What are the Primary Factors that determine the Near shore Fish Population Structure and Productivity around Antigua, West Indies?

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ABSTRACT

What factors whether natural, biotic, abiotic, the composite marine habitats or the geographic location, determine the abundance, density and species composition of near shore fish populations around Antigua? This is the question we tried to answer using four contrasting sites around the island. We also tried to use the data collected to come up with preliminary estimates of productivity at each site. The sites chosen were located along the north, north east, south west and south east coasts of the island. Each of these sites faces different levels of development and fishing pressure. In addition, the current regime, and composite habitats have markedly different characteristics among the sites. We conducted visual surveys and fisher interviews, documented the level of coastal development at each site and employed nets and fish traps with the hope of isolating the factors having the greatest influence on the populations of fish observed. Additionally, habitat maps were used to characterize the sites by size, geomorphology and habitat composition. Although in some areas fishing pressure seemed to play an apparent role, because many of our surveys were conducted fairly close to shore and fishers generally fish at sites much further out to sea, this impact was not always an important determinant. Overall, we were able to show that the composite marine habitats in an area were the primary factor determining the structure of fish populations at our selected sites.

KEY WORDS: abundance, density, species composition, productivity, current regime, fishing pressure, composite marine habitats

¿Cuáles son los Factores Principales que determinan la Estructura y Productividad de las Poblaciones de Peces alrededor de Antigua, isla del Caribe?

¿Qué factores, sean naturales, bióticos, abióticos, por la composición de su medio habitad o su ubicación geográfica, determinan la abundancia, densidad y composición de las poblaciones de peces alrededor de Antigua? Esta es la pregunta que tratamos de responder usando cuarto sitios contrastantes alrededor de la isla. También tratamos de utilizar los datos recapturas para llegar a estimativas preliminares de la productividad de cada sitio. Los sitios escapturas se situaban a lo largo de las costas norte, noreste, este, suroeste y sureste de la isla. Cada uno de estos sitios sufre distintos niveles de desarrollo y presión de pesca. Además, el régimen de las corrientes y los habitad tienen características muy diferentes entre los sitios. Realizamos encuestas visuales y entrevistas con los pescadores, documentamos el nivel desarrollo costera en cada sitio y utilizamos mallas (redes) y trampas con la esperanza de aislar los factores de mayor influencia sobre las poblaciones de peces observados. En algunas áreas la presión de pesca parecía jugar un papel importante, porque muchas de nuestras encuestas fueron realizadas relativamente cerca de la costa y los pescadores generalmente pescan en sitios más lejos de la costa este impacto no fue siempre un factor importante. Pudimos comprobar que la composición de los habitad marianos en un sitio fueron el factor principal en determinar la estructura de las poblaciones de peces en nuestros sitios seleccionados.

PALABRAS CLAVES: abundancia, densidad, composición de las especies, productividad, régimen de las corrientes, presión de pesca, composición del habitad marina.

INTRODUCTION

Tropical nearshore habitats differ due to dissimilar combinations of natural, anthropogenic, abiotic and biotic characteristics that influence the biological communities that settle in these habitats. Fish in particular respond to many physical and biological aspects of the habitat, which in turn determines their diversity, distribution and abundance (Öhman & Rajasuriya 1998). Numerous studies have shown that reef fish communities are structured by several interacting factors including recruitment from the planktonic larva phase, interactions among species and the history of disturbances such as physical, biotic and fishing (Hixon 1991, Russ & Alcala 1998, Ferreira *et al*. 2001). Apart from these post-settlement processes, fish assemblages in marine areas may be influenced by pre-settlement processes. Settlement of fish larvae may be controlled by a number of factors (Dorenbosch *et al*. 2006) including availability of suitable habitat, current regime, temperature, salinity, dissolved oxygen and pH.

There is extensive literature investigating the effects of substratum variables on reef fish community structure (Luckhurst & Luckhurst 1978, Roberts & Ormond 1987, Öhman & Rajasuriya 1998). Based on the results of these studies and many others (Chabanet *et al*. 1997, Jenkins and Wheatley 1998, Gratwicke & Speight 2005a, Gratwicke & Speight 2005b) it is well accepted that more complex habitats (complexity in terms of topographic complexity, substratum diversity, variety of refuge hole sizes, vertical relief, percentage live cover, and percentage hard substratum) (Gratwicke & Speight 2005b), tend to have higher fish species richness, abundance and density than less complex ones. Subsequently, characteristics of nearshore habitats and their accompanying physical and biological environment may result in unique combinations that may directly influence the structure of fish assemblages.

The aim of this study was to analyze different aspects of the biological and physical characteristics of a site and to determine how they influence the structure of the resident fish communities. Thus, the following two questions were asked: 1) Is the species distribution, diversity and abundance different at the four sampling sites? and 2) What factors, (whether natural, biotic, abiotic, or composite marine habitats *i.e.* the unique combination of substratum components seen along a transect *e.g.* sponges, coral heads, patchy seagrass, coral rubble) are the most important predictors of fish species distribution, diversity and abundance at the sites?

