Promising yet variable performance of cross-taxon biodiversity surrogates: a test in two marine habitats at multiple times

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Abstract

Surrogates are a potential solution to the often-cited problem of there being insufficient information for biodiversity assessments or conservation planning. Cross-taxon surrogacy is the ability of a group of well-known taxa to represent variation in other poorly known taxa. To date, tests of the effectiveness of cross-taxon surrogacy in marine environments have yielded variable results and a significant qualification to the outcomes of tests that have demonstrated surrogacy is the near absence of tests for its persistence through time. This study tested for cross-taxon surrogacy and its persistence through time for three surrogates (crustaceans, molluscs, polychaetes). We used data on biodiversity variables and species assemblages of the surrogates and their targets that had been collected during multiple sampling events over 2.5 yr in two habitats (seagrass, unvegetated sediment) in a large bay in south-eastern Australia. We tested surrogacy by fitting a series of linear models using generalized least squares for biodiversity variables and by Mantel tests of dissimilarity matrices of species assemblages. We also tested whether the type of data transformation affected Mantel tests. We found that each of the groups were effective surrogates for some but not all biodiversity variables (with molluscs or polychaetes being effective surrogates for species richness in both habitats), that none of the groups were effective surrogates for species assemblages, and that the outcomes of Mantel tests of dissimilarity matrices of surrogates and their targets were unaffected by the data transformation used. We conclude that while our results for surrogacy for biodiversity variables are promising the inconsistent results from other studies argues for caution about their application beyond the area and context in which they were assessed. The lack of evidence that we found for surrogates of species assemblages, and similar lack of evidence from other studies, suggests that assemblage-level surrogates are unlikely to be useful in biodiversity surveys.

Keywords Biodiversity assessment, Conservation planning, Ecological indicators, Jervis Bay, *Posidonia*, Species richness

Introduction

In the absence of detailed information on the distribution of biodiversity, assessment or conservation planning, some form of surrogacy is typically used (Margules and Pressey 2000). A surrogate represents spatial and temporal variation in biodiversity and when used in conservation planning (as a proxy for detailed information on a biodiversity conservation target) leads to adequate representation of the target in reserves (Sutcliffe et al. 2015). The need for a surrogate approach to conservation planning in the marine realm arises from the limited information on the extent and distribution of biodiversity and its patterns of temporal variation, and the logistical (e.g. time, finances) and technical (e.g. incomplete taxonomy) constraints to obtaining detailed information on biodiversity in a planning region in the typical time scales of conservation decision-making (Fisher et al. 2011, Menegotto and Rangel, 2018, Valesini et al. 2018).

The ability of a group of well-known taxa to represent variation in other poorly known taxa is called cross-taxon surrogacy. Surrogacy is a pragmatic approach to conservation planning in the face of limited information on biodiversity and the pressures to make planning decisions (Grantham et al. 2009). Studies of cross-taxon surrogacy performance have tested for spatial congruence between putative surrogates and their targets in patterns of species richness, species composition, or sets of representative reserves. A number of comprehensive reviews of these studies have found variable evidence for surrogate effectiveness and cautioned against the general application of the cross-taxon surrogacy approach in terrestrial (Rodrigues and Brooks 2007, Eglington et al. 2012, Westgate et al. 2014, Oberprieler et al. 2019) and freshwater aquatic ecosystems (Allen et al. 1999, Heino 2010, Velghe and Gregory-Eaves 2013).

Tests of the effectiveness of cross-taxon surrogacy in marine environments have similarly yielded variable results. Molluscs on coastal, intertidal rocky shores and in estuarine habitats effectively represented spatial variation in species richness of other organisms (Gladstone 2002, Smith 2005, Shokri et al. 2009), and simulated conservation reserves planned using molluscs

71 performed significantly better than random selection of sites at representing other species
72 (Gladstone 2002, Shokri et al. 2009). The species richness of polychaetes predicted the species
73 richness of other groups in coastal Europe (Olsgard et al. 2003) and in a single estuary in Australia
74 (Shokri et al. 2009). The species richness of corals and fishes was correlated at a trans-oceanic scale
75 (Hughes et al. 2002) but not at the scale of a single bay (Beger et al. 2003). Spatial patterns in the
76 species richness and assemblages of algae, macro-invertebrates and fishes on coastal sub-tidal reefs
77 in south-east Australia are uncorrelated and none of the putative surrogates performed better than
78 random selection in representing their target groups in simulated reserve networks (Gladstone and
79 Owen 2005). On the shelf seabed of the Great Barrier Reef there was little congruency amongst
80 different assemblages of different groups of organisms (Sutcliffe et al. 2012). Spatial variations in
81 assemblages of macro- and meiofauna inhabiting soft-sediments in a bay in Brazil were significantly
82 correlated, suggesting one group was an effective surrogate of the other (Corte et al. 2017). Rarity
83 values of a range of phyla from subtidal rocky reefs in Brittany (western France) were poorly
84 correlated, indicating no potential for cross-taxon surrogacy (Leroy et al. 2017). Ciliated protozoans
85 are suitable surrogates for the diversity of the eukaryotic microperiphyton community (Xu et al.
86 2015).

87 This variability in the existence of surrogacy is also emphasised when the outcomes of
88 studies on the same group of organisms are compared. Polychaetes have been shown to be useful
89 surrogates by some studies (Olsgard et al. 2003, Magierowski and Johnson 2006, Shokri et al. 2009)
90 but not others (Olsgard and Somerfield 2000). Molluscs have been shown to be useful surrogates by
91 some studies (Gladstone 2002, Smith 2005) but not others (Olsgard and Somerfield 2000,
92 Magierowski and Johnson 2006). And, while some studies concluded that crustaceans were suitable
93 surrogates (Magierowski and Johnson 2006) others found no evidence of surrogacy (Olsgard and
94 Somerfield 2000, Smith 2005).

95 The lack of a clear and consistent outcome from the different tests of cross-taxon surrogacy
96 can be attributed to a number of interacting causes: the range of spatial scales and habitats that
97 have been used; the existence (or non-existence) of an environmental gradient in the study area;
98 differences in the ecologies and life histories of surrogates and their targets; latitudinal differences
99 among the published studies; variation in sampling effort (i.e. size of sampling unit and number of
100 replicate samples); differences in the units of assessment (i.e. species or assemblages); and the use
101 of different variables and statistical analyses to assess surrogate effectiveness and decide on its
102 presence or absence (Hess et al. 2006, Lawler and White 2008, Grantham et al. 2010, Westgate et al.
103 2014, 2017).

104 Notwithstanding these possible explanations for the lack of consistent evidence for cross-
105 taxon surrogacy, a significant qualification to the conclusions of studies that have demonstrated
106 cross-taxon surrogacy is the near-absence of tests for temporal consistency (Mellin et al. 2011,
107 Westgate et al. 2014). A significant correlation between a putative surrogate and its target groups
108 based on one period of sampling could be a one-off result (e.g. a spurious correlation arising from
109 incomplete sampling, Neeson et al. (2013)) and not representative of long-term or underlying
110 relationships among taxa. If so, this could be a major limitation to the application of this form of
111 surrogacy in biodiversity assessment, marine conservation planning, and environmental assessment.
112 In addition, tests for the existence of cross-taxon surrogacy based on multivariate assemblages
113 typically use correlations of similarity matrices with some form of data transformation prior to
114 analysis. Transformation of species' abundances in multivariate data sets is done to reduce the
115 influence of numerically dominant species or erratic differences between sampled locations (Clarke
116 and Gorley 2015). Tests of surrogates of multivariate assemblages have typically used only a single
117 data transformation e.g. presence-absence (Beger et al. 2003), log(X+1) (Corte et al. 2017), square
118 root (Olsgard and Somerfield 2000), or fourth root (Magierowski and Johnson 2006). Given the
119 findings that other types of analyses of multivariate assemblages are affected by the choice of data

120 transformation (Anderson et al. 2005) it is important to understand whether the type of data
121 transformation affects analyses of surrogacy effectiveness.

122 Therefore, the aim of this study was to test for cross-taxon surrogacy and its persistence through
123 time. We used data on three groups of marine invertebrates (crustaceans, molluscs, polychaetes)
124 that had been collected during multiple sampling events over 2.5 yr. In order to improve the
125 generality of the results we undertook the study in two habitats (seagrass, unvegetated sediment) at
126 the same location. Specifically, we tested the following null hypotheses: (1) biodiversity variables of
127 the surrogates are not related to the same variables in their target through time and in different
128 habitats; (2) pairwise patterns among sites of assemblage dissimilarity for a surrogate and its target
129 are not correlated; and (3) the size of the correlations between the dissimilarity matrices of a
130 surrogate and its target are unaffected by the type of data transformation used.

131

132 **Materials and methods**

133 **Study area**

134 This study was undertaken in Jervis Bay, a marine embayment in southern New South Wales (NSW),
135 Australia (35˚08'S, 150˚45'E) (Fig. 1). At depths <10 m the predominant habitats are either beds of
136 the seagrass *Posidonia australis* or rocky reefs and at depths >10 m the predominant habitat is
137 unvegetated sandy mud. Jervis Bay is currently managed by two marine protected areas: the NSW
138 State-managed Jervis Bay Marine Park, and the Commonwealth of Australia-managed Booderee
139 National Park. Much of the surrounding terrestrial area is within State national parks with limited
140 residential development and no major rivers flowing into the Bay. At the time of this study, Jervis
141 Bay was regarded as relatively pristine. Water temperatures during the study varied between 14-
142 15^{o}C (July-August) and 23-24.5^{o}C (January-February) (CSIRO 1993). As the sampling sites spanned the

143 extent of Jervis Bay, the spatial extent of this study was the area of the Bay i.e. 102 km^2 (Hutchings
144 and Jacoby 1994).

145 **Field sampling**

146 Four sites in beds of the seagrass *P. australis* and six sites of sandy/muddy substratum that was
147 unvegetated (hereafter called unvegetated sediment) that spanned the breadth of Jervis Bay were
148 sampled (Fig. 1). The seagrass sites were in depths of 2-6 m (mean±SE=4.0±0.9 m) and the
149 unvegetated sediment sites were in depths of 12-20 m (14.7±1.7 m). Each site was sampled on nine
150 occasions between February 1989 and June 1991, with intervals of 2-5 mo between successive
151 sampling events.

