set of positive Akaike weights (w_i) summing to 1 (Burnham and Anderson, 2002). Finally, evidence ratios (w_1 / w_i, where model 1 is the estimated 'best' in the set) were calculated to examine the relative likelihood of each model compared to the estimated 'best' model. Note that, according to Burnham and Anderson's (2002) convention for calculating evidence ratios, a ratio of 2.7 indicates, for example, that model i is 2.7 times less likely to be the 'best' model than model 1. The aforementioned authors have also suggested that in cases where a number of models exhibit small evidence ratios, multi-model inference should be employed to identify the relative importance of each of the variables (metrics) across all, or an appropriate subset of, models. An analogous weight of evidence approach was thus adopted for selecting those metrics that exhibited the most pronounced and consistent inter-annual differences, based on their relative importance among the models in the $\Delta_i \leq 2$ subset. Only those metrics which occurred in >50% of the models in this subset were selected.

It is recognised that the above approach to metric selection can only fit linear combinations of the fish metrics to the model matrix. The second approach to metric selection thus employed the BEST routine in PRIMER, which is a less constrained, fully non-parametric method which caters for non-linear functions (Clarke and Ainsworth, 1993). A similar structure for identifying sets of near optimum models through the BEST procedure might have been adopted (for example, by cutting off the subset of models at a level of correlation considered significant by the global BEST test) but, in the present case, we elected to simply use BEST in a secondary capacity to detect any metrics that the linear DISTLM approach may have missed. This second approach, in which the reference (model) resemblance matrix and complementary set of explanatory fish metric residual data were the same as those used in the DISTLM routine, employed the BIOENV or BVSTEP procedures in the BEST routine to search for that subset of fish metrics whose pattern of rank order of resemblances between samples best matched that defined by the model matrix of differences between years. In each case, the null hypothesis of no similarities in rank order pattern between the complementary matrices was rejected if the significance level (p) associated with the test statistic (Spearman's rank 'matrix correlation' coefficient [ρ_s]) was ≤ 0.05 (Clarke et al., 2008). The extent of any significant differences was determined by the magnitude of ρ_s, i.e. values close to zero indicate little correlation in rank order pattern whereas those close to +1 indicated a near perfect agreement. BIOENV was used to search all possible metric combinations for the 21 and 41 m and gill net data sets, whilst the far larger number of samples in the 102-133 m data set necessitated the application of the BVSTEP routine, which searches only a subset of possible metric combinations. The forward selection/backward elimination algorithm of BVSTEP was repeated multiple times, starting with different, randomly selected subsets of one to six metrics, to minimise the chances of not detecting the most suitable subset (Clarke and Warwick, 1998).

Finally, a weight of evidence approach was adopted for consolidating, into a single set, those metrics which were consistently identified as among the 'best' in the DISTLM and BIOENV/BVSTEP analyses of the 21, 41 and 102-133 m data sets. Thus, a metric was selected for inclusion in the nearshore index of estuarine health if it was identified by more than one of the six analyses. Given the small number of metrics identified by the DISTLM and BIOENV analyses of the gill net data set, and the fact that only two metrics were selected by both analyses, the decision rule for metric selection was modified to include a metric in the offshore index if it was identified by either of the two analyses.

3. Results

3.1. Nearshore data sets

The DISTLM analysis of the fish metric data derived from the 21 m data set identified eight metrics (*No species, Dominance, Prop trop spec, No trop spec, Prop trop gen, Prop est spawn, Prop P. olorum, Tot no P. olorum*) as $\mathrm{AIC}_{c(\min)}$, i.e. as the combination of metrics that best modelled the 0-1 model matrix and thus exhibited the most consistent inter-annual differences. However, the Akaike weights for each of the resultant models revealed that none had a high probability of being the single best, and the application of multi-model inference was thus shown to be appropriate. A subset of 20 models with r^2 values ranging between 0.194 and 0.216 were identified as being within two units of $\mathrm{AIC}_{\mathrm{c(min)}}$ ($\Delta_i \leq 2$), and were thus also considered to be substantially supported by the evidence (Table 4). The metrics that occurred at a relative frequency of >50% among the models in this subset, and which were thus considered to have been selected by the DISTLM routine, are listed in Table 5.

Similarly, the results of the DISTLM analysis carried out on the fish metric data calculated from the 41 m data set (Appendix B) demonstrated that a model containing seven metrics (*Prop trop spec, No trop spec, Prop detr, No benthic, Prop est spawn, No est spawn, Prop P. olorum*) was the estimated ‘best’ ($\mathrm{AIC}_{\mathrm{c(min)}}$), although a set of 66 models with r^2 values ranging from 0.237 to 0.329 were also identified as having substantial support from the evidence ($\Delta_i \leq 2$). Akaike weights again revealed that none of these fish metric combinations had a high probability of being the single best model. The metrics that occurred at a relative frequency of >50% among the models in the $\Delta_i \leq 2$ subset are highlighted in Table 5.

DISTLM of the fish metric data calculated from the 102-133 m data set identified a model containing nine metrics (*No species, Dominance, Prop trop spec, No trop spec, Prop detr, Prop benthic, No benthic, Feed guild comp, No est spawn*) as the estimated ‘best’ ($\mathrm{AIC}_{\mathrm{c(min)}}$), although a set of 51 models with r^2 values ranging from 0.133 to 0.145 were also identified as having substantial support from the evidence (Appendix C). Table 5 again lists those metrics which occurred at a relative frequency of >50% among the models in the $\Delta_i \leq 2$ subset.

BIOENV determined that, for the 21 m data set, the metrics *No trop spec, Prop detr, Prop P. olorum* and *Tot no P. olorum* best matched the underlying pattern of rank order resemblances between all pairs of samples in the model matrix (ρ_s = 0.128, p = 0.01; Table 5) and thus differed the most consistently between years. For the 41 m data set, BIOENV showed that *No trop gen, Prop detr, Prop benthic* and *Prop est spawn* were most highly correlated with the model matrix (ρ_s = 0.176, p = 0.01), while for the 102-133 m data set, BVSTEP identified the metrics *Prop trop spec, No benthic* and *No est spawn* as being the best matched to the inter-annual model matrix (ρ_s = 0.071, p = 0.001). Although each of the above correlations were significant, their extents were low in all cases, thus indicating a weak match between the inter-annual patterns exhibited by the fish metrics and those defined by the model matrix. This agrees with the findings of the DISTLM approach, where r^2 values were also low, noting that r^2 and ρ are broadly comparable since the latter is a matrix correlation, not a direct correlation.

Given the above findings, neither DISTLM nor BIOENV/BVSTEP alone could be considered to have selected a definitive, best set of fish metrics for the nearshore waters of the Swan Estuary. Consideration of the combined outputs of these analyses via a weight of evidence approach was therefore appropriate for identifying the most reliable, informative metric subset from which to build a nearshore index of estuarine health. The set of 11 metrics selected for inclusion in this index, namely those selected by more than one of the six analyses, are shown in Table 5.