METHODS

Study Area

This study was carried out in the Eastern Caribbean Island of Antigua (Figure 1). This island is located in the Lesser Antillean island chain between 17º 00' N and 17º 44' N and 61º 21' and 61º 55' W. The Atlantic Ocean washes its eastern shores and the Caribbean Sea the western shores. It has a total land area of 280 km². Antigua and its sister island Barbuda sits on a shelf area of approximately 3,568 km². The island has an intricate coastline which is deeply indented and fringed by nearshore and offshore coral reefs, shoals, rock islands, and sand bars (CCA 1991). Antigua has three fairly distinct topographical regions; volcanic in the southwest, central plain, and limestone in the north and east (CCA 1991). The movement of sea currents around Antigua is primarily wind driven, and flows northwest to west. This study was carried out at four sites around Antigua: Cades Reef (CAD) located on the southwest coast; Willoughby Bay (WILL) located on the southeast coast; the north coast of the island from Boon Point to Shoal Point (JB); and around Guiana Island (GI) located on the northeast coast of the island.

Visual Surveys and Habitat Sampling

During a four week period prior to the initiation of actual visual survey data collection, baseline data on the fish communities present in the study areas were collected. Fish species composition, diversity and abundance and also substrate composition were estimated at the four sampling sites using randomly placed 100 x 2 m transects. An *a prior* number of transects were completed at each site based on the total area of the site, such that a minimum of 25% of the entire site area was covered. In order to avoid diver impacts while surveying, fish counts were started 5 - 10 minutes after the measuring tape had been laid out. Fish counts were always conducted by the same observer and during the mid morning to minimize bias in the fish abundance caused by diurnal variation. Fish species were

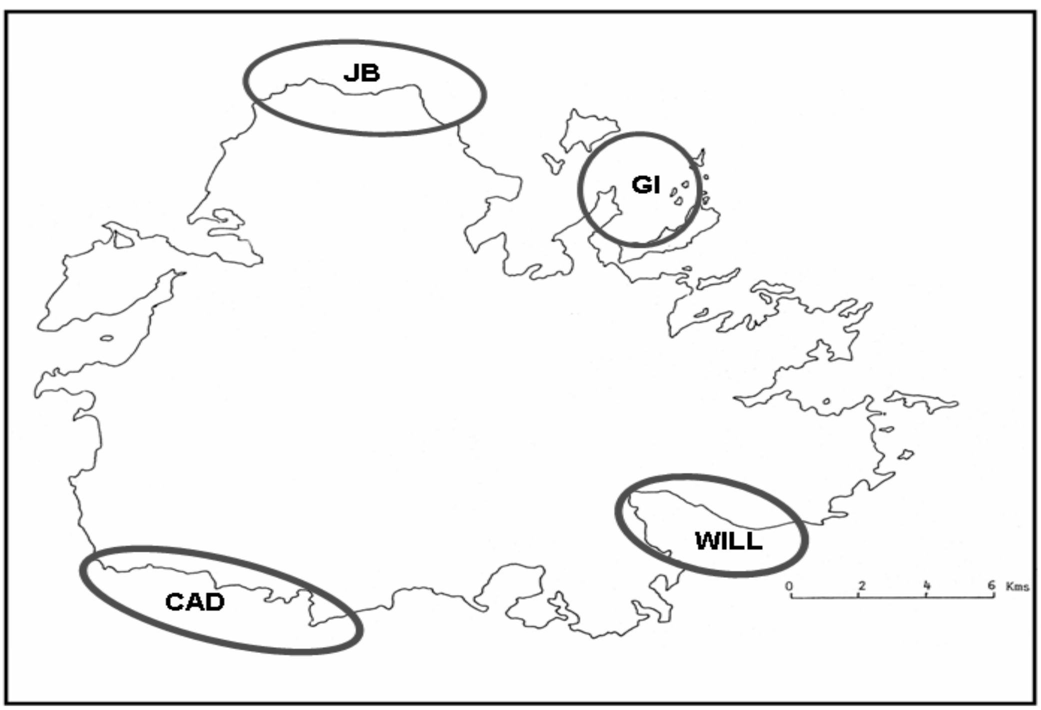

Figure 1. Map of Antigua showing the location of the four contrasting study sites: Cades Reef (CAD) located on the southwest coast; Willoughby Bay (WILL) located on the southeast coast; the north coast of the island from Boon Point to Shoal Point (JB); and around Guiana Island (GI) located on the northeast coast.

grouped into the following abundance categories; 1 - a single individual was observed, 2- between 2 and 10 individuals observed, 3 – between 11 and 100 individuals observed, and 4 – over 100 individuals observed. After the fish data were recorded, a second transect swim was completed in order to collect data on the following substrate and benthos categories: dense seagrass, patchy seagrass, sparse seagrass, algae, isolated hard coral heads, soft corals, sponges, and coral rubble. The average depth of each transect was determined by measuring the depth at the shallowest and deepest parts of each transect. Temperature was recorded at the site of each transect and water samples were collected and analyzed in the laboratory for pH, salinity, and turbidity. Habitat maps were used to characterize the sites by broad scale habitat composition.

Arrowhead fish traps with 1⅝" mesh size and gill nets with 3" mesh were used to supplement the data collected from the visual surveys, however due to logistical problems this data were only collected at WILL, CAD and GI. Traps were hauled on average every 7 days and the nets were set for approximately 1 hour. The composition and weight of each catch was recorded.

