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A comparison of statistical approaches to analyzing community convergence between natural and constructed oyster reefs

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Abstract

Evaluating the success of habitat creation or restoration depends primarily on the selection of appropriate goals, relevant metrics and robust analytic approaches. For intertidal oyster reefs, the goal of restoring ecological function often is as important as the production of harvestable oysters, especially since oysters are the habitat. Assessing differences in resident faunal composition between created and natural reefs is one possible metric for evaluating ecological success. Yearly changes in the resident faunal composition on constructed and natural intertidal oyster reefs at one South Carolina restoration site were analyzed with a variety of statistical approaches to determine the most effective method(s) for documenting possible convergence in the similarity of reef assemblages over time. Two datasets were defined by the level of taxonomic identification, all taxa or a subset of common taxa, and the level of taxa reduction; all taxa, taxa >1% of total abundance, and taxa significantly contributing to variation. Data were analyzed using "classic" multivariate analysis of variance (MANOVA), null model analysis of co-occurrence (ECOSIM), nonparametric analysis of similarity (ANOSIM), and permutation tests for multivariate analysis of similarity (PERMANOVA). Taxa abundance was used to weight MANOVA and ECOSIM analyses, while the Bray–Curtis dissimilarity index was used to weight ANOSIM and PERMANOVA analyses. Initial constraints on the analytic design and data manipulations resulted in only one test where convergence of the constructed and natural reef assemblages was indicated. Prescribed reductions in the suite of taxa considered did not alter appreciably the results. The analytic approaches varied in suitability and effectiveness at discriminating among changes in compositional similarity, even when initial constraints were relaxed. MANOVA results indicated either no difference or a significant difference in resident faunal composition between reefs, but were compromised by the inability to transform the data sufficiently to test for multivariate homogeneity violations even in analyses with reduced taxa numbers. Interpretation of ECOSIM results suggested fewer taxa in common even on natural reefs and were affected by a lack of design alternatives and the possible inflation of Type I error that weighting by abundance may cause. ANOSIM results identified no significant reef treatment effects and also suffered from design constraints and an inability to generate enough permutations to test for significant differences in datasets with relatively small sample sizes. All test results from PERMANOVA analyses except one indicated unambiguously that resident faunal assemblages on constructed reefs generally were not yet similar to natural reefs even after 7 years. Convergence of constructed and natural reef resident assemblages was suggested by PERMANOVA tests only for the dataset with the fewest taxa. The negligible limitations of PERMANOVA, flexible design options, and ability to generate significance tests for small sample sizes make the approach powerful. The ongoing development of effective statistical approaches for testing the significance of taxonomic compositional changes among habitats makes the determination of whether restoration

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projects are successful less dependent on the choice of analytic technique. More critical, biological questions including whether convergence of taxa abundance and composition is a valid indicator of similar ecological function remain to be answered.
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1. Introduction

The creation or restoration of marine and estuarine habitats is viewed increasingly as a necessary and potentially sufficient response to anthropogenic effects (e.g., coastal development and related impacts, overharvesting, introduced species). A number of different habitat types including seagrass beds (Fonseca et al., 2000; Bell et al., 2001; Sheridan, 2004), salt marshes (Levin et al., 1996; Craft et al., 1999; Desmond et al., 2002), offshore hard or live-bottom reefs (Beets, 1989; Edwardo et al., 2002; Relini et al., 2002), and intertidal and subtidal oyster reefs (Coen et al., 1999b; Lenihan et al., 2001; Peterson et al., 2003; Luckenbach et al., 2005) have been created and evaluated over the past decades. Although restoration efforts for some habitats date from the 1970s (e.g., Seneca et al., 1985; Broome et al., 1986), questions about the cost, value, and success of efforts remain widespread (Moy and Levin, 1991; Zedler, 1993; Weinstein et al., 1997; Craft et al., 1999; Block et al., 2001; Peterson and Lipcius, 2003; Luckenbach et al., 2005).

A major difficulty associated with evaluating the success of restoration efforts is the identification of appropriate goals and metrics (e.g., Coen and Luckenbach, 2000; Luckenbach et al., 2005). For example, if the goal of salt marsh restoration is to establish natural plant coverage then plant stem density probably is a reasonable assessment metric. Existing evidence based on stem density would indicate the near universal success of most marsh restoration projects (e.g., Broome et al., 1986). However, if the goal is to restore the numerous ecological functions of a natural marsh then stem density alone is insufficient. Suitable metrics for measuring marsh function can vary from breeding bird success (Zedler, 1993) to sediment biogeochemical cycling (Craft et al., 1999). The existence of multiple metrics suggests that evaluation of restoration success may be influenced by the metric selected (see Palmer et al., 1997; Thayer et al., 2003, 2005; Bernhardt et al., 2005; Luckenbach et al., 2005; Palmer et al., 2005).

Assessing the success of oyster reef restoration also is influenced by identification of goals and appropriate metrics. A consistent goal for reef restoration has been the production of harvestable (generally 75 mm) oysters, but reefs contribute many other ecological functions that are reasonable restoration goals (reviewed in Coen et al., 1999b; Lenihan, 1999; Coen and Luckenbach, 2000; Dame et al., 2001). Reefs can improve water quality (Nelson et al., 2004; Newell, 2004), stabilize shorelines (Meyer et al., 1997; Coen et al., submitted for publication), reduce predation (Grabowski, 2004), and provide habitat for both transient and resident fauna (Posey et al., 1999; Peterson et al., 2003; Luckenbach et al., 2005). An economic assessment of oyster reefs may suggest that restoration of ecological function may be as important as production of harvestable oysters (Coen et al., 1999b; Peterson and Lipcius, 2003; Peterson et al., 2003; Luckenbach et al., 2005).

Almost as critical as the choice of restoration goal and associated assessment metric(s) is the ability to evaluate the prescribed metric statistically to determine whether the restoration effort truly is successful. The statistical analysis of many relevant metrics (e.g., oyster density, benthic-pelagic coupling, associated community) presumably is a straightforward comparison between constructed and natural or reference habitats (Thayer et al., 2003, 2005 and references therein). However, evaluating other aspects of ecological function require more complex multivariate data and analyses. For example, assessing the temporal convergence of resident faunal similarity between constructed and natural reefs could provide a sensitive test of functional equivalency (Philippi et al., 1998). The variety of statistical approaches that exist to analyze community compositional change can be divided into analyses based on: (1) direct measures of abundance, percent cover and biomass for a ‘species’ or other ecological grouping (e.g., Navarrete et al., 2000; Lotze et al., 2001; Micheli et al., 2002; Chase, 2003; Allison, 2004) or (2) conversion of compositional data into a similarity index or other distance measure (e.g., Clarke, 1993; Legendre and Anderson, 1999; Langlois et al., 2005, Terlizzi et al., 2005; Wassenaar et al., 2005). Statistical models applied to one or the other types of compositional data include: (1) “classic” multivariate analyses (Johnson and Wichern, 1998; Rencher, 1998); (2) null models (Gotelli, 2000); (3) non-parametric analysis of among sample similarity (Clarke and Warwick, 2001); and (4) multivariate permutation analyses of distance

measures (Anderson, 2001; McArdle and Anderson, 2001). The data, either species abundances or distance measures, analyzed and the analytic technique applied may influence one's ability to conclude whether constructed oyster reefs have met the selected restoration goal(s).

In this paper we evaluate whether established and more recent analytic approaches are capable of detecting the potential convergence of resident faunal assemblages on a dataset derived from an ongoing intertidal oyster restoration program consisting of constructed and natural (or reference) oyster reefs in South Carolina (Coen et al., 1999a; Coen and Luckenbach, 2000). The similarity in taxonomic composition and abundance is one possible metric of ecological function, and the ability to document similar faunal assemblages between constructed and natural treatments may be considered a sufficient evaluation of reef restoration success.

