Coastal Fish Communities of The Bahamas

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ABSTRACT

We completed surveys of coastal fish communities and benthic flora at different study sites, seasons, and years to identify differences in fish communities as well as to determine the features of the benthic flora that were most responsible for the observed differences in fish community composition. Fish communities were significantly different at different sites, seasons, and sample sequences (site-season-year combinations). Multivariate analyses identified cover of specific species and functional forms of benthic flora as the major factors determining species abundances. Total flora cover and seagrass cover were more important in influencing species and trophic group biomasses than abundances. Univariate analyses also highlighted the effects of total flora cover and cover of various functional groups on the number of species, diversity, and mean total biomass. In general, univariate analyses tended to provide stronger (more significant) results than multivariate analyses. We conclude that there is a strong relationship between benthic flora and fish community composition, and that different floral parameters affect different aspects of coastal fish communities.

KEY WORDS: Fish communities, benthic flora, benthic interactions

Análisis Univariante y Multivariante de las Relaciones Entre Macroalgas/Hierba Marinas y Agregaciones de Peces en Habitates Costeros de Las Bahamas

Realizamos muestreos en comunidades de peces costeros y flora bentónica en diferentes localidades, estaciones y años, con los objetivos de determinar las diferencias entre las comunidades de peces y tambien que características de la flora bentónica presentan un mayor efecto sobre las comunidades de peces. Las comunidades de peces fueron significativamente diferentes en las distintas localidades, estaciones y la secuencia de muestreo (*i.e.* las combinaciones sitio-estación–año).El análisis multivariado identifico a la cobertura de especies y el grupo funcional de la flora bentónica como los principales factores que determinan la abundancia de especies. El total de cobertura vegetal y de *Thalassia testudinum* tuvo mayor importancia afectando la biomasa de especies y grupos tróficos. Análisis univariados enfatizan los efectos de la cobertura vegetal total y las coberturas de *Thalassia testudinum* y *Batophora oerstedii* sobre las abundancias totales, biomasas y diversidad. En general, los análisis univariados tienden a ser mas fuertes (*i.e.* mas significativos) que los análisis multivariados. Concluimos que hay una fuerte relación entre la flora bentónica y la composición de la comunidad de peces, y que diferentes parámetros afectan diferentes aspectos de la comunidad de peces costeros.

PALABRAS CLAVES: Macroalgas, hierbas marinas, peces, análisis, Bahamas

INTRODUCTION

Habitat structure and complexity have been considered to be some of the primary factors that influence marine, estuarine, and freshwater fish communities worldwide (Huston 1979, Crowder and Cooper 1982, Roberts and Ormond 1987, McClanahan et al. 2000, Able et al. 2002). Coastal habitats, by their very nature, are influenced by oceanic and terrestrial influences, and consequently are shaped by a variety of terrestrial and aquatic characteristics (both abiotic and biotic) that can directly determine habitat quality, structure, and complexity, and indirectly determine fish community composition.

The first objective of this study was to determine the differences in fish communities at different coastal sites of Andros Island, The Bahamas. We then investigated how differences in the benthic flora contributed to observed differences in fish communities. By comparing fish communities to a suite of floral characteristics, we determined which features are most important in influencing fish communities. We predicted that fish community structure was not random and could be at least partially explained by some measures of floral composition. Because different habitat characteristics may influence different aspects of a fish community (e.g. diversity, species densities, or size spectra), we analyzed a variety of dependent variables commonly used to describe fish community composition. At a multivariate level, we analyzed individual species' abundances and biomasses, while at a univariate level, we analyzed Shannon-Weiner diversity, total abundances, number of species, and mean total biomass.

Some characteristics of an environment can likely target specific types of fish more than others. For example, the availability and types of flora may influence the occurrences of herbivores more than invertebrate feeders or piscivores. Thus, we hypothesized that floral-related differences in fish communities might also be detected at trophic group levels of analyses.