Data Analysis

The relationship between fish species distribution, diversity and abundance; and biotic and abiotic factors, composite marine habitats, and geographic location were investigated using multivariate analysis. Summary statistics on the number of species, number of families and the most common species and families found at each site were completed. Multivariate analyses were conducted using the "PRIMER" set of programs from Plymouth Marine Laboratory, England. In this study each sample represents one transect. The first analyses performed were diversity measures. These are exploratory analyses that furnish information on species richness and equitability (Clarke and Warwick 2001). The analyses completed were 1) Shannon-Wiener diversity index, 2) Margalef's index and 3) the Simpson index. The species data were fourth root transformed and the Bray-Curtis similarity coefficient was calculated to generate rank similarity matrices. Hierarchical cluster analyses were then completed to determine the natural grouping of samples (which samples are most similar to each other). Prior to the data being analyzed by Multi Dimensional Scaling (MDS), the Bray-Curtis similarity analysis was performed on the square root transformed data. The rank similarity matrix produced was converted into an MDS ordination. A Principal Components Analysis (PCA) was completed. The objective of this ordination was similar to that of the cluster analysis and the MDS ordination: to map samples in two or three dimensions such that the placement of samples reflects the similarity of their fish communities (Clarke and Warwick 2001). The first step in doing the PCA was to delete all the rare species; those that represented less that 3% of the total abundance from the spreadsheet. Thus, only 46 species remained. An ANOSIM for the 1-way layout was performed to test the null hypothesis that there is no difference in community composition at the four sites. In order to examine H_0, three main steps were performed: 1) compute the test statistic, 2) re-

Table 1. A summarized description of each sampling site

Site	Description					
	Location	Broad Scale Habitats	Small Scale Habitats	Fishing	Hotels	Tourism Related Activities
WILL	Southeast	Mangroves, Seagrass, Coral Reefs	*Curve of the bay* - large mangrove stand, dense seagrass, little coral development, very turbid water *Mouth of bay* – extensive reef development, coral rubble, dense seagrass, clear water with good visibility	No record of fishing activities	None	Very little (surfing)
CAD	Southwest	Mangroves, Seagrass, Coral Reefs	Two main mangrove stands, dense seagrass, majority of site lined by coral reef/hardbar which stretches from shore to over to 300 m	Gill netting, Handlining, Spearing, Trapping	Few	Numerous (diving, snorkeling, sport fishing, jet skiing *etc.*)
JB	North	Seagrass, Coral Reefs	Dense seagrass, discontinuous coral reef up to 90 m offshore	Gill netting, Trapping	Numerous (all along the coastline)	Numerous (diving, snorkeling, sport fishing, jet skiing *etc.*)
GI	Northeast	Mangroves, Seagrass, Coral Reefs	Much of coastline fringed by mangroves, dense seagrass, numerous patch reefs.	Gill netting, Spearing, Trapping	Single	Few (diving, snorkeling)

compute the statistic under permutation, and 3) calculate the significance level. One of the major aims of this study was to match the fish community data collected to a suite of environmental variables measured at the same sites. In order to examine the extent to which the environmental data was related to or explained the observed biological pattern, the BIO-ENV procedure was completed. The factors compared were temperature, pH, salinity, turbidity, composite habitats and depth.

RESULTS

Approximately 100 species from 40 families were seen at the four sites (Figure 2). Seventy-one species from 27 families were observed at WILL, 98 species from 38 families at CAD, 93 species from 35 families at JB, and 79 species from 32 families at GI. The species distribution across all samples was lognormally distributed, such that there were a few very abundant species and a large number of rare species. Beaugregorys (*Stegastes leucostictus*)), slippery dicks (*Halichoeres bivittatus*) and juvenile striped parrotfish (Scarus iserti) were observed at >87% of all transects and were usually the species occurring in the highest abundances. At each site a few families dominated the fish community composition. At WILL the dominant family was Labridae with 8 species observed. At CAD Labridae, Pomacentridae, and Haemulidae all had the most representative species (9 each). At JB the dominant family was Haemulidae (10 species) and at GI Labridae was dominant with 8 species. Overall the most common families seen at the four sites were Labridae, Scaridae, Pomacentridae, Haemulidae, Lutjanidae, Holocentridae and Serranidae.

A review of the abundance values showed that CAD had the highest abundance, then WILL, then GI, then JB (Figure 3).

GI had the highest values of Margalef's index, Shannon-Weiner diversity index and Simpson index. CAD had the next highest values for the three diversity indices investigated, then JB, and WILL.