2. Methods and materials

2.1. Constructed and natural (reference) oyster reefs

Intertidal oyster reefs were constructed and natural reference reefs selected at two tidal creek locations near Charleston, South Carolina (see Coen et al., 1999a; Coen and Luckenbach, 2000; Luckenbach et al., 2005 for details). Toler's Cove is drained by a small tidal creek (≤ 3 m depth) and surrounded by *Spartina alterniflora* marsh and a 100+ slip marina. In part because Toler's Cove is a highly developed site (marinas and condos), results from the site are considered elsewhere (Coen et al., submitted for publication). Inlet Creek is a tidal creek bordered by extensive *S. alterniflora* marshes with minimal adjacent development and extensive, existing oyster reefs. A total of three reefs (24 m^2 each) were constructed in October 1994 at the Inlet Creek location. Each constructed reef consisted of 156 plastic trays ($0.46 \times 0.31 \times 0.11$ m) arranged in a 6×26 array (8.2×2.9 m). Trays were lined with 1.3 mm fiberglass window screening and filled to the top with clean oyster shell (ca. 8 kg). Sites were prepared for reef construction by removing all live oyster clusters. Separate, undisturbed natural reefs adjacent to constructed reefs were identified and warning signs placed around the entire site to limit future harvesting. Additional details on reef location and construction can be found in Coen et al. (1999a), Coen and Luckenbach (2000), and Luckenbach et al. (2005).

Constructed and natural reefs were sampled at low tide in July 1995, biannually (January and July) from 1996 to 1999, and in January of 2000 and 2001. Only results from January are considered here to provide the maximum yearly coverage and avoid potential seasonal effects; see Coen et al. (1999a,b), Coen and Luckenbach (2000), and Luckenbach et al. (2005) for details on seasonal patterns. Each January, replicate samples (3 trays) were removed from constructed (=experimental) reefs and comparable sized quadrats were excavated from the identified natural reef areas adjacent to constructed sites. Trays were sampled randomly with replacement at low tide, but no tray was resampled (Coen et al., 1999a). Natural reef samples were collected from areas of densest oyster coverage. Samples were sorted on a 0.5-mm-mesh sieve and all fauna remaining were identified as 'residents.' All faunal residents collected from 1996 to 1998 were identified to lowest possible taxon and enumerated. After January 1998 only bivalves, decapods, and the ectoparasitic gastropod *Boonea impressa* were identified to lowest possible taxon and enumerated to reduce processing effort.

2.2. Faunal resident data

The enumerated resident fauna were divided into two datasets: Data Set 1 (DS-1), a complete list of taxa identified from 1996 to 1998, and Data Set 2 (DS-2), a subset of taxa identified from 1996 to 2001. The datasets consist of different taxa, with some overlap, and different time intervals since initial reef construction (1994), 4 and 7 years, respectively. Taxa within each dataset represent a mix of different taxonomic resolutions, from individuals identified to genus-species (e.g., *Panopeus herbstii*) to higher levels of classification (e.g., Xanthidae). Classification level often was necessitated by juvenile stages for which accurate keys or easily identified characteristics do not exist. Including taxa that possibly consist of multiple species in the analyses may influence our results, but studies suggest that quantitative differences in compositional similarity often are maintained even at different levels of taxonomic resolution (see Chapman, 1998; Clarke and Warwick, 1998; Warwick and Clarke, 1998). We chose to include higher taxonomic groupings along with actual species in our analyses because identification was unlikely to be biased towards either reef treatment, and the presence of juveniles may be an important indicator of reef success. Also a majority of habitat restoration studies typically do not enumerate taxa to the generic or specific level (personal observation).

Data Sets 1 and 2 also were analyzed for taxa that constituted >1% of the total faunal abundance and for taxa that contributed to explaining the most variation in

total taxa abundance. Setting a lower abundance limit for taxa inclusion is common (e.g., Micheli et al., 2002) and effectively excludes very rare taxa that may affect analyses but have little consequence within the overall community or assemblage. Principal component analysis (PCA) was used to reduce the data to include only taxa that explain the most variation (e.g., Johnson and Wichern, 1998; Khattree and Naik, 2000). The covariance matrix of each dataset was analyzed with PCA, non-rotated factors explaining a reasonable percentage of the overall variation (typically >90%) identified, and taxa with greater factor loadings (non-standardized values >1) were selected. The selected taxa are ones that contributed most to explaining overall differences in taxa abundance.

2.3. Analytic approaches

Average Bray–Curtis dissimilarity was calculated for total taxa in both datasets to provide an initial examination of the trend in composition between reef treatments. Within (sample) and among reef data were combined and the dissimilarity between constructed and natural reef resident faunal assemblages determined for each year. Compositional dissimilarity for combined samples within reefs also was calculated among constructed or natural reef assemblages separately. The level of dissimilarity among constructed and natural reefs was expected to decline with time and the dissimilarity among constructed reefs was expected to approach that among natural reefs if resident reef assemblages are converging (see Wassenaar et al., 2005).

Changes in resident faunal composition on constructed and natural reefs were analyzed using two different taxa abundance approaches, multivariate analysis of variance (MANOVA; SPSS, 1999) and analysis of expected species compositional similarity (ECOSIM; Gotelli and Entsminger, 2004), and two different taxa similarity approaches, a nonparametric analysis of compositional similarity (ANOSIM; Clarke and Warwick, 2001; Clarke and Gorley, 2001) and permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001, 2005; McArdle and Anderson, 2001). Each approach has advantages and disadvantages that may or may not affect results and/or interpretation of the results (Table 1). The complete experiment is a multivariate repeated-measures design with taxa abundances from samples collected within-reefs, within-treatments across years, but not every approach considered allows for a repeated-measures design. The use of even MANOVA, which does have the capacity to analyze repeated measures, would require the application of a complex, doubly multivariate model. To provide a consistent comparison of the various analyses, the model design was simplified across statistical approaches wherever possible. Differences in compositional similarity between constructed and natural (reference) reef treatments were analyzed for the initial sampling date, 1996, and final sampling date of the different datasets, 1998 or 2001. A nested model with samples ($n=3$) within reefs and reefs ($n=3$) within treatments was used for MANOVA, ANOSIM and PERMANOVA analyses, but was not applicable for ECOSIM.

2.3.1. Multivariate analyses of variance

The use of MANOVA to analyze community compositional change has been criticized (Legendre

Table 1
Summary of the different analytic approaches used to analyze residential taxa compositional similarity among reef treatments