MATERIALS AND METHODS

Study Sites

Four study sites located along a 16 km stretch of coastline of eastern North Andros were incorporated into this study. SC1 and SC2 were spatially the closest (< 1 km apart), but varied in their physical properties. See Nero & Sealey (In press) for details of the study sites. Sites were visited in the summers of 2003 and 2004 and the winter of 2004, except for site SC2, which was only sampled in 2003.

Beach Seining

Beach seining followed standard seine protocol, and was completed with a seine net that was 20 m long and 1.5 m high, with a 1.2 m wide central pocket. The sampling schedule included a minimum of 15 seine events at each site in order to incorporate natural variability due to different tides and times of day (Nero & Sealey, In press).

Species and total abundances were recorded. In cases where large schools of atherinids were caught, these individuals were identified down to the family level (referred to as Atherinidae spp.), and their abundances were estimated. Fish were measured on a gridded tray and their lengths were then applied to standard length-weight relationships to obtain biomass estimates.

Environmental Data

Benthic flora variables were measured at each site once per sample sequence. Point intercept analysis was used to obtain cover estimates for each flora species. Each species was also assigned a functional group based on its morphology, and cover of each functional group was obtained by summing the cover of all representative species in that functional group. Presence/absence surveys of macroalgae and seagrass were used to determine Shannon-Weiner diversity.

Data Analysis

Analyses included univariate approaches (using SYSTAT v 10.2 and PRIMER v 5) and multivariate approaches (using PRIMER v 5). Analyses were based on abundance and biomass datasets, with data being analyzed first at the species level, then at the trophic group level. Species were sorted into trophic groups using PRIMER's 'aggregate' function and a master taxonomy list which assigned each species to a trophic level. Species were categorized as herbivores, primary predators (feeding mainly on small invertebrates), and secondary predators (feeding on large invertebrates and fish).

All data were fourth-root transformed, which allowed the estimated abundances of schooling silversides (Atherinidae) to be properly considered. Cluster analyses were used to identify outliers (defined as being less than 20% similar) to each data set. These outliers reflected minimal to no catch and were most likely due to poor seining or weather conditions; consequently, these outliers were omitted from future analyses. ANOSIM, PRIMER's multivariate equivalent to ANOVA, was used to test for effects of site, season, and sample sequence on individual seine events. The SIMPER routine identified the main species/trophic groups responsible for differences.

In order to address the influences of benthic flora features on the fish communities, data were averaged to yield one estimate per site and sampling sequence. Averaging of the data was completed using PRIMER's 'average' function. Environmental features, which represented conditions for each site at each sampling season/year, could then be matched to fish communities for each site/sampling year. Thus, there were 10 final data points, representing

Summer 2003, Winter 2004, and Summer 2004 for three sites (SC1, SH5, and BS2), and a Summer 2003 survey for site SC2, which could not be re-sampled in 2004 due to time constraints.

PRIMER's BIOENV routine identified the key benthic flora variables that best explained the variation in abundances and biomasses of species and trophic groups. Backward stepwise multiple regression was used to test for the effects of the various benthic features on univariate measurements of fish diversity, number of species, number of individuals, and mean total biomass. Correlation analysis (data not presented) verified that none of these dependent univariate variables was correlated to any other dependent variable.

RESULTS

Variability in Seine Events

ANOSIMS on individual seine events showed significant effects of site, season and sample sequence (significance = 0.1% for each) on fish species abundances and biomasses. Trophic group abundances were affected only by sample sequence (significance = 0.1%), while trophic group biomasses were only affected by site (significance = 4.2%).

SIMPER helped identify the sources of differences between different sites, and the species that accounted for differences in species abundances and biomasses are summarized in Table 1. It was often the case that the species that contributed to pairwise differences in abundances were not the same species that contributed to pairwise differences in biomasses. For example, BS2 was distinguished from SC2 by a higher abundance of *Eucinostomus melanopterus*, but higher biomasses (and larger individuals) of *Albula vulpes* and *Sphyraena barracuda*.