Cluster analyses were performed on an individual site basis and on all the samples combined. When all samples were combined the cluster analysis indicated that the similarity between JB and WILL was 82%, while that between CAD and GI was 80.5% (Figure 4). The similarity between the JB/WILL and CAD/GI combinations was 79.1%. This value is not significantly different from the between site percentages. This pattern therefore indicates that although JB and WILL are more similar to each other than to either CAD or GI and CAD and GI are more similar to each other than to either JB or WILL the sites are not significantly different from each other. For the cluster analysis performed on an individual site basis, the top 13 relationships that represented between 95.91% and 85.17% similarity

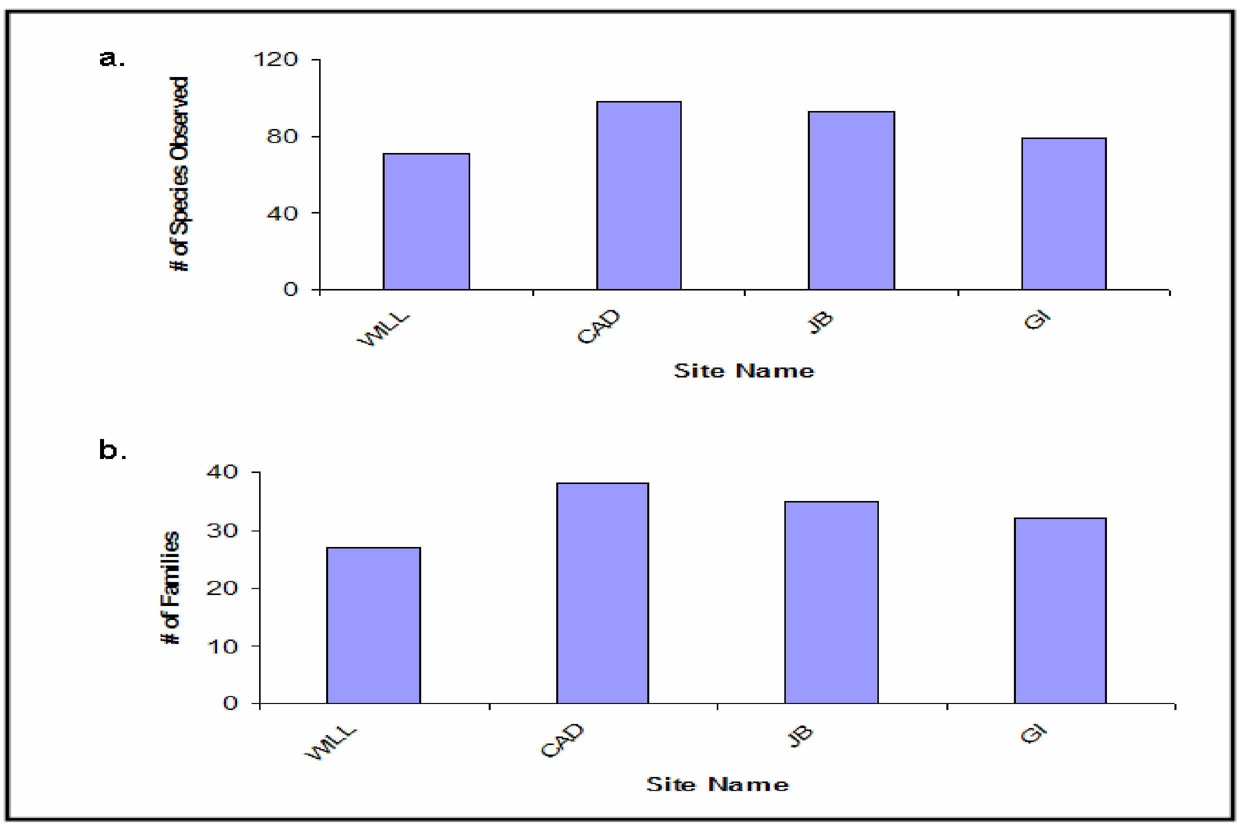

Figure 2. a) Number of species observed at each site; b) Number of families observed at each site.

between samples were all between GI transects. After this the next two pairs of most similar sites were from WILL. The two least similar sites were both from WILL and they were only 56.66% similar to each other.

The MDS ordination (Figure 5) showed a general clustering of samples by site but more importantly many of the samples from the four different sites clustered together. WILL had the most outliers, followed by JB.

The PCA analysis separated the samples to represent the similarity of their geographical communities. GI and CAD samples were separated along PC2 indicating that these communities are more similar to each other than any other (Figure 6). The WILL and JB samples were separated along PC1 indicating the similarities of these communities. PC 1 accounted for 19.2% of the variability and PC2 7.1%. The seven species contributing the highest to the variability accounted for by PC1 were in order of contribution sailors choice (*Haemulon parra*), blackear wrasse (*Halichoeres poeyi*), rock hind (*Epinephelus adscensionis*), unidentified juvenile grunts, slippery dick (*Halichoeres bivittatus*), bicolor damselfish (*Stegastes partitus*), and foureye butterflyfish (*Chaetodon capistratus*).

The null hypothesis tested using ANOSIM for the 1-way layout was that there is no difference in community composition at the 4 study sites. The value obtained for the sample statistic (Global R) was 0.196 at a significance level of 0.1% (Figure 7).