152 Samples from unvegetated sediment sites were collected by Smith-McIntyre grab (sample
153 area 0.06 m^2 and sample volume 4.7 L) deployed from a boat. At each site, five replicate samples
154 were collected from an area of several hundred square metres by allowing the boat to drift. All grab
155 samples were collected on the same day. Samples at the seagrass sites were collected by SCUBA
156 divers using hand-operated corers. The corers had an internal diameter of 0.11 m and sampled an
157 area of 0.0095 m^2 and a volume of 0.95 L of sediment (when pushed into the sediment to a depth of
158 0.10 m). At each site four replicate cores were collected from each of two plots (2 m x 2 m) that
159 were approximately 50 m apart, at each sampling event. The vegetated sites were sampled over a
160 number of days during the same week as the grab samples were collected and all field sampling in
161 each sampling event was completed within one week. For consistency in the field collection the
162 same two divers collected all seagrass samples throughout the study, the same crew operated the
163 grabs, and the same people sorted samples in the lab. Different sampling techniques were used in
164 the two habitats because the seagrass beds were too shallow for effective deployment of a grab,
165 and the unvegetated sediment sites were too deep for repetitive diving over a limited number of
166 days. The data were analysed separately for each habitat, and interpretations limited to the
167 temporal variation in cross-taxon surrogacy within each habitat rather than a comparison between

168 the habitats, to avoid confounding because of the different methods and physical scales of sampling
169 in the two habitats.

170 In the field, the collected samples were put into bags made of 1.0 mm mesh, quickly washed
171 to remove sediment then immediately placed in a polydrum containing 7% neutralised seawater
172 formalin and Biebricht Scarlet (to stain all living organisms) and gently agitated. After 4-5 d the mesh
173 bags were removed and carefully washed under a running tap to remove all the formalin and
174 remaining sediment and then the contents of each bag placed into 70% alcohol. Samples were then
175 sorted in the laboratory under a dissecting microscope and identified to species with a reference
176 collection being deposited at the Australian Museum.

177 **Data analyses**

178 Analyses were done for two data sets: four sampling events (that spanned 10 mo), and nine
179 sampling events (that spanned 28 mo). In the test of four sampling events the surrogates tested
180 were crustaceans, molluscs, and polychaetes and their target groups were, respectively, molluscs +
181 polychaetes, crustaceans + polychaetes, and crustaceans + molluscs. In the test of nine sampling
182 events the surrogate was molluscs and the target was polychaetes (data for crustaceans were
183 unavailable), and we recognise that because it is a bivariate relationship the results are
184 interchangeable (i.e. polychaetes as a surrogate). The following biodiversity variables were
185 calculated for each surrogate and its target group: species richness; total number of individuals;
186 Margalef's index of species richness, which accounts for the numbers of individuals in a sample;
187 Pielou's evenness index, which measures how equitability individuals are distributed among the
188 species in a sample; and Shannon-Wiener diversity index (calculated to log base e) (Magurran 2003).
189 Variables were calculated using PRIMER 7 software (PRIMER-E, Plymouth).

190 In the analyses that follow correlations ≥0.7 were used as evidence of strong relationships
191 between surrogates and their targets, with the surrogate being suitable for biodiversity surveys and

192 conservation planning (Vellend et al. 2008, Heino 2010). In the tests of the biodiversity variables the
193 relevant correlation was the partial correlations ($_p$r) after taking time into account, and in the tests of
194 assemblages, the relevant correlation was the Mantel correlation coefficient (r_M).

195 To test the null hypothesis that biodiversity variables of the surrogates are not related to the
196 same variables in their target through time we fit a series of linear models using generalized least
197 squares in R (R Core Team 2019). Each model determined whether an individual taxon (crustaceans,
198 molluscs, polychaetes) was an effective biodiversity surrogate for the other two taxa combined. For
199 example, the species richness of crustaceans (the surrogate) was modelled in relation to the
200 combined species richness of molluscs and polychaetes. Separate models to examine the strength of
201 such taxon surrogacy in each habitat (seagrass, unvegetated sediment) were built for each of the
202 five biodiversity variables. The mean values of each variable at each site at each time were used. To
203 account for repeated measurements over time at the same sites, we used the nlme package
204 (Pinheiro et al. 2019) and the function corAR1 to specify a temporal autocorrelation structure of
205 order one in the models (Mangiafico 2016). After including time as a potential source of variation in
206 the models in this way, we were able to determine the strength of each taxon as a surrogate over
207 and above any influence of time through the use of partial correlation coefficients ($_p r$). We used a
208 likelihood ratio (LR) test via the nagelkerke function (Mangiafico 2016) to assess statistical
209 significance and to calculate pseudo R^2 values (from which $_p r$ values were calculated) for each taxon
210 as a surrogate (Crawley 2012). The LR tests assessed the significance of the change in deviance (χ^2)
211 when the full model (surrogate and time) was compared with a reduced model (time only). All
212 models were inspected for normality of residuals and homogeneity of variances, with species
213 richness log-transformed in seagrass habitat to meet model assumptions.

214 For the assessment of multivariate assemblages of surrogates and their targets, the mean
215 abundance of each species at each site was used (n=4 seagrass sites, n=6 unvegetated sediment
216 sites). Patterns of assemblage dissimilarity among sites were visualised by non-metric MDS

ordination plots, based on Bray-Curtis dissimilarity matrices of square-root transformed abundance data, for each pair of surrogate and target for each sampling event, in each habitat. Analyses were done with PRIMER 7 software (PRIMER-e, Quest Research Ltd). The null hypothesis that the pairwise patterns among sites of assemblage dissimilarity for a surrogate and its target are not correlated was tested by Mantel test (Heino 2010, Ilg and Oertli 2016, Yong et al. 2018). Mantel correlation coefficients (R_M) were calculated from the Bray-Curtis dissimilarity matrices of the surrogate and its target. Surrogate-target relationships with $R_M \geq 0.7$ were further investigated by partial Mantel correlation coefficients (pR_M), using a third matrix of pairwise physical distances between sites (see also Su et al. 2004, Padial et al. 2012, Ilg and Oertli 2016), to account for the possibility that the correlations were confounded by the different pairwise distances among sites (Fig. 1). Mantel tests were conducted with PC-Ord v 7.08 (McCune and Mefford 2018).The statistical significance of the pR_M values is not reported because the small number of maximum possible permutations of the dissimilarity matrices did not allow for meaningful estimates of *P*-values (Manly 1997).

Prior to the above analyses, separate dissimilarity matrices were constructed in which the abundance data of each species were transformed to square-root, log(X+1), or presence-absence to account for the possible effect of transformation on the Mantel test (Olsgard et al. 1997, Anderson et al. 2005, Mueller et al. 2013). One-way analysis of variance (ANOVA) was used to test the null hypothesis that mean R_M did not differ among data transformations for each of the data sets of four and nine sampling events in each habitat. Data transformation was analysed as a fixed factor with 3 levels (square-root, log(X+1), presence-absence). The replicates for each level were the set of R_M-values for all times, in each habitat. The assumption of equality of variances was tested prior to ANOVA by Levene's test.

Results

Biodiversity

The data set for the four sampling events included (i) crustaceans: 154 species (981 individuals) in seagrass and 185 species (16,391 individuals) in unvegetated sediment; (ii) molluscs: 72 species (1,779 individuals) in seagrass and 110 species (4,300 individuals) in unvegetated sediment; and (iii) polychaetes: 85 species (1,666 individuals) in seagrass and 141 species (8,351 individuals) in unvegetated sediment. The data set for the nine sampling events included (i) molluscs: 97 species (3,335 individuals) in seagrass and 178 species (9,537 individuals) in unvegetated sediment; and (ii) polychaetes: 105 species (2,815 individuals) in seagrass and 166 species (15,248 individuals) in unvegetated sediment.

Biodiversity variables

Seagrass

In the set of four sampling events each of the three surrogates showed statistically significant relationships with their targets for most biodiversity variables through time (Table 1, Fig 2). The only exceptions were for the surrogate crustaceans (Margalef's index), molluscs (total number of individuals, Pielou's evenness index) and polychaetes (Pielou's evenness index). The surrogate relationships that exceeded the r=0.7 threshold were crustaceans (total number of individuals $_{p}r=0.89$), molluscs (species richness $_{p}r=0.79$, Shannon-Weiner diversity index $_{p}r=0.81$), and polychaetes (species richness $_{p}r=0.73$, Shannon-Weiner diversity index $_{p}r=0.76$). For the test of molluscs as a surrogate of polychaetes in the set of nine sampling events, relationships between surrogate and target were statistically significant for most biodiversity variables (with the exception of total number of individuals); however, none of the tests exceeded the r=0.7 threshold (Table 1, Fig 3). The largest correlation was for species richness ($_{p}r=0.60$).

Unvegetated sediment

In the set of four sampling events there was a statistically significant relationship between each surrogate and its target through time for most biodiversity variables, except for crustaceans (Pielou's evenness index, Shannon-Weiner diversity index), molluscs (Pielou's evenness index, Shannon-

Weiner diversity index), and polychaetes (Shannon-Weiner diversity index) (Fig. 3, Table 2). The surrogate-target relationships that exceeded the r=0.7 threshold included crustaceans (species richness $_p$r=0.75, total number of individuals $_p$r=0.75), molluscs (species richness $_p$r=0.89, total number of individuals $_p$r=0.82), and polychaetes (species richness $_p$r=0.73). In the set of nine sampling events the relationship between the surrogate (molluscs) and target (polychaetes) was statistically significant for all biodiversity variables except Pielou's evenness index and Shannon-Weiner diversity index, and none of the tests had $_p$r of at least 0.7 (Fig.4, Table 2).

Assemblages

Mean R_M values between surrogates and targets did not significantly differ among the three different data transformations (square-root, log(X+1), presence-absence) in both seagrass and unvegetated sediment (Fig. 5). The error bars indicate that R_M values varied among the sampling events for all transformations, and in some sampling events R_M values were negative. When this occurred, the R_M values were negative for all transformations. As a result of the lack of significant differences among data transformations, only analyses of the square root-transformed data are presented in the following section.

Seagrass

nMDS ordination plots of surrogates and targets that showed the spread of sites according to relative dissimilarity of assemblages showed few concordant pattens for each of the four (Fig 6) or nine (Fig 7) sampling events. For example, in event 1 there was a near-equidistant spread of all sites for crustaceans (the putative surrogate) but a distinct cluster of sites 1 and 2 for the target (the assemblage of molluscs and polychaetes). There was a similar pattern of difference in event 4 between surrogate (molluscs) and target (crustaceans and polychaetes). In event 7 (Fig 7) Sites 3 and 4 clustered close together for the mollusc assemblage but were widely separated for the polychaete assemblage. There were few examples of concordant patterns of dissimilarity among sites of the

surrogate and target in the four sampling events (e.g. polychaetes as surrogate (event 1), molluscs as surrogate (event 3)) or nine sampling events (e.g. event 4).