3.2. Offshore data set

The estimated 'best' model ($\mathrm{AIC}_{c(min)}$) identified by DISTLM as that which demonstrated the most consistent inter-annual differences in the offshore waters of the Swan Estuary contained the fish metrics *No species, No trop spec, No trop gen, Prop benthic* and *Prop est spawn*. However, a subset of 66 models with r^2 values ranging between 0.098 and 0.329 were again identified as having substantial support from the evidence (Appendix D). As for the nearshore data sets, Akaike weights demonstrated that none of these models had a high probability of being the single best. Selection of those metrics occurring at a relative frequency of >50% among the models in this subset generated the set of metrics highlighted in Table 6.

The BIOENV routine identified a set of five metrics (*Sh-div*, *No trop spec*, *No trop gen*, *Prop detr* and *Prop benthic*) as being best matched to the model matrix of inter-annual differences for the offshore data set ($\rho_s = 0.068$, $p = 0.07$; Table 6). Although this correlation was weak, it was close to statistical significance at $p = 0.05$, and was thus accepted for further consideration as part of the broader, evidence-based approach for constructing the offshore health index. As only two metrics were selected by both the DISTLM and BIOENV analyses of the gill net data set, the modified decision rule, to select a metric for inclusion in the offshore index if it was identified by either of the two analyses, subsequently generated a set of seven metrics (Table 6).

4. Discussion

Multi-metric biotic indices derived using an objective, statistical approach to metric selection are widely regarded as being more robust than those based on expert judgement alone (Hering et al., 2006; Roset et al., 2007). This study has produced a generally applicable and multifaceted statistical approach for selecting the most responsive and parsimonious subset of metrics for inclusion in a biotic index of ecosystem health. In particular, this novel methodology allows the objective selection of health index metrics in situations where independent data on ecosystem condition is unavailable, and can be applied to any type of biota in any ecosystem. Moreover, by modifying the model matrix to reflect available information, this approach could equally be applied to any situation in which there is sound evidence for specific patterns or directions of change in the health of an ecosystem over time or space.

In addition to the above, the current approach to metric selection also adheres to a range of accepted recommendations for multi-metric index development that have been documented in the relevant literature. Firstly, as recommended by Roset et al. (2007), the metrics selected for inclusion in the ecosystem health index were chosen from an initial, large candidate list using statistical tests of metric redundancy and sensitivity. Secondly, as recommended by Hering et al. (2006) among others, the current approach excluded erratically variable and highly correlated metrics in order to increase the reliability and reduce the redundancy, respectively, of the resultant candidate metric set. Finally, selection from among those remaining candidate metrics was carried out using statistical testing of metric sensitivity to a model matrix, the latter of which can readily be tailored to reflect a range of spatio-temporal trends.

The novel statistical approach adopted here, which employed a combination of multivariate analyses and information-theoretic multi-model inference techniques, allowed metrics to be selected according to the weight of evidence from multiple analyses of numerous data sets, each of which was collected over differing periods and employed divergent sampling techniques.

The adoption of novel statistical approaches for selecting metrics requires that the use of these techniques be justified. Although the use of AIC and AIC$_c$ for establishing the importance of predictor variables in ‘explaining’ the underlying patterns in a response cloud has been criticised by some authors (Link and Barker, 2006; Murray and Conner, 2009), Burnham and Anderson (2002) have shown that the relative importance of each variable may be calculated by summing the Akaike weights for each model containing the variable of interest and calculating ratios of those summed weights. This enables variables to be ranked and selected according to their relative importance among multiple competing models. In the present case, however, direct calculation of the relative importance of variables (fish metrics) in the manner outlined above was invalid, as individual metrics were not balanced in terms of the frequency with which they occurred among multiple models in the output of the DISTLM routine. Therefore, the current study has adapted this method by ranking the relative importance of individual metrics according to their relative frequency among the likely ‘best’ ($\Delta_i \leq 2$) subset of models identified by DISTLM. Given that all possible combinations of metrics have been tested and that some metrics occurred more consistently than others among this 'best' subset, the weight of evidence suggests that metrics which are present among >50% of those models are likely to be the most consistently sensitive to inter-annual differences in estuarine condition, and thus most appropriate for inclusion in an estuarine health index. Although the selection of variables via exhaustive testing of all possible models has been identified as ‘data dredging’ and cautioned against (Burnham and Anderson, 2002), the aim in the present case was not to determine statistically significant explanatory variables and thus fit parameters to model causative relationships, but rather to identify the most useful signals from which to construct an estuarine health index, which will subsequently be validated using larger data sets. The weight of evidence approach adopted in this study thus accounts for model uncertainty and is compatible with the ideological demands of constructing a multi-metric index that integrates information from a range of attributes of the fish community.

The Swan Estuary is an example of one of the many estuarine systems throughout south-western Australia and, indeed, the world, for which robust, independent data on ecosystem condition are not available at appropriate spatio-temporal scales. Unlike the situation for many estuaries throughout Europe, the United States and South Africa, there is thus no objective framework against which the sensitivity of candidate fish metrics for a biotic index of ecosystem health for these systems might be assessed. Existing indicators developed for the Swan Estuary focus on various aspects of water quality, (e.g. salinity, temperature, total suspended solids, the concentrations of chlorophyll *a* and several key nutrients) and counts of various phytoplankton groups. However, they provide little or no information on the ecological status of the estuarine fauna and exhibit trends which are highly inconsistent, often contrary and difficult to interpret (Henderson and Kuhnert, 2006; Kuhnert and Henderson, 2006).

When the current approach was applied to the specific example of the fish fauna in the Swan Estuary, the respective sets of 11 and seven metrics selected for the nearshore and offshore waters were shown to represent a broad range of fish community characteristics including species composition and diversity, trophic structure, life history and habitat functions and, in the case of the nearshore index, a potential sentinel species. Biotic indices constructed from a broad range of metrics such as this are more likely to reflect the integrated ecological effects of multiple and diverse stressors, and thus reveal their impacts on the condition of the estuary as a whole (Barbour et al., 1995). These metric sets are currently being used to construct a multi-metric health index for the Swan Estuary (the first such scheme to be developed for assessing and monitoring the health of estuaries in Australia), whose sensitivity and reliability will be tested in subsequent studies

Despite the prior elimination of highly correlated metrics to reduce redundancy among the candidate metric set for the Swan Estuary fish fauna, the results of the distance-based linear modelling analyses of multiple data sets highlighted considerable redundancy among the remaining candidate metrics, and indicated substantial uncertainty regarding the particular subset of metrics that best responded to inter-annual differences. Moreover, the consistently low r^2 and ρ_S values from the DISTLM and BIOENV/BVSTEP analyses, respectively, revealed that no single combination of metrics explained a large proportion of the inter-annual patterns in the model resemblance matrix. Therefore, for each of the nearshore and offshore data sets analysed, acceptance of a single ‘best’ model was inappropriate, and weight of evidence-based multi-model inference techniques were thus applied to identify the set of metrics whose responses were most consistent over time and across data sets.

It is universally recognised, however, that the final suite of metrics selected for inclusion in a multi-metric index should include those that are sensitive to human disturbance (Barbour et al., 1995; United States Environmental Protection Agency, 2006; Roset et al., 2007; Niemeijer and de Groot, 2008). Thus, while the current approach provides an avenue for circumventing any *a priori* demonstration of the relationships between the selected metrics and independent measures of anthropogenic degradation (i.e. where the latter data is not available), it should be reiterated that, in cases such as these, *a posteriori* tests of metric sensitivity, redundancy and consistency are essential to demonstrate their ecological relevance and robustness before they can be used to construct a health index. This is the subject of continuing research for the example of the Swan Estuary presented in this study.