BIO-EVN was performed in order to determine which

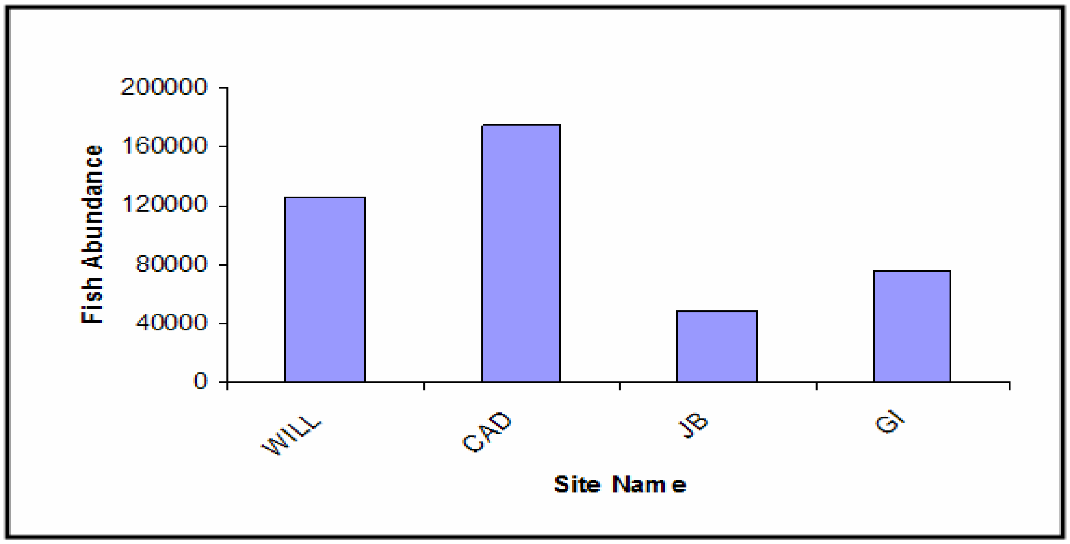

Figure 3. Fish abundance recorded at each site

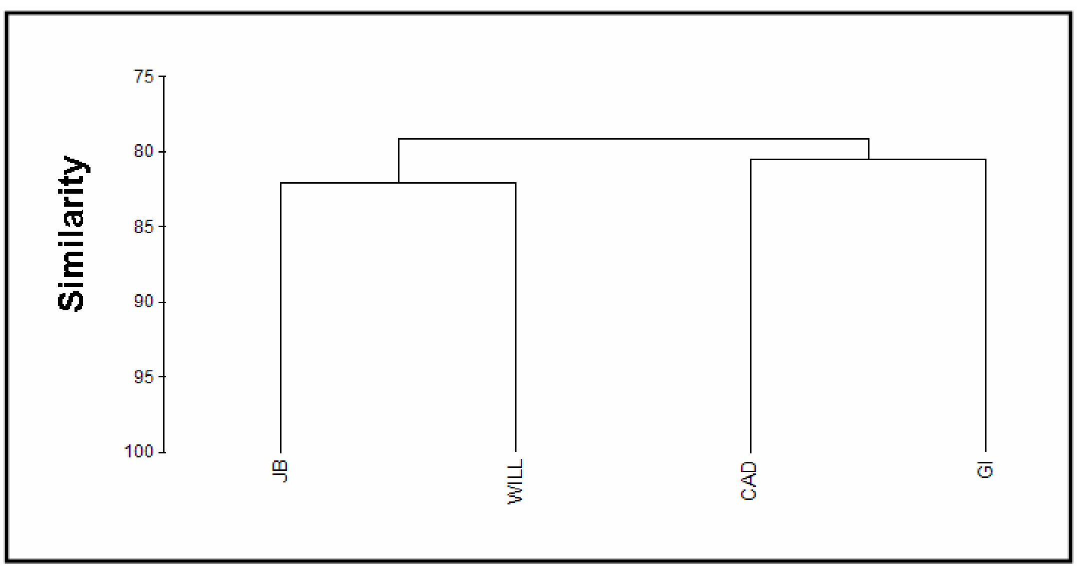

Figure 4. Hierarchical cluster analysis results illustrating the similarities among the study sites.

characteristics of a site were most important in determining the community structure observed. The Spearman Rank correlation value was 0.281. One hundred percent of the 20 best results generated by PRIMER had composite habitats as the determining factor. Temperature was partly responsible in 50% of the results, pH and salinity partly responsible in 40% of the results, and depth and turbidity partly responsible in 20% of the results. The top result showed that the factor composite habitats was 100% responsible for the community composition patterns seen.

The netting/trapping data was used to help support the result of the visual surveys. The MDS plot generated from these data also showed a clustering of samples by site (Figure 8).

DISCUSSION

There are two important descriptors of any biological community: physiognomy (physical structure) and the number of species present and their relative abundances (species richness and diversity). Species diversity has received the greatest amount of attention in community ecology because diversity is an emergent property of the community. Species richness is a number representing the total number of species present (Clarke and Warwick 2001) and

