POLLUTION DETECTION MODELS AND HABITAT PREFERENCE OF THE CRYPTOFAUNA ASSOCIATED WITH THE CORAL *MADRACIS MIRABILIS*

by

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Abstract

The crustacean cryptofauna associated with the coral Madracis mirabilis (Duchassaing and Michelotti) was sampled to test several hypotheses concerning pollution in tropical ecosystems. Six stations along the west coast of Barbados, W.I. were monitored for environmental quality parameters to reaffirm earlier work that found a pollution gradient was present. Trends in nitrite, phosphate, and suspended particulate matter concentrations as well as water clarity generally supported this hypothesis. Samples of M. mirabilis were collected and the cryptofauna used to show that log-normal plotting and dominance curves may be ineffective in differentiating between the fauna of highly polluted and less polluted sites. Greater success was attained with classification and ordination using Bray-Curtis dissimilarities, which did separate the highly polluted sites from those that were less polluted. An F-test showed that there are 8 possible indicator species, all of which were less common at the high pollution sites. The cryptofauna associated with small isolated heads of M. mirabilis was compared to the fauna found in large monospecific stands of the same species, and classification and ordination clearly separated the faunas of the two growth forms. Analysis of covariance performed to establish how the faunas differed in richness, and analysis of variance performed to compare densities showed that isolated heads possessed greater numbers of species and individuals of large cryptofaunal organisms (decapods and amphipods) while large stands were found to support more species and individuals of smaller organisms (copepods and isopods). This difference may be

a function of the greater habitat seen in the large stands. Evenness was reduced in isolated head compared to the monospecific beds, perhaps as a result of an "island effect" where low migration between coral heads would result in little variation in available habitat and dominance by a few strongly competitive species. To show how richness and evenness may be biased in many current studies, linear regression analysis was performed to show that there is a strong positive relationship between richness and abundance of individuals and a strong negative relationship between evenness and abundance of individuals. Analysis of richness and evenness without correction for differences in abundance showed a number of inconsistencies with results obtained using ANCOVA. An intuitive explanation is provided of why this problem of abundance dependence exists and how researchers can avoid bias in such analyses.

RÉSUMÉ

La cryptofaune carcinogène associée au corail Madracis mirabilis (Duchassaing et Michelotti) fut échantillonnée afin de vérifier plusieurs hypothèses concernant les écosystèmes tropicaux. Nous avons échantillonné six stations de la côte ouest de la Barbade (Antilles) dans le but de confirmer un des aspects d'un travail antérieur qui y montra la présence d'un gradient de pollution. À cet égard, nos concentrations de nitrites, de phosphates et de matière particulaire en suspension ainsi que la transparence de l'eau en font foi. L'application d'un graphique log-normal et de courbes de dominance aux échantillons de M. mirabilis et de sa cryptofaune associée se révéla inefficace pour séparer la faune d'un milieu très pollué de celle d'un milieu qui l'est moins. L'application d'une méthode d'ordination et de classification tel que celle de dissimilaritées de Bray-Curtis sépara avec succès les sites plus pollués de ceux qui l'étaient moins. Un test du F montra qu'il y a huit espèces indicatrices possibles toutes moins communes aux sites très pollués. La cryptofaune associée à de petits îlots de M. mirabilis fut comparée à celle accompagnant de vastes champs monospécifiques de la même espèce. Grâce à la classification et à l'ordination on a reconnu deux faunes distinctes. L'analyse de covariance réalisée afin de détecter des différences de richesse, et l'analyse de variance réalisée afin de détecter des differences d'abondance montra que les îlots possédaient un plus grand nombre de grosses espèces cryptofauniques (décapodes et amphipodes) alors que les champs vastes supportaient plus de

petites espèces (copépodes et isopodes). Ces différences seraient attribuables à l'habitat plus large que constituent des champs étendus. L'équitabilité réduite des îlots par rapport à celle des champs monospécifiques résulterait d'un effet d'isolement favorisant une migration faible entre îlots coralliens qui réduirait la variation de l'espace habitable et encouragerait la dominance de quelques espèces en compétition vive. Pour illustrer comment les calculs de richesse et d'équitabilité peuvent être erronés, on utilisa une droite d'estimation qui montra un lien positif fort entre la richesse et l'abondance des individus et un lien négatif fort entre l'équitabilité et l'abondance. Une analyse de la richesse et de l'équitabilité sans correction entre les différences d'abondance favorise un certain nombre d'incohérences rattachées aux résultats obtenus par l' ANCOVA. Nous suggérons aussi une explication empirique quant à l'existence du problème de dépendance dû à l'abondance et comment les chercheurs peuvent l'éviter au cours de leurs analyses.

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Many people have helped in the completion of this thesis, and the contribution of every one of them was of great importance. I can only list these people in order of occurrence since the contributions of all are equally appreciated. First, I would like to thank Dr. John Lewis for his supervision and support (both moral and financial) throughout the thesis work. This was particularly felt when things were not going well, and Dr. Lewis always had encouraging words. Further financial support was provided by a Postgraduate Scholarship from the Natural Sciences and Engineering Research Council of Canada, who also dangled the carrot that drove me to complete the thesis as quickly as possible. Early discussions with Dr. Tom Tomascik and John Boers helped formulate some of the ideas and methodology for the work, and were much appreciated. Dr. Brian Marcotte had some useful suggestions in the early stages and enthusiasm and mind-broadening ideas throughout. Criticism of an early thesis draft was also extremely valuable.

Dr. Wayne Hunte offered encouragement and suggestions while I was at Bellairs Research Institute, and also did a very helpful critique on an early draft of this thesis. My field work could not have been completed without my dive partner and valued friend Barbara Conlin, who endured many bone chilling dives without complaint. All of the Bellairs employees helped at some point while I was in the field and I thank them all. Other people who helped out while I was at Bellairs include Drs. Hazel Oxenford and Julia Horricks, Jill Hambrook, Sarah McLean, and Ione Hunt von Herbing. Heather Kaye and John Boers were responsible for

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Preface

1.) Statement of contribution to original knowledge:

To the best of my knowledge, at the time of writing the material presented in this thesis is original in that; (i) it is the first quantification of pollution effects on a tropical biological community using techniques developed in cold water ecosystems; (ii) it is the first quantitative comparison of the cryptofauna associated with two different growth forms of the same coral species (Madracis mirabilis); (iii) it is the first attempt to provide an intuitive understanding of the problems marine investigators have been ignoring in their analyses of diversity, richness, and evenness.

2.) Historical statement of relevant work:

A historical review may be found in the general introduction, while more extensive background material is found in the introduction and text of the individual chapters.

3.) Declaration of assistance:

The candidate acknowledges the supervision and advice of Dr. J.B. Lewis who will appear as co-author on future manuscripts from the thesis. In accordance with section 7 of the Thesis Guidelines, the candidate declares that the study design, field and laboratory work, data analysis and interpretation, and writing of chapters was undertaken by the candidate alone.

4.) Thesis format:

In accordance with Section 7 of the Thesis Guidelines, this thesis has been prepared as a series of chapters which will be used as manuscripts for submission to refereed scientific journals for publication. Therefore, each chapter contains an Abstract, Introduction, Materials and Methods, Results, Discussion and Literature cited. Because the material in the different chapters is related, some degree of repetition is necessary. Every effort has been made to reduce this as much as possible. This format has been approved by the thesis committee and by the Chairman of the Department.

The format of the chapters corresponds to that required by the journal Marine Biology, to whom these papers will be submitted early in 1987.

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General Introduction

Within the last 25 years, there has been a rapid increase in tropical marine research. Much of this work has centered on coral reefs, including studies on coral distribution (review by Stoddart, 1969), pollution effects on coral (reviews by Loya and Rinkevich,1980; Howard and Brown, 1984; Brown and Howard, 1985), and coral reef productivity (review by Lewis, 1977). Though coral reef cryptofauna has received less attention, a number of recent studies have examined coral associated organisms (e.g. Tsuchiya et al.,1986; Abele, 1984). McCloskey (1970) and Grassle (1973) have provided early indications of the diversity of organisms present, and sampling methods began to improve as a result of experiments by Porter and Porter (1977), McWilliams et al. (1980), and an overview by Hutchings (1978). Such work has made possible the examination of other biological phenomena related to cryptofaunal distribution.

Great effort has also been directed toward pollution detection in biological communities (reviews by Gray and Pearson, 1982; Hargrove and Thiel, 1983; Sundberg, 1983), but most of this work has focused on temperate and boreal communities (e.g. Gray and Mirza, 1979; Rafaelli and Mason, 1981; Shaw et al., 1983). As a result, models for pollution detection have been developed in cold water ecosystems. Though response of coral communities to pollution stress has been documented (reviews by Pastorok and Bilyard, 1985; Brown and Howard, 1985), models used to describe biological response to pollution have not been well tested in tropical ecosystems.

Several aspects of cryptofaunal communities make them ideal subjects for tropical pollution studies. Because numerous samples may be taken without damaging reefs and organisms may be identified later in a laboratory, the excessive amounts of field time required by many other types of studies (e.g. coral transects) may be avoided. Cryptofaunal densities (numbers of individuals per unit volume of coral) are very high and the community is diverse (McCloskey, 1970; Grassle, 1973). These are both critical assumptions of many pollution detection models (Gray and Pearson, 1982).

Madracis mirabilis (Duchassaing and Michelotti) was chosen as a cryptofaunal habitat for the present study because it is one of the few coral species available in Barbados at numerous sites (see Lewis, 1960) along the pollution gradient on the island's west coast (see Tomascik and and Sander, 1985). Six sites were selected along the west coast of the island to represent various levels of pollution loading (Fig. 1 of chapter 1). At five of these sites, M. mirabilis grows in large monospecific beds that may be up to a metre in depth and tens of metres in diameter. However, at one of the sites (Paynes Bay), M. mirabilis grows in small, discrete heads. The branches of both growth forms provide numerous crevices and spaces for cryptic fauna where effects of fish predation and environmental fluctuations may be reduced.