Only one test of surrogacy in the four sampling events had a Mantel correlation coefficient (R_M) ≥0.7: polychaetes in event 1 (R_M=0.83, Table 3). This correlation decreased (but still exceeded the 0.7 threshold) when the effect of distance between the sites was controlled for (pR_M=0.71). Values of R_M changed considerably among sampling events for each of the surrogates tested, including changing from positive to negative values. In the test of nine sampling events R_M for molluscs and polychaetes was high for only one sampling event (event 9) and the value of R_M did not alter when the distances between sites was controlled for. Otherwise, values of R_M changed considerably from one sampling event to the next.

Unvegetated sediment

In unvegetated sediment there were distinct differences between surrogates and targets in the arrangement of the sites in the nMDS ordination plots for the set of four sampling events (Fig 8 e.g. event 1 with crustaceans as the surrogate, and event 3 with polychaetes as the surrogate) and the set of nine sampling events (Fig 9 e.g. events 1, 5 and 8). The arrangements of sites for the surrogate and target appeared to be similar for molluscs as the surrogate in event 4. There were no obvious examples of similar arrangements of sites for molluscs or polychaetes in any of the nine sampling events.

Results of the Mantel tests showed a high value of R_M (0.78) for only one test of surrogacy in the four sampling events: molluscs in event 1 (Table 4). This value increased slightly when the distances between sites were controlled for (pR_M=0.79). Other Mantel tests varied considerably for each of the surrogates in each of the sampling events and none approached 0.7. Only one Mantel test returned a high value in the set of nine sampling events for molluscs and polychaetes: 0.84 in event 9. This increased to pR_M=0.88 when distances among sites were controlled for.

Discussion

Performance of surrogates

Previous research has revealed no consistency in the performance of cross-taxon surrogates in different habitats, spatial scales, and among different groups of fauna (Westgate et al. 2014), and highlighted the lack of understanding about the persistence of cross-taxon surrogacy through time (Mellin et al. 2011, Westgate et al. 2017). We used data sets of marine invertebrates that were collected at regular intervals for periods of 10 and 28 mo to test for the existence of cross-taxon surrogacy and its persistence through time, and we tested for it in two habitats (seagrass, unvegetated sediment). We assessed cross-taxon surrogacy by using generalised linear models (that included time as a factor) to test for relationships between surrogates and their targets for several biodiversity variables and by Mantel correlations to test for relationships between the dissimilarity matrices of surrogates and their targets. Based on a threshold correlation of ≥0.7 as evidence of surrogacy, we found that: (i) each of the tested surrogates had a strong relationship with its target that persisted through time for one or more biodiversity variables in each habitat; (ii) there was no consistent evidence for surrogacy in the species assemblages of either seagrass or unvegetated sediment; and (iii) data transformation did not affect the size of Mantel correlation coefficients.

We defined *a priori* the evidence needed to reject the null hypothesis of no relationship between a surrogate and its target, which was the magnitude of the correlation coefficient and its persistence through time. An *r*-value of ≥0.70 indicates that a substantial proportion of the variation in the target could be explained by variation in the surrogate (Lovell et al. 2007, Vellend et al. 2008, Heino 2010). A correlation of $r \geq 0.70$ after time has been taken into account, or in a majority of sampling events, indicates that the correlation between surrogate and target is unlikely to be a statistical anomaly (Neeson et al. 2013). Reasons for rejecting cross-taxon surrogacy in other studies have included the non-significance of correlations (Beger et al. 2003, Gladstone and Owen 2007), significant but small correlations (e.g. <0.30 by Hirst 2008), or a combination of non-significance and

339 significant but small correlations (Karakassis et al. 2006, Leroy et al. 2017). Similarly, surrogacy has
340 been accepted as proven for a range of magnitudes of correlation coefficients (Gladstone 2002,
341 Olsgard et al. 2003, Smith 2005, Magierowski and Johnson 2006, Shokri et al. 2009, Corte et al.
342 2017). While the use of a standard criterion (e.g. $r \geq 0.70$) for accepting the existence of cross-taxon
343 surrogacy would potentially facilitate the application of surrogacy in conservation planning and
344 comparisons among studies, it would need to be established that the criterion was independent of
345 habitat, spatial scale, sampling effort, latitude, and the diversity of the putative surrogate group and
346 its targets.

347 Notwithstanding differences in the criteria used to decide whether or not surrogacy exists,
348 the results of this study show that conclusions about a group's performance as a cross-taxon
349 surrogate are not transferable. We found that crustaceans, molluscs and polychaetes were suitable
350 surrogates for some biodiversity variables in both seagrass and unvegetated sediment. While some
351 other studies also found that polychaetes (Olsgard and Somerfield 2000, Olsgard et al. 2003,
352 Magierowski and Johnson 2006, Shokri et al. 2009), molluscs (Gladstone 2002, Smith 2005), and
353 crustaceans (Magierowski and Johnson 2006) were effective surrogates, others have concluded that
354 polychaetes (Olsgard and Somerfield 2000), crustaceans (Olsgard and Somerfield 2000, Smith 2005)
355 and molluscs (Olsgard and Somerfield 2000, Magierowski and Johnson 2006) were unsuitable as
356 cross-taxon surrogates. Whilst some of these differences can be attributed to the different ways
357 surrogate effectiveness was judged, these studies were also conducted in different environments,
358 over different time scales, in different biogeographical regions, and with faunas of different
359 diversities. This further reinforces the caution expressed by other authors about the application of
360 conclusions about surrogates beyond the area and context in which they have been assessed (Mellin
361 et al. 2011, Westgate et al. 2014).

362 For one-third of the studies reviewed by Mellin et al. (2011) there was no relationship
363 between surrogates and their targets, and when there was a relationship the predictive power was

364 weak. Cross-taxon surrogates are expected to perform well when the surrogate and target co-vary
365 spatially and temporally and this may be more likely to occur at smaller spatial scales, when there is
366 a strong ecological or disturbance gradient that favours a surrogate, when the surrogate has a
367 diversity of life histories and ecologies that overlap those of the target group of species, or in low
368 complexity environments (Gaston and Williams 1996, Olsgard and Somerfield 2000, Mellin et al.
369 2011). Mellin et al. (2011) found that marine habitat type was the best predictor of surrogate
370 effectiveness, with low complexity marine habitats such as soft bottoms being best. We found, for
371 biodiversity variables, a similar number of acceptable surrogacy relationships in unvegetated
372 sediment and seagrass (a more complex marine habitat). We also found no difference between
373 these habitats in the lack of surrogacy relationships for species assemblages.

374 Each of the tested surrogates represented a variety of ecological roles and life histories that
375 we expected to overlap with the roles and life histories of their targets and to therefore be suitable
376 as surrogates. For example, the polychaetes in our data set were diverse and represented a range of
377 families, life cycles (from a few months to several years), reproductive strategies (from breeding
378 once then dying, to those which breed annually over several years), larval phases and durations
379 (including long-lived pelagic larvae, a very short larval phase, no larval phase), and a range of feeding
380 strategies (carnivores, filter-feeders, herbivores, opportunistic) (Hutchings 1998, Beesley et al. 2000,
381 Rouse and Pleijel 2006, Jumars et al. 2015). The molluscs were similarly diverse in ecological roles
382 and life histories: the bivalves include suspension feeders, deposit feeders, microcarnivores and
383 some obtain their nutrition via bacteria or zooxanthellae. Gastropods are equally diverse with
384 carnivores and grazers and some with symbioses, others are suspension feeders, parasites,
385 coprophages, and life cycles ranged from annual species to those that lived for several years (Brusca
386 et al. 2016, Lindberg et al. 2004, Ponder and Lindberg 2008). The absence of surrogacy in the test of
387 nine sampling events, which were based on a surrogate (molluscs) and a single target (polychaetes),
388 could be due to smaller degree of overlap in the above features compared to the test of a surrogate
389 and the combined set of two target groups.

The lack of evidence for surrogacy in the species assemblages of both habitats mirrors results from other studies that have reported correlations that, while statistically significant, were small in marine (Karakassis et al. 2006, Hirst 2008), aquatic (Heino 2010, Padial et al. 2012, Ilg and Oertli 2016) and terrestrial environments (Irwin et al. 2014, Yong et al. 2018). These conclusions have been consistent across a variety of methods used to test surrogacy of species assemblages, including Mantel tests, Procrustes analysis, and RELATE tests (Beger et al. 2003, Hirst 2008, Heino 2010, Padial et al. 2012, Corte et al. 2017). A possible explanation for this poor performance of assemblage-level surrogates in marine environments is environmental variation that differentially affected the range of species comprising the surrogate and the target groups. For example: spatial heterogeneity in the features of each habitat that differed among the sampled sites and influenced the invertebrate biodiversity (Bell et al. 1988, Macfarlane and Booth 2001, Edgar and Barrett 2002, Radke et al. 2011), temporal variation in the features of each habitat that influenced invertebrate biodiversity (Duarte 1989, Ysebaert and Herman 2002, van der Wal et al. 2017), or the absence of a strong ecological gradient in Jervis Bay among the sites sampled within each habitat (Przeslawski et al. 2009, Clark et al. 2015).

Temporal variation in surrogacy

There are examples in the published literature of cross-taxon surrogacy studies that used biodiversity data from a single sampling event, assessed surrogacy in the same ways as this study, and concluded that surrogacy had been demonstrated (Gladstone 2002, Olsgard et al. 2003, Smith 2005, Shokri et al. 2009) or was absent (Beger et al. 2003, Hirst 2008, Sutcliffe et al. 2012). There are fewer examples of studies that have directly tested for the persistence of surrogacy through time. Magierowski and Johnson (2006) found changes through time in the magnitude of the goodness of fit between some putative surrogates (molluscs, echinoderms) and their targets, and no changes for some other putative surrogates (for assemblages of macroinvertebrates inhabiting artificial kelp holdfasts) over a total study time of 13 mo. Corte et al. (2017) found significant and large

correlations between assemblages of macro- and meiofauna in each of four time periods (spanning 11 mo), and concluded surrogacy was present. Olsgard and Somerfield (2000) tested cross-taxon surrogacy in three different years that spanned six years and found that the correlations between some putative surrogates and their targets varied dramatically among the three years (from small to large correlation coefficients), while others were consistently large, showed less variation, and were therefore suitable surrogates. Other approaches to testing surrogacy have integrated the influence of time by pooling multiple samples that had been collected through time and analysing a larger single data set and have concluded that surrogacy existed (Olsgard et al. 2003, Xu et al. 2015) or was absent (Gladstone and Owen 2007). While we applied criteria of a specific and strong correlation coefficient and its persistence through time, such threshold criteria have not been used in other marine studies that assessed surrogacy through time.