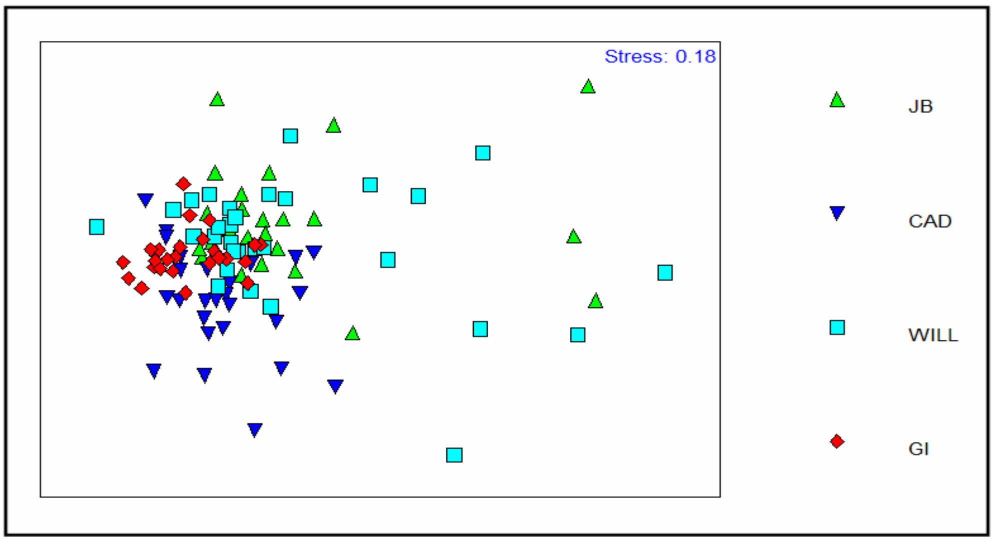

Figure 5. MDS ordination illustrating the clustering of samples based on their similarities.

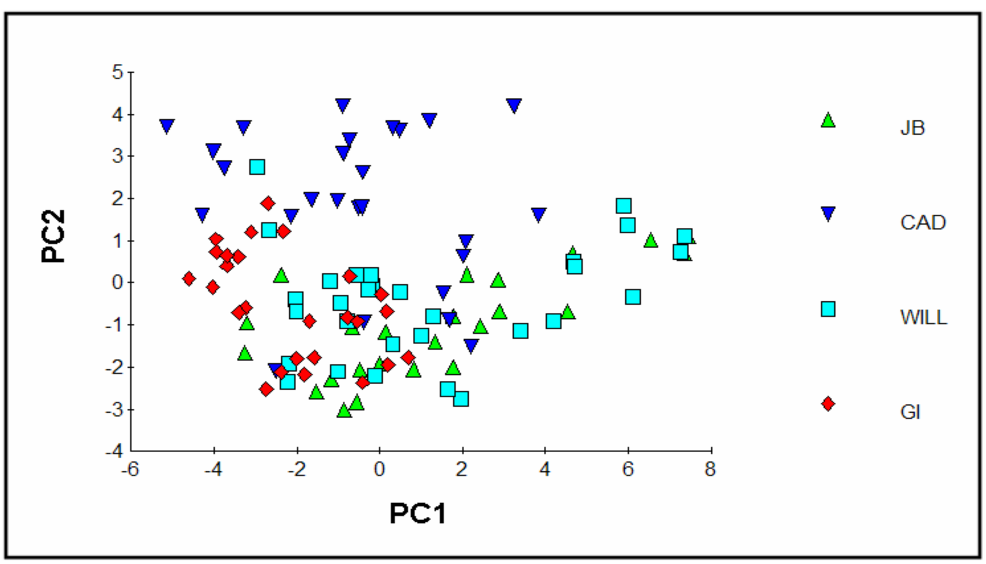

Figure 6. PCA ordination illustrating the separation of samples based on the similarity among their fish assemblages.

is often incorrectly used as the estimator for the diversity of a community. However, in order to have an effective measure of diversity, we need to account for both species richness and the evenness with which individuals are distributed among different species (Margalef 1958, Llyod 1964). Thus, most species diversity indices usually incorporate some combination of these two features of the sample information (Clarke and Warwick 2001).

In this study the three diversity indices used were the Shannon-Wiener, Margalef and Simpson. Interestingly, these indices showed that GI was the most diverse community, then CAD, JB, and finally WILL. However, a simple count of the total number of species found at each site resulted in CAD having 98 species, JB 93 species, GI 79 species and WILL 71 species. The key to explaining this somewhat contradictory result may be the fact that diversity indices take into account both the number of species and the evenness of with which individuals are distributed among species. Thus, if one were to pick apart the number of species and the equitability of distribution and look at

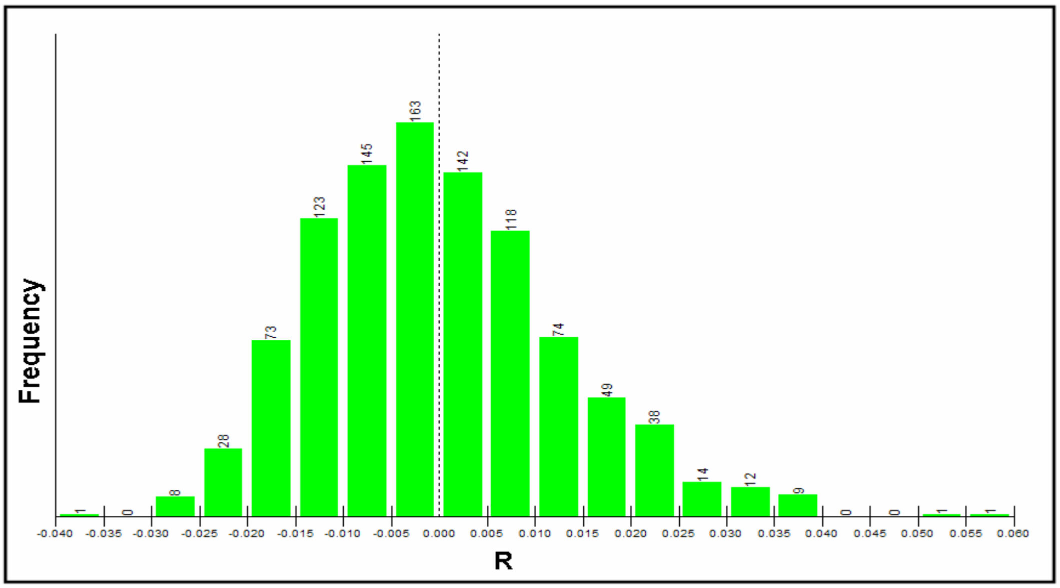

Figure 7. Results of the ANOSIM for the 1-way layout. The global R value is 0.196.