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Figure Legends

Fig. 1. Location of the Swan Estuary, Western Australia (inset), illustrating the regions of the estuary in which historical and current sampling of the estuarine fish community was carried out. CH = Channel, BA = Basin, CR = Canning River, LS = Lower Swan River, MD = Middle-Downstream Swan River, MU = Middle-Upstream Swan River, US = Upper Swan River.

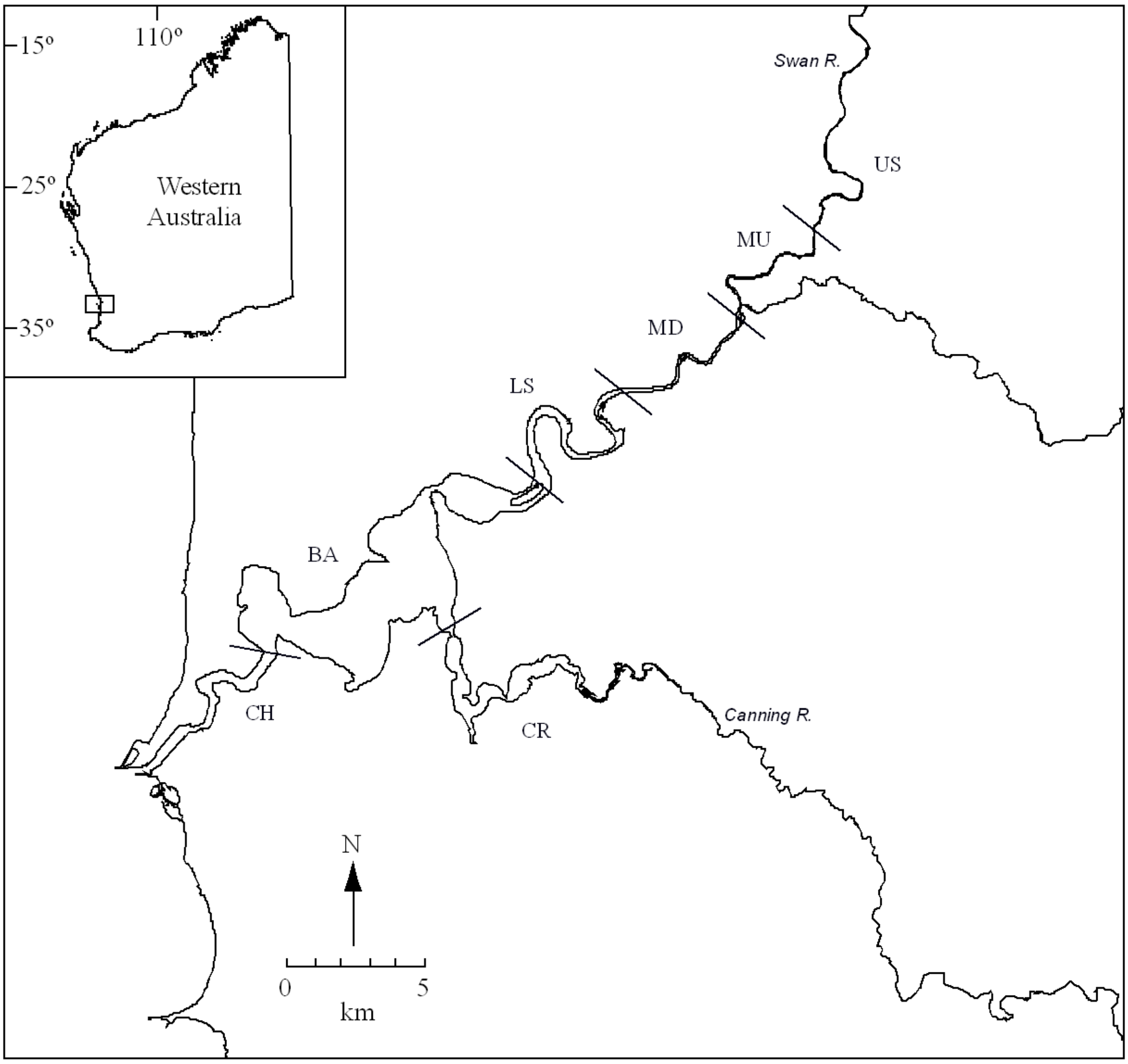
15°
110°
25°
Western
Australia
35°
Swan R.
US
MU
MD
LS
BA
CH
CR
Canning R.
N
0
5
km

Table 1

Fish species abundance data sets employed in the selection of metrics sensitive to temporal ecosystem change in the Swan Estuary, illustrating the regions of that system sampled seasonally during each study and the methods employed to sample them. CH = Channel, BA = Basin, CR = Canning River, LS = Lower Swan River, MD = Middle-Downstream Swan River, MU = Middle-Upstream Swan River, US = Upper Swan River. Locations of the regions of the Swan Estuary are shown in Fig. 1.

	Sampling method			
	Nearshore waters			**Offshore waters**
Study (Period)	**21.5 m seine net**	**41.5 m seine net**	**102-133 m seine net**	**Gill net**
	21.5 m long, 1.5 m deep, 9 mm mesh (wings), 3 mm mesh (pocket)	41.5 m long, 1.5 m deep, 25 mm mesh (wings), 9 mm mesh (pocket)	102.5-133 m long, 2 m deep 25.4 mm mesh (wings), 15.9 mm mesh (pocket)	6-8 x 20 m-long panels, Mesh sizes 35-127 mm in increments of 12-16 mm
Loneragan [a] (1976-1982)			CH, BA, CR, LS, MD, MU, US	
Sarre [b] (1993-1994)				LS, MD, MU
Kanandjembo [c] (1995-1997)		LS, MD		LS, MD
Hoeksema [d] (1999-2001)	MD, MU, US			
Hoeksema [e] (2003-2004)		LS, MD		LS, MD, MU
Valesini [f] (2005-2007)	MD, MU, US			
Current study (2007-2009)		LS, MD		LS, MD, MU

[a] Loneragan et al., 1989; Loneragan and Potter 1990; [b] Sarre, unpublished data; [c] Kanandjembo et al., 2001; [d] Hoeksema and Potter 2006; [e] Hoeksema, unpublished data; [f] Valesini et al., unpublished data.

Table 2

List of candidate metrics for possible inclusion in a biotic index of estuarine health for the Swan Estuary. ‘Trophic Specialist’ comprises the feeding mode guilds Zooplanktivore, Zoobenthivore, Herbivore, Piscivore; ‘Trophic Generalist’ comprises the feeding mode guilds Omnivore, Opportunist; ‘Benthic’ comprises the habitat guilds Benthopelagic, Small Benthic, Demersal; ‘Estuarine Spawner’ comprises the habitat guilds Estuarine species and Semi-Anadromous. * Where appropriate, two variants of each metric were tested, namely ‘number of taxa’ and ‘proportion of total individuals’ (variants not shown for brevity).