The limited understanding of temporal variation in the existence or absence of surrogacy has been highlighted by other authors (Mellin et al. 2011, Westgate et al. 2017). We used persistence through time as one criterion for evidence of surrogacy. We found that for some surrogates and some biodiversity variables, strong correlations persisted through time. We also found that surrogacy relationships in species assemblages did not persist through time. Our results highlight the importance of sampling at multiple times to assess surrogacy performance. A single sampling event done at the time of sampling event 1 would have concluded that polychaetes (in seagrass) and molluscs (in unvegetated sediment) were suitable surrogates for the species assemblages of the target groups crustaceans and molluscs, and crustaceans and polychaetes respectively. A strong correlation between a surrogate and its target would be expected to persist through time if both groups varied in the same way in most or all the sampled sites.

Effect of data transformation

Sampled invertebrate assemblages typically include a few species with much greater abundances that may vary differently through time (e.g. Morrisey et al. 1992, Ysebaert and Herman 2002,

Marshall et al. 2018) and therefore some form of data transformation is required. While tools are available to assist decisions about the transformation to use (e.g. Clarke et al. 2014, Clarke and Gorley 2015), the decision in a test related to a biodiversity assessment or conservation objective should depend on the hypothesis being tested or the objective of the assessment or conservation planning (e.g. conservation of species' occurrences, or representative assemblages) and is therefore ultimately an *a priori* decision. Tests of multivariate cross-taxon surrogacy have typically used only a single data transformation including presence-absence (Beger et al. 2003), log(X+1) (Corte et al. 2017), square root (Olsgard and Somerfield 2000), and fourth root (Magierowski and Johnson 2006). Other types of analyses of multivariate assemblages are affected by the choice of data transformation (Anderson et al. 2005) and it is therefore important to understand the effect of transformation on analyses of surrogacy effectiveness. Shokri et al. (2009) compared two transformations and found only slight differences in the magnitudes of correlation coefficients that did not alter their conclusions about surrogate effectiveness. However, if they had used the same threshold criterion of $r \geq 0.70$ their conclusions would have been influenced by the type of transformations. We showed in this study that the magnitude of the correlation coefficients, and therefore the decision about the existence of surrogacy, was not influenced by the type of transformation used.

Conclusions

Along with this study, studies of the usefulness of cross-taxon surrogacy in biodiversity assessments have yielded variable results. Our study, which also incorporated a test of temporal consistency, found that if the objective is to assess species richness in seagrass or unvegetated sediment then molluscs or polychaetes would be suitable surrogates. Considering the two habitats separately, crustaceans or molluscs would be suitable surrogates in seagrass, and molluscs or polychaetes would be suitable surrogates in unvegetated sediment. None of the surrogates we tested were suitable as surrogates for species assemblages. Our results highlighted the importance of testing surrogacy at

multiple times. We showed that conclusions about the performance of a group as a surrogate are not transferable, and while our results for surrogacy for biodiversity variables are promising the inconsistent results from other studies argues for caution about their application beyond the area and context in which they were assessed. While studies of surrogates of species assemblages have applied a range of data transformations prior to creation of dissimilarity matrices, and results of ecological studies are affected by the type of data transformation used, we found that different data transformations did not significantly affect the outcomes of Mantel tests, and authors should adopt the transformation relevant to the characteristics of sampled assemblage and/or the objective of the research. The lack of support that we found for surrogates of species assemblages in both habitats, and evidence from other studies also showing weak correlations, suggests that surrogates for assemblages are unlikely to be useful in biodiversity surveys.

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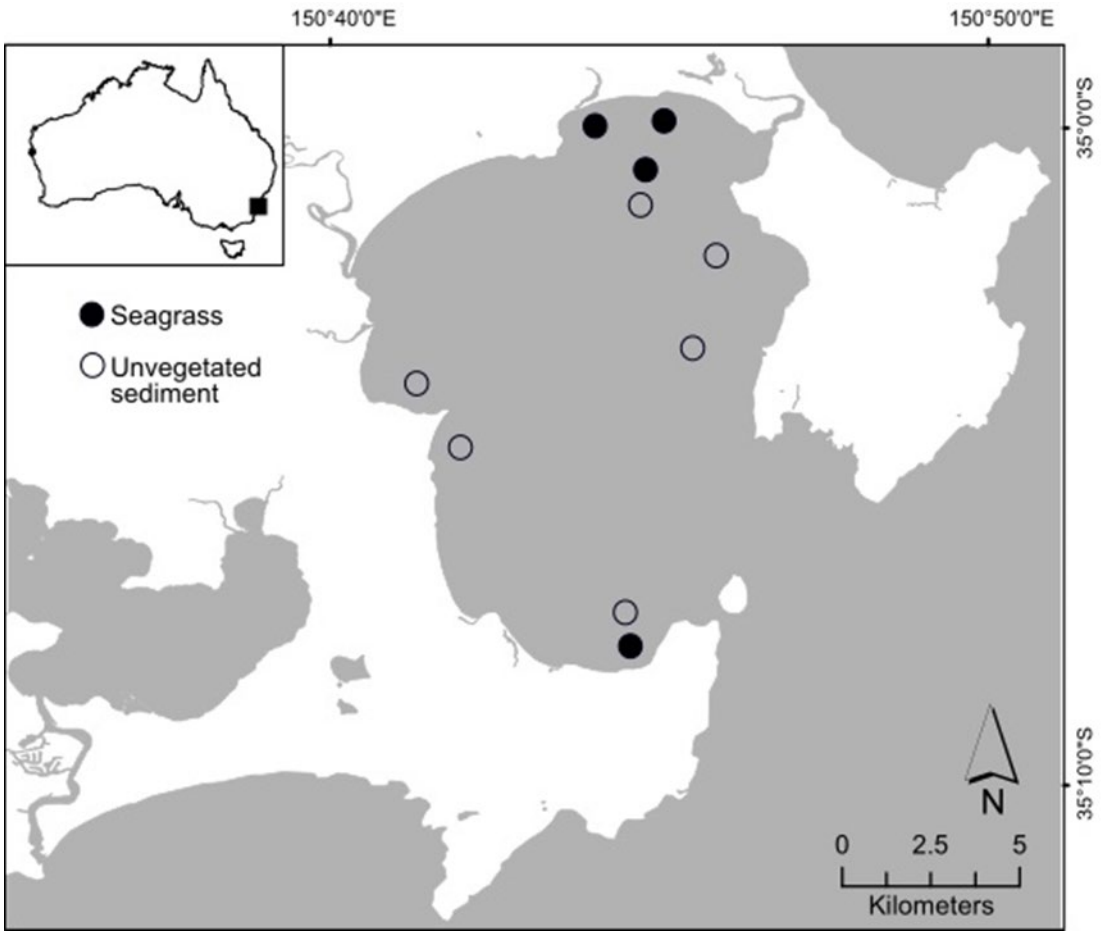


Fig. 1 The study area in Jervis Bay, Australia, showing relative positions of sites in seagrass and unvegetated sediment habitats (source of polygon: Crossman and Li 2015)

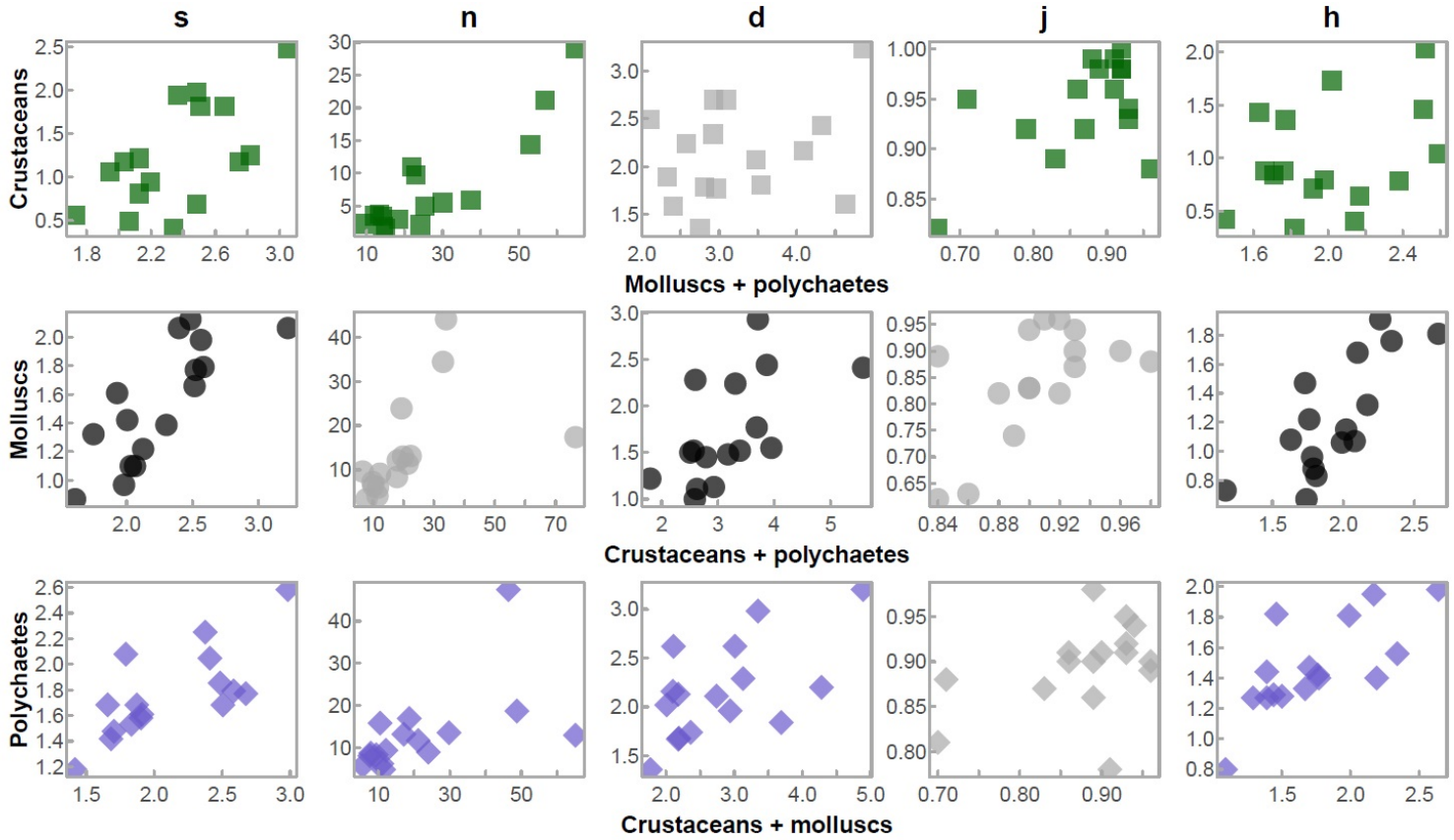


Fig 2 Seagrass: Relationships between surrogates (X-axes) and targets (Y-axes) for univariate measures of biodiversity (s species richness, n total no. individuals, d Margalef's index, j Pielou's evenness index, h Shannon-Wiener diversity index). Points are mean values from each site at each sampling event. Coloured symbols indicate a significant relationship between surrogate and target and grey symbols indicate a non-significant relationship.