	Statistical approaches	ECOSIM	ANOSIM	PERMANOVA
Assumptions	Independence, Normality, Homogeneity	Taxa pool defined Equal dispersal abilities	'Distribution free'	Observation units exchangeable and independent
Data Analyzed	Abundance, Proportion, Biomass	Presence/absence and row or column weighted presence/absence	Similarity or distance index (based on abundance, proportion, or biomass)	Similarity or distance index (based on abundance, biomass, or proportion)
Test	F-statistic Range 0 to $+\infty$	C-score (obs. vs. exp.) (Stone and Roberts, 1990) Range 0 to $\sum S_i S_j/(R(R-1)/2)$	Global R (Clarke and Warwick, 2001) range -1 to 1	Pseudo F-ratio (Anderson, 2005) range 0 to $+\infty$
Designs	All ANOVA designs (e.g., factorial, blocked, nested, +)	2-cell design (obs. and exp.)	1-way, 2-way, 2 level nested	All ANOVA designs
Limitations	Sufficient replicates for number of dependent variables	Variable Type I and II errors based on row and column constraints and test index	Small sample size restriction, sensitive to group spread (homogeneity), index dependence	Only balanced designs, sensitive to group spread (homogeneity), index dependence (?)
Comments	Many taxa and/or "0" observations more difficult to satisfy assumptions	Design limitations, careful selection of test, recognition of errors required	Effective multivariate test for simple experimental designs and sufficient sample sizes	Similar to ANOVA approach w/o limits from assumptions

and Anderson, 1999; Clarke and Warwick, 1998; Hooper et al., 2004) but is included as an approach that may have application if specific recommendations are followed (e.g., Table 1). MANOVA is analogous to the well known ANOVA procedures except that the single dependent variable is replaced by multiple dependent variables. Resident taxa are the dependent variables and reef treatment (constructed or natural) and reefs (1–3) are the independent variables. Similar to ANOVA, MANOVA is constrained by the same assumptions (Table 1), but unlike ANOVA testing for assumption violations is not as straight forward (see Rencher, 1995). Data characteristics and model assumptions were first examined for each analyzed dataset, the appropriate data manipulations including transformations applied if necessary, and finally any remaining violations taken into account when presenting the final analyses and results.

2.3.2. Co-occurrence null models

Analyzing community composition with null models (e.g., Connor and Simberloff, 1979; Service and Walters, 1991; Acosta and Robertson, 2002) remains controversial (e.g., Wiens, 1989; Gotelli and Graves, 1996). The null model approach involves comparing the observed taxa by sample matrix to a series of randomized or expected matrices generated under specific constraints. As in Gotelli (2000), we will not focus on a philosophical defense of the approach but rather an examination of the usefulness of null models for analyzing co-occurrence patterns in resident reef fauna. The statistical validity of the various null model algorithms and indices has been compared systematically by Gotelli (2000). Taxa co-occurrence patterns among samples were examined with the "Co-occurrence" option in ECOSIM (Gotelli and Entsminger, 2004) using an abundance-weighted row constraint. The weighting of taxa selection by abundance while maintaining fixed column or taxa numbers in each sample increases the chance of a Type I error (Gotelli, 2000), but was necessary to maintain consistency with the other statistical approaches. Constructed and natural reef taxa co-occurrence patterns were compared in the analyses using the *C*-score (Stone and Roberts, 1990). Greater observed relative to expected *C*-scores indicate fewer taxa in common than by chance and is the anticipated result for constructed reefs, especially in 1996. Natural reefs were expected to have taxa compositions that either were not different from random or more common than indicated from random simulations.

2.3.3. Nonparamentric analyses of similarity

Differences in resident faunal compositional similarity on constructed and natural reefs were analyzed using the ANOSIM routine of PRIMER v5 (Clarke and Warwick, 2001). The taxon by sample matrix was converted to a similarity matrix and then analyzed by a nonparametric permutational procedure applied to similarity ranks. A variety of similarity indices and approaches exist to convert a taxon by sample matrix (e.g., Legendre and Legendre, 1998; Podani and Miklüs, 2002). In order to maintain consistency among analyses the Bray–Curtis index (Bray and Curtis, 1957) was used to generate dissimilarity matrices. Data transformations were not applied initially unless necessary to satisfy assumptions of the actual statistical model (see Table 1). In addition to satisfying model assumptions, transformations of abundance data (e.g., 4th root, $\log(x+1)$) can be used to reduce the importance of abundant taxa and permit taxa with low or rare occurrences to contribute to similarity groupings (Clarke and Warwick, 2001). Other indices and approaches exist to minimize difficulties such as "0" observations (e.g., Legendre and Gallagher, 2001), but only the effects of different data treatments were investigated after initial comparisons among the analytic approaches.

2.3.4. Permutation multivariate analyses

Similar to the ECOSIM and ANOSIM approaches, PERMANOVA relies on comparing the observed value of a test statistic (pseudo *F*-ratio) against a recalculated test statistic generated from random re-ordering (permutation) of the data (Anderson, 2001). The stated advantage of the permutation approach is that the resulting test is "distribution free" and not constrained by many of the typical assumptions of parametric statistics. Although the history of data randomization in statistical tests dates to the early 1900s (e.g., Fisher, 1935), resolution of the appropriate methods for applying permutation tests to complex experimental designs is ongoing (see Anderson, 2001). Availability of a user-friendly computer package to calculate the appropriate tests also is recent (Anderson, 2005). As with ANOSIM, the PERMANOVA approach for taxa by sample data begins by calculating a similarity or distance matrix. Again, the Bray–Curtis dissimilarity index was used for consistency with our other statistical approaches.

3. Results

3.1. Dataset compositions

A total of 59 taxa were identified in DS-1 and 11 in DS-2 (Table 2). Except for one taxon, the hard clam *Mercenaria mercenaria*, DS-2 is a subset of all taxa

Table 2
A list of the Inlet Creek oyster reef associated taxa employed in Data Set 1 (1996–1998) and Data Set 2 (1996–2001)

Taxon	Data Set 1			Data Set 2		
	Total	>1%	PCA	Total	>1%	PCA
Nereis succinea	17.467	18.972	18.481			
Acarinids	14.404	15.645	15.240			
Brachidontes exustus	8.831	9.592	9.343	23.974	24.257	25.365
Geukensia demissa	8.004	8.693	8.468	22.706	22.974	24.023
Boonea impressa	7.579	8.232	8.019	30.679	31.041	32.459
Melampus bidentatus	7.479	8.123	7.913			
Gammarus palustris	5.803	6.303	6.140			
Eurypanopeus depressus	4.847	5.264	5.128	7.115	7.199	7.528
Dolichopodidae	4.746	5.155	5.022			
Heteromastus filiformis	4.451	4.835	4.710			
Xanthidae	2.797	3.038	2.960	10.043	10.161	10.625
Streblospio benedicti	2.596	2.820	2.747			
Melita nitida	1.791	1.945	1.895			
Panopeus herbstii	1.273	1.382		4.317	4.368	
Anurida maritima	0.948					
Uca spp.	0.870		0.921			
Uca pugnax	0.755		0.799			
Uca pugilator	0.733		0.776			
Eteone heteropoda	0.726					
Phyllodocidae	0.705		0.746			
Marphysa sanguinea	0.654		0.692			
Polydora cornuta	0.360					
Panopeus spp.	0.295					
Panopeus obesus	0.280			0.653		
Sabellidae	0.244					
Nemertinea	0.209					
Uhlorchestia spp.	0.144					
Eurytium limosum	0.129			0.168		
Cassidinidea ovalis	0.093					
Hargeria rapax	0.079					
Collembolids	0.072					
Sphenia antillensis	0.072					
Gemma gemma	0.065					
Insecta larvae	0.065					
Sesarma reticulatum	0.058					
Upogebia affinis	0.050					
Glycera americana	0.036					
Neopanope sayi	0.036			0.065		
Amphitrite ornata	0.029					
Monocorophium acherusicum	0.029					
Nereiphylla fragilis	0.029					
Sphaerosyllis longicauda	0.022					
Syllidae sp A	0.022					
Cirratulidae	0.014					
Sesarma spp.	0.014					
Tellinidae	0.014					
Alpheus heterochaelis	0.007					
Amphipoda	0.007					
Corbula sp	0.007					
Hydroides dianthus	0.007					
Insecta pupae	0.007					
Lembos smithi	0.007					
Mulinia lateralis	0.007					
Pelecypoda (Bivalvia)	0.007					
Petrolisthes armatus	0.007			0.270		
Polychaeta	0.007					

Table 2 (*continued*)

Taxon	Data Set 1			Data Set 2		
	Total	>1%	PCA	Total	>1%	PCA
Syllidae	0.007					
Tanystylum orbiculare	0.007					
Uca minax	0.007					
Mercenaria mercenaria				0.009		
Total abundance	**13,906**	**12,803**	**13,143**	**10,724**	**10,599**	**10,136**

The percent abundance in both constructed and natural reefs are reported for total taxa sampled, only taxa >1% of the total abundance, and only taxa identified by PCA as contributing most to the overall variation in abundances. Data Set 1 total taxa are sorted from most to least abundant.

collected within the first 4 years after reef construction. The two most abundant taxa in DS-1 were the polychaete species *Nereis succinea* and mites. The next most abundant taxa in DS-1 and most abundant in DS-2 were the bivalves *Brachidontes exustus* and *Geukensia demissa* and the pyramidellid gastropod *B. impressa*.