Metric	**Metric description***
Species diversity / composition / abundance	
Species richness	Total number of species present
Dominance	Number of species comprising 90% of total individuals
Total density	Total number of individuals
Introduced	Contribution of alien/introduced species
Native	Contribution of native species
Shannon diversity	Shannon Diversity Index
Pielou’s evenness	Pielou’s Evenness Index
Trophic structure	
Trophic Specialist	Contribution of trophic specialist species
Carnivore	Contribution of carnivorous species
Piscivore	Contribution of piscivorous species
Omnivore	Contribution of omnivorous species
Opportunist	Contribution of opportunist species
Trophic Generalist	Contribution of trophic generalist species
Detritivore	Contribution of detritivorous species
Feeding Guild Composition	The number of different trophic guilds present (after Coates et al., 2007)
Habitat / life history function	
Benthic	Contribution of benthic associated species
Estuarine Spawner	Contribution of estuarine spawning species
Estuarine Resident	Contribution of estuarine resident species
Sentinel species	
P. olorum	Contribution of *Pseudogobius olorum*

Table 3

Refined list of candidate metrics for possible inclusion in a biotic index of estuarine health for the Swan Estuary.

Metric	**Metric code**	**Metric description**
Species diversity / composition / abundance		
Species richness	*No species*	Total number of species present
Dominance	*Dominance*	No. of species comprising 90% of total individuals
Shannon diversity	*Sh-div*	Shannon's diversity index
Trophic structure		
Proportion of trophic specialists	*Prop trop spec*	Trophic specialists as a proportion of total individuals
Number of trophic specialists	*No trop spec*	Number of trophic specialist species
Proportion of trophic generalists	*Prop trop gen*	Trophic generalists as a proportion of total individuals
Number of trophic generalists	*No trop gen*	Number of trophic generalist species
Proportion of detritivores	*Prop detr*	Detritivores as a proportion of total individuals
Number of detritivores	*No detr*	Number of detritivorous species
Feeding Guild Composition	*Feed guild comp*	Number of different trophic guilds present
Habitat / life history function		
Proportion of benthic species	*Prop benthic*	Benthic associated as a proportion of total individuals
Number of benthic species	*No benthic*	Number of benthic associated species
Proportion of estuarine spawners	*Prop est spawn*	Estuarine spawners as a proportion of total individuals
Number of estuarine spawning species	*No est spawn*	Number of estuarine spawning species
Proportion of estuarine residents	*Prop est res*	Estuarine residents as a proportion of total individuals
Number of estuarine resident species	*No est res*	Number of estuarine resident species
Sentinel species		
Proportion of *P. olorum*	*Prop P. olorum*	*P. olorum* as a proportion of total individuals
Total density of *P. olorum*	*Tot no P. olorum*	Total abundance (density) of *P. olorum*

Table 4

The subset of models (fish metric combinations) identified as being substantially supported by evidence ($\Delta_i \leq 2$) from distance-based linear modelling of the 21 m data set. Selection criterion (AIC$_c$) and associated measures of the evidence in favour of each model are presented. The estimated ‘best’ model, termed AIC$_{c(min)}$, is italicised.

AIC$_c$	**Number of metrics**	**Metrics selected ***	**AIC$_c$ difference (Δ_i)**	**log-likelihood**	**Akaike weight (w_i)**	**Evidence ratio**
-338.28	*8*	*1,2,4,5,6,11,13,14*	*0*	*1.00*	*0.09*	*1.00*
-338.01	7	1,4,5,6,11,13,14	0.27	0.87	0.08	1.14
-337.71	8	1,3,4,5,6,11,13,14	0.57	0.75	0.07	1.33
-337.44	9	1,2,4,5,6,11,12,13,14	0.84	0.66	0.06	1.52
-337.38	7	4,5,7,11,12,13,14	0.90	0.64	0.06	1.57
-337.32	7	4,5,6,7,11,13,14	0.96	0.62	0.06	1.62
-337.29	8	2,4,5,6,7,11,13,14	0.99	0.61	0.06	1.64
-337.10	9	1,3,4,5,6,11,12,13,14	1.18	0.55	0.05	1.80
-337.00	8	1,4,5,6,11,12,13,14	1.28	0.53	0.05	1.90
-336.97	8	3,45,6,7,11,13,14	1.31	0.52	0.05	1.93
-336.76	9	1,2,4,5,6,9,11,13,14	1.52	0.47	0.04	2.14
-336.69	8	3,4,5,7,11,12,13,14	1.59	0.45	0.04	2.21
-336.59	8	1,4,5,6,9,11,13,14	1.69	0.43	0.04	2.33
-336.57	8	2,4,5,7,11,12,13,14	1.71	0.43	0.04	2.35
-336.37	9	1,2,4,5,6,7,11,13,14	1.91	0.38	0.04	2.60
-336.36	8	1,4,5,6,7,11,13,14	1.92	0.38	0.04	2.61
-336.35	9	1,2,4,5,6,10,11,13,14	1.93	0.38	0.04	2.62
-336.30	9	2,4,5,6,7,11,12,13,14	1.98	0.37	0.03	2.69
-336.29	9	1,2,4,5,6,8,11,13,14	1.99	0.37	0.03	2.70
-336.28	9	1,3,4,5,6,9,11,13,14	2.00	0.37	0.03	2.72

* **Metric Numbers (see Table 3 for explanation of metric abbreviations):** 1. *No species*; 2. *Dominance*; 3. *Sh-div*; 4. *Prop trop spec*; 5. *No trop spec*; 6. *No trop gen*; 7. *Prop detr*; 8. *Prop benthic*; 9. *No benthic*; 10. *Feed guild comp*; 11. *Prop est spawn*; 12. *No est spawn*; 13. *Prop P. olorum*; 14. *Tot no P. olorum*

Table 5

Summary of the fish metrics selected by the DISTLM and BIOENV/BVSTEP analyses of the nearshore data sets (light highlight), including those metrics selected by multiple analyses and thus identified as appropriate for incorporation into a nearshore estuarine health index for the Swan Estuary (dark highlight). Numbers shown represent the relative frequency (%) of the metric among the 'best' model subset. See Table 3 for explanation of metric abbreviations.

Metric	**21 m data set**		**41 m data set**		**102-133 m data set**		**Selected**
	DISTLM	BIOENV	DISTLM	BIOENV	DISTLM	BVSTEP	
No species	65		58		100		■
Dominance	45		3		63		
Sh-div	25		6		39		
Prop trop spec	100		91		57	▨	■
No trop spec	100	▨	100		100		■
No trop gen	85		27	▨	29		■
Prop detr	65	▨	71	▨	100		■
Feed guild comp	5		5		100		
Prop benthic	15		56	▨	86		■
No benthic	5		86		100	▨	■
Prop est spawn	100		53	▨	39		■
No est spawn	85		59		100	▨	■
Prop P. olorum	100	▨	73		20		■
Tot no P. olorum	100	▨	5		12		■

Table 6

Fish metrics selected by the DISTLM or BIOENV analyses of the offshore data set (light highlight) and thus identified as appropriate for incorporation into an offshore estuarine health index (dark highlight). Numbers shown represent the relative frequency (%) of the metric among the ‘best’ model subset. See Table 3 for explanation of metric abbreviations.