Initial examination of the cryptofaunal samples indicated that the fauna of discrete heads differed markedly from the fauna of large beds. For this reason, the study was divided into two components presented as two chapters. In the first, analyses are

performed on the five sites with large M. mirabilis beds to establish whether pollution affected the cryptofaunal species composition and to apply several pollution monitoring models. In the second, analyses were performed to establish how cryptofaunal composition differs between the discrete coral head growth form and the large beds adjacent to the Payne's Bay site where the discrete heads were sampled. Though several studies have shown that different substrates harbour different densities of cryptofaunal groups (e.g. Alldredge and King, 1977; McWilliams et al., 1981; Ohlhorst, 1985), little effort has been directed toward measuring species richness and evenness, and how these factors may be related to differences in density.

During analysis of the cryptofauna of the two growth forms it became apparent that many of the analyses of composite diversity, richness, and evenness in current studies may be biased. This bias is a result of differences in abundances (numbers of individuals collected) in the different communities under investigation, and the phenomenon requires elaboration and clarification. A third chapter is therefore presented to show show how many previous studies have inadvertently introduced bias. Cryptofaunal analysis is repeated without correction for abundance differences to emphasize how inaccurate such results can be.

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Chapter 1

Pollution Detection Models and their Application to a Tropical Ecosystem: Response of a Cryptofaunal Community Along a Pollution Gradient

ABSTRACT

Concentrations of nitrites, phosphates, and suspended particulate matter, as well as light absorbance were measured at 6 sites along the west coast of Barbados, W.I. to reaffirm earlier work suggesting that a pollution gradient was present. A general trend of decreasing concentrations of nitrites, phosphates, and suspended particulate matter was observed as distance from Bridgetown increased in a northern direction, and light absorbance was lowest at the northern stations. The crustacean cryptofauna associated with the coral Madracis mirabilis (Duchassaing and Michelotti) was used to test whether several of the pollution detection models developed for cold water ecosystems may be readily applied to tropical ecosystems. At 5 of the 6 sites monitored for environmental quality, core samples of M. mirabilis were taken. The motile crustacean cryptofauna inhabiting the coral stands were collected from these core samples to test whether any biological response to the environmental gradient was evident. Dominance plots based on relative abundance (species percentage composition) and log-normal plotting methods were ineffective in segregating highly polluted from less polluted stations. However, ordination (multidimensional scaling) and classification (group average clustering) based on Bray-Curtis dissimilarity measures, did separate highly polluted stations from those that were less polluted. Ordination was found to be the preferable technique, since minor changes to the data set caused major realignment of the cluster dendrogram. Several species were found to differ

markedly in density between the highly polluted and less polluted sites, but all of these species showed population decreases at the polluted sites. There is a noticeable absence of pollution tolerant species, and given the results is is suggested that pollution detection models developed for cold water ecosystems should not be indiscriminantly applied to tropical communities. Classification and ordination techniques are the most promising, but more tropical data sets are needed before general models can be assumed.

INTRODUCTION

Biological systems can only endure a minimal level of pollution before the community reacts (e.g. Sheppard, 1980; Dollar and Grigg, 1981). It is therefore of interest to detect community response at the earliest possible stage, so that the pollution can be reduced or stopped before severe ecological damage is done.

In a series of papers (Gray and Mirza, 1979; Gray, 1979; Gray, 1981; Gray and Pearson, 1982; Ugland and Gray, 1982), it has been suggested that plotting cumulative percentage of species against geometric class of individuals may be an effective means of demonstrating a community response to pollution at the earliest possible stage. Shaw et al. (1983) and Platt and Lambshead (1985) criticize this method, on the grounds that its interpretation is ambiguous in many examples and flawed in its basic assumption that benthic communities may be expected to conform to a log-normal distribution. Despite these criticisms, log-normal analyses continue to appear in the literature (e.g. Valderhaug and Gray, 1984; Hartnoll et al., 1985), along with alternative multivariate approaches (e.g. Green and Vascotto, 1978; Field et al., 1982; Collins and Williams, 1982; Lambshead, 1986).

Much of this work has focused on boreal or temperate communities (e.g. Gray and Mirza, 1979; Rafaelli and Mason, 1981; Hargrove and Thiel, 1983), and little quantitative work has been done on the response of tropical assemblages to pollution stress. Brown and Howard (1985) reviewed the numerous studies on tropical marine organisms and physiological responses to stress. Several

studies have also addressed the issue of pollution induced changes in coral communities (e.g. Loya, 1975; Tomascik and Sander, in press), but little work has been done with other tropical systems (Coles, 1980). As a result, it remains unclear whether the analyses developed for temperate communities may be applied to tropical ecosystems. For example, log-normal analysis is based on the assumption that species intermediate in numerical abundance react quickly to disturbance by increasing in number before rarer species have disappeared. Gray and Mirza (1979) base this on a definition of pollution stress as the disturbance of community equilibrium by organic or industrial waste input. The whole question of equilibrium has been a cause of much debate, and in several tropical ecosystems the existence of a community equilibrium has been questioned (Connell, 1978; Talbot et al., 1978). Furthermore, tropical ecosystems are considered to be much more complex, and the degree of interaction among species is much greater (e.g. Sanders, 1968; Petipa, 1978). If this is indeed the case, then the relative abundance patterns of tropical multispecies data sets may not show the same characteristic changes shown for temperate environments. A similar problem may occur with dominance based indices that have been effective in describing temperate ecosystems (e.g. Shaw et al., 1983; Swartz et al.,1986) but are ambiguous in the few tropical systems tested (e.g. Hodda and Nicholas, 1986).

The present study investigates changes in the crustacean cryptofauna associated with Madracis mirabilis (Duchassaing and Michelotti) in Barbados, West Indies. M. mirabilis is an erect, branching coral that develops long, thin, pencil-like branches in

dense monospecific beds (Lewis, 1960). Between the branches are numerous spaces and crevices which harbour a diverse fauna of sessile and motile organisms. Hutchings (1978) summarized the known cryptofauna of other corals and suggested that many species of bivalves, sponges, polychaetes, and crustaceans may be present. For example, an extensive list of the taxonomic groups associated with the coral Oculina arbuscula is found in McCloskey (1970).

Stands of M. mirabilis may range from several metres to tens of metres in width and may be 7 cm to over a metre in depth. Only the tips of the coral are living, therefore below about 3 cm in depth the coral is dead and extremely brittle. This fragility makes M. mirabilis patches an ideal habitat for quantitative, replicable sampling of coral for associated macrobenthic cryptofauna, since cores may be taken with minimal disturbance and effort.

Tomascik and Sander (1985) demonstrated that a pollution gradient exists along the west coast of Barbados, and that water quality at the southern reefs is poor as a result of elevated concentrations of phosphates, nitrates, nitrites, and suspended particulate matter. Using Rosen's (1982) definition of stress, in which stress is defined as some influence between optimal conditions and the limits of community survival, they suggested that the eutrophication gradient has created greater stress on corals at the southern reefs than on those at the northern reefs. The present study is designed to examine how this type of stress affects the species rich cryptofauna of Madracis mirabilis, and,

in doing so, to test the applicability of analytical models developed to monitor pollution in temperate or boreal climates for tropical macrobenthos.