Averaged Site and Sample Sequence Values

Typically, fish community diversity (Figure 1a) at any given site tended to be higher in the winter sample sequence than in the two summer seasons. However, SC1 showed very little difference in fish diversity between Winter 2004 and Summer 2004. The fish community at BS2 had the highest diversity in Summer 2003 and Winter 2004, but the SC1 fish community was most diverse in Summer 2004. A similar pattern of increased biomass (Figure 1b) at winter was also observed, except again for site SC1, where there was little difference between Winter 2003 and Summer 2004. One seine event in Summer 2004 at SC1 resulted in over 600 mixed jacks being collected; this unusually high seine event is likely responsible for the inflated mean biomass for Summer 2004. In most cases, the error bars are very large, especially for biomass estimates, indicating a very high degree of variability among individual seines.

Table 1. Results of SIMPER analyses for pairwise comparisons of sites. Percent values represent the average dissimilarity between the two sites. Cells above the diagonal represent analyses completed on species biomasses, while cells below the diagonal represent analyses completed on species abundances. Species listed represent those which contributed to the top 50% of pairwise dissimilarity. Species in bold were more abundant or had higher biomass at the site above the cell, while species not in bold were more abundant or in higher biomass at the site to the left of the cell.

	BS2	SC1	SC2	SH5
BS2		82.52% ***Trachinotus goodei*** *Albula vulpes* ***Trachinotus falcatus*** *Eucinostomus melanopterus*	74.59% ***Trachinotus goodei*** *Albula vulpes* *Sphyraena barracuda* ***Gerres cinereus***	80.87% ***Trachinotus goodei*** *Sphyraena barracuda* *Eucinostomus melanopterus* *Albula vulpes*
SC1	75.58% *Atherinidae spp.* *Trachinotus falcatus* *Trachinotus goodei* ***Eucinostomus melanopterus***		64.58% *Trachinotus goodei* *Trachinotus falcatus* ***Gerres cinereus*** ***Eucinostomus melanopterus***	66.48% *Trachinotus goodei* *Trachinotus falcatus* ***Eucinostomus melanopterus***
SC2	62.10% *Atherinidae spp.* *Trachinotus goodei* ***Eucinostomus melanopterus*** *Gerres cinereus*	62.22% ***Atherinidae spp.*** ***Trachinotus falcatus*** ***Trachinotus goodei*** *Eucinostomus melanopterus*		66.75% *Trachinotus goodei* *Eucinostomus melanopterus* *Gerres cinereus* *Strongylura notata*
SH5	72.05% ***Eucinostomus melanopterus*** ***Sphyraena barracuda*** *Atherinidae spp.* *Trachinotus falcatus*	64.16% ***Atherinidae spp.*** ***Trachinotus falcatus*** ***Trachinotus goodei*** ***Albula vulpes***	60.75% ***Eucinostomus melanopterus*** *Atherinidae spp.* *Trachinotus goodei* *Harengula humeralis*	