Metric	**Gill net data set**		**Selected**
	DISTLM	BIOENV	
No species	80		■
Dominance	24		
Sh-div	39	▒	■
Prop trop spec	12		
No trop spec	88	▒	■
No trop gen	42	▒	■
Prop detr	39	▒	■
Feed guild comp	44		
Prop benthic	100	▒	■
No benthic	18		
Prop est spawn	100		■
No est spawn	21		

Appendices

Appendix A. List of fish species identified from the Swan Estuary during previous (1976-2007) and current (2007-2009) studies, and the functional guilds to which they were allocated. Abbreviations: P – large pelagic; D – demersal (species closely associated with substrate, rocks or weed); BP – bentho-pelagic; SP – small pelagic; SB – small benthic; MS – marine straggler; MM – marine migrant (includes marine estuarine opportunists); SA – semi-anadromous; ES – estuarine species; FM – freshwater migrant or straggler; PV – piscivore; ZB – zoobenthivore; ZP – zooplanktivore; DV – detritivore; OV – omnivore; HV – herbivore; OP – opportunist.

Species name	**Common name**	**Habitat**	**Estuarine Use**	**Feeding Mode**
Carcharinas leucas	Bull shark	P	MS	PV
Myliobatis australis	Southern eagle ray	D	MS	ZB
Elops machnata	Giant herring	BP	MS	PV
Hyperlophus vittatus	Sandy sprat	SP	MM	ZP
Spratelloides robustus	Blue sprat	SP	MM	ZP
Sardinops neopilchardus	Australian pilchard	P	MS	ZP
Sardinella lemuru	Scaly mackerel	P	MS	ZP
Nematalosa vlaminghi	Perth herring	BP	SA	DV
Engraulis australis	Southern anchovy	SP	ES	ZP
Galaxias occidentalis	Western minnow	SB	FM	ZB
Carassius auratus	Goldfish	BP	FM	OV
Cnidoglanis macrocephalus	Estuarine cobbler	D	MM	ZB
Tandanus bostocki	Freshwater cobbler	D	FM	ZB
Hyporhamphus melanochir	Southern sea garfish	P	ES	HV
Hyporhamphus regularis	Western river garfish	P	FM	HV
Gambusia holbrooki	Mosquito fish	SP	FM	ZB
Atherinosoma elongata	Elongate hardyhead	SP	ES	ZB
Leptatherina presbyteroides	Presbyter's hardyhead	SP	MM	ZP
Atherinomorus vaigensis	Ogilby's hardyhead	SP	MM	ZB
Craterocephalus mugiloides	Mugil's hardyhead	SP	ES	ZB
Leptatherina wallacei	Wallace's hardyhead	SP	ES	ZP
Cleidopus gloriamaris	Pineapplefish	D	MS	ZB
Stigmatophora nigra	Wide-bodied pipefish	D	MS	ZB
Vanacampus phillipi	Port Phillip pipefish	D	MS	ZB
Phyllopteryx taeniolatus	Common seadragon	D	MS	ZB
Hippocampus angustus	Western Australian seahorse	D	MS	ZP
Stigmatophora argus	Spotted pipefish	D	MS	ZP
Urocampus carinirostris	Hairy pipefish	D	ES	ZP
Filicampus tigris	Tiger pipefish	D	MS	ZP
Pugnaso curtirostris	Pugnose pipefish	D	MS	ZP
Gymnapistes marmoratus	Devilfish	D	MS	ZB
Chelidonichthys kumu	Red gurnard	D	MS	ZB
Platycephalus laevigatus	Rock flathead	D	MS	PV
Platycephalus endrachtensis	Bar-tailed flathead	D	ES	PV
Leviprora inops	Long-head flathead	D	MS	PV
Platycephalus speculator	Southern blue-spotted flathead	D	ES	PV
Pegasus lancifer	Sculptured seamoth	D	MS	ZB
Amniataba caudavittata	Yellow-tail trumpeter	BP	ES	OP

Pelates octolineatus	Eight-line trumpeter	BP	MM	OV
Pelsartia humeralis	Sea trumpeter	BP	MS	OV
Edelia vittata	Western pygmy perch	BP	FM	ZB
Apogon rueppelli	Gobbleguts	BP	ES	ZB
Siphamia cephalotes	Woods siphonfish	BP	MS	ZB
Sillago bassensis	Southern school whiting	D	MS	ZB
Sillago burrus	Trumpeter whiting	D	MM	ZB
Sillaginodes punctata	King George whiting	D	MM	ZB
Sillago schomburgkii	Yellow-finned whiting	D	MM	ZB
Sillago vittata	Western school whiting	D	MM	ZB
Pomatomus saltatrix	Tailor	P	MM	PV
Trachurus novaezelandiae	Yellowtail scad	P	MS	ZB
Pseudocaranx dentex	Silver trevally	BP	MM	ZB
Pseudocaranx wrightii	Sand trevally	BP	MM	ZB
Arripis georgianus	Australian herring	P	MM	PV
Arripis esper	Southern Australian salmon	P	MS	PV
Gerres subfasciatus	Roach	BP	MM	ZB
Pagrus auratus	Snapper	BP	MM	ZB
Acanthopagrus butcheri	Southern black bream	BP	ES	OP
Rhabdosargus sarba	Tarwhine	BP	MM	ZB
Argyrosomus japonicus	Mulloway	BP	MM	PV
Pampeneus spilurus	Black-saddled goatfish	D	MS	ZB
Enoplosus armatus	Old wife	D	MS	ZB
Aldrichetta forsteri	Yellow-eye mullet	P	MM	OV
Mugil cephalus	Sea mullet	P	MM	DV
Sphyraena obtusata	Striped barracuda	P	MS	PV
Haletta semifasciata	Blue weed whiting	D	MS	OV
Siphonognathus radiatus	Long-rayed weed whiting	D	MS	OV
Neoodax baltatus	Little weed whiting	D	MS	OV
Odax acroptilus	Rainbow cale	D	MS	OV
Parapercis haackei	Wavy grubfish	D	MS	ZB
Petroscirtes breviceps	Short-head sabre blenny	SB	MS	OV
Omobranchus germaini	Germain's blenny	SB	MS	ZB
Parablennius intermedius	Horned blenny	D	MS	ZB
Istiblennius meleagris	Peacock rockskipper	D	MS	HV
Cristiceps australis	Southern crested weedfish	D	MS	ZB
Pseudocalliurichthys goodladi	Longspine stinkfish	D	MS	ZB
Eocallionymus papilio	Painted stinkfish	D	MS	ZB
Nesogobius pulchellus	Sailfin goby	SB	MS	ZB
Favonigobius lateralis	Long-finned goby	SB	MM	ZB
Afurcagobius suppositus	Southwestern goby	SB	ES	ZB
Pseudogobius olorum	Blue-spot / Swan River goby	SB	ES	OV
Amoya bifrenatus	Bridled goby	SB	ES	ZB
Callogobius mucosus	Sculptured goby	SB	MS	ZB
Callogobius depressus	Flathead goby	SB	MS	ZB
Papillogobius punctatus	Red-spot goby	SB	ES	ZB
Tridentiger trigonocephalus	Trident goby	SB	MS	ZB
Pseudorhombus jenynsii	Small-toothed flounder	D	MM	ZB
Ammotretis rostratus	Longsnout flounder	D	MM	ZB
Ammotretis elongata	Elongate flounder	D	MM	ZB
Cynoglossus broadhursti	Southern tongue sole	D	MS	ZB
Acanthaluteres brownii	Spiny-tailed leatherjacket	D	MS	OV
Brachaluteres jacksonianus	Southern pygmy leatherjacket	D	MS	OV
Scobinichthys granulatus	Rough leatherjacket	D	MS	OV
Meuschenia freycineti	Sixspine leatherjacket	D	MM	OV
Monacanthus chinensis	Fanbellied leatherjacket	D	MM	OV
Eubalichthys mosaicus	Mosaic leatherjacket	D	MS	OV
Acanthaluteres vittiger	Toothbrush leatherjacket	D	MS	OV
Acanthaluteres spilomelanurus	Bridled leatherjacket	D	MM	OV
Torquigener pleurogramma	Banded toadfish	BP	MM	OP
Contusus brevicaudus	Prickly toadfish	BP	MS	OP
Polyspina piosae	Orange-barred puffer	BP	MS	OP
Diodon nichthemenus	Globefish	D	MS	ZB
Scorpis aequipinnis	Sea sweep	P	MS	ZP
Neatypus obliquus	Footballer sweep	P	MS	ZP