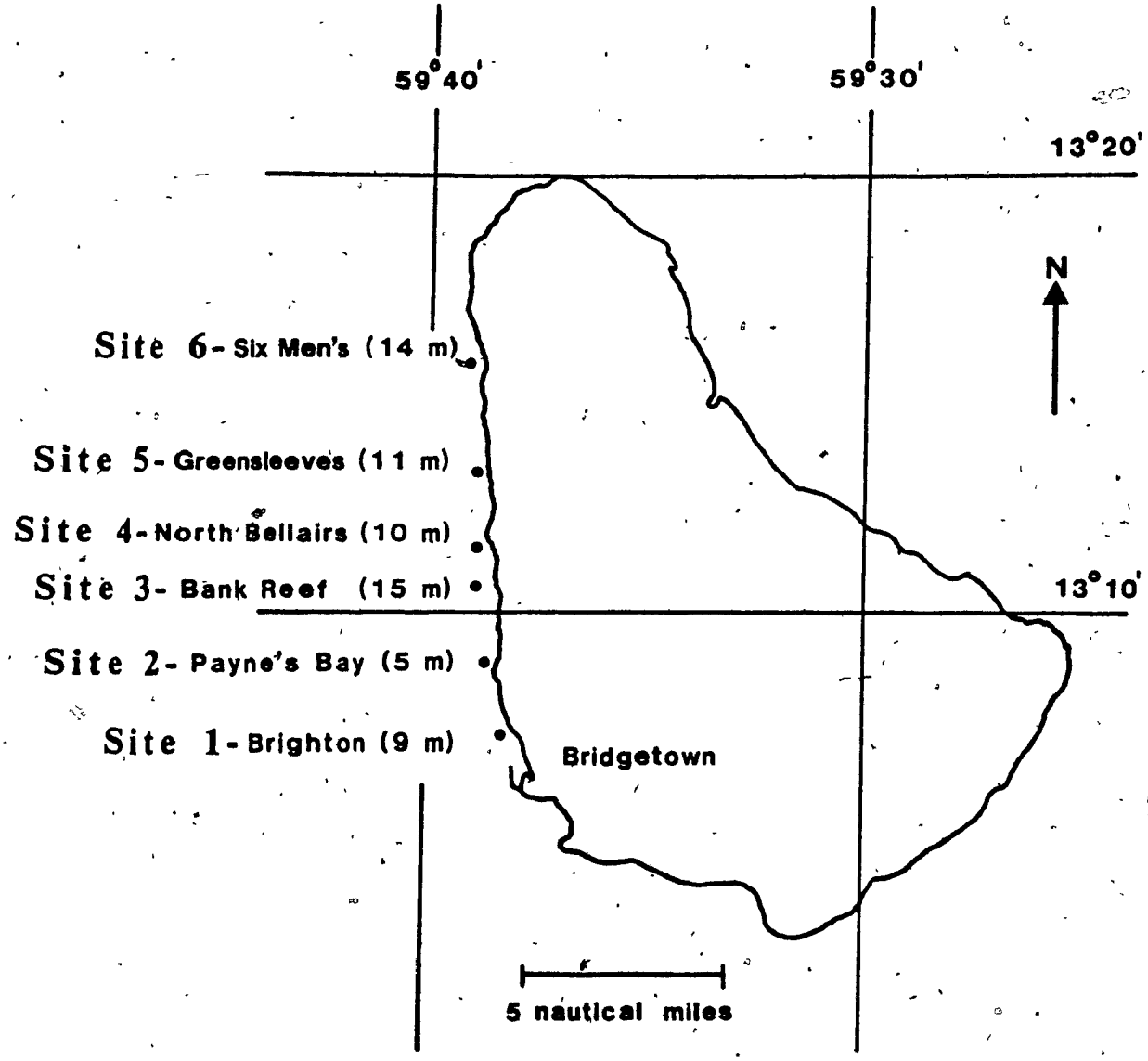
MATERIALS AND METHODS

Environmental Variables

Six sampling stations, were selected along the west coast of Barbados, West Indies (Fig. 1), in water ranging from 5 to 15 metres in depth. Stations were chosen along a gradient of environmental stress in the vicinity of the reefs examined in 1983 by Tomascik and Sander (1985).

To determine whether there was any change in the environmental gradient from its previous condition, water quality was examined at each site from May to November, 1985. The following variables were measured: nitrites, phosphates, suspended particulate matter, and percentage of light absorbed in the upper 5 metres of the water column. Water samples were collected at approximately monthly intervals for the first four months and at approximately 2 week intervals for the last three months. Sampling effort was increased during the season of heavy rain since this was expected to be a period of high variation in environmental parameters (Tomascik and Sander, 1985). Because Sander (1981) showed that the water column along the coast of Barbados is well mixed, only surface samples were collected. At each of the six stations, a van Dorn sampler was used to collect samples. Nalgene polyethylene bottles (300 ml volume) were filled from the sampling bottle and transported in a cooler to Bellairs Research Institute. Sampling was confined to the period 1000 to 1400 hours and, to further minimize diel effects, was performed at the stations in random order. At the same time as the water samples

Fig. 1. Map of Barbados, W.I. showing the six sites sampled for environmental quality. With the exception of Payne's Bay, the same sites were also sampled for Madracis mirabilis cryptofauna. Bottom depths at each site are given in brackets.


59°40'
59°30'
13°20'
13°10'
N
Site 6- Six Men's (14 m)
Site 5- Greensleeves (11 m)
Site 4- North Bellairs (10 m)
Site 3- Bank Reef (15 m)
Site 2- Payne's Bay (5 m)
Site 1- Brighton (9 m)
Bridgetown
5 nautical miles

were collected, a QSI-140 Integrating Quantum Scalar Irradiance meter was used to measure illumination at 1 m above the water surface and at 5 m depth.

The 300 ml samples were filtered through pre-washed, pre-combusted, and pre-weighed GF/C glass fiber filters. The filters were then dried for 1 hour at 100 C and placed in a desiccator overnight before a second weighing to determine the weight of the suspended particulate matter.

The filtrate obtained by this process was used for determination of reactive phosphate (PO_4^{-3}) and nitrite (NO_2^-) concentrations according to the methods outlined in Strickland and Parsons (1972). Reactive phosphate was usually measured on fresh samples while filtered seawater was frozen at -15 C for the later nitrite analysis. Analysis of frozen samples was always completed within four weeks. Samples were also collected for nitrate analysis but the extreme variation observed in the data raised some doubt as to their validity and the results were discarded.

Statistical analyses

Because day to day variation in nutrient level was extremely high, the data were ranked from 1 (lowest concentration) to 6 (highest concentration) within each sampling day over the six sites. These ranked data were then used in regression analysis. Regression analysis requires that several assumptions be met, including normality of the y variates and normality of residuals. The former was tested using the Shapiro-Wilk, W, statistic and visual inspection of residual plots provided a means of

detecting heteroscedasticity. Since the normality checks showed no significant deviations from normality and the residual plots did not reveal any trends, regressions were then performed to test whether distance from Bridgetown (measured for each of the six sites) was a significant predictor of ranked concentrations of nitrite, phosphate and suspended particulate matter.

Percentage of light absorbed in the upper 5 m of the water column was calculated by subtracting light levels at 5 m from those measured at the surface, dividing the difference by surface light levels, and multiplying the ratio by 100. Parametric analyses of this variable proved impossible as the variates were not normally distributed and could not be normalized using the various transformations available (see Sokal and Rohlf, 1981). The entire data set was then ranked and normalized using Blom's (1958) method. A Shapiro-Wilk, W, normality test and F-max test (Zar, 1984) revealed that the assumptions of parametric analyses had then been met. A General Linear Model procedure (a form of ANOVA) was performed to test whether there were any discernable differences in light absorbance at the six stations. When a difference was found, a Tukey multiple comparisons test (SAS Institute Inc., 1985) was performed to determine which of the stations differed from one another.

Biological Variables

The sites monitored for environmental conditions were also sampled for cryptofauna, but the absence of Madracis mirabilis beds at site 2 (Paynes Bay) necessitated its exclusion. Large beds of M. mirabilis were located by swimming transects

perpendicular to the shore, and when a large bed was found it was marked and used for the remainder of the study. Sampling began in early June, 1985 and ended in October, 1985. Each of the five stations was visited three times during this period, and 5 replicate samples were taken during each visit.

The samples consisted of cores which were obtained with a section of PVC tubing 6.0 cm in length and 10.5 cm in diameter. Piping larger than 10.5 cm in diameter was found to be difficult to manipulate and seal underwater. At the top of the pipe a 64 u mesh was fastened and metal handles were attached to the sides of the pipe to facilitate manipulation. Sections of the Madracis mirabilis patch were selected for sampling by swimming along the edge of the patch until an area was found where sponges were not predominant between the coral branches. Heavy sponge infestation made coring difficult and would have resulted in the sampling of a predominantly sponge associated cryptofauna rather than the coral associated organisms. Cores of M. mirabilis were then taken by quickly forcing the pipe into the coral and then inserting a sharp metal plate to cut off the core at the base of the branches. The tube containing the sample was then pulled away from the M. mirabilis patch, a polyurethane bag was wrapped tightly around the metal plate and the base of the tube, and the coral allowed to fall into the bag. After the contents had settled the tube and metal plate were gently removed and the bag was sealed.

To standardize core size, a constant depth of 18 cm was always attempted. However, variation in the depth of the M. mirabilis branches made it impossible to maintain a constant core depth and

some variation did occur. A core 10.5 cm in diameter and 18 cm in depth contains approximately 1 dm^3, the volume Clausade (1970) recommended for inclusion of most cryptofaunal species in the Pacific corals she sampled.

Once samples were collected, they were quickly transported to Bellairs Research Institute for overnight treatment with a mixture of 20 ml 4% formalin and 51 ml seawater as suggested by Brander et al. (1971). This solution acted as an irritant and therefore helped drive cryptic species out of cracks and crevices as well as fixing them.

Early the following morning, the coral samples were thoroughly washed over a .297 mm sieve and then fixed in 5% formalin. This particular sieve size was selected on the basis of earlier work by Hessler and Jumars (1974), although they chose to subdivide samples into macrofaunal and meiofaunal elements based on taxonomic affinities. The organisms collected in the washing were stored separately in small vials, and the coral samples were all stored in larger jars prior to the examination of each piece of coral under a dissecting microscope. All non-colonial organisms were removed, stored in vials and, after all coral was examined, the volume displacement and dry weights of the coral were measured. This procedure provided a means of standardizing abundances of organisms according to the amount of coral sampled. As a final step the washings were also carefully examined and all crustaceans sorted into appropriate taxonomic groups. Specimens were later identified, or at least separated, to species. Decapod crabs were numerically rare, and severe damage to many of the

specimens made identification impossible. Therefore this group was omitted from the study. The identity of selected specimens has been verified by the following authorities: E.J. Bousfield, Canadian National Museum (amphipods); G.A. Boxshall, British Museum (siphonotomitoids); M. Dardeau, Dauphin Island Sea Lab (Synalpheid decapods); B. Kensley, Smithsonian Institute (isopods); B.M. Marcotte, McGill University (harpacticoids); and F.Rafi, Canadian National Museum (isopods and tanaids). Representative material has been deposited with these people. A complete species list is found in Appendix A along with the number of individuals of each species collected at each site.

Statistical analysis

To examine the effectiveness of log-normal plots in detecting pollution effects, the individuals within each species from all 15 samples at each site were combined. These totals were then placed in geometric classes as described by Ugland and Gray (1982) and a plot of cumulative percentage of species versus geometric class of individuals was generated for each of the five sites.

Shaw et al. (1983) used a simple dominance index to demonstrate the effects of pollution. Species abundance (expressed as a percentage of the total population) was plotted against species rank. To use the entire data set would have been impractical, therefore only mean values of the 25 most abundant species were plotted.

To establish whether volume of coral sampled or densities of organisms differed at the 5 sites, an analysis of variance was performed on both variables. Shapiro-Wilk, W, tests of normality

and F-max tests (Zar, 1984) revealed no violations of the assumptions of parametric analysis with either of the two variables. When differences in means were detected, a Tukey multiple comparisons test was used to determine which of the sites differed.