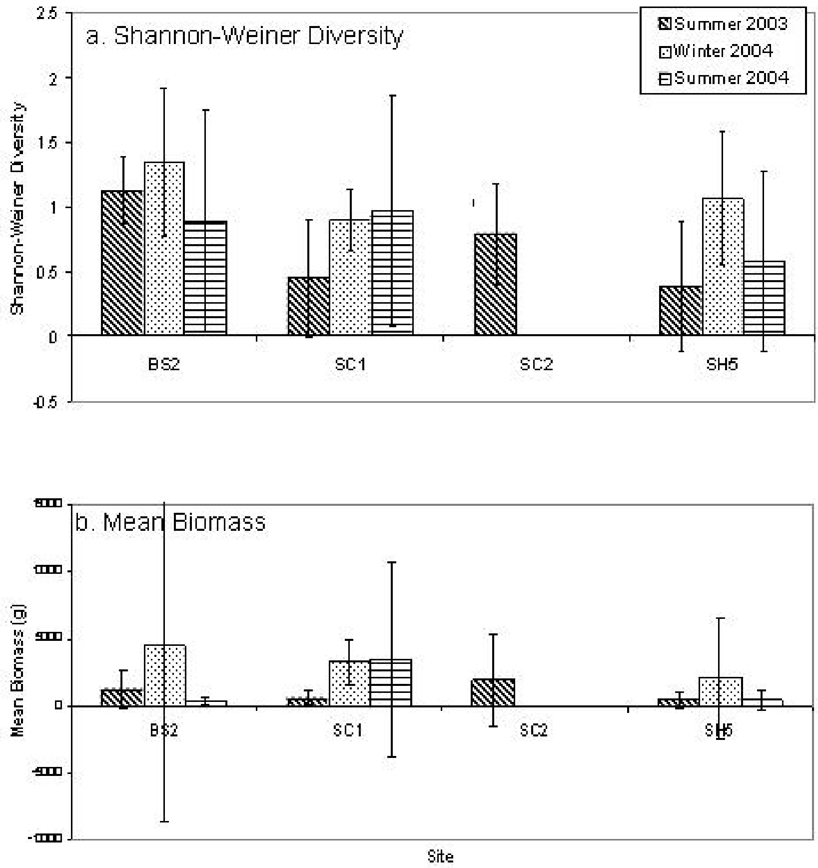

Figure 1. Values of mean a) Shannon-Weiner Diversity and b) Total biomass at the different site and sample sequence combinations. Error bars represent the 95% confidence interval. SC2 was only sampled in Summer 2003.

The two-dimensional MDS plot (Figure 2) indicated that species abundances show strong seasonal and site influences. The plot shows that communities from the same site (e.g. BS2) but different sample sequences are very similar, but in other cases (e.g. SC1 and SH5), fish communities from the sample sequence but different sites are more similar. In particular, there is a noticeable separation between the Winter 2004 communities and all summer communities of those sites. The MDS plot indicates that the BS2 fish community is most unlike those of the other sites.