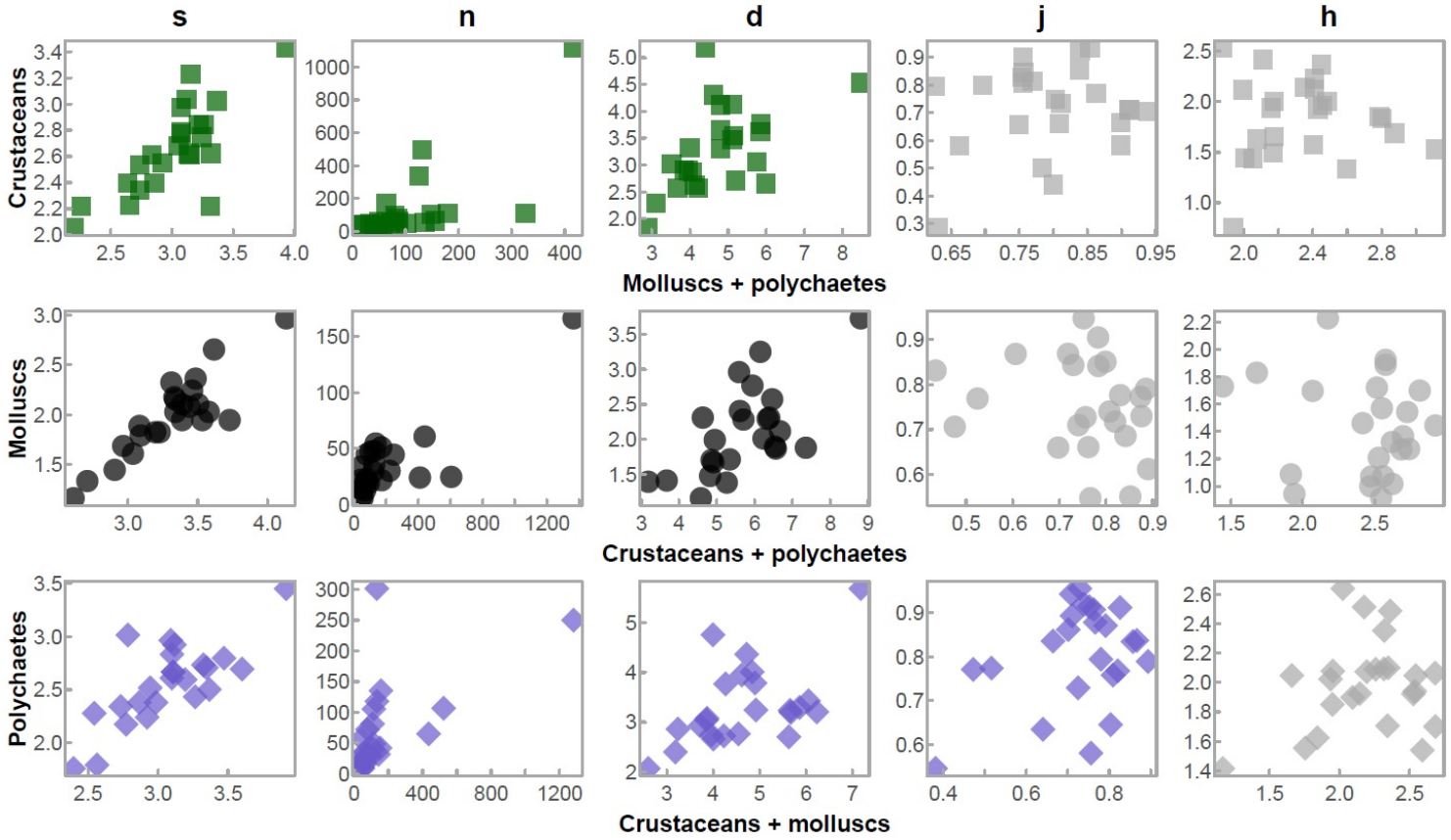


Fig 3 Unvegetated sediment: Relationships between surrogates (X-axes) and targets (Y-axes) for univariate measures of biodiversity (s species richness, n total no. individuals, d Margalef's index, j Pielou's evenness index, h Shannon-Wiener diversity index). Points are mean values from each site at each sampling event. Coloured symbols indicate a significant relationship between surrogate and target and grey symbols indicate a non-significant relationship.

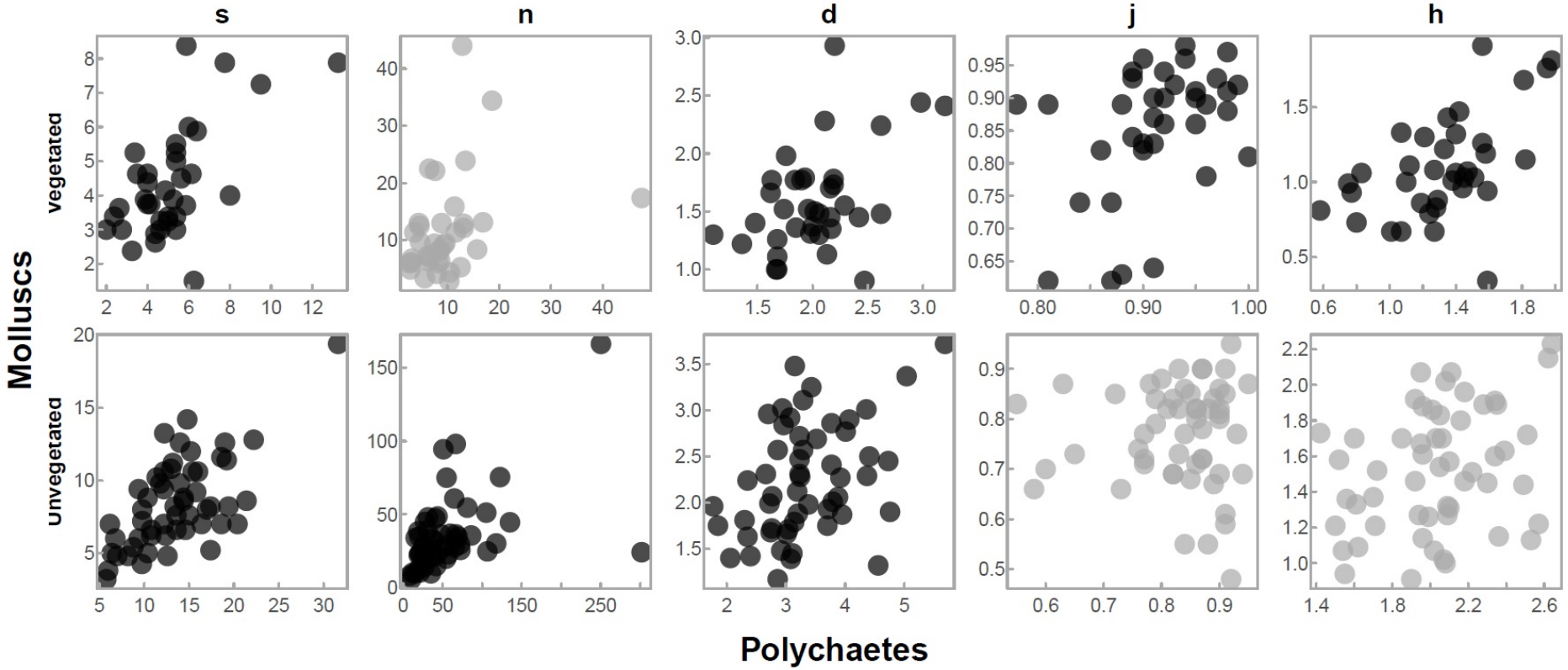


Fig 4 Relationships between surrogate (X-axes) and target (Y-axes) for univariate measures of biodiversity (s species richness, n total no. individuals, d Margalef's index, j Pielou's evenness index, h Shannon-Wiener diversity index) in seagrass (vegetated) and unvegetated sediment (unvegetated). Points are mean values from each site (n=4 seagrass sites, n=6 unvegetated sediment sites) at each sampling event (n=9). Black symbols indicate a significant relationship between surrogate and target and grey symbols indicate a non-significant relationship.