Subsequent analyses required the conversion of species abundances (number of individuals collected) to densities (number of individuals per unit volume of coral sampled). For normal or q-type analysis, which is designed to group biologically similar stations, several forms of data reduction were necessary. First, the mean density of each species was calculated for each sampling date at each station (where station refers to the mean of 5 replicates taken at a given site on a given day). This reduced the raw data of 15 samples at each of 5 sites to 3 stations at each site, for a total of fifteen station means. Day et. al. (1971) were able to show that rare species do not affect normal sample analyses, although they do increase computing time. Therefore, species that did not contribute more than one percent to any one of the fifteen station mean abundance totals were dropped. This reduced the number of species groups from 137 to 33, and created a data set of more manageable dimensions.

The species densities were first root-root transformed to reduce the weighting of very abundant species (Green and Vascotto, 1978; Downing, 1979; Field et al., 1982). The transformed densities were then used to construct a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957), which is the most common index used to contrast samples in recent marine benthic

analyses (e.g. Shin, 1982; Collins and Williams, 1982; Lambshead, 1986). Bloom (1981) reviewed dissimilarity measures and their properties, including the Bray-Curtis index. The formulation of the Bray-Curtis measure is:

$$\delta_{jk} = \frac{\sum|Yij-Yik|}{\sum(Yij+Yik)}$$

where Yij = density of the ith species at the jth station; Yik = density of the ith species at the kth station; and δ_{jk} = dissimilarity between the jth and kth stations summed over all species (s). δ_{jk} can range from 0 (complete similarity, or identical scores for all species) to 1 (complete dissimilarity, or no species in common), and is unaffected by joint absences (Field and McFarlene, 1968). It has the further advantage of giving greater weight to more abundant species, which is desirable in any analysis of distribution patterns where presence-absence data may be insufficient. The values calculated for δ_{jk} were then arranged in a 15 by 15 dissimilarity matrix.

A number of ordination methods based on multidimensional scaling (MDS) have recently appeared in the literature (e.g. Field et al., 1982; Lambshead, 1986). For the present study, the SAS program MLSCALE (Ramsey, in press) was employed. This type of MDS is not as flexible as the non-metric analysis used by Field et al. (1982) but does offer several advantages. Non-metric analyses tend to be sensitive to the initial data configuration and the non-metric analysis offered in SAS (Young et al.,1982) squares dissimilarities before analysis. This also results in the squaring of the error associated with each of the values (Ramsey, 1982), therefore the accuracy of the ordination mapping is

reduced.

Although interpretation of the MDS output is explained by Ramsey (1982), the novelty of this method in biological applications necessitates some introduction. Chi-square values are used to test the fit of the configuration using the formula:

$$X^2 = 2(\text{log likelihood for data configuration}) - 2(\text{log likelihood of random fit})$$

Degrees of freedom are calculated by doubling the number of stations contrasted in the comparison less one, and subtracting from this value the number of parameters ~~needed~~ for a zero dimensional representation (1). A multiple correlation coefficient is also provided as an additional method of assessing the amount of variation that the MDS map and the actual data have in common.

MLSCALE also allows the investigator to test whether increased flexibility is needed for the data set. By subtracting the chi-square value obtained for the fit of a power transformation from that obtained for a spline transformation, a statistic is generated (a chi-square with 2 degrees of freedom - one for each of the new parameters introduced by the spline analysis). This statistic indicates whether increased flexibility is needed, by testing whether the fit is significantly improved.

Generally, ordination results are presented with a complementary dendrogram (e.g. Tomascik and Sander, in press; Lambshead, 1986), as a result of its visual simplicity and ease of interpretation. However, there are a number of disadvantages

in using dendrograms, several of which relate to the type of data being examined here (Field et. al., 1982). The present study was designed to examine pollution effects along a pollution gradient, but dendrograms "seek out" discontinuities and may artificially force data into discrete groupings. Only discontinuities supported by an ordination mapping are irrefutable, therefore classification is presented here only as an aid in the interpretation of the MDS plot. The same Bray-Curtis matrix generated for the MDS analysis was also used in group average sorting to produce a similarity dendrogram.

Once patterns in distribution have been discerned, it is useful to know which species are important in creating the observed configurations. One method that has been suggested is the information statistic (I-) which has been used by Field (1969) and Velimirov et al. (1979) to establish indicator species. This method relies on presence-absence information only, and as Gray (1979) points out, it is often change in abundances, rather than elimination of species, that is a more sensitive pollution indicator.

An F-ratio (Sokal and Rohlf, 1981) has also been used to define indicator species (e.g. Shin, 1982), and has the great advantage of utilizing abundance as well as presence-absence. Samples from sites 6, 5 and 3 were grouped to represent less polluted sites, and samples from sites 1 and 4 were grouped to represent highly polluted sites. The root-root transformed data were again used, although rare species were not tested because of the error associated with low density sampling. Samples from the two misclassified site 6 stations were also omitted, since

findings on their affiliations were ambiguous. It should be noted that an F-ratio is a parametric test and for rigorous application should meet the asssumptions of parametric analyses. With species abundance data such assumptions are rarely met (Field et al., 1982), and the ratio is used as a yardstick to extract indicator species rather than as a hypothesis testing tool.

RESULTS

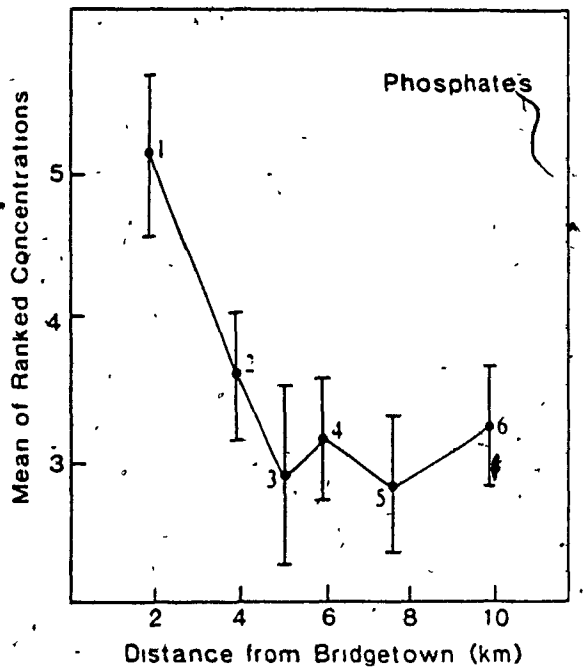
Environmental Variables

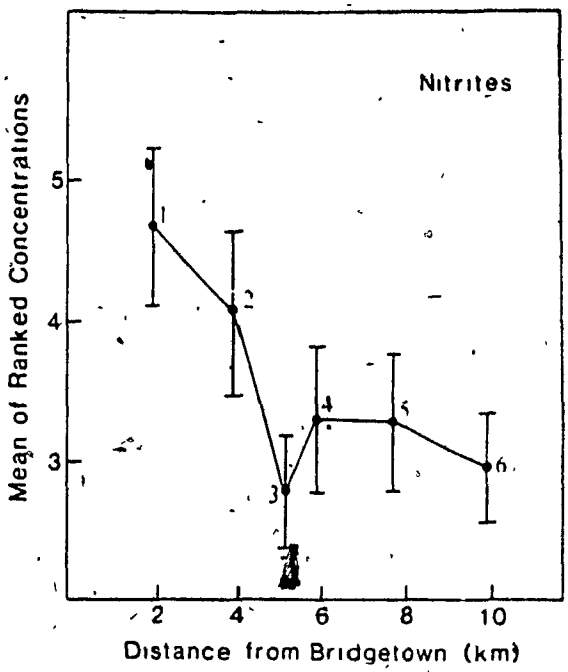
Figure 2 shows mean rank values for the environmental variables at the six sites plotted against distance from Bridgetown. A general trend of decreasing ranked concentrations of nitrite, phosphate, and suspended particulate matter with increased distance from Bridgetown is evident. It should be noted that one site strongly deviated from this linear trend. Site 3 was lower in phosphates and nitrites compared to the adjacent sites.

The slopes of the regressions of ranks of nitrite concentration ($r=.11$, $p<.014$, $n=54$), phosphate concentration ($r=.12$, $p<.009$, $n=54$) and suspended particulate matter ($r=.13$, $p<.001$, $n=48$) on distance from Bridgetown were all negative. They were all statistically discernible ($p<0.02$) supporting the suggestion by Tomascik and Sander (1985) that a gradient of nitrite, phosphate, and suspended particulate matter existed along the west coast. However, the amount of variation explained by these regressions (r^2) is extremely low, thus casting doubt on the validity of distance from Bridgetown as an accurate predictor of nutrient values.

The General Linear Model procedure also showed discernible differences among mean values of light absorbance at the six sites ($F_{5,48}=4.29$, $p<.003$). The Tukey multiple comparisons test shows that site 5 and site 3 did not differ from each other but surface water did absorb discernibly less light than at site 4. No other differences could be detected.

Fig. 2. Mean rank values of concentrations of nitrites, phosphates, and suspended particulate matter versus distance from the main sewage outfall (Bridgetown). Points represent means and bars represent standard errors. Numbers next to points denote sites, and corresponding names may be found in Table 1.