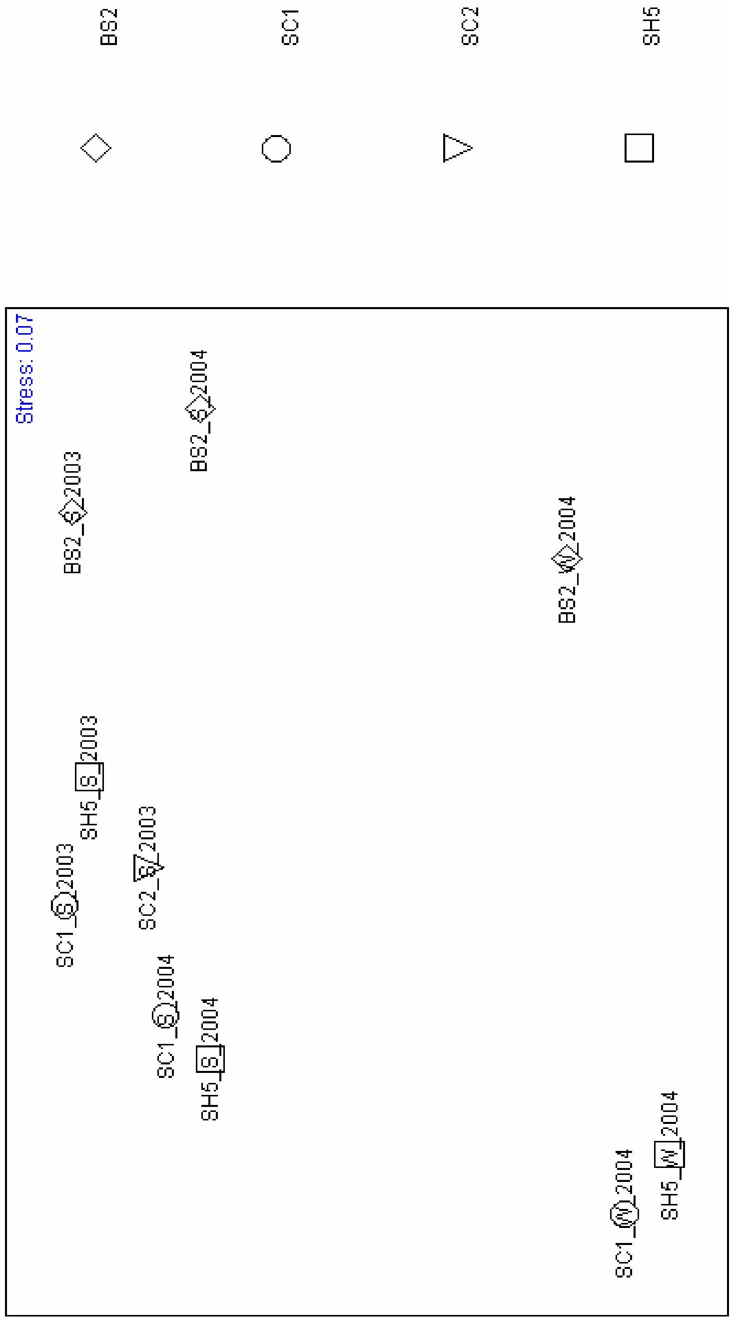

Figure 2. MDS plot based on abundances of fish species averaged for each site and sample sequence combination. Seasons are denoted as S (Summer) or W (Winter).

Relationships between Benthic Flora and Fish Communities

BIOENV provided the five best models for each fish parameter, and the strongest influences are summarized in Figure 3. For fish species abundances, each of the five best models explained a moderate degree of variation, with values of Spearman's rank correlation, ρ_s, ranging from 0.457 to 0.465. Cover of *Batophora oerstedii* and the branching functional group were the most common variables included in the best models, although cover of *Udotea spp.* and *Dasycladus vermicularis* were also important factors influencing species abundances.

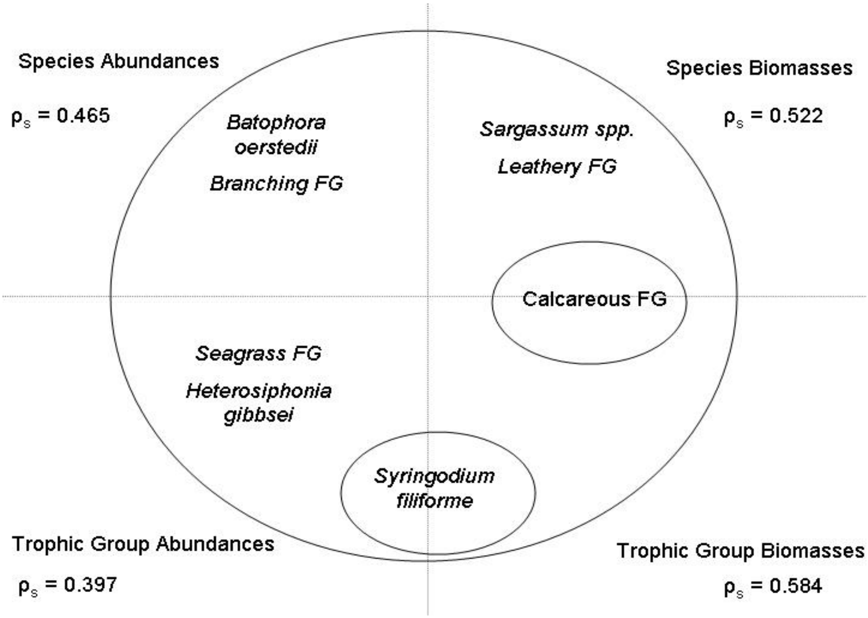

Figure 3. Representation of benthic flora features' effects on fish species and trophic groups abundances and biomasses. Factors that affect a single parameter are included only in that parameter's quadrant, while factors that affect more than one parameter are included in circles that span all affected parameters.