Appendix B. The subset of models (fish metric combinations) identified as being substantially supported by evidence ($\Delta_i \leq 2$) from distance-based linear modelling of the 41 m data set. Selection criterion (AIC_c) and associated measures of the evidence in favour of each model are presented. The estimated 'best' model, termed $AIC_{c(min)}$, is italicised.

AIC_c	**Number of metrics**	**Metrics selected ***	**AIC_c difference (Δ_i)**	**Log-likelihood**	**Akaike weight (w_i)**	**Evidence ratio**
-111.54	*7*	*4,5,7,9,11,12,13*	*0*	*1.00*	*0.03*	*1.00*
-111.48	7	4,5,7,8,9,12,13	0.06	0.97	0.03	1.03
-111.35	8	4,5,7,8,9,11,12,13	0.19	0.91	0.03	1.10
-111.19	6	4,5,7,8,12,13	0.35	0.84	0.02	1.19
-111.09	6	1,4,5,7,9,11	0.45	0.80	0.02	1.25
-111.04	6	1,4,5,6,9,11	0.50	0.78	0.02	1.28
-110.86	7	4,5,7,8,11,12,13	0.68	0.71	0.02	1.40
-110.72	5	1,4,5,9,11	0.82	0.66	0.02	1.51
-110.71	7	1,4,5,7,9,11,13	0.83	0.66	0.02	1.51
-110.68	7	4,5,6,7,8,12,13	0.86	0.65	0.02	1.54
-110.66	8	1,4,5,7,8,9,12,13	0.88	0.64	0.02	1.55
-110.62	7	1,4,5,6,9,11,13	0.92	0.63	0.02	1.58
-110.56	8	1,4,5,6,8,9,12,13	0.98	0.61	0.02	1.63
-110.44	6	4,5,7,9,11,12	1.10	0.58	0.02	1.73
-110.40	6	5,7,8,9,11,12,13	1.14	0.57	0.02	1.77
-110.35	6	5,7,8,9,12,13	1.19	0.55	0.02	1.81
-110.34	5	1,5,7,9,11	1.20	0.55	0.02	1.82
-110.32	5	5,7,8,12,13	1.22	0.54	0.02	1.84
-110.29	8	4,5,6,7,8,11,12,13	1.25	0.54	0.02	1.87
-110.28	7	1,4,5,8,9,12,13	1.26	0.53	0.02	1.88
-110.27	6	1,4,5,9,11,13	1.27	0.53	0.02	1.89
-110.20	6	4,5,7,9,12,13	1.34	0.51	0.02	1.95
-110.19	7	1,4,5,7,9,12,13	1.35	0.51	0.02	1.96
-110.16	5	1,4,5,6,9	1.38	0.50	0.01	1.99
-110.14	7	1,4,5,7,8,9,11	1.40	0.50	0.01	2.01
-110.12	8	1,4,5,7,9,11,12,13	1.42	0.49	0.01	2.03
-110.12	6	1,4,5,6,8,9	1.42	0.49	0.01	2.03
-110.12	5	1,4,5,7,9	1.42	0.49	0.01	2.03
-110.11	7	1,4,5,6,9,12,13	1.43	0.49	0.01	2.04
-110.10	7	1,4,5,6,8,9,11	1.44	0.49	0.01	2.05
-110.10	6	1,4,5,7,8,9	1.44	0.49	0.01	2.05
-110.09	7	1,4,5,6,8,9,13	1.45	0.48	0.01	2.06
-110.05	6	1,4,5,9,12,13	1.49	0.47	0.01	2.11
-109.99	7	1,4,5,9,11,12,13	1.55	0.46	0.01	2.17
-109.97	6	1,5,7,9,11,13	1.57	0.46	0.01	2.19
-109.96	8	1,4,5,6,8,9,11,13	1.58	0.45	0.01	2.20
-109.96	8	3,4,5,7,9,11,12,13	1.58	0.45	0.01	2.20
-109.96	8	1,4,5,7,8,9,11,13	1.58	0.45	0.01	2.20
-109.94	8	1,4,5,6,9,11,12,13	1.60	0.45	0.01	2.23
-109.92	9	1,4,5,7,8,9,11,12,13	1.62	0.44	0.01	2.25
-109.90	8	2,4,5,7,8,9,12,13	1.64	0.44	0.01	2.27
-109.89	8	4,5,7,8,9,12,13,14	1.65	0.44	0.01	2.28
-109.86	8	3,4,5,7,8,9,12,13	1.68	0.43	0.01	2.32

-109.85	7	1,4,5,7,8,9,13	1.69	0.43	0.01	2.33
-109.80	7	1,4,5,6,7,9,11	1.74	0.42	0.01	2.39
-109.80	9	1,4,5,6,8,9,11,12,13	1.74	0.42	0.01	2.39
-109.78	6	1,4,5,6,9,13	1.76	0.41	0.01	2.41
-109.75	8	4,5,6,7,8,9,12,13	1.79	0.41	0.01	2.45
-109.73	9	4,5,7,8,9,11,12,13,14	1.81	0.40	0.01	2.47
-109.73	7	5,7,8,9,11,12,13	1.81	0.40	0.01	2.47
-109.68	8	4,5,7,9,10,11,12,13	1.86	0.39	0.01	2.53
-109.65	6	4,5,6,7,8,13	1.89	0.39	0.01	2.57
-109.64	7	1,4,5,7,9,10,11	1.90	0.39	0.01	2.59
-109.64	7	4,5,7,8,12,13,14	1.90	0.39	0.01	2.59
-109.62	9	3,4,5,7,8,9,11,12,13	1.92	0.38	0.01	2.61
-109.61	7	2,4,5,7,8,12,13	1.93	0.38	0.01	2.62
-109.61	6	4,5,7,8,9,12	1.93	0.38	0.01	2.62
-109.60	6	1,4,5,7,9,13	1.94	0.38	0.01	2.64
-109.60	6	1,4,5,8,9,11	1.94	0.38	0.01	2.64
-109.59	7	1,3,4,5,7,9,11	1.95	0.38	0.01	2.65
-109.59	8	1,4,5,8,9,11,12,13	1.95	0.38	0.01	2.65
-109.59	7	1,4,5,7,9,11,12	1.95	0.38	0.01	2.65
-109.58	8	4,5,7,8,9,10,12,13	1.96	0.38	0.01	2.66
-109.58	9	4,5,6,7,8,9,11,12,13	1.96	0.38	0.01	2.66
-109.54	5	4,5,7,9,11	2.00	0.37	0.01	2.72
-109.54	7	1,4,5,7,8,12,13	2.00	0.37	0.01	2.72