Phosphates
Mean of Ranked Concentrations
5
4
3
1
2
3
4
5
6
2
4
6
8
10
Distance from Bridgetown (km)


Nitrites
Mean of Ranked Concentrations
5
4
3
1
2
3
4
5
6
2
4
6
8
10
Distance from Bridgetown (km)

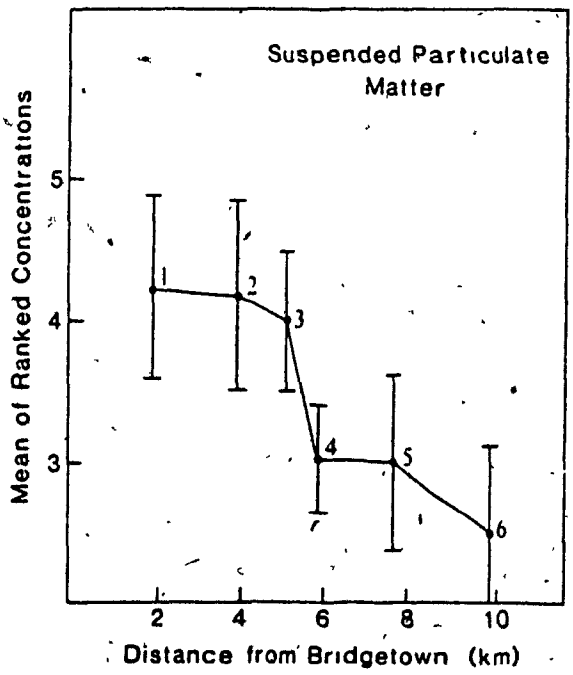

Suspended Particulate Matter
Mean of Ranked Concentrations
5
4
3
1
2
3
4
5
6
2
4
6
8
10
Distance from Bridgetown (km)

Table 1 summarizes results obtained for the environmental variables, and indicates station designations used for the biological multivariate analyses below. These results further indicate that water quality at site 1 is poorer than that at sites 3, 5, or 6. This is apparent in values of phosphates, nitrites, suspended particulate matter, and light absorbance which are all very high at site 1. Slight elevation of phosphates and nitrites as well as discernibly reduced water clarity at site 4 relative to adjacent stations indicate this site may also suffer from poor water quality. Although a rapid increase in suspended particulate matter is not evident, more extensive sampling by Tomascik and Sander (1985) found elevated concentrations of suspended particulate matter, phosphates, nitrates and light absorbance in this area. A study on groundwater discharge in the same area by Lewis (1985) found extremely high phosphate concentrations in water being discharged onto the reefs. In view of these more extensive data sets, there is little doubt that this area is more stressed than the adjacent sites.

Biological Variables

Appendix A summarizes the biological data collected at the 5 sites. In all, 8383 individuals were collected and sorted into 137 species categories. Approximately 80% of all individuals collected at each site consisted of isopods, tanaids, or copepods. The isopods and tanaids collectively contributed around 50% with the copepods generally contributing about 30%. The remaining 20% consisted primarily of amphipods and some decapods.

Figure 3 shows plots of cumulative percentage of species

Table 1. Mean values for concentrations of nitrites, phosphates and suspended particulate matter at 15 stations on the west coast of Barbados. Values for standard errors are given in brackets. The term station is used to designate the mean of 5 replicate biological samples taken on a given day at a given site.

Site (distance*)	Station	Nitrites (ug-at l^{-1})	Phosphates (ug-at l^{-1})	SPM** (mg l^{-1})	Light Absorbance***
Site 6	A	0.022	0,123	5.58	72.2
Six Men's	B	(0.008)	(0.032)	(0.64)	(3.52)
(9.8 km)	C	n=9	n=9	n=8	n=9
Site 5	D	0.027	0.112	6.33	62.1
Greensleeves	E	(0.008)	(0.036)	(0.85)	(5.01)
(7.5 km)	F	n=9	n=9	n=8	n=9
Site 3	G	0.015	0.104	6.23	64.8
Bank Reef	H	(0.006)	(0.034)	(0.70)	(2.52)
(5.1 km)	I	n=8	n=9	n=8	n=9
Site 4	J	0.025	0.129	5.88	80.2
North Bellairs	K	(0.007)	(0.032)	(0.69)	(2.14)
(5.7 km)	L	n=9	n=9	n=8	n=9
Site 2	No Madracis	0.095	0.151	6.52	70.0
Paynes Bay	beds found	(0.052)	(0.044)	(0.969)	(2.80)
(4.0 km)		n=9	n=9	n=8	n=9
Site 1	M	0.117	0.312	6.58	75.0
Brighton	N	(0.043)	(0.091)	(0.68)	(2.80)
(1.5 km)	O	n=9	n=9	n=8	n=9

*Distance from Bridgetown.
**Suspended particulate matter
***Percentage of surface light absorbed in upper 5 m.

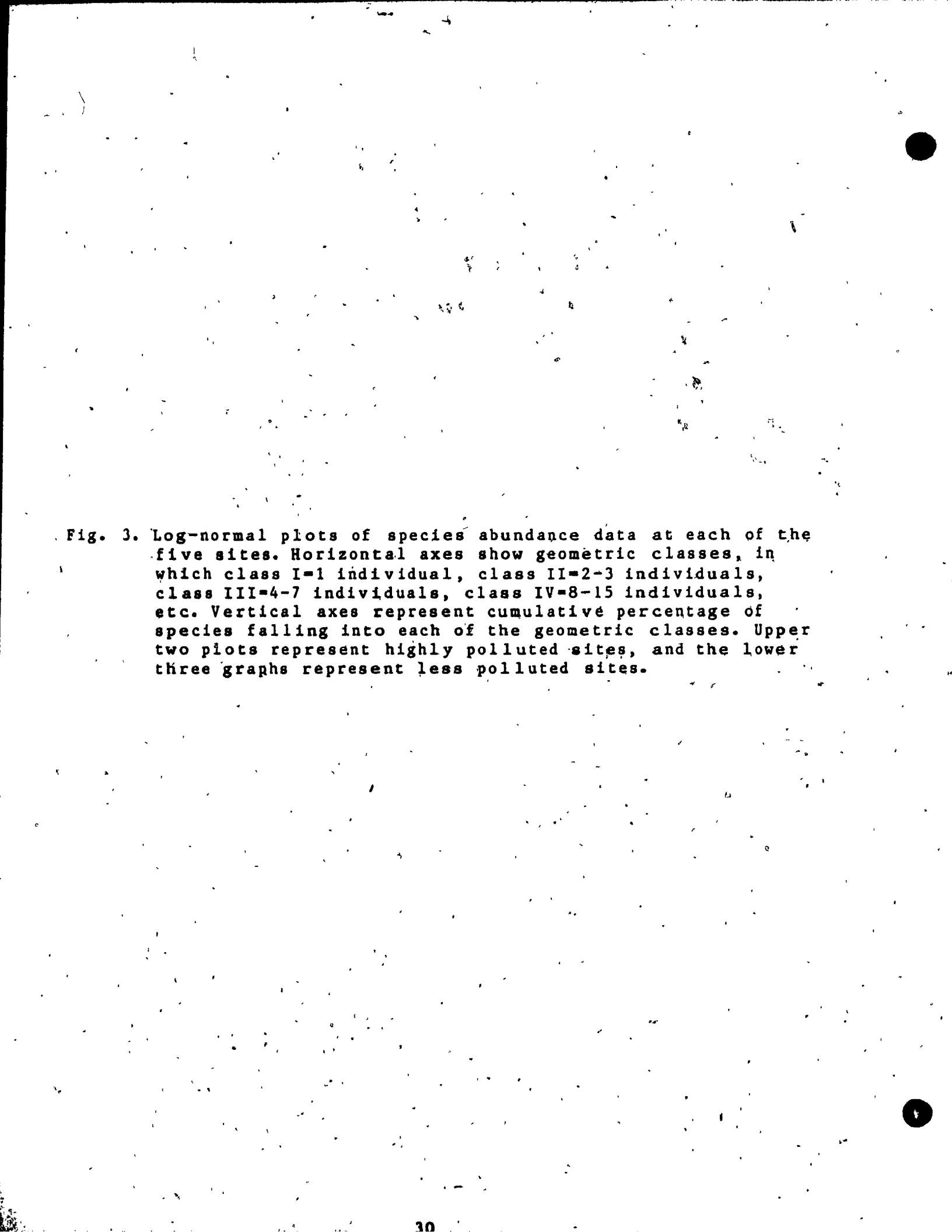
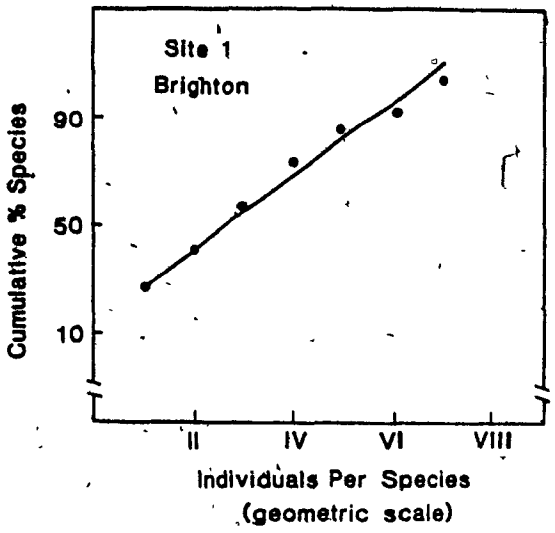
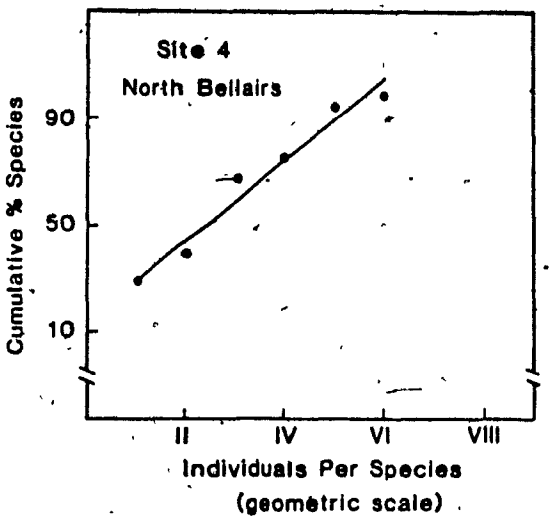
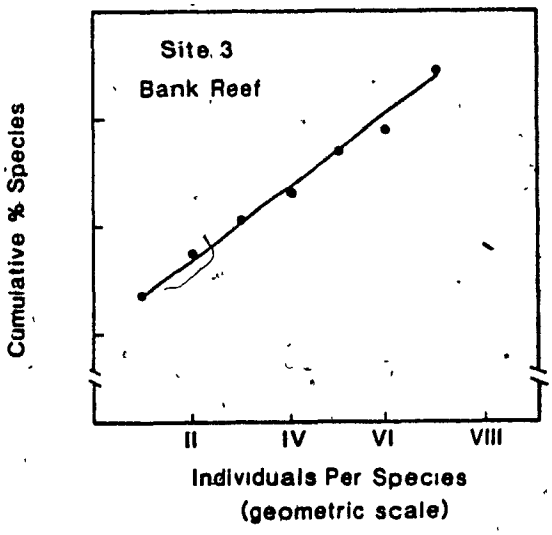
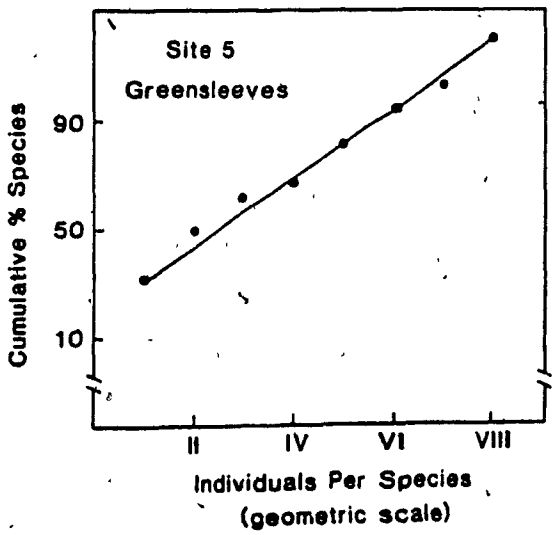