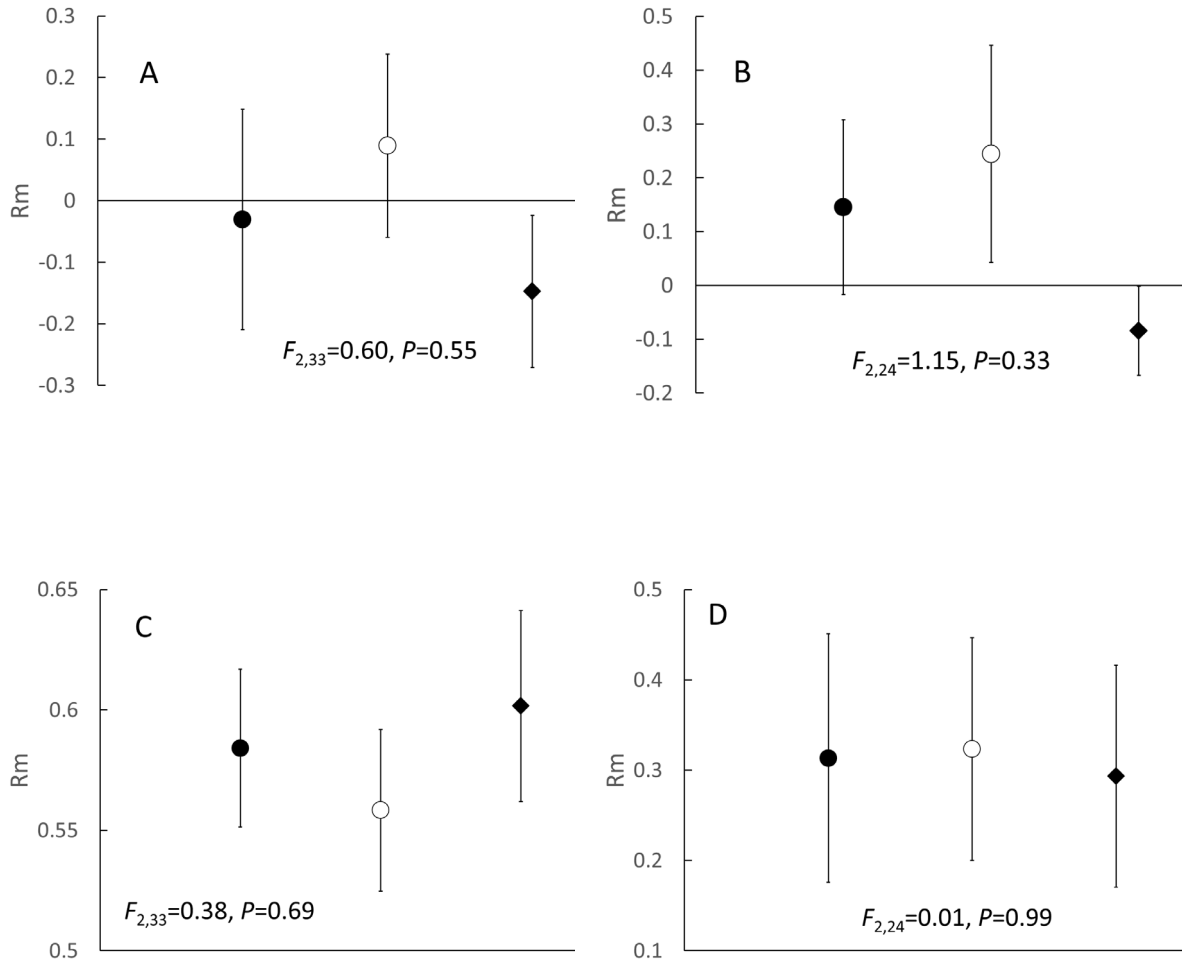


Fig. 5 The effect of data transformation (● square root, ○ log (X+1), ♦ presence-absence) on the magnitude of the Mantel correlation coefficient (R_M) between the Bray-Curtis dissimilarity matrices of surrogates and their targets. Values shown are mean R_M-values (± standard error) for (A) seagrass for 4 sampling events (n=12), (B) seagrass for 9 sampling events (n=9), (C) unvegetated sediment for 4 sampling events (n=12), and (D) unvegetated sediment for 9 sampling events (n=9). Results of one-way ANOVA testing for significant differences among mean R_M-values are also shown (Levene's tests done prior to ANOVAs were all non-significant)

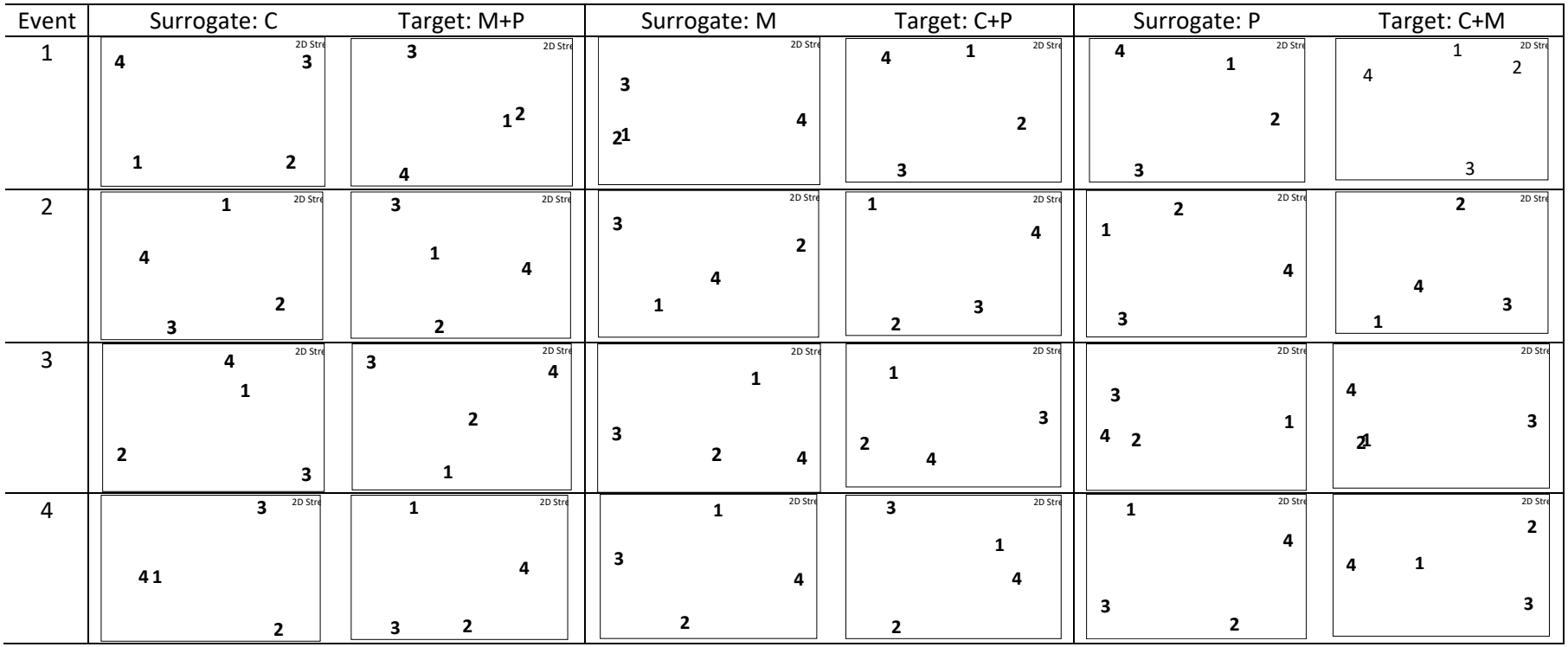
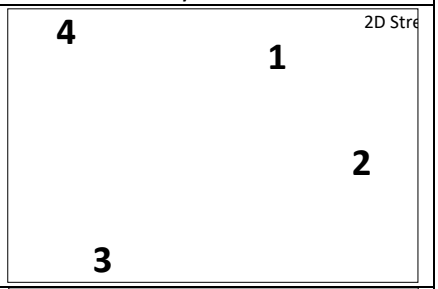
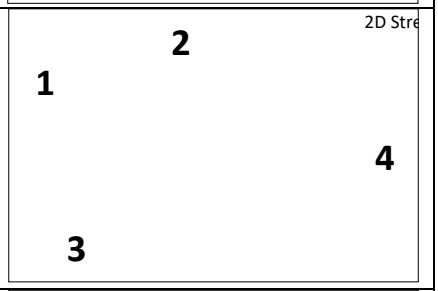
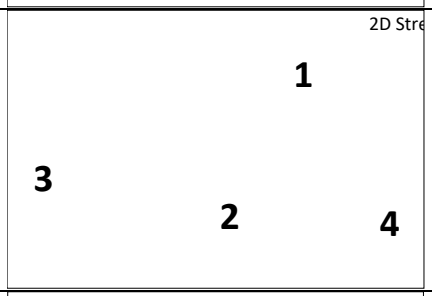
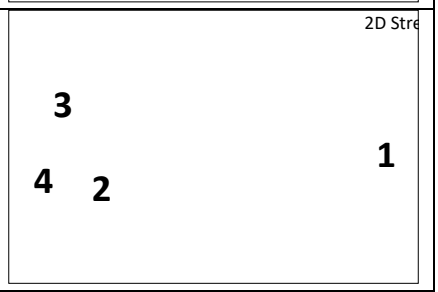
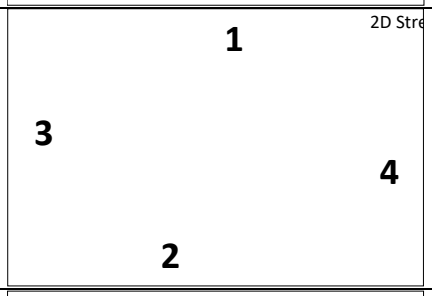
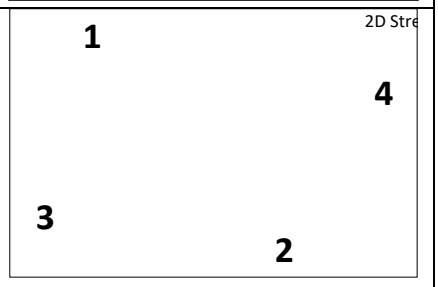
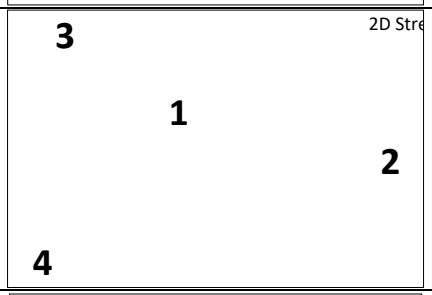
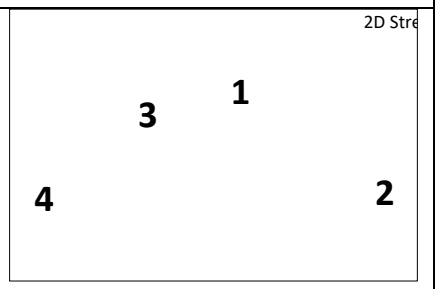
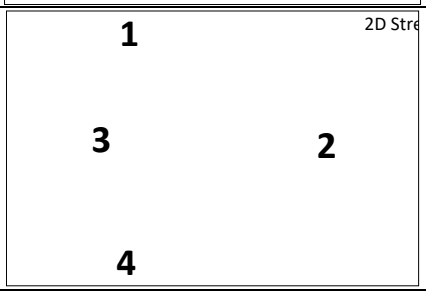
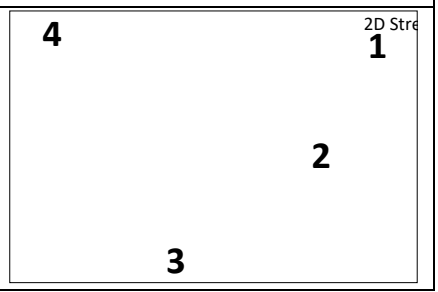


Fig 6. Seagrass: nMDS ordination plots (based on Bray-Curtis dissimilarity matrices of square-root transformed abundances) comparing dissimilarities among sites (numbered 1-4) for assemblages of surrogates and their targets in each of four sampling events. C Crustaceans, M Molluscs, P Polychaetes.