* **Metric Numbers (see Table 3 for explanation of metric abbreviations):** 1. *No species*; 2. *Dominance*; 3. *Sh-div*; 4. *Prop trop spec*; 5. *No trop spec*; 6. *No trop gen*; 7. *Prop detr*; 8. *Prop benthic*; 9. *No benthic*; 10. *Feed guild comp*; 11. *Prop est spawn*; 12. *No est spawn*; 13. *Prop P. olorum*; 14. *Tot no P. olorum*

Appendix C. The subset of models (fish metric combinations) identified as being substantially supported by evidence ($\Delta_i \leq 2$) from distance-based linear modelling of the 102-133 m data set. Selection criterion (AIC_c) and associated measures of the evidence in favour of each model are presented. The estimated 'best' model, termed $AIC_{c(min)}$, is italicised.

AIC_c	**Number of metrics**	**Metrics selected ***	**AIC_c difference (Δ_i)**	**log-likelihood**	**Akaike weight (w_i)**	**Evidence ratio**
-638.51	*9*	*1,2,4,5,7,8,9,10,12*	*0*	*1.00*	*0.04*	*1.00*
-638.23	8	1,4,5,7,8,9,10,12	0.28	0.87	0.03	1.15
-638.11	10	1,2,3,4,5,7,8,9,10,12	0.40	0.82	0.03	1.22
-637.94	9	1,2,5,7,8,9,10,11,12	0.57	0.75	0.03	1.33
-637.82	8	1,2,5,7,8,9,10,12	0.69	0.71	0.03	1.41
-637.75	10	1,2,4,5,7,8,9,10,12,13	0.76	0.68	0.03	1.46
-637.72	10	1,2,4,5,6,7,8,9,10,12	0.79	0.67	0.03	1.48
-637.70	9	1,2,5,6,7,8,9,10,12	0.81	0.67	0.03	1.50
-637.66	9	1,3,4,5,7,8,9,10,12	0.85	0.65	0.03	1.53
-637.58	10	1,2,4,5,7,8,9,10,11,12	0.93	0.63	0.02	1.59
-637.48	9	1,4,5,6,7,8,9,10,12	1.03	0.60	0.02	1.67
-637.42	10	1,2,5,6,7,8,9,10,11,12	1.09	0.58	0.02	1.72
-637.36	11	1,2,3,4,5,7,8,9,10,12,13	1.15	0.56	0.02	1.78
-637.29	10	1,2,4,5,7,8,9,10,12,14	1.22	0.54	0.02	1.84
-637.27	9	1,2,4,5,7,9,10,11,12	1.24	0.54	0.02	1.86
-637.22	9	1,2,3,5,7,8,9,10,12	1.29	0.52	0.02	1.91
-637.19	9	1,2,5,7,8,9,10,12,13	1.32	0.52	0.02	1.93
-637.18	10	1,2,3,5,7,8,9,10,11,12	1.33	0.51	0.02	1.94
-637.16	8	1,5,6,7,8,9,10,12	1.35	0.51	0.02	1.96
-637.16	11	1,2,3,4,5,6,7,8,9,10,12	1.35	0.51	0.02	1.96
-637.14	7	1,5,7,8,9,10,12	1.37	0.50	0.02	1.98
-637.12	8	1,2,4,5,7,9,10,12	1.39	0.50	0.02	2.00
-637.06	10	1,2,5,7,8,9,10,11,12,13	1.45	0.48	0.02	2.06
-637.03	9	1,4,5,7,8,9,10,12,14	1.48	0.48	0.02	2.10
-637.01	10	1,3,4,5,7,8,9,10,12,13	1.50	0.47	0.02	2.12
-637.01	11	1,2,3,4,5,7,8,9,10,11,12	1.50	0.47	0.02	2.12
-636.99	10	1,3,4,5,6,7,8,9,10,12	1.52	0.47	0.02	2.14
-636.93	10	1,2,3,5,6,7,8,9,10,12	1.58	0.45	0.02	2.20
-636.93	9	1,4,5,7,8,9,10,11,12	1.58	0.45	0.02	2.20
-636.92	11	1,2,3,4,5,7,8,9,10,12,14	1.59	0.45	0.02	2.21
-636.92	9	1,4,5,7,8,9,10,12,13	1.59	0.45	0.02	2.21
-636.90	9	1,3,5,6,7,8,9,10,12	1.61	0.45	0.02	2.24
-636.78	9	1,2,5,7,8,9,10,12,14	1.73	0.42	0.02	2.38
-636.77	8	1,3,5,7,8,9,10,12	1.74	0.42	0.02	2.39
-636.77	11	1,2,4,5,6,7,8,9,10,12,13	1.74	0.42	0.02	2.39
-636.75	10	1,2,5,6,7,8,9,10,12,13	1.76	0.41	0.02	2.41
-636.74	9	1,3,5,7,8,9,10,11,12	1.77	0.41	0.02	2.42
-636.71	10	1,2,3,4,5,7,9,10,11,12	1.80	0.41	0.02	2.46
-636.71	10	1,2,5,7,8,9,10,11,12,14	1.80	0.41	0.02	2.46
-636.70	8	1,2,5,7,9,10,11,12	1.81	0.40	0.02	2.47
-636.67	11	1,2,4,5,7,8,9,10,11,12,13	1.84	0.40	0.02	2.51

-636.66	11	1,2,4,5,6,7,8,9,10,11,12	1.85	0.40	0.02	2.52
-636.65	9	1,2,3,4,5,7,9,10,12	1.86	0.39	0.02	2.53
-636.64	10	1,3,4,5,7,8,9,10,12,14	1.87	0.39	0.02	2.55
-636.64	8	1,4,5,7,9,10,11,12	1.87	0.39	0.02	2.55
-636.60	11	1,2,3,5,6,7,8,9,10,11,12	1.91	0.38	0.01	2.60
-636.60	8	1,5,7,8,9,10,11,12	1.91	0.38	0.01	2.60
-636.60	10	1,2,3,5,7,8,9,10,12,13	1.91	0.38	0.01	2.60
-636.56	10	1,3,4,5,7,8,9,10,11,12	1.95	0.38	0.01	2.65
-636.55	9	1,2,5,6,7,9, 10,11,12	1.96	0.38	0.01	2.66
-636.54	10	1,3,5,6,7,8,9,10,11,12	1.97	0.37	0.01	2.68

* **Metric Numbers (see Table 3 for explanation of metric abbreviations):** 1. *No species*; 2. *Dominance*; 3. *Sh-div*; 4. *Prop trop spec*; 5. *No trop spec*; 6. *No trop gen*; 7. *Prop detr*; 8. *Prop benthic*; 9. *No benthic*; 10. *Feed guild comp*; 11. *Prop est spawn*; 12. *No est spawn*; 13. *Prop P. olorum*; 14. *Tot no P. olorum*

Appendix D. The subset of models (fish metric combinations) identified as being substantially supported by evidence ($\Delta_i \leq 2$) from distance-based linear modelling of the gill net data set. Selection criterion (AIC$_c$) and associated measures of the evidence in favour of each model are presented. The estimated 'best' model, termed AIC$_{c(min)}$, is italicised.