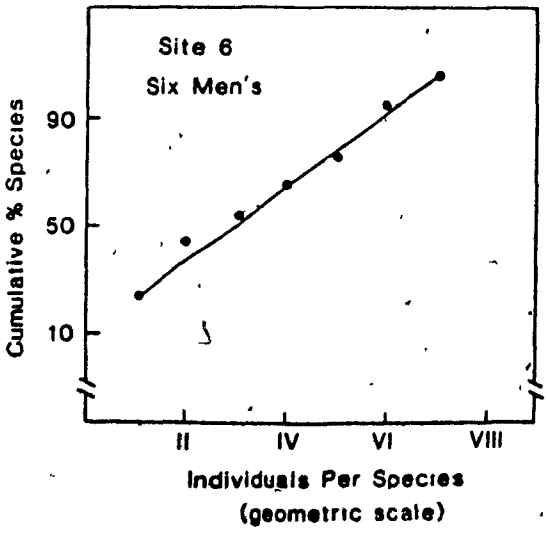
Fig. 3. Log-normal plots of species abundance data at each of the five sites. Horizontal axes show geometric classes, in which class I=1 individual, class II=2-3 individuals, class III=4-7 individuals, class IV=8-15 individuals, etc. Vertical axes represent cumulative percentage of species falling into each of the geometric classes. Upper two plots represent highly polluted sites, and the lower three graphs represent less polluted sites.


Site 1
Brighton
Cumulative % Species
90
50
10
II
IV
VI
VIII
Individuals Per Species
(geometric scale)


Site 4
North Bellairs
Cumulative % Species
90
50
10
II
IV
VI
VIII
Individuals Per Species
(geometric scale)


Site 3
Bank Reef
Cumulative % Species
II
IV
VI
VIII
Individuals Per Species
(geometric scale)


Site 5
Greensleeves
Cumulative % Species
90
50
10
II
IV
VI
VIII
Individuals Per Species
(geometric scale)


Site 6
Six Men's
Cumulative % Species
90
50
10
II
IV
VI
VIII
Individuals Per Species
(geometric scale)

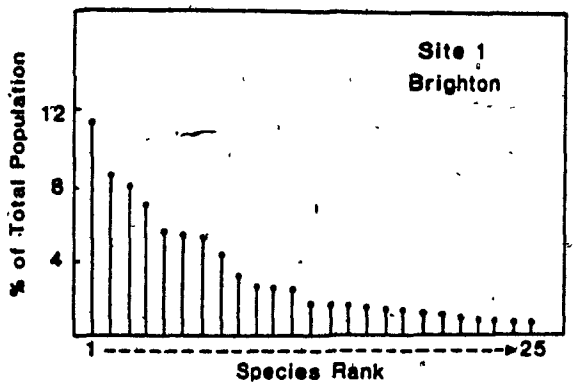
versus geometric classes of individuals. According to the criteria of Ugland and Gray (1982) all five of the plotted distributions indicate healthy biological communities, since no deviations from a straight line are evident.

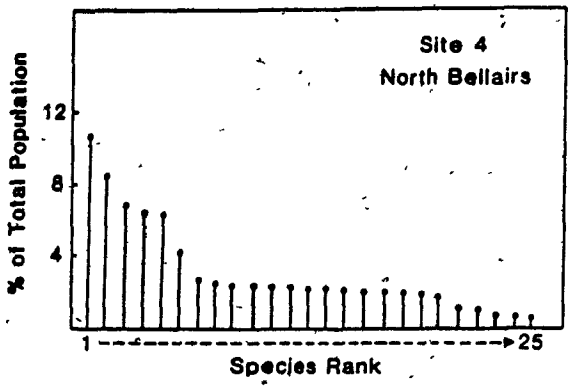
Figure 4 shows rank species abundance curves for each of the five sites. Shaw et al. (1983) suggested that polluted communities are characterized by a very dominant first rank species. This creates a very steep curve which differs from the relatively flat distribution expected for unpolluted sites. No decreasing trend in dominance is evident as distance from Bridgetown increases, and thus there is no indication of variation in the degree of pollution stress. Plotting the data on a semi-log scale was also ineffective in distinguishing the sites.

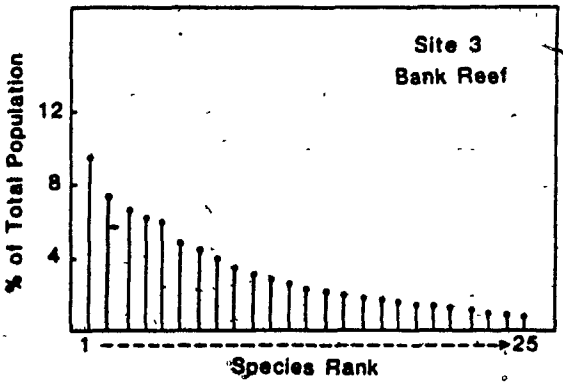
The ANOVA to compare volumes of coral sampled at the 5 sites shows no discernible differences. Densities, however, do show several differences (Table 2). Of the 5 sites where biological samples were collected, the 2 sites that appear to be poorest in water quality (sites 1 and 4) also have the lowest total densities (Table 2).

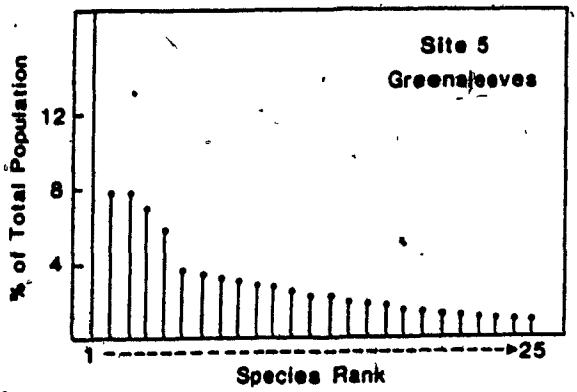
Figure 5 is the dendrogram produced by group average sorting of stations using the Bray-Curtis dissimilarity matrix. At an arbitrary similarity level of 40% stations A, C, J, K and L separate on their own, while two large groupings are seen. The first group consists of stations M, N, and O. All stations in the second grouping are from sites with superior water quality (Table 1). Except for stations A and C (site 6), stations that separate on their own or fall into the first group are from sites with

Fig. 4. Dominance plots for species abundance data at each of the five sites. Horizontal axes represent ranked species abundance for 25 most abundant species. Vertical axes represent percent abundance of each species. Species involved, and their relative importance may be found in Appendix A