Event	Molluscs	Polychaetes
1		
2		
3		
4		
5		
6		

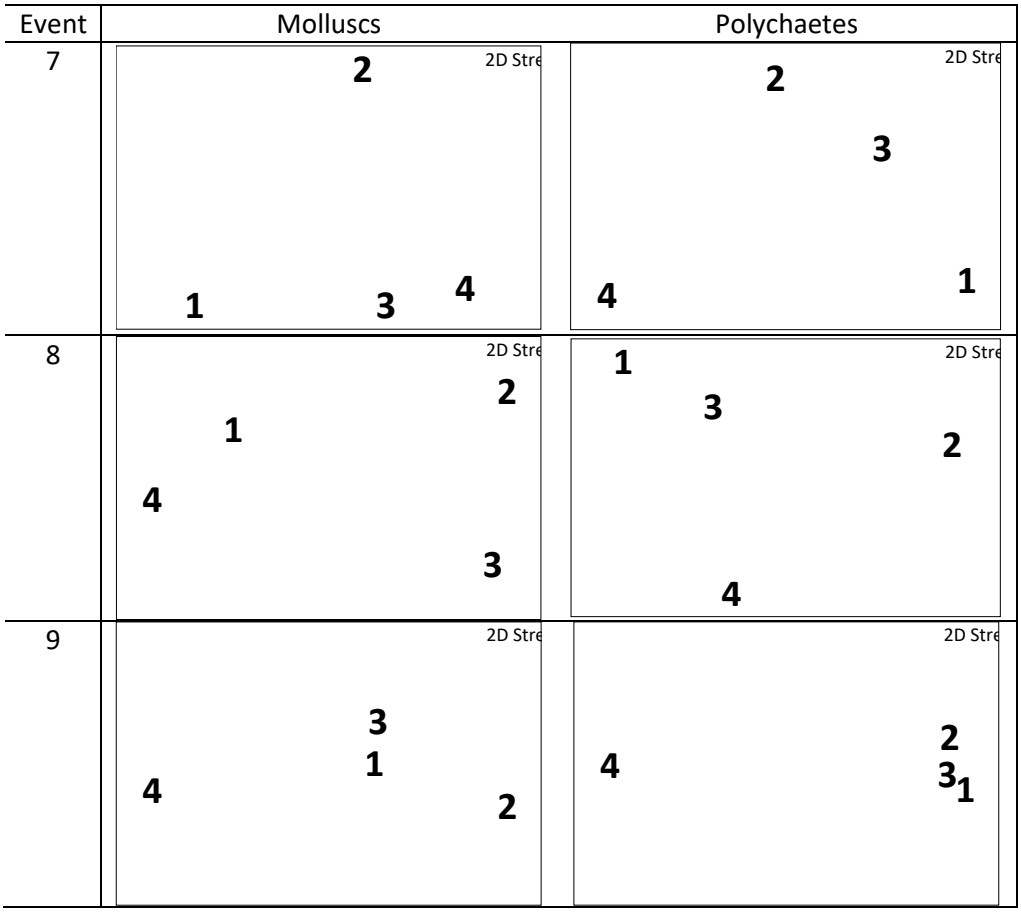


Fig 7. Seagrass: nMDS ordination plots (based on Bray-Curtis dissimilarity matrices of square-root transformed abundances) comparing dissimilarities among sites (numbered 1-4) for assemblages of molluscs and polychaetes in each of nine sampling events.

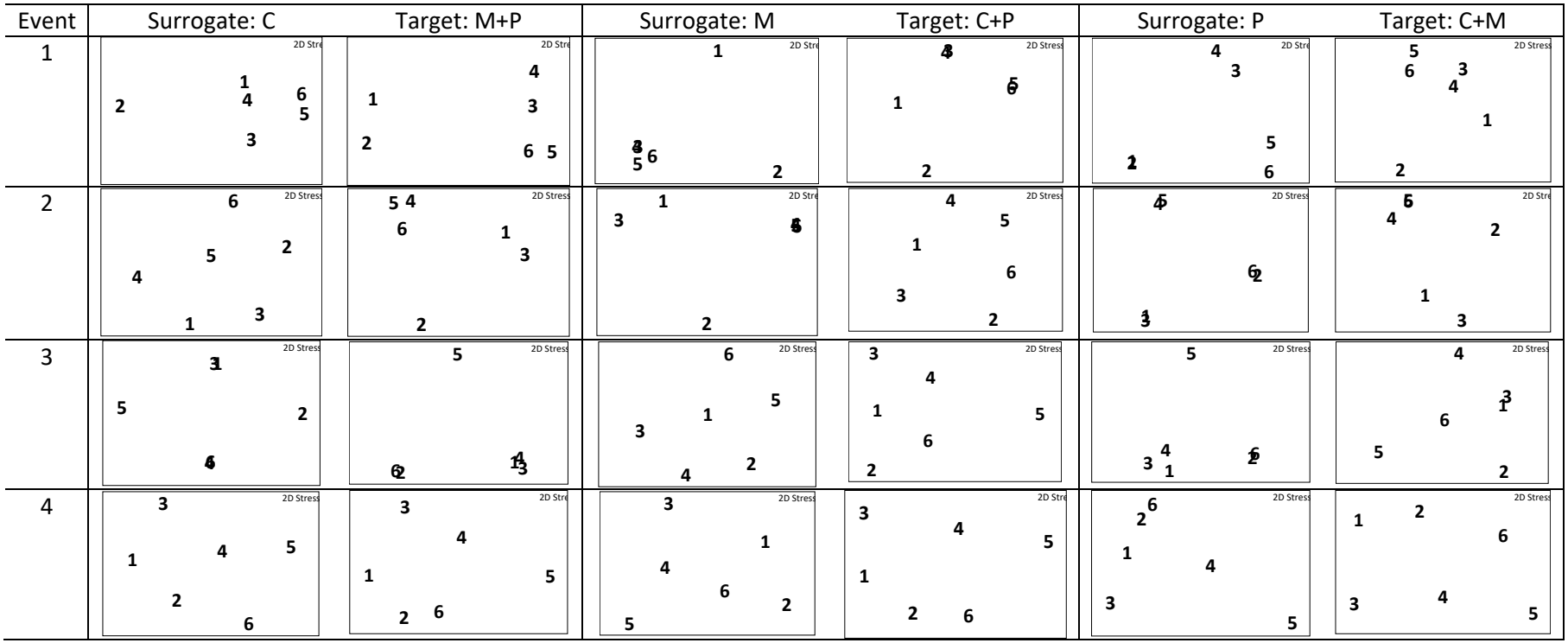
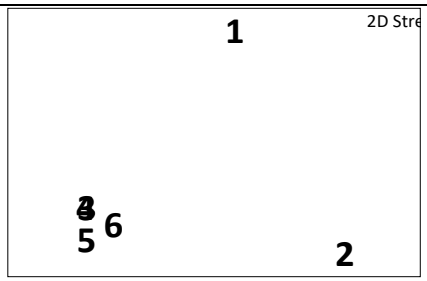
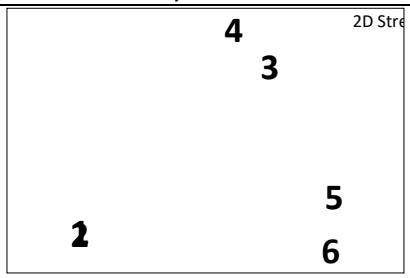
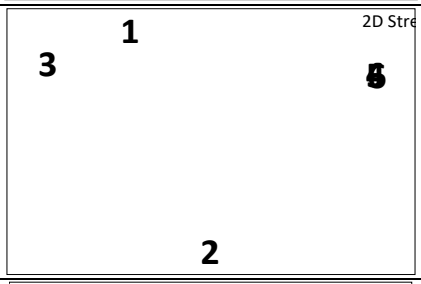
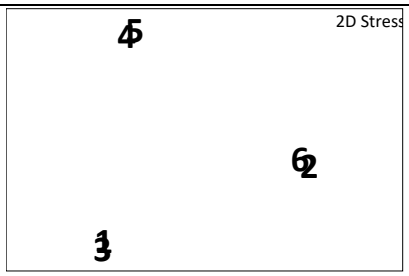
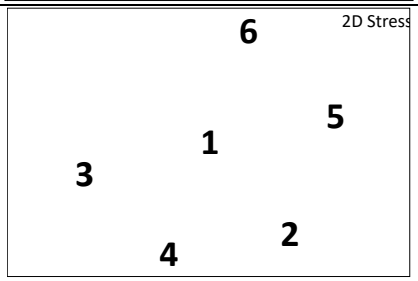
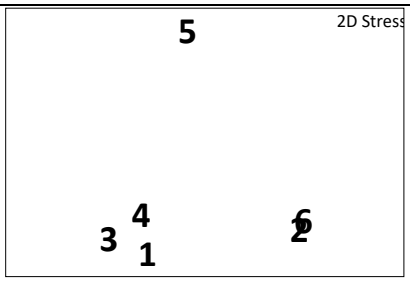
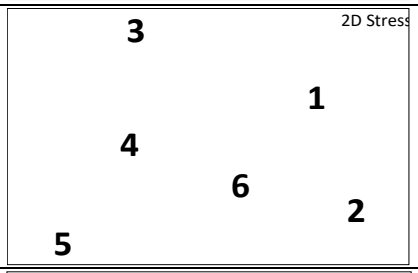
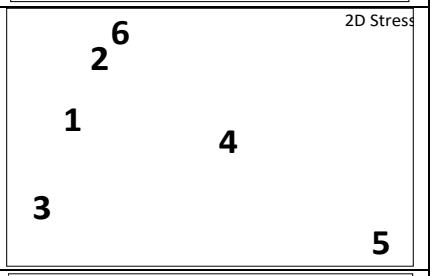
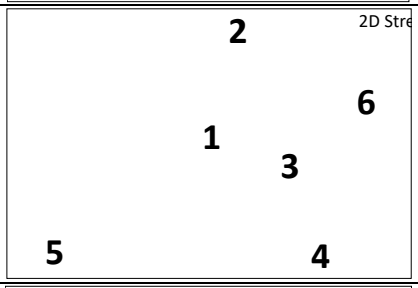
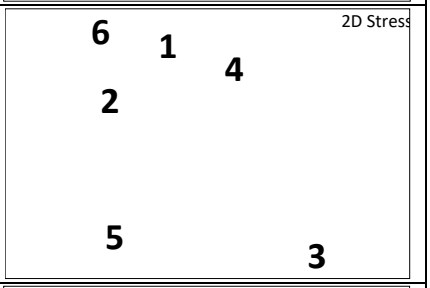
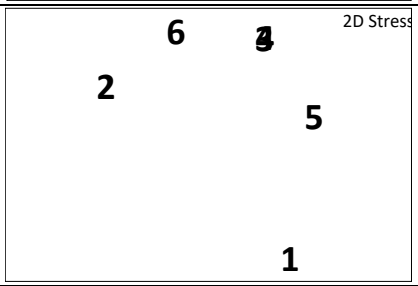
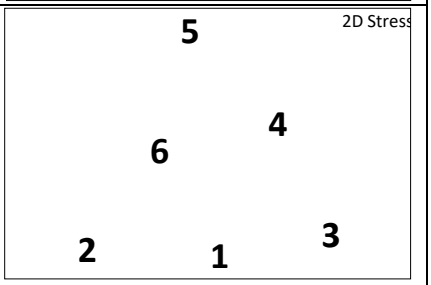