Use of an abundance minima or PCA appreciably reduced the number of taxa considered in compositional analyses of resident fauna (Table 2). Including taxa that constituted >1% of the total abundance reduced the number of taxa by 76% and 46% in DS-1 and DS-2, respectively. The first three axes explained 74% of the overall variation in DS-1 and consideration of five axes explained 86% but did not alter the taxa included in the reduced dataset. Taxa included in DS-1 were reduced by 70% through the use of PCA (Table 2). The first two axes explained 95% of the overall variation in DS-2 and inclusion of the 3rd axis, explaining 98%, did not alter taxa selection. Use of PCA reduced the DS-2 taxa included by 54% (Table 2).

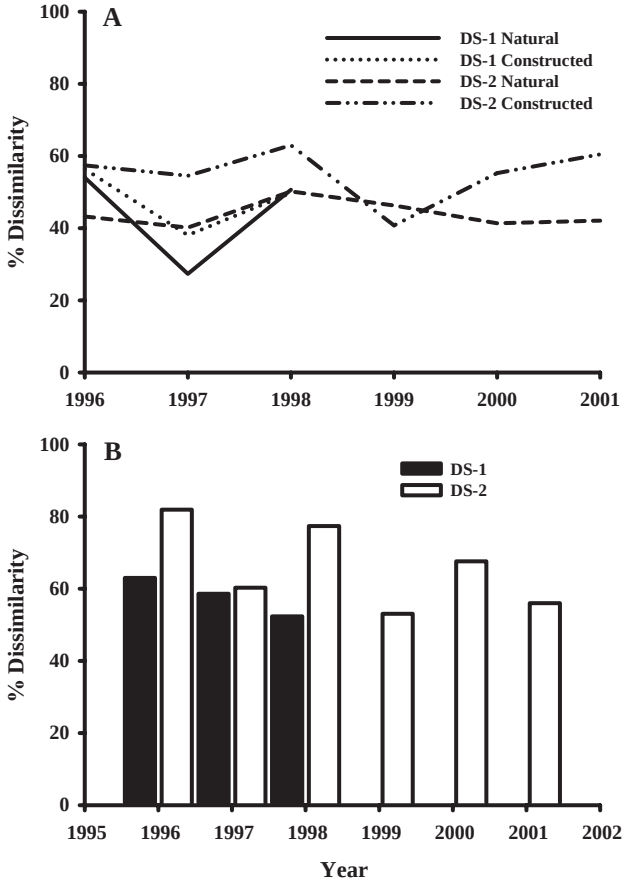

Fig. 1. Yearly changes in the (A) Bray–Curtis dissimilarity among reefs within constructed or natural treatments for DS-1 and DS-2 and (B) averaged Bray–Curtis dissimilarity between constructed and natural reefs for DS-1 and DS-2.

3.2. Taxa dissimilarity patterns

Compositional dissimilarity among reefs varied more in DS-1 than DS-2, but typically ranged between 40% and 60% for most dates (Fig. 1A). Except for 1997, taxa compositions were only ca. 60% similar among even natural reefs. Species numbers on reefs also remained relatively unchanged varying in DS-2 between 6–8 on constructed and 5–9 on natural reefs.

The average Bray–Curtis dissimilarity in taxa composition among DS-1 and DS-2 samples collected from constructed and natural reefs is shown in Fig. 1B. Compositional dissimilarity between reef treatments was initially greater for DS-2 and tended to decline slowly over the years (Fig. 1B).

3.3. Taxa abundance approaches

Convergence of constructed and natural reef assemblages was not indicated in MANOVA analyses for either DS-1, where reef compositions were not significantly different between dates, or DS-2, where reef treatments were significantly different on each date (Table 3). Results were comparable for total, >1% and PCA selected taxa compositions except for within-reef treatment effects that were significant for >1% DS-1 taxa in 1998 and not significant for >1% and PCA selected DS-2 taxa in 1996. Both dataset analyses suggest no significant differences in taxa composition between dates, but no significant reef effects existed for the greater number of taxa in DS-1 whereas significant reef effects existed on both dates for the more restricted taxa list in DS-2 (Table 3).

Additional analyses were conducted to examine questions of power and design. Each sample was treated as a replicate lumping reef and sample variation to focus on treatment effects and possibly increase the power of the test. Results for the DS-2 total taxa pool were not different from Table 3 with significant treatment effects in 1996 ($F_{8,9}=16.52$, $p<0.001$) and 2001 ($F_{8,9}=5.31$, $p<0.02$). Changing the design to include year as an additional nesting factor resulted in no change in DS-1 total results, but the addition of a significant year effect in DS-2 total ($F_{10,19}=9.40$, $p<0.001$).

Interpretation of MANOVA results was complicated by the inability to test critical assumptions for the analyses. Raw abundance data did not permit calculation of Box's M test of homogeneity of covariance

Table 3
A summary of analyses of compositional abundance between constructed and natural oyster reefs using taxa abundance data

Year/ Analyses	Source of variation	Total		>1%		PCA	
		Test Statistic	Significance	Test Statistic	Significance	Test Statistic	Significance
Data Set 1							
1996							
MANOVA	Trt	4.70	n.s.	0.99	n.s.	3.42	n.s.
	Reef(Trt)	2.04	n.s.	1.30	n.s.	1.64	n.s.
ECOSIM	Const.	1.75>	<0.001	0.85	n.s.	0.98	n.s.
	Nat.	1.60>	<0.001	0.63	n.s.	1.15>	<0.006
1998							
MANOVA	Trt	2.17	n.s.	10.48	n.s.	8.95	n.s.
	Reef(Trt)	1.13	n.s.	2.30	<0.04	1.76	n.s.
ECOSIM	Const.	1.91>	<0.001	1.11	n.s.	1.63>	<0.05
	Nat.	1.99>	<0.001	0.68>	<0.03	1.20>	<0.001
Data Set 2							
1996							
MANOVA	Trt	62.62	<0.001	21.39	<0.001	28.47	<0.001
	Reef(Trt)	2.40	<0.009	1.70	n.s.	1.80	n.s.
ECOSIM	Const.	2.50	n.s.	2.33	n.s.	3.1	n.s.
	Nat.	0.00	n.s.	0.00	n.s.	0.00	n.s.
2001							
MANOVA	Trt	6.64	<0.05	6.20	<0.02	8.04	<0.007
	Reef(Trt)	2.48	<0.008	4.32	<0.001	5.20	<0.001
ECOSIM	Const.	0.32	n.s.	0.27	n.s.	0.30	n.s.
	Nat.	0.57	n.s.	0.00	n.s.	0.00	n.s.