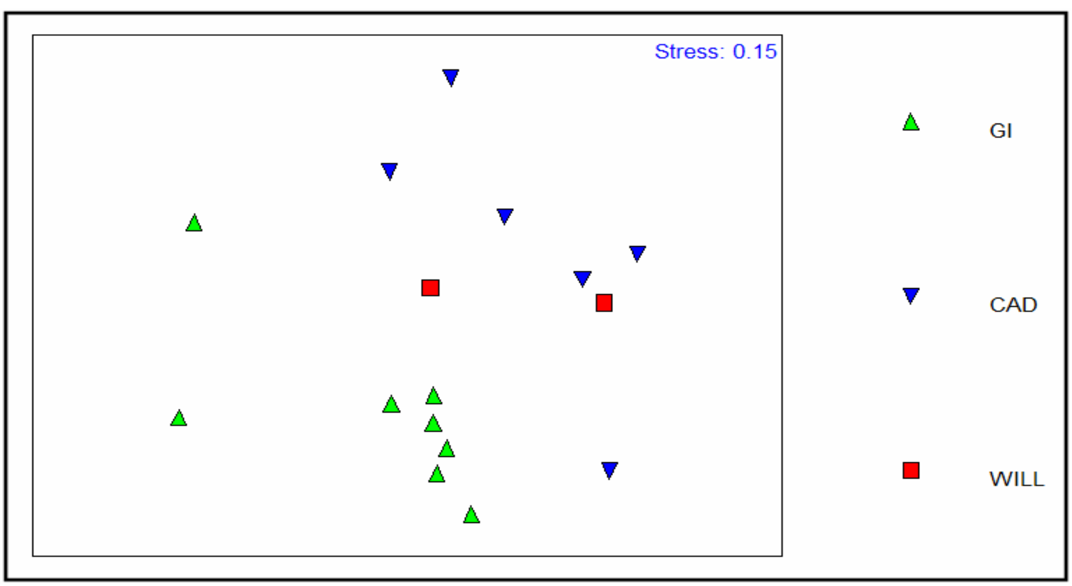

Figure 8. MDS ordination generated form netting/trapping data. The clustering of samples is based on their similarities.

them separately, it would appear that GI must have the highest evenness value, thereby skewing the diversity data in its favor. The results of the cluster analyses may also help explain this finding. When cluster analyses were performed on an individual site basis, the top 13 relationships that represented between 95.91% and 85.17% similarity between samples were all between GI samples. Cluster analyses aim to find natural groupings of samples such that samples within a group are more similar to each other than samples in different groups (Clarke and Warwick 2001). This similarity is in terms of both numbers and evenness. Evenness is important because any large variances in the distribution of the rare or abundant species will have a large effect on the similarity coefficients obtained between samples. Thus, the GI samples must have had similar numbers of species and there must have been a fairly equitable distribution.

The BIOEVN procedure showed that the variable, "composite habitats" was the most important in determining the community structure observed. This variable was more important than water temperature, pH, salinity, turbidity, and depth. This result is not unexpected as numerous studies (Roberts & Ormond 1987, Chabanet *et al*. 1997, Jenkins and Wheatley 1998, Öhman & Rajasuriya 1998, Gratwicke & Speight 2005a, Gratwicke & Speight 2005b) have documented the importance of habitat complexity in structuring fish communities. Although a few broad scale habitat differences exist among the different sites they generally contain the same basic habitats with one exception; no mangroves fringe the coastline at JB.

Willoughby Bay (WILL) is located on the south eastern coast of Antigua. On a broad scale, the habitats present in this area are mangroves, seagrass and coral reefs (Table 1). The majority of the coastline along both sides of WILL is composed of coastal trees/shrubs such as *Acacia* and there is little tourism-related development or activities. The only mangroves in this area is a large stand located at the curve of the bay. The area of the Bay closest to the mangroves is very turbid and is the result of runoff from a number of agricultural farms located behind the mangrove stand. Generally, there are lush, luxuriant dense seagrass beds all around WILL. There are isolated coral heads and small rock formations in numerous areas all around the bay, but the extensive reef development occurs close to the mouth of the bay. This area is colonized by mountains of *Montastraea annularis* and there are also large areas where coral rubble has been piled up by Hurricane Hugo. At its mouth, the bay receives flushing from the incoming sea currents so the waters are clear with good visibility.