Site 1
Brighton
% of Total Population
12
8
4
1
25
Species Rank


Site 4
North Bellairs
% of Total Population
12
8
4
1
25
Species Rank


Site 3
Bank Reef
% of Total Population
12
8
4
1
25
Species Rank


Site 5
Greensleeves
% of Total Population
12
8
4
1
25
Species Rank

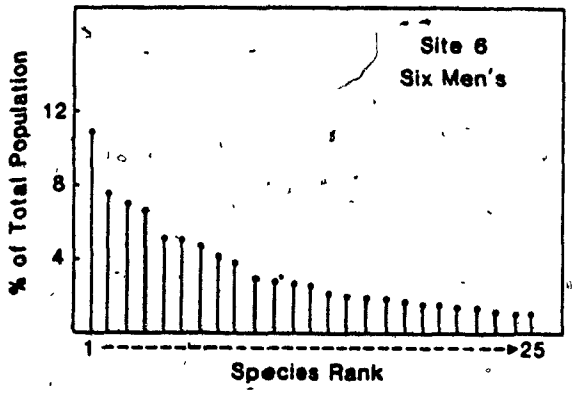
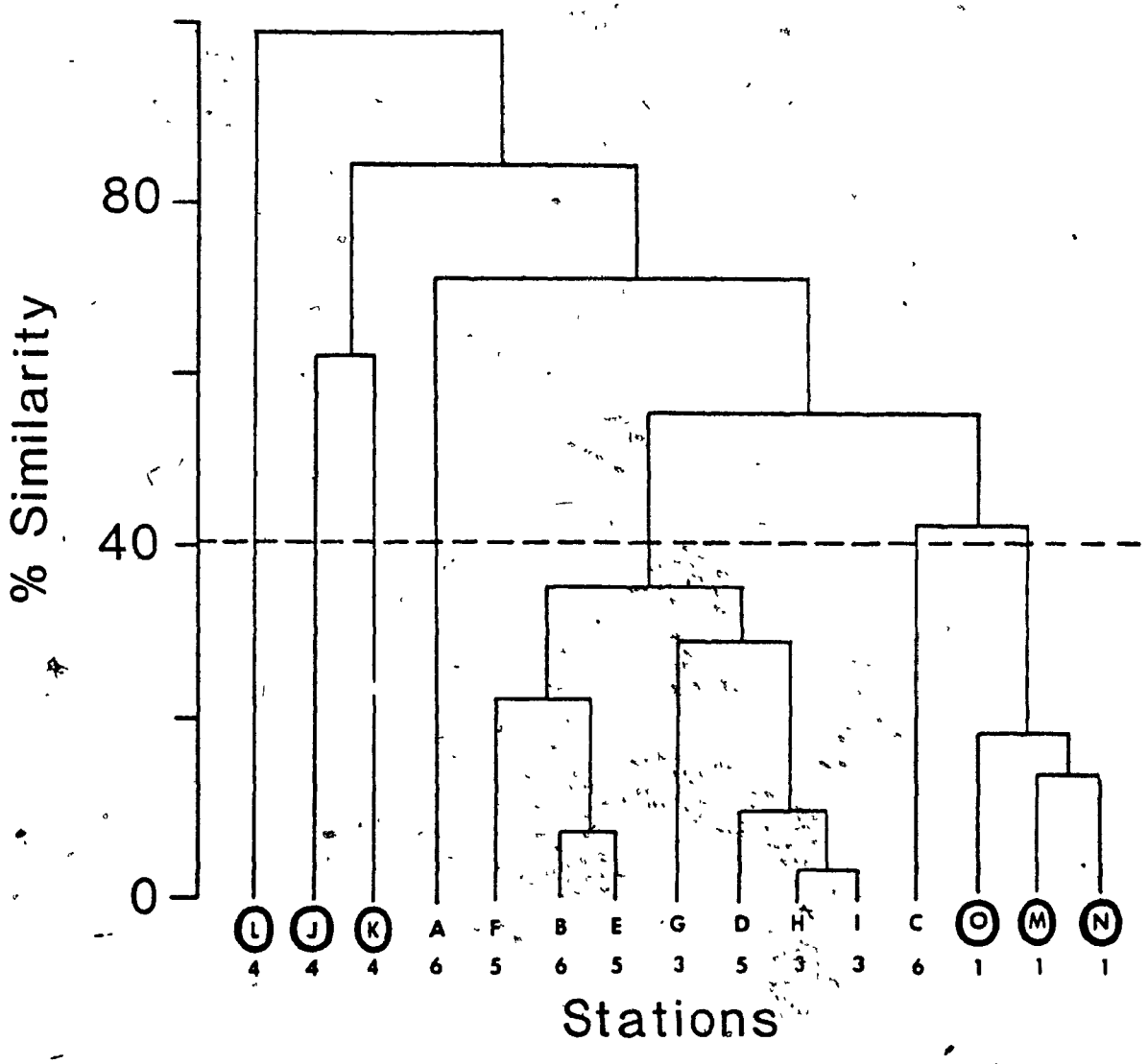

Site 6
Six Men's
% of Total Population
12
8
4
1
25
Species Rank

Table 2. Comparison of mean sample densities of all organisms collected at each of the 5 sites with Tukey's multiple comparison of means to show which densities are significantly different. * indicates statistically different means (α=0.05) and N.S. indicates no significant difference.

Site	Mean Density (#/dm^3)	Tukey's Comparison of Means: Six Men's	Green-sleeves	Bank Reef	Brighton	North Bellairs
Six Men's	558.4	-	N.S.	N.S.	*	*
Greensleeves	531.4		-	N.S.	N.S.	*
Bank Reef	455.9			-	N.S.	N.S.
Brighton	350.8				-	N.S.
N. Bellairs	296.0					-

Fig. 5. Dendrogram showing classification of 15 stations along the west coast of Barbados based on faunal densities of 34 most common species. Each station represents a mean of five samples taken on a given day. Densities were root-root transformed before comparison using group-average sorting of Bray-Curtis dissimilarities. Sites corresponding to station letters are listed in table 2. Numbers listed below letters correspond to sites as listed in Fig. 1.


% Similarity
80
40
0
L J K A F B E G D H I C O M N
4 4 4 6 5 6 5 3 5 3 3 6 1 1 1
Stations

poorer water quality.

Figure 6 is the configuration produced by the MDS analysis using a power transformation (a spline transformation did not statistically improve the chi-square value). The fit is very strong (X^2=347.02, d.f.=27, p .001), as is the correlation between the MDS mapping and the actual distribution of data points (r^2=1.00, n=45, p .001). There are no tight clumps or discontinuities visible, but there is a general segregation of stations from sites 1 and 4 (both lower water quality) from those at sites 3, 5 and 6 (all higher water quality). For clarity, the stations from sites 1 and 4 have been circled, and groupings from the clustering have been superimposed on the MDS by outlining the clusters obtained at a 40% similarity level.

Table 3 summarizes the results of the F-tests. At an arbitrary cut-off level of F=5.00, there are 8 potential indicator species: Minyanthura coralicola, Peltidinum sp., Porcellidium trisetosum, Eisothistos teri, Gnathia rathi, Paralaophonte sp., Amphilochus sp. a, and Amphioscopsis sp. It is interesting to note that the density of all of these species is lower at the polluted sites, and no indicator species increased in density at polluted sites.

Fig. 6. MDS ordination of 15 stations along the west coast of Barbados based on the faunal densities of the 34 most common species. Each station represents a mean of 5 samples taken on a given day. Densities were root-root transformed before comparison using Bray-Curtis dissimilarities. Sites corresponding to station letters are shown as subscripts of letters and are also listed in table 2. Scales of axes are arbitrary and are therefore omitted.

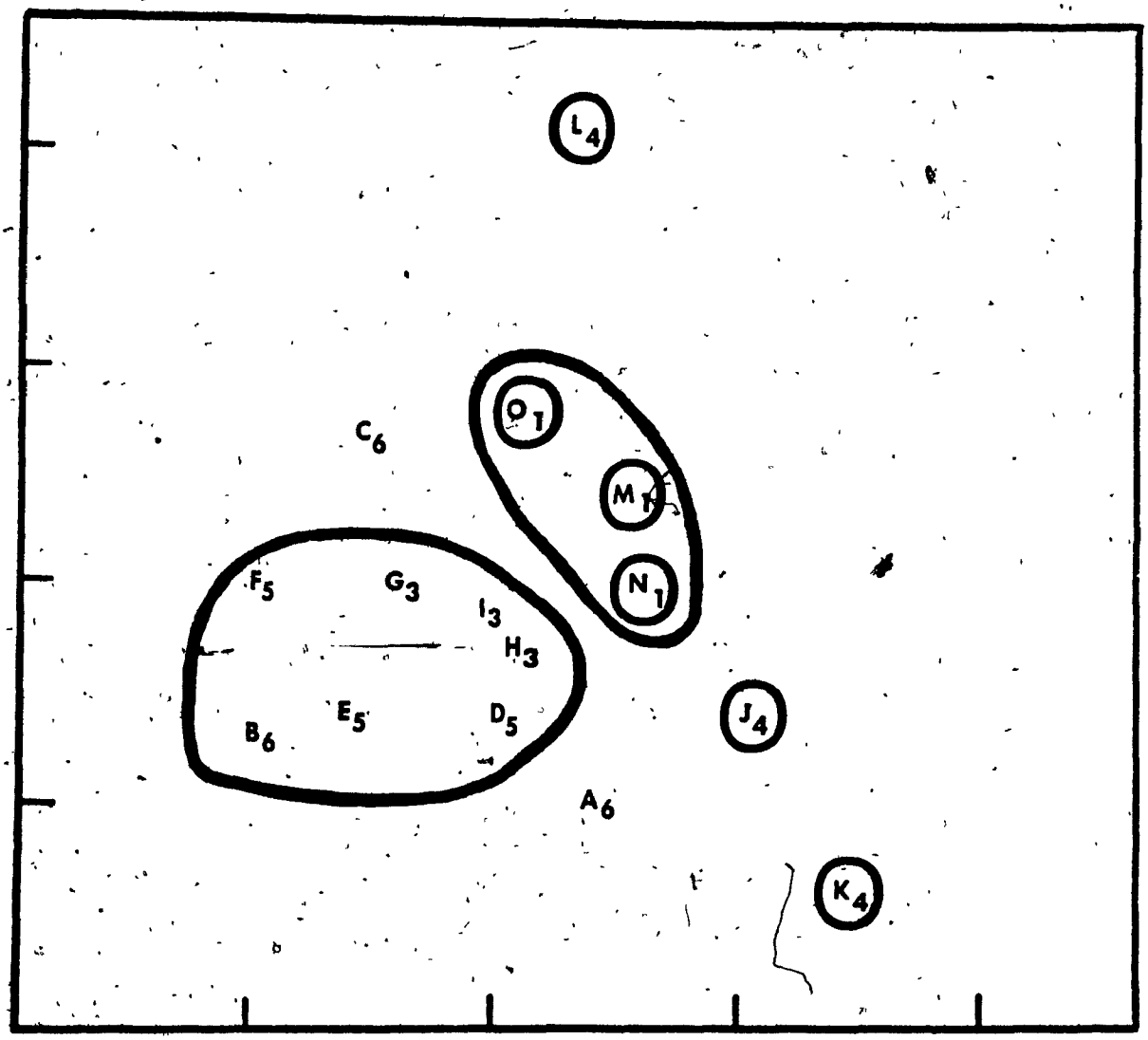

L4
O1
C6
M1
N1
F5
G3
I3
H3
E5
D5
B6
J4
A6
K4

Table 3. Results of F-tests to compare densities of the 34 most common species at the highly polluted and less polluted sites. Probabilities are not given since the test is not statistically rigorous for abundance data: A=amphipod, D=decapod, C=copepod, I=isopod, O=ostracod, T=tanaid.