AIC$_c$	**Number of metrics**	**Metrics selected ***	**AIC$_c$ difference (Δ_i)**	**log-likelihood**	**Akaike weight (w_i)**	**Evidence ratio**
-240.16	*5*	*1,5,6,8,11*	*0*	*1.00*	*0.03*	*1.00*
-239.97	6	1,5,7,8,10,11	0.19	0.91	0.03	1.10
-239.93	5	1,5,8,10,11	0.23	0.89	0.03	1.12
-239.85	6	1,5,6,8,10,11	0.31	0.86	0.03	1.17
-239.78	4	6,7,8,11	0.38	0.83	0.02	1.21
-239.58	5	1,5,7,8,11	0.58	0.75	0.02	1.34
-239.50	4	1,5,8,11	0.66	0.72	0.02	1.39
-239.49	7	1,2,3,5,6,8,11	0.67	0.72	0.02	1.40
-239.38	6	1,3,5,6,8,11	0.78	0.68	0.02	1.48
-239.30	3	6,8,11	0.86	0.65	0.02	1.54
-239.24	6	1,5,6,7,8,11	0.92	0.63	0.02	1.58
-239.17	5	1,3,5,8,11	0.99	0.61	0.02	1.64
-239.12	6	1,3,5,8,10,11	1.04	0.59	0.02	1.68
-239.11	6	1,2,3,5,8,11	1.05	0.59	0.02	1.69
-239.10	6	1,5,8,9,10,11	1.06	0.59	0.02	1.70
-239.10	7	1,2,3,5,8,10,11	1.06	0.59	0.02	1.70
-239.08	7	1,5,7,8,9,10,11	1.08	0.58	0.02	1.72
-238.97	6	1,5,6,8,9,11	1.19	0.55	0.02	1.81
-238.95	8	1,2,3,5,6,8,10,11	1.21	0.55	0.02	1.83
-238.94	7	1,5,6,7,8,10,11	1.22	0.54	0.02	1.84
-238.91	5	1,5,8,9,11	1.25	0.54	0.02	1.87
-238.91	6	1,5,7,8,9,11	1.25	0.54	0.02	1.87
-238.90	7	1,5,7,8,10,11,12	1.26	0.53	0.02	1.88
-238.88	6	1,5,6,8,11,12	1.28	0.53	0.02	1.90
-238.86	8	1,2,3,5,6,8,11,12	1.30	0.52	0.02	1.92
-238.83	7	1,3,5,6,8,10,11	1.33	0.51	0.02	1.94
-238.80	6	1,5,8,10,11,12	1.36	0.51	0.02	1.97
-238.71	6	5,7,8,9,10,11	1.45	0.48	0.01	2.06
-238.67	7	1,4,5,7,8,10,11	1.49	0.47	0.01	2.11
-238.66	5	5,8,9,10,11	1.50	0.47	0.01	2.12
-238.65	7	1,5,6,8,9,10,11	1.51	0.47	0.01	2.13
-238.63	6	1,5,7,8,11,12	1.53	0.47	0.01	2.15
-238.61	6	5,7,8,10,11,12	1.55	0.46	0.01	2.17
-238.57	8	1,2,3,5,6,8,9,11	1.59	0.45	0.01	2.21
-238.55	6	1,3,5,7,8,11	1.61	0.45	0.01	2.24
-238.55	7	1,5,6,8,10,11,12	1.61	0.45	0.01	2.24
-238.54	5	1,5,8,11,12	1.62	0.44	0.01	2.25
-238.51	7	1,3,5,7,8,10,11	1.65	0.44	0.01	2.28
-238.50	6	1,3,4,5,8,11	1.66	0.44	0.01	2.29
-238.49	6	1,4,5,7,8,11	1.67	0.43	0.01	2.30
-238.47	6	1,4,5,8,10,11	1.69	0.43	0.01	2.33

-238.43	5	2,6,7,8,11	1.73	0.42	0.01	2.38
-238.42	6	1,4,5,6,8,11	1.74	0.42	0.01	2.39
-238.42	7	1,2,3,4,5,8,11	1.74	0.42	0.01	2.39
-238.42	4	5,8,10,11	1.74	0.42	0.01	2.39
-238.42	5	3,6,7,8,11	1.74	0.42	0.01	2.39
-238.41	6	1,2,5,6,8,11	1.75	0.42	0.01	2.40
-238.41	7	1,3,5,6,8,11,12	1.75	0.42	0.01	2.40
-238.38	5	5,8,10,11,12	1.78	0.41	0.01	2.44
-238.35	5	6,7,8,11,12	1.81	0.40	0.01	2.47
-238.32	7	1,3,5,6,8,9,11	1.84	0.40	0.01	2.51
-238.32	6	1,3,5,8,9,11	1.84	0.40	0.01	2.51
-238.31	9	1,2,3,5,6,8,10,11,12	1.85	0.40	0.01	2.52
-238.27	5	5,7,8,10,11	1.89	0.39	0.01	2.57
-238.26	7	1,2,3,5,8,9,11	1.90	0.39	0.01	2.59
-238.24	7	1,2,3,8,11,12	1.92	0.38	0.01	2.61
-238.24	7	1,2,5,7,8,10,11	1.92	0.38	0.01	2.61
-238.24	5	1,6,7,8,11	1.92	0.38	0.01	2.61
-238.23	5	1,4,5,8,11	1.93	0.38	0.01	2.62
-238.22	7	1,2,3,5,7,8,11	1.94	0.38	0.01	2.64
-238.22	8	1,2,3,5,7,8,10,11	1.94	0.38	0.01	2.64
-238.21	5	4,6,7,8,11	1.95	0.38	0.01	2.65
-238.21	5	6,7,8,10,11	1.95	0.38	0.01	2.65
-238.19	8	1,2,3,5,8,10,11,12	1.97	0.37	0.01	2.68
-238.19	7	1,3,5,6,7,8,11	1.97	0.37	0.01	2.68
-238.18	7	1,3,4,5,8,10,11	1.98	0.37	0.01	2.69

*** Metric Numbers (see Table 3 for explanation of metric abbreviations):** 1. *No species*; 2. *Dominance*; 3. *Sh-div*; 4. *Prop trop spec*; 5. *No trop spec*; 6. *No trop gen*; 7. *Prop detr*; 8. *Prop benthic*; 9. *No benthic*; 10. *Feed guild comp*; 11. *Prop est spawn*; 12. *No est spawn*