Pillai's trace (see Johnson and Field, 1993) was used as the MANOVA test statistic calculated for ln $(x+1)$ data. The *C*-score (see Gotelli, 2000) was used as the ECOSIM test statistic and direction of the difference indicated by >(obs ≥ exp) or <(obs ≤ exp).

matrices or Bartlett's sphericity test of the residual covariance matrices and resulted in many significant Levene's univariate homogeneity tests for each individual taxa (DS-1 = 54 out of 59, DS-2 = 10 out of 11). Transformations were applied to the raw data and ln $(x+1)$ selected as the most appropriate for the reported analyses in Table 3. Unfortunately, fewer than two nonsingular matrices resulted even with the transformed data and Box's M still could not be calculated in all tests. The transformation did reduce the number of significant univariate Levene's tests (DS-1 = 45 out of 59, DS-2 = 6 out of 11) and resulted in significant Bartlett sphericity tests for a majority of DS-2 analyses, suggesting dependent variables were not a linear function of two or more other variables.

Results from the ECOSIM analyses suggested that the composition of resident faunal assemblages on either constructed or natural reefs either was not different from random or had significantly less co-occurrence than expected by chance on each date (Table 3). The hypothesized greater than expected compositional similarity on 1998 or 2001 constructed reefs or on natural reefs of either date was not observed. None of the reef comparisons for DS-2 indicated non-randomness of resident fauna sampled on either date for both constructed and natural reefs. For all taxa sampled a few comparisons indicated randomly expected co-occurrence, but most suggested fewer taxa in common than expected by chance.

3.4. Taxa similarity approaches

Nonparametric analyses of taxa dissimilarities did not indicate a significant temporal change in composition for either DS-1 or DS-2 (Table 4). All analyses suggest that taxa compositions were as dissimilar on constructed and natural reefs in 1996, with only ca. 1 year since initial reef construction, as in 1998 or 2001. ANOSIM results in Table 4 are for untransformed data, but results were not altered appreciably by initial 4th root transformation of the data. For example, treatment and reef within treatment effects (Global $R = 0.56$ and 0.14, respectively) for 1998 PCA selected taxa abundances were not significant, the same as for untransformed data (Table 4). Insufficient power (Clarke and Warwick, 2001) or insufficient possible permutations to calculate a reasonable test (Clarke, 1993; Anderson, 2005) are possible explanations for the lack of significant reef treatment differences even in 1996. One suggested solution to the problems of limited

Table 4
A summary of analyses of compositional abundance between constructed and natural oyster reefs using taxa similarity data

Year/Analyses	Source of variation	Total		>1%		PCA	
		Test Statistic	Significance	Test Statistic	Significance	Test Statistic	Significance
Data Set 1							
1996							
ANOSIM	Trt	−0.28	n.s.	0.15	n.s.	0.96	n.s.
	Reef(Trt)	0.69	<0.002	0.97	n.s.	0.19	n.s.
PERMANOVA	Trt	1.31	n.s.	10.17	<0.001	10.81	<0.001
	Reef(Trt)	3.56	<0.001	1.46	n.s.	1.49	n.s.
1998							
ANOSIM	Trt	0.00	n.s.	0.63	n.s.	0.63	n.s.
	Reef(Trt)	0.45	<0.005	0.14	n.s.	0.13	n.s.
PERMANOVA	Trt	3.07	<0.02	8.53	<0.001	8.91	<0.001
	Reef(Trt)	2.97	<0.001	1.81	<0.04	1.76	<0.05
Data Set 2							
1996							
ANOSIM	Trt	0.14	n.s.	1.00	n.s.	1.00	n.s.
	Reef(Trt)	1.00	n.s.	0.06	n.s.	0.70	n.s.
PERMANOVA	Trt	15.70	<0.001	14.37	<0.001	14.13	<0.001
	Reef(Trt)	1.48	n.s.	1.11	n.s.	1.27	n.s.
2001							
ANOSIM	Trt	−0.06	n.s.	−0.07	n.s.	−0.07	n.s.
	Reef(Trt)	0.26	<0.04	0.29	<0.05	0.30	<0.03
PERMANOVA	Trt	3.68	<0.004	3.80	<0.004	1.25	n.s.
	Reef(Trt)	3.08	<0.002	3.25	<0.002	1.09	n.s.

Global R (see Clarke and Gorley, 2001) was used as the ANOSIM test statistic. The multivariate F-score and permutation p-value (see Anderson, 2005) was used as the PERMANOVA test statistic.

sample sizes if no significant differences exist for a nested factor and the possible risks of invalid results are recognized is "pooling" samples (Clarke and Warwick, 2001). To examine the effects of pooling, ANOSIM designs were collapsed for analyses with no significant differences in dissimilarity among reefs. The one-way ANOSIM results did not alter conclusions about differences between years, no convergence in compositions, but did suggest reef assemblages were significantly dissimilar (e.g., DS-1, >1%; 1996 Global $R=0.68$, $p<0.002$; 1998 Global $R=0.58$, $p<0.002$).

Compositional differences between years were identified in only 33% of the possible analyses using PERMANOVA (Table 4). Taxa dissimilarity was not different between reef treatments in 1996 but was different in 2001 for DS-1 total, and was different between treatments in 1996 but not 2001 for DS-2 PCA selected taxa. Only the results for DS-2 PCA selected taxa are consistent with an interpretation of restored ecological function; constructed reefs initially are more dissimilar, but exhibit the same level of dissimilarity as natural reefs with time. Including year as a factor in the design resulted in no significant year effect for DS-1 total ($F_{1,2}=1.86$, $p>0.05$) but a significant year effect for DS-2 total ($F_{1,2}=5.21$, $p<0.002$). Pairwise comparisons between years and reef treatments for DS-2 total taxa indicated that composition in 1996 was more dissimilar than in 2001 ($t=1.69$, $p<0.03$) and constructed were more dissimilar than natural reefs in both 1996 ($t=3.74$, $p<0.001$) and 2001 ($t=1.56$, $p<0.04$).

4. Discussion

A consensus of analytic approaches employed here indicated that resident faunal composition on constructed and adjacent natural intertidal oyster reefs had not converged after 7 years, but the ability to interpret results varied among the datasets analyzed and the statistical tests performed. Data reduction approaches substantially decreased the number of taxa considered within an analysis (e.g., in DS-1 from 59 to 14 taxa), but generally did not alter the observed conclusions about compositional similarity between the two reef treatments. In one instance, DS-2 PCA selected taxa, decreasing the number of taxa considered did result in the only test where convergence of resident assemblages on constructed and natural reefs appeared to occur (Table 4). The apparent convergence was explained less by increasing taxa similarity, all taxa were present on all reef treatments on all dates, than by increasing numbers on the constructed reefs (90–563 total individuals) and decreasing numbers on the natural reefs (1490–912 total individuals). As with all data reduction approaches, decreasing the number of taxa included in an analysis can convert a test of differences in taxa composition and abundance essentially into a test of only abundance differences. Alternative approaches to using either an abundance minima or contribution to overall variation criteria to reduce the number of taxa considered exist (e.g., Manté et al., 1995). However, other methods for selecting taxa do not obviate the fundamental question of whether inclusion of rare taxa is critical or not to assessing reef restoration success.

Results among total, >1%, and PCA compositions for DS-1 also varied when analyzed with ECOSIM. Resident faunal compositions on constructed reefs were more likely not to differ from random using the reduced species pool datasets. Natural reefs had fewer taxa in common than expected by chance alone in virtually all instances. The apparent random or segregated assortment of taxa on constructed and natural reefs respectively can have multiple interpretations (e.g., sampling, competition, life histories). Less than expected taxa co-occurrence could be explained by a patchy distribution of natural reef residents on spatial scales greater than the size of our sampling quadrat. Patterns in faunal composition also can be explained by differences in the levels of competition on reefs. Fewer taxa in common on natural reefs may result from greater competitive interactions among taxa. Less competition on constructed reefs, possibly owing to lower oyster and resident densities, could explain the observed random assortment of taxa. Differences in resident faunal life histories also suggest an alternative explanation for the greater segregation observed on natural reefs. Haphazard recruitment of larvae or adults can develop into segregated co-occurrence patterns (see Gotelli and McCabe, 2002). The ectoparasite *B. impressa* is one possible taxa where dispersal patterns may have lead to the observed "over" abundance in some samples and absence in others. If larval recruitment was responsible, then the difference between random constructed and segregated natural reef co-occurrence patterns should not be interpreted as constituting a fundamental lack of compositional similarity.