BIOENV analyses showed that the cover of *Sargassum spp.*,the calcareous functional group, and the leathery functional group were most influential in affecting fish species biomasses. *Dasycladus vermicularis* and filamentous functional group were also commonly included in the best models. The five best models had Spearman's rank correlation coefficients ranging from 0.495 to 0.522.

Cover of *Syringodium filiforme, Heterosiphonia gibbesei*, and the seagrass functional group were included in each of the five best BIOENV models explaining patterns in trophic group abundances. The five best models had ρ_s values ranging from 0.386 to 0.397. Cover of *Dictyota spp.* and *Chondria spp.* were also included in several of the models.

BIOENV models that determined relationships between benthic flora features and trophic group biomasses were highly variable. The top five models had Spearman's rank correlation coefficients that ranged from 0.560 to 0.584, and included 10 different species. The features common to all five top models were cover of *Syringodium filiforme* and the calcareous functional group, although cover of the turf functional group and *Laurencia* spp. was also important.

Multiple regression analyses, summarized in Table 2, investigated the effects of benthic flora factors on univariate dependent variables. The total number of individuals was not significantly influenced by any of the independent variables investigated. Cover of different species and functional groups affected different parameters, although overall cover of benthic flora was also often incorporated into the models.

Table 2. Results of stepwise backward multiple regression analyses. Variables were omitted one by one until only significant variables remained in the model.

Parameter	Significant Variables	*p* value	R^2 value
Number of Species	Flora diversity	0.019	0.935
	Flora cover	0.001	
	Halodule wrightii cover	0.016	
	Turf cover	0.001	
	Batophora oerstedii cover	0.001	
Number of Individuals	No significant variables	n/a	n/a
Shannon-Weiner Diversity (at the species level)	Flora cover	0.003	0.990
	Thalassia testudinum cover	0.006	
	Branching algae cover	0.006	
	Laurencia intricata cover	0.000	
	Calcareous algae cover	0.000	
Mean Total Biomass	Flora diversity	0.041	0.733
	Calcareous algae cover	0.020	

DISCUSSION

There were clear distinctions in the types, numbers, and biomasses of fish associated with each site. The fish communities from BS2, which was characterized by having benthic flora assemblages most unlike those of other sites, were the most disparate, and included many unique species, such as *Sphoeroides testudinus*, *Sphoeroides spengleris*, and *Hippocampus erectus*. We conclude that there is a direct link between the environmental features and the fish community at a site. Furthermore, we conclude that different specific benthic features affect different aspects of fish communities. Species and trophic group abundances were most influenced by species and/or functional groups that were characteristically tall and/or complex (e.g. seagrasses and branching algae). Species and trophic group biomasses tended to be most influenced by the cover of tougher morphologies, such as leathery and calcareous morphologies. In general, analyses of the environmental data showed strong effects of benthic flora characteristics on univariate parameters (high R^2 values) and moderate effects on multivariate parameters (moderate Spearman's Rank Coefficient values).

In our studies, some species, such as *Eucinostomus melanopterus* and Atherinid spp. were ubiquitous, but their relative abundances and/or biomasses varied greatly and contributed to a great deal of the variation between different sites. *Albula vulpes*, for example, was observed at all sites, and in fairly similar abundances. However, the individuals observed at BS2 samples were *much* larger adults, compared to the smaller, post-recruitment sized individuals observed at all other sites. Benthic flora features at sites SC1, SC2, and SH5 may be more favorable to recently settled *Albula vulpes*, while benthic flora features of BS2 may provide better resource for adults.