Fig 8. Unvegetated sediment: nMDS ordination plots (based on Bray-Curtis dissimilarity matrices of square-root transformed abundances) comparing dissimilarities among sites (numbered 1-6) for assemblages of surrogates and their targets in each of four sampling events. C Crustaceans, M Molluscs, P Polychaetes

Event	Molluscs	Polychaetes
1		
2		
3		
4		
5		
6		

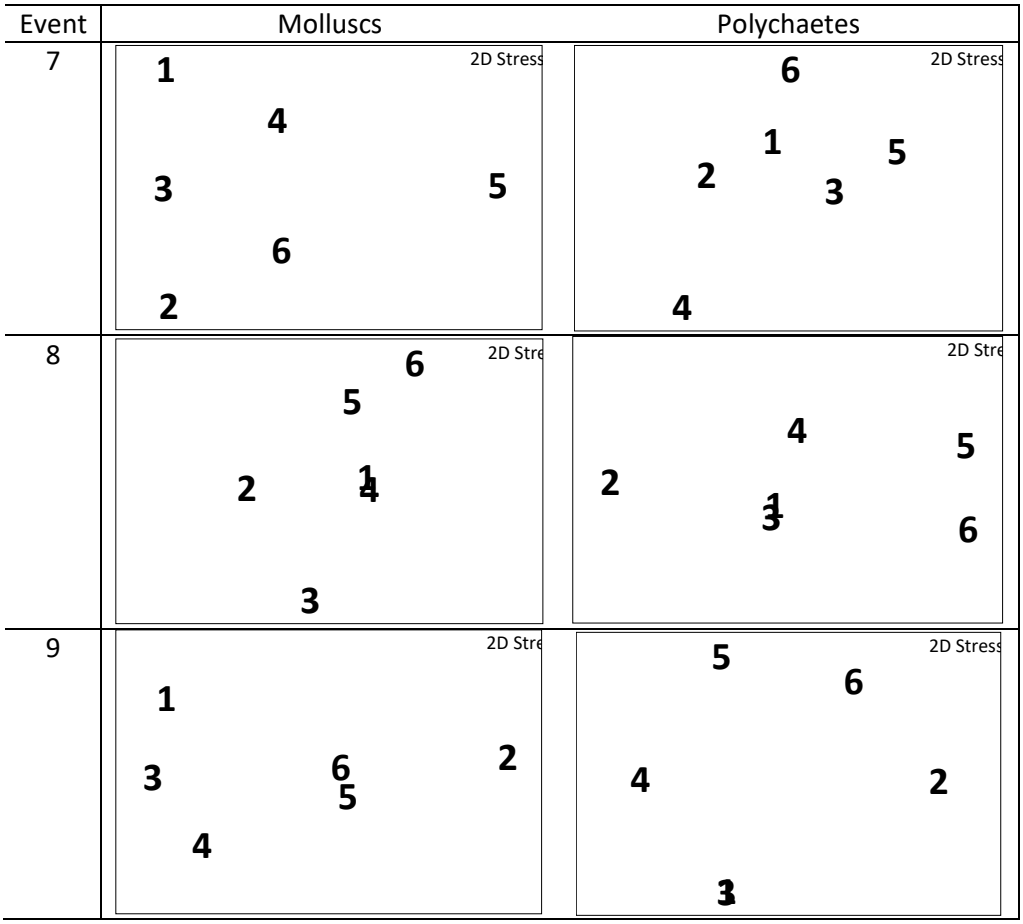


Fig 9. Unvegetated sediment: nMDS ordination plots (based on Bray-Curtis dissimilarity matrices of square-root transformed abundances) comparing dissimilarities among sites (numbered 1-6) for assemblages of molluscs and polychaetes in each of nine sampling events

Table 1 Seagrass: Results of generalized least squares analyses to fit linear models between surrogates and targets for each biodiversity variable across four and nine sampling events. Biodiversity variables tested were species richness (s), total number of individuals (n), d Margalef's index, j Pielou's evenness index, and h Shannon-Wiener diversity index

(a) Four sampling events

Surrogate	Target	Response variable	χ^2	Df	*P*	$_pr^2$	$_pr$
Crustaceans	Molluscs + Polychaetes	s	9.04	1	0.003	0.4	0.63
		n	51.56	1	<0.0001	0.8	0.89
		d	2.09	1	0.10	0.07	0.26
		j	24.52	1	<0.0001	0.36	0.60
		h	4.12	1	0.04	0.17	0.41
Molluscs	Crustaceans + Polychaetes	s	25.04	1	<0.0001	0.62	0.79
		n	3.54	1	0.06	0.21	0.46
		d	11.52	1	0.0007	0.37	0.61
		j	1.75	1	0.20	0.14	0.37
		h	53.33	1	<0.0001	0.65	0.81
Polychaetes	Crustaceans + Molluscs	s	17.51	1	<0.0001	0.54	0.73
		n	5.21	1	0.02	0.3	0.55
		d	9.23	1	0.002	0.26	0.51
		j	0.66	1	0.40	0.08	0.28
		h	34.23	1	<0.0001	0.58	0.76

(b) Nine sampling events

Surrogate	Target	Response variable	χ^2	Df	*P*	$_pr^2$	$_pr$
Molluscs	Polychaetes	s	11.50	1	0.0007	0.36	0.60
		n	2.06	1	0.20	0.09	0.30
		d	7.22	1	0.007	0.22	0.47
		j	4.01	1	0.045	0.08	0.28
		h	5.09	1	0.02	0.27	0.52

Table 2 Unvegetated sediment: Results of generalized least squares analyses to fit linear models between surrogates and targets for each biodiversity variable across four and nine sampling events. Biodiversity variables tested were species richness (s), total number of individuals (n), d Margalef's index, j Pielou's evenness index, and h Shannon-Wiener diversity index

(a) Four sampling events

Surrogate	Target	Response variable	χ^2	Df	*P*	$_pr^2$	$_pr$
Crustaceans	Molluscs + Polychaetes	s	28.43	1	<0.0001	0.57	0.75
		n	33.80	1	<0.0001	0.57	0.75
		d	7.78	1	0.005	0.29	0.54
		j	1.33	1	0.20	0.05	0.22
		h	0.61	1	0.40	0.03	0.17
Molluscs	Crustaceans + Polychaetes	s	66.58	1	<0.0001	0.79	0.89
		n	44.83	1	<0.0001	0.68	0.82
		d	15.89	1	<0.0001	0.47	0.69
		j	1.05	1	0.30	0.05	0.22
		h	0.37	1	0.50	0	0
Polychaetes	Crustaceans + Molluscs	s	21.27	1	<0.0001	0.53	0.73
		n	13.53	1	0.0002	0.39	0.62
		d	6.94	1	0.008	0.28	0.53
		j	4.43	1	0.04	0.16	0.40
		h	0.72	1	0.40	0.05	0.22

(b) Nine sampling events

Surrogate	Target	Response variable	χ^2	Df	*P*	$_pr^2$	$_pr$
Molluscs	Polychaetes	s	34.45	1	<0.0001	0.37	0.61
		n	12.67	1	0.0004	0.21	0.46
		d	8.96	1	0.003	0.14	0.37
		j	1.38	1	0.20	0.01	0.10
		h	2.81	1	0.09	0.05	0.22

Table 3 Seagrass: Mantel (R_M) correlation coefficients between dissimilarity matrices of surrogates and targets. Partial Mantel correlation coefficients (pR_M) controlling for the effects of physical distances between sites were calculated for surrogates with $R_M \geq 0.7$. Tests were done on Bray-Curtis dissimilarity matrices with abundance data transformed to square-root

(a) Four sampling events

Event	Surrogate	Target	R_M	pR_M
1	Crustaceans	Molluscs + Polychaetes	0.49	
	Molluscs	Crustaceans + Polychaetes	0.57	
	Polychaetes	Crustaceans + Molluscs	0.83	0.71
2	Crustaceans	Molluscs + Polychaetes	-0.68	
	Molluscs	Crustaceans + Polychaetes	-0.73	
	Polychaetes	Crustaceans + Molluscs	-0.97	
3	Crustaceans	Molluscs + Polychaetes	-0.42	
	Molluscs	Crustaceans + Polychaetes	0.26	
	Polychaetes	Crustaceans + Molluscs	-0.49	
4	Crustaceans	Molluscs + Polychaetes	0.25	
	Molluscs	Crustaceans + Polychaetes	0.69	
	Polychaetes	Crustaceans + Molluscs	-0.17	

(b) Nine sampling events

Event	Surrogate	Target	R_M	pR_M
1	Molluscs	Polychaetes	0.66	
2	Molluscs	Polychaetes	-0.82	
3	Molluscs	Polychaetes	-0.29	
4	Molluscs	Polychaetes	0.08	
5	Molluscs	Polychaetes	0.57	
6	Molluscs	Polychaetes	0.18	
7	Molluscs	Polychaetes	0.05	
8	Molluscs	Polychaetes	0.17	
9	Molluscs	Polychaetes	0.71	0.71

Table 4 Unvegetated sediment: Mantel (R_M) correlation coefficients between dissimilarity matrices of surrogates and targets. Partial Mantel correlation coefficients (pR_M) controlling for the effects of physical distances between sites were calculated for surrogates with $R_M \geq 0.7$. Tests were done on Bray-Curtis dissimilarity matrices with abundance data transformed to square-root

(a) Four sampling events

Event	Surrogate	Target	R_M	pR_M
1	Crustaceans	Molluscs + Polychaetes	0.51	
	Molluscs	Crustaceans + Polychaetes	0.78	0.79
	Polychaetes	Crustaceans + Molluscs	0.56	
2	Crustaceans	Molluscs + Polychaetes	0.59	
	Molluscs	Crustaceans + Polychaetes	0.59	
	Polychaetes	Crustaceans + Molluscs	0.66	
3	Crustaceans	Molluscs + Polychaetes	0.54	
	Molluscs	Crustaceans + Polychaetes	0.31	
	Polychaetes	Crustaceans + Molluscs	0.54	
4	Crustaceans	Molluscs + Polychaetes	0.68	
	Molluscs	Crustaceans + Polychaetes	0.62	
	Polychaetes	Crustaceans + Molluscs	0.63	

(b) Nine sampling events

Event	Surrogate	Target	R_M	pR_M
1	Molluscs	Polychaetes	0.69	
2	Molluscs	Polychaetes	0.56	
3	Molluscs	Polychaetes	0.23	
4	Molluscs	Polychaetes	0.52	
5	Molluscs	Polychaetes	-0.03	
6	Molluscs	Polychaetes	0.1	
7	Molluscs	Polychaetes	-0.5	
8	Molluscs	Polychaetes	0.41	
9	Molluscs	Polychaetes	0.84	0.88