Mangroves, coral reefs and seagrass beds are also present at CAD (Table 1). This site has two main mangrove stands. One located in the middle of the site (closer to the western end) and is separated from the sea grass beds and coral reef communities by a ridge of coral rubble, which is only inundated when the tide is high. At low tide, the mangroves and their accompanying biological communities are separated from the other habitats by this ridge. The other mangrove stand fringes Cades Bay. The majority of this site is lined by a coral reef/hardbar area which stretches from the shore to over 300 m out to sea in some areas, and then there is a fairly steep drop off to seagrass and sand. Generally, the seagrass communities at this site are very dense.

JB has a large area of discontinuous coral reef that is located approximately 90 m off shore in certain areas and at closer or further distances in others. These structures rise out of the water in many locations and are exposed regardless of the tides. These structures are very tall in places and provide numerous crevices and holes that provide shelter to the fish resident there. Much of the corals were killed and piled up by Hurricane Hugo. However, there are numerous live staghorn (*Acropora prolifera*) coral heads. The seagrass beds are very dense and luxurious.

GI has an abundance of mangroves, coral reefs and seagrass (Table 1). Much of the coastline at this site is fringed with red mangroves (*Rhizophra mangle*). Dense seagrass meadows spread out all around the area and numerous coral reefs are located all over the site. Coral reef types range from reef flats to back reef area down to 40 ft. with *M. annularis* and staghorn coral (*A. prolifera* and *A. cervicornis)* among other coral species.

It is understandable why CAD sites have the most species and most families. At this site there is more reef area present than at the other areas, and therefore there are many different habitat combinations for fish to exploit. Studies have shown that tropical marine habitats are connected by organism movements, nutrient exchange and energy flow (Ogden and Ziemen 1977, Beck *et al*. 2001). These movements are typified by feeding migrations (Hobson 1965, McFarland *et al*. 1979, Tulevech and Recksiek 1993, Beets *et al*. 2003), spawning migrations (Smith 1972, Claro and Lindeman 2003), and ontogenetic shifts in habitat use with increase in size or age (Longhurst and Pauly 1987). Therefore, the greater the diversity of habitats in an area the more resources and spaces available for fish to carryout their life processes.

The MDS plot and PCA showed both a clustering of samples by site but also that many of the samples from the four different sites clustered together. This clustering indicates a large amount of similarity among samples within a site and among the four sites. In the MDS plot, WILL had the most outliers, a result which was corroborated by the cluster analysis data which showed that the sites that were most dissimilar were WILL sites. The reason for this difference may be partially explained by the habitat characteristics of this site. A perusal of the individual sample data from WILL showed that the data from the sites that were located at the mouth of the bay were similar to each other but were very different from the sites located in the turbid area at the curve in the bay. Recall that there is extensive reef development at the mouth of the bay and this area is flushed by sea currents, but the area around the curve is very turbid and there is little reef development with only isolated coral heads and rock formations.

The Global R value generated from the ANOSIM was low (0.196) indicating that there exists a degree of discrimination between sites such that in some cases some samples within sites are more similar to each other, while for other cases samples from different sites are more similar than samples from the same site. This result is also supported by the cluster analysis data which showed that some samples at a site (example the top 13 relationships that represented between 95.91% and 85.17% similarity between samples were all between GI transects) are more similar to each other than any other. However, the cluster analysis data also showed that many of the most similar samples were from different sites. The MDS ordination from the trapping/netting data also showed a clustering of samples from the same site but also that two samples from different sites (CAD and WILL) were more similar to each other than any other samples.

Based on fisher interviews and data from the Antigua Fisheries Division, JB is the least fished area among the four sites. In fact, for the duration of the survey it was not possible to identify any commercial fishermen that engage in fishing activities at this site. CAD is a multi-use area and has been designated an MPA since 1999, however the management plan has yet to be implemented. A number of fishers do gill netting, handlining, spearing and trapping at this site. The only area of WILL that is fished is at the mouth of the Bay where the mature coral reef development is located. At this site fishers use fish traps and gill nets but on a small scale. In addition, some of the fishers that work this site only spend part of the year fishing in this area so that the level of fishing effort expended fluctuates throughout the year. At GI fish trap, spearing and gill net fishermen predominate. Although there is a high level of fishing activity going on at this site, it is a very diverse and large area so the fishermen have many choices of where to set their gear. Overall the commercial fishing effort per unit area is greatest at CAD, then at GI, then WILL and the lowest at JB. This result is surprising since CAD experiences the highest amount of fishing but is also the site where the greatest number of species and highest abundance was observed. Although there was no evidence of commercial fishing at JB it had the lowest fish abundance values. It is therefore clear that although fishing pressure seemed to play an apparent role, this impact was not always an important determinant of the fish community structure observed at a site.

The coastal areas of JB are the most developed of all the sites (Table 1). There are a number of hotels along the entire stretch of the coastline of this site. In addition, numerous tourism-related activities are carried out in this area. Due to accessibility, WILL is the least developed area in terms of construction of buildings but there are agricultural farms located at this site. There is one major tourist resort at GI, and there are some other tourism-related activities that take place. CAD is a multi-use area. At this site, the coastline is not as physically developed as JB and there aren't as many hotels, but there is widespread use of the area for touristic activities such as diving, snorkeling, jet skiing *etc*.

It is arguable that the low abundance of fish at JB may be the result of anthropogenic influences, however, CAD also experiences high anthropogenic influences. Therefore, one can conclude that although coastal development may affect the fish communities present, it is not the most important factor influencing the fish community trends observed.

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