Relationships between flora and fishes tended to be stronger in analyses completed at the fish species level than at the trophic group level. Such results suggest that studies of responses of fish communities to environmental features are best understood at species levels, rather than at broader, taxa-reducing scales. Reducing 41 species down to only three trophic groups may have accounted for the decrease in occurrence and/or strength of relationships between benthic flora and fishes. Furthermore, since different species have different reproductive, dietary, and behavioral patterns, it can be expected that responses to different environmental and temporal states will be detected at the species level. In our study, the species that would most likely be affected by changes in the benthos are herbivores and invertebrate feeders, which rely on the benthos for a direct or indirect food supply. However, because there were many species that were reduced down to these two groups, it is possible that natural species-level variations clouded out trophic group responses. Ideally, analyzing the data at the trophic-group level would provide insight into how coastal fish communities respond to resource availabilities (i.e. availability of flora for herbivores or invertebrates for primary predators), but our analyses provided less than optimal results. To provide more meaningful results, future studies of such trophic group responses should incorporate a finer scale of trophic level assignments and/or more frequent sampling of fishes and environments.

The weakest relationship was that between benthic flora and trophic group abundances, whose BIOENV analysis has the lowest Spearman's rank coefficient value of 0.397. Past work has shown that abundances of various trophic groups on reefs are significantly influenced by flora assemblage composition (McClanahan et al. 2001) and coral cover and topographic complexity (Connell and Kingsford 1998). However, responses of fishes on reefs (which consist mainly of adult fishes on a consolidated substrate) may be quite different than responses of fishes in coastal habitats (which are typically composed of sub-adult individuals in an unconsolidated substrate dominated by benthic flora).

Although it is a common notion that diversity begets diversity, our univariate analyses lead us to conclude that this is not necessarily always the case. Our results suggest that benthic flora cover, and not flora diversity, was much more important in influencing fish diversity. Parker et al. (2001) also determined that indices of epifaunal diversity were more strongly related to total plant surface area than to plant diversity. We believe that there are very few species-specific qualities that determine the resource-providing abilities of different flora species. Thus, parameters that measure some aspect of total flora abundance (e.g. benthic flora cover) or cover of similar morphologies (e.g. branching floral forms) are probably better predictors of fish diversity.

Overall, the values of Spearman's Rank Coefficients for the various BIOENV routines were relatively low. Thus, it is possible that the environmental factors investigated were not the most important in influencing fish communities, and that other site-specific factors not considered by this study, (such as temperature, prey densities, and wave energy), may be more critical than those addressed here. Additionally, as concluded by a similar study (Hovel et al. 2002), it is possible that processes operating at larger spatial scales, such as regional storm events and larval delivery by currents, may be a source of influence on coastal fish community composition. This is likely the case, since nearshore habitats are commonly occupied by young recruits (Mateo and Tobias 2001) that rely at least partially on oceanographic influences for long-distance transport to settlement sites (Underwood and Keough 2001).

The combination of multivariate and univariate analyses helped to elucidate the benthic factors most affecting various aspects of fish communities. In some cases, the two types of analyses stressed the effects of different floral features. For example, univariate analyses commonly highlighted the role of total floral cover in shaping fish communities, but this feature was not important in any of the multivariate analyses. Conversely, the multivariate analyses featured the importance of many floral species or functional groups that were not highlighted by univariate analyses. In this case, multivariate analyses alone probably gives a better understanding than do univariate analyses alone, but omission of either type of analysis leads to an incomplete picture of the wide array of factors that may influence the composition of fish communities.

In conclusion, we have demonstrated that there is a clear link between the benthic floral composition of a site and that site's fish community. The relationships between flora and fauna are not easily discerned, however, because different aspects of the flora influence different univariate and multivariate fish parameters. Our results indicate that fish are responsive to their habitat, suggesting that changes in the benthos due to natural (e.g. storms) or anthropogenic (e.g. eutrophication or sedimentation) activities can affect fish community composition.

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