Testing of separate hypotheses for constructed and natural (reference) reefs was necessitated by the design constraints of ECOSIM. Rather than compare compositional differences by calculating a similarity index that can suffer from interpretative difficulties (see Henderson and Heron, 1977; Raup and Crick, 1979), ECOSIM compares an index that summarizes co-occurrence patterns in the raw taxa by site matrix with the same index generated from a random reassortment of the data

matrix. The approach as stipulated is not suited to testing directly compositional differences among different treatments. Along with design constraints the ECOSIM approach can be compromised by additional limitations. Degenerate matrices (0 row or column), weighting by taxa abundance, and selection of the co-occurrence index can increase the rejection frequency for the null hypothesis (Gotelli, 2000).

Differences in the composition of constructed and natural reefs as indicated by MANOVA were not significant on either date for all DS-1 analyses, but consistently significant for all DS-2 analyses. Test interpretations are inconsistent between the datasets: DS-1 results suggest no difference in faunal composition even after only 2 years while DS-2 results suggest constructed and natural reef assemblages are still not similar after 7 years. Although MANOVA has been used extensively to analyze differences in community compositions (e.g., Menge et al., 1997; Hillebrand et al., 2000; Navarrete et al., 2000; Forbes and Chase, 2002; Micheli et al., 2002; Hoeinghaus et al., 2003; Allison, 2004), the approach is controversial (Legendre and Anderson, 1999; Clarke and Warwick, 1998; Hooper et al., 2004). The controversy over the use of MANOVA to analyze compositional similarity typically breaks in three directions: (1) data limitation, (2) model approach, and (3) assumptions. The data or sample size limits the number of dependent variables (taxa) that can be included in the model because each dependent variable subtracts from the overall degrees of freedom requiring collection of sufficient replicates. For our oyster reef data, sample size did not restrict the number of taxa that could be included in the analyses even in DS-1. MANOVA is suited for detecting statistically significant differences among treatments and such an approach may be unsuited to analyzing the convergence of constructed and natural communities (A.J. Underwood, personal communication). Initially the composition of constructed and natural reef communities may be significantly dissimilar, but the question is whether the difference disappears with time. Using MANOVA to assess a lack of significant difference (i.e., failing to reject the null hypothesis of no difference among treatments in favor of the alternative) may be inappropriate. In addition, MANOVA, similar to ANOVA, is constrained by the same assumptions of independence, normality and homogeneity of variance. Different from univariate ANOVAs, testing for a violation of the assumptions in MANOVA is not straightforward (Rencher, 1995). For example, the standard test for violation of the homogeneity of covariance matrices assumption, the Box M test, is very sensitive to departures from normality. Although MANOVA is robust to violations of assumptions (see Rencher, 1998 and references therein), test statistics are affected by high levels of heteroscedasticity (Johnson and Field, 1993). Also the presence of many "0" cells in a typical taxa by sample matrix may make the technique unsuited for use with such data (Legendre and Anderson, 1999; Clarke and Warwick, 1998). An alternative approach to analyzing strict taxa by sample data that could reduce or eliminate "0" cells would be to pool taxa into functional groups (e.g., Allison, 2004). Whatever data modification is applied, the potential difficulties in applying MANOVA to taxa by site data suggest any result should be interpreted with caution.

The results of ANOSIM and PERMANOVA tests were different even though both approaches are similar in a reliance on some measure of similarity and permutation of the original similarity matrix to generate a "distribution free" test. For ANOSIM, no reef treatment effect was detected even when samples were pooled. A lack of identifiable differences is more likely a result of design limitations, too few samples for sufficient permutations to generate a powerful test, and not a lack of real differences (e.g., 6 species and 163 individuals on 1996 DS-2 constructed reefs versus 8 species and 1537 individuals on natural reefs). PERMANOVA results consistently indicated that constructed and natural reefs were dissimilar in resident faunal composition in all instances except two: DS-1 total and DS-2 PCA. The lack of a difference in similarity in 1996 DS-1 is puzzling given the almost 2-fold difference in total abundance between constructed and natural reefs. Results for DS-2 PCA, a relatively small dataset of only 5 taxa, were the only unambiguous indication of convergence between constructed and natural reef assemblages. However, the decreasing F-scores between years (Table 4) are a possible indication of a trend towards increased similarity among resident faunal communities. The time required for restored habitats to reach natural levels can vary dramatically among metrics (e.g., Craft et al., 1999). Given the level of dissimilarity among natural reefs, 5 years likely is not long enough to expect constructed and natural oyster reef resident communities to be similar.

As a test of compositional similarity PERMANOVA has a number of advantages that include powerful "distribution free" tests of compositional similarity, extensive design possibilities similar to ANOVA, and no restrictive sample size limitations. To generate tests for complex designs with more than one factor, PERMANOVA does estimate parameters, making the

procedure "semi-parametric" and not completely non-parametric like ANOSIM (Anderson, 2005). Direct modeling of the distance matrix places a premium on careful selection of the distance measure. The only apparent additional limitations include balanced design requirements and a sensitivity to variability among groups (Anderson, 2005), and reliance on some form of similarity index that may or may not suffer from unknown statistical properties (see Gotelli and Ellison, 2004). PERMANOVA does provide for a variety of indices and transformations and the empirical correspondence of different data treatments could provide the basis for a robust conclusion.

Additional approaches to analyzing changes in community composition over time exist and include principal coordinates analysis (Rundle and Jackson, 1996), principal response curves (Van den Brink and Ter Braak, 1999), multivariate distance decay (Wassenaar et al., 2005), redundancy analysis (e.g., Langlois et al., 2005), ordination techniques (e.g., Anderson and Willis, 2003; Hewitt et al., 2005), and the use of complex samples general linear models (see Walters, 1991). The suitability of the above cited or other approaches to evaluate community convergence was not examined here, but our attempts to analyze changes in resident faunal assemblages on South Carolina intertidal oyster reefs identified a number of critical considerations when selecting a technique for analyzing compositional similarity. Specifically, considerations include: (1) an ability to handle complex experimental designs; (2) a method to effectively account for "0" occurrences; (3) a technique with a minimum of or easily tested assumptions; and (4) a method that is relatively insensitive to different input data (e.g., similarity indices).

The multivariate evaluation of community change over time has and continues to be a challenge (e.g., Philippi et al., 1998) that additionally is complicated when results are applied to assessing the success of habitat restoration efforts. The existence of adequate analytic approaches to assess reef community convergence does not address questions about the choice of natural reefs for comparison or whether resident faunal composition is a critical metric of reef success. The choice of natural (or reference) reefs and how reefs are sampled is critical to the generation of an unbiased assessment of progress. In many situations natural or reference habitats for comparison often are unavailable or compromised because of degraded conditions, especially for subtidal oyster reef habitats. Our natural reefs were in proximity to constructed reefs within the same tidal creek system (hundreds of meters), but history and sampling methodology could have confounded comparisons between reef treatments. Compositional variability between natural reef systems is typical (Coen, personal observation; Coen et al., submitted for publication) likely reflecting differences in reef history and local conditions. Even within the same location, resident faunal compositions on natural reefs are dissimilar (Inlet Creek = 35–55%). Although samples were collected from the "best" or more densely packed oyster populations, the observed level of dissimilarity among natural reefs could result from a sample size effect. Relative differences between the scale of our sampling effort (three 0.14 m^2 quadrats per reef) and the distribution of resident taxa may increase the level of natural reef dissimilarity.

The resident component of the reef assemblage/community was identified as one of the critical metrics for assessing the success of both subtidal and intertidal restoration efforts at a recent workshop attended by oyster reef restoration experts from across the US (http://www.coastal.edu/marine/sgoyster). Of the metrics highlighted by the group, most agreed that resident fauna: (1) are indicative of the enhanced biodiversity associated with reef structure and development; (2) are provided a significant refuge from predators within the oyster reef; and (3) offer a dependable food resource for other resident and transient predators. Each of the reasons for considering resident fauna is part of the subset of total ecosystem services that resource managers are trying to enhance and/or restore through reef construction. In time the specific relationships (e.g., habitat linkages and species interactions) will receive enough attention to generate sufficient biological information in order to predict which are the most critical species required for fully functioning reefs.

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References

Acosta, C.A., Robertson, D.N., 2002. Diversity in coral reef fish communities: the effects of habitat patchiness revisited. Mar. Ecol. Prog. Ser. 227, 87–96.

Allison, G., 2004. The influence of species diversity and stress intensity on community resistance and resilience. Ecol. Monogr. 74, 117–134.

Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci. 58, 626–639.

Anderson, M.J., 2005. PERMANOVA: A FORTRAN Computer Program for Permutational Multivariate Analysis of Variance. Department of Statistics, University of Aukland, New Zealand.

Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84, 511–525.

Beets, J., 1989. Experimental evaluation of fish recruitment to combinations of fish aggregating devices and benthic artificial reefs. Bull. Mar. Sci. 44, 973–983.

Bell, S.S., Brooks, R.A., Robbins, B.D., Fonseca, M.S., Hall, M.O., 2001. Faunal response to fragmentation in seagrass habitats: implications for restoration efforts in a marine environment. Biol. Conserv. 100, 115–123.

Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L., Powell, B., Sudduth, E., 2005. Synthesizing U.S. river restoration efforts. Science 308, 636–637.

Block, W.M., Franklin, A.B., Ward, J.P., Ganey, J.L., White, G.C., 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. Restor. Ecol. 9, 293–303.

Bray, R.J., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.

Broome, S.W., Seneca, E.D., Woodhouse, W.W., 1986. Long-term growth and development of the transplants of the salt-marsh grass *Spartina alterniflora*. Estuaries 9, 63–74.

Chapman, M.G., 1998. Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. Mar. Ecol. Prog. Ser. 162, 71–78.

Chase, J.M., 2003. Strong and weak trophic cascades along a productivity gradient. Oikos 101, 187–195.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. Aust. J. Ecol. 18, 117–143.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35, 523–531.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edition. PRIMER-E, Plymouth, UK.

Clarke, K.R., Gorley, R.N., 2001. PRIMER v5: User Manual/Tutorial. PRIMER-E, Plymouth, UK. 91 pp.

Coen, L.D., Luckenbach, M.W., 2000. Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? Ecol. Eng. 15, 323–343.

Coen, L.D., Knott, D.M., Wenner, E.L., Hadley, N.H., Ringwood, A.H., Bobo, M.Y., 1999a. Intertidal oyster reef studies in South Carolina: design, sampling and experimental focus of evaluating habitat value and function. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 133–158.

Coen, L.D., Luckenbach, M.W., Breitburg, D.L., 1999b. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. In: Benaka, L.R. (Ed.), Fish Habitat: Essential Fish Habitat and Rehabilitation. Am. Fisheries Soc., Symposium, vol. 22. Bethesda, MD, pp. 438–454.

Coen, L.D., Wilber, D.H., Knott, D.M., submitted for publication. Development of intertidal oyster reef resident communities in the southeastern United States: An analysis of natural and constructed reefs over time. Mar. Ecol. Prog. Ser.

Connor, E.F., Simberloff, D., 1979. The assembly of species communities: chance or competition? Ecology 60, 1132–1140.

Craft, C., Reader, J., Sacco, J.N., Broome, S.W., 1999. Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. Ecol. Appl. 9, 1405–1419.

Dame, R., Bushek, D., Prins, T., 2001. The role of suspension feeders as ecosystem transformers in shallow coastal environments. In: Reise, K. (Ed.), The Ecology of Sedimentary Coasts. Springer-Verlag, Berlin, pp. 11–37.

Desmond, J.S., Deutschman, D.H., Zedler, J.B., 2002. Spatial and temporal variation in estuarine fish and invertebrate assemblages: analysis of an 11 year data set. Estuaries 25, 552–569.

Edwardo, A.S., Tito, G., Almeida, C.M., Zalmon, I.R., 2002. Fish assemblages and environmental variables on an artificial reef north of Rio de Janeiro, Brazil. ICES J. Mar. Sci. 59, S138–S143.

Fisher, R.A., 1935. Design of experiments. Oliver and Boyd, Edinburgh, UK.

Fonseca, M.S., Julius, B.E., Kenworthy, W.J., 2000. Integrating biology and economics in seagrass restoration: how much is enough and why? Ecol. Eng. 15, 227–236.

Forbes, A.E., Chase, J.M., 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96, 433–440.

Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. Ecology 81, 2606–2621.

Gotelli, N.J., Ellison, A.M., 2004. A Primer of Ecological Statistics. Sinauer Associates, Inc., Sunderland, MA. 510 pp.

Gotelli, N.J., Entsminger, G.L., 2004. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. and Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim.htm.

Gotelli, N.J., Graves, G.R., 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C. 400 pp.

Gotelli, N.J., McCabe, D.J., 2002. Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. Ecology 83, 2091–2096.

Grabowski, J.H., 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade in oyster-reef communities. Ecology 85, 995–1004.

Henderson, R.A., Heron, M.L., 1977. A probabilistic method of paleobiogeographic analysis. Lethaia 10, 1–15.

Hewitt, J.E., Anderson, M.J., Thrush, S.F., 2005. Assessing and monitoring ecological community health in marine systems. Ecol. Appl. 15, 942–953.

Hillebrand, H., Worm, B., Lotze, H.K., 2000. Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. Mar. Ecol. Prog. Ser. 204, 27–38.

Hoeinghaus, D.J., Layman, C.A., Arrington, D.A., Winemiller, K.O., 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. Env. Biol. Fish. 67, 379–387.

Hooper, E.R., Legendre, P., Condit, R., 2004. Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. Ecology 85, 3313–3326.

Johnson, C.R., Field, C.A., 1993. Using fixed-effects model multivariate analysis of variance in marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. 31, 177–221.

Johnson, R.A., Wichern, D.W., 1998. Applied Multivariate Statistical Analysis, 4th ed. Prentice Hall, New Jersey, USA. 816 pp.

Khattree, R., Naik, D.N., 2000. Multivariate Data Reduction and Discrimination with SAS Software. SAS Institute, Carey, North Carolina, USA. 558 pp.

Langlois, T.J., Anderson, M.J., Babcock, R.C., 2005. Reef-associated predators influence adjacent soft-sediment communities. Ecology 86, 1508–1519.

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1–24.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd ed. Elsevier, Amsterdam, The Netherlands. 853 pp.

Lenihan, H.S., 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecol. Monogr. 69, 251–275.

Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecol. Appl. 11, 764–782.

Levin, L.A., Talley, A., Thayer, G., 1996. Succession of macrobenthos in a created salt marsh. Mar. Ecol. Prog. Ser. 141, 67–82.

Lotze, H.K., Worm, B., Sommer, U., 2001. Strong bottom-up and top-down control of early life stages of macroalgae. Limnol. Oceanogr. 46, 749–757.

Luckenbach, M.W., Coen, L.D., Ross Jr., P.G., Stephen, J.A., 2005. Oyster reef habitat restoration: relationships between oyster abundance and community development based on two studies in Virginia and South Carolina. J. Coast. Res. SI40, 64–78.

Manté, C., Dauvin, J.-C., Durbec, J.-P., 1995. Statistical method for selecting representative species in multivariate analysis of long-term changes of marine communities. Applications to a macrobenthic community for the Bay of Morlaix. Mar. Ecol. Prog. Ser. 120, 243–250.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.

Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997. Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proc. Natl. Acad. Sci. 94, 14530–14535.

Meyer, D.L., Townsend, E.C., Thayer, G.W., 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. Restor. Ecol. 5, 93–99.

Micheli, F., Peterson, C.H., Mullineaux, L.S., Fisher, C.R., Mills, S.W., Sancho, G., Johnson, G.A., Lenihan, H.S., 2002. Predation structures communities at deep-sea hydrothermal vents. Ecol. Monogr. 72, 365–382.

Moy, L.D., Levin, L.A., 1991. Are Spartina marshes a replaceable resource? A functional approach to evaluation of marsh creation efforts. Estuaries 14, 1–16.

Navarrete, S.A., Menge, B.A., Daley, B.A., 2000. Species interactions in intertidal food webs: prey or predation regulation of intermediate predators? Ecology 81, 2264–2277.

Nelson, K.A., Leonard, L.A., Posey, M.H., Alphin, T.D., Mallin, M. A., 2004. Using transplanted oyster beds to improve water quality in small tidal creeks: a pilot study. J. Exp. Mar. Biol. Ecol. 298, 347–368.

Newell, R.I.E., 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve mollusks: a review. J. Shellfish Res. 23, 51–61.

Palmer, M.A., Ambrose, R.F., Poff, N.L., 1997. Ecological theory and community restoration ecology. Restor. Ecol. 5, 291–300.

Palmer, M.A., Bernhardt, E.S., Allen, J.D., Lake, P.S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C.N., Follstad Shah, J., Galat, D.L., Loss, S.G., Goodwin, P., Hart, D.D., Hassett, B., Jenkinson, R., Kondolf, G.M., Lave, R., Meyer, J.L., O'Donnell, T. K., Pagano, L., Sudduth, E., 2005. Standards for ecologically successful river restoration. J. Appl. Ecol. 42, 208–217.

Peterson, C.H., Lipcius, R.N., 2003. Conceptual progress towards predicting quantitative ecosystem benefits of ecological restorations. Mar. Ecol. Prog. Ser. 264, 297–307.

Peterson, C.H., Grabowski, J.H., Powers, S.P., 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar. Ecol. Prog. Ser. 264, 251–266.

Philippi, T.E., Dixon, P.M., Taylor, B.E., 1998. Detecting trends in species composition. Ecol. Appl. 8, 300–308.

Podani, J., Miklüs, I., 2002. Resemblance coefficients and the horseshoe effect in principal coordinates analysis. Ecology 83, 3331–3343.

Posey, M.H., Alphin, T.D., Powell, C.M., 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 229–237.

Raup, D.M., Crick, R.E., 1979. Measurement of faunal similarity in paleontology. J. Paleontol. 53, 1213–1227.

Relini, G., Relini, M., Torchia, G., Palandri, G., 2002. Ten years of censuses of fish fauna on the Loano artificial reef. ICES J. Mar. Sci. 59, S132–S137.

Rencher, A.C., 1995. Methods of Multivariate Analysis. J. Wiley & Sons Inc., New York, NY. 627 pp.

Rencher, A.C., 1998. Multivariate Statistical Inference and Applications. J. Wiley & Sons, Inc., New York, NY. 559 pp.

Rundle, H.D., Jackson, D.A., 1996. Spatial and temporal variation in littoral-zone fish communities: a new statistical approach. Can. J. Fish. Aquat. Sci. 53, 2167–2176.

Seneca, E.D., Broome, S.W., Woodhouse, W.W., 1985. The influence of duration-of-inundation on development of a man-initiated *Spartina alterniflora* Loisel. marsh in North Carolina. J. Exp. Mar. Biol. Ecol. 94, 259–268.

Service, S.K., Walters, K., 1991. Use of null models to assess patterns of size class migrations in the copepod *Zausodes arenicolus*. Mar. Ecol. Prog. Ser. 69, 17–23.

Sheridan, P., 2004. Comparison of restored and natural seagrass beds near Corpus Christi, Texas. Estuaries 27, 781–792.

SPSS, 1999. SPSS Advanced models 10.0. SPSS Inc, Chicago. 333 pp.

Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. Oecologia 85, 74–79.

Terlizzi, A., Denedetti-Cecchi, L., Bevilacqua, S., Fraschetti, S., Guidetti, P., Anderson, M.J., 2005. Multivariate and univariate asymmetrical analyses in environmental impact assessment: a case study of Mediterranean subtidal sessile assemblages. Mar. Ecol. Prog. Ser. 289, 27–42.

Thayer, G.W., McTigue, T.A., Bellmer, R.J., Burrows, F.M., Merkey, D.H., Nickens, A.D., Lozano, S.J., Gayaldo, P.F., Polmateer, P.J., Pinit, P.T. (Eds.), 2003. Science-Based Restoration Monitoring of Coastal Habitats, Volume One: A Framework for Monitoring Plans Under the Estuaries and Clean Waters Act of 2000 (Public Law 160-457). NOAA Coastal Ocean Program Decision Analysis Series, vol. 23. NOAA National Centers for Coastal Ocean Science, Silver Spring, MD. 35 pp. plus appendices.

Thayer, G.W., McTigue, T.A., Salz, R.J., Merkey, D.H., Burrows, F.M., Gayaldo, P.F. (Eds.), 2005. Science-Based Restoration Monitoring of Coastal Habitats, Volume Two: Tools for Monitoring Coastal Habitats. NOAA Coastal Ocean Program Decision Analysis Series, vol. 23. NOAA National Centers for Coastal Ocean Science, Silver Spring, MD. 628 pp. plus appendices.

Van den Brink, P.J., Ter Braak, C.J.F., 1999. Principal response curves: analysis of time-dependent multivariate responses of biological community to stress. Environ. Toxicol. Chem. 18, 138–148.

Walters, K., 1991. Influences of behavior, abundance, species composition and ontogenetic stage on active emergence of meiobenthic copepods in subtropical habitats. Mar. Biol. 108, 207–215.

Warwick, R.M., Clarke, K.R., 1998. Taxonomic distinctness and environmental assessment. J. Appl. Ecol. 35, 532–543.

Wassenaar, T.D., van Aarde, R.J., Pimm, S.L., Ferreira, S.M., 2005. Community convergence in disturbed subtropical dune forests. Ecology 86, 655–666.

Weinstein, M.P., Balletto, J.H., Teal, J.M., Ludwig, D.F., 1997. Success criteria and adaptive management for a large-scale wetland restoration project. Wetlands Ecol. Manag. 4, 111–127.

Wiens, J.A., 1989. The ecology of bird communities. In: Barnes, R.S. K., Birks, H.J.B., Connor, E.F., Paine, R.T. (Eds.), Foundations and Patterns. Cambridge Studies in Ecology, vol. 1. Cambridge University Press, Cambridge, UK.

Zedler, J.B., 1993. Canopy architecture of natural and planted cordgrass marshes: selecting habitat evaluation criteria. Ecol. Appl. 3, 123–138.