Family	Species	F-value (d.f. 1,64)	Mean Unpoll*	Mean Poll**
Apanthuridae(I)	Minyanthura corallicola	83.06	85.7	1.5
Peltidae(C)	Peltidinum sp.	21.30	20.4	2.0
Porcellidium(C)	Porcellidium trisetosum	20.45	8.8	0.9
Anthuridae(I)	Eisothistos teri	12.74	13.3	5.4
Gnathiidae(I)	Gnathia rathi	9.42	12.5	5.3
Laophontidae(C)	Paralaophonte sp.	6.73	5.2	1.5
Amphilochidae(A)	Amphilochus sp.	5.95	8.2	5.0
Diosaccidae(C)	Amphioscopsis sp.	5.94	7.4	3.8
Alpheidae(D)	Synalpheus paraneptunus	4.52	11.6	3.3
Ostracoda(O)	Undetermined	3.66	5.9	2.9
Diosaccidae(C)	Amphiascus sp.	3.34	26.1	18.7
Peltidae(C)	Undetermined	2.92	2.4	0.1
Sphyrapidae(T)	Undetermined	1.98	20.6	32.5
Isaeidae(A)	?Megamphopus b.	1.50	39.7	24.5
Apseudidae(T)	Apseudomorpha sp.	1.44	9.7	16.3
Stenetriidae(I)	Stenetrium spathulicarpus	1.26	8.1	8.9
Anthuridae(I)	Chalixanthura lewisi	1.21	6.3	8.0
Paratanaidae(T)	?Heterotanais sp. b	1.12	8.4	6.4
Stenetriidae(I)	Stenetrium patulipalmis	0.50	18.4	11.4
Leucothoidae(A)	Leucothoella sp.	0.45	12.5	9.2
Hippolytidae(D)	Lysmata rathbunae	0.27	2.0	2.3
Leucothoidae(A)	Leucothoe sp.	0.23	3.2	1.7
Artotrigidae(C)	Acontophorus sp. nov.	0.23	1.1	2.1
Janiridae(I)	Carpias minutus	0.20	31.4	33.5
Diosaccidae(C)	Undetermined sp.	0.19	11.5	10.0
Paratanaidae(T)	?Heterotanais sp.a	0.18	16.7	13.1
Tisbidae(C)	?Tisbe sp.	0.17	2.3	4.1
Lichomoglidae(C)	Undetermined sp.	0.10	6.3	6.3
Laophontidae(C)	Laophonte bulbifera?	0.08	3.5	5.8
Ectinosomatidae(C)	Pseudobradya sp.	0.08	2.1	2.4
Paratanaidae(T)	?Heterotanais sp. c	0.04	5.0	4.2
Asterocheridae(C)	Asterocheres sp.	0.01	14.7	25.7
Tetragonoceptidae	Phyllopodopsyllus sp.	0.01	5.2	3.6

*Mean density (individuals/dm^3) for each species at less polluted sites (sites 3, 5, and 6).
**Mean density (individuals/dm^3) for each species at highly polluted sites (sites 1 and 4).

DISCUSSION

Work on the fringing reefs of Barbados by Tomascik and Sander (1985) has produced a powerful data base for the examination of biological reaction to pollution stress. They showed that a large power plant and rum refinery north of Bridgetown are contributing to the eutrophication on the west coast reefs. The effluents from these plants are likely carried up the coast of the island by a north-northwest current (Murray et al., 1977; Peck, 1978), and diluted somewhat by mixing with offshore water. This eutrophication is further enhanced by nutrient rich groundwater runoff all along the coast (Lewis, 1985), and a large tourist complex near Bellairs Research Institute (Tomascik and Sander, 1985). Together these inputs create a gradient of eutrophication along the west coast. A general improvement in a number of water quality parameters is observed with increased distance from Bridgetown. The exception to this trend is site 4, the area immediately around Bellairs Research Institute where several environmental parameters markedly increase in value and indicate a reduction in water quality. Tomascik and Sander (1985) found that a number of physicochemical and biological parameters indicated high pollution levels in this area, and coral growth (Tomascik and Sander, 1985) and composition (Tomascik and Sander, in press) were both markedly affected by eutrophication.

The results of the present study support this finding. Concentrations of both nitrites (Fig. 2a) and phosphates (Fig. 2b) decreased with distance from Bridgetown as far as site 4, where marked increases in concentrations were seen. Light

absorbance was highest at site 4, and differed from values obtained at adjacent sites (5 and 3). The clearer water at these two sites may be an important contributer to the healthier coral communities observed by Tomascik and Sander (in press), since sedimentation and turbidity are known to have negative effects on corals (e.g. Dodge and Vaisnys, 1977; Hudson, 1981). Finally suspended particulate matter (Fig. 2c) also showed a decreasing trend, and although a marked increase at site 4 is not observed, the light absorbance results also suggest some enhanced eutrophication at this site.

This eutrophication pattern allowed the examination of biological response with an "interspersion of treatments", where the two high eutrophication sites and three lower eutrophication sites were geographically intermixed (Fig. 1). This circumvented the problem of pseudoreplication (Hurlbert, 1984) and ensured that differences between the highly polluted and less polluted sites could not merely be a function of geographic cline.

The effects of nutrient enrichment and increased production have been well documented for tropical waters (e.g. Kinsey and Domm, 1974; Laws and Redalje, 1979). Response of coral communities to eutrophication has also been shown (e.g. Smith et. al., 1981; Walker and Ormond, 1982: Tomascik and Sander, 1986). However, aside from the study of Coles (1980) on the decapods associated with dead and living Pocillopora, little is known about the effect of stress on cryptofaunal communities. Since Johannes (1970, 1971) warned that coral ecosystems were being irreparably damaged in many areas, some attention has shifted toward coral reef conservation. However, monitoring and testing

programmes continue to be developed in temperate industrialised areas (Rafaelli and Mason, 1981; Field et al.,1982; Shaw et al., 1983), and have not been well applied in economically poorer tropical countries.

The use of log-normal plots in detecting disturbance was frequently used (e.g. Andrews and Rickard, 1980; Hicks, 1980; Crenna and Bonvicini, 1980; Bonsdorff and Koivisto, 1982) before criticism by Shaw et al. (1983) and Platt and Lambshead (1985) diminished its popularity. The results of this study (Fig. 3) further indicate that this method is not universally applicable. Despite the fact that stress on the coral community has been demonstrated (Tomascik and Sander, in press), the log-normal plotting of macrofauna suggested that healthy cryptofaunal communities existed all along the coast of the island. This is indicated by the straight-line plots and the steepness of the slopes, both of which are characteristic of healthy communities (Gray and Mirza, 1979). It is unclear whether the ineffectiveness of this method reflects a different response in tropical communities, or merely further indicates that log-normal plotting is a poor means of stress detection. In either case, these results should discourage future investigators from using a single log-normal plot to determine whether a given reef community is under stress.

In criticising log-normal analyses, Shaw et al. (1983) suggested that plotting a simple dominance index may be an effective monitoring approach. A similar method was proposed by Frontier (1985). However, with the present data this method failed

to show any differences in the high-stress and low-stress sites (Fig. 4). This is not surprising given that log-normal plotting also depends on a change in dominance, and was shown to be ineffective. In fact, visual inspection of the coral data of Tomascik and Sander (in press) indicates that dominance is also ineffective in diagnosing stressed coral communities. This may reflect a different stress response in tropical communities, where relative abundance patterns may not show the same changes characteristic of temperate ecosystems. If this is the case, an entirely different approach to pollution monitoring may be needed for tropical biologists before a general theory of ecosystem structure and response may be possible.

Perhaps the least controversial methods seen in recent pollution monitoring studies are multivariate ordinations (e.g. Field et al., 1982; Lambshead, 1986). Though the precise techniques involved have varied somewhat, ordination seems to have gained universal acceptance. In contrast to the log-normal and dominance plotting methods, MDS did segregate the highly polluted stations from those that were less polluted (Fig. 6). Though a distinct discontinuity was not observed, a sudden shift in relative abundance is not necessarily expected along an environmental gradient, as opposed to an environmental discontinuity. However, despite the fact that the stations from site 3 (low pollution) lie geographically between sites 1 and 4 (both high pollution), they are still mapped closer to the low stress stations. This is the strongest evidence that the faunal shift observed was a function of environmental degradation and not a geographic cline.

Although the dendrogram showed a general clustering of high pollution and low pollution stations, it did separate 2 of the stations from site 6 and all 3 of the stations from site 4. The separation of the stations from site 4 is almost certainly a result of the low density of individuals sampled there. Because so few individuals were taken, samples were likely too small numerically to show strong consistency. This would explain why these 3 stations not only show little affinity with any other sites, but also show little similarity to each other. This becomes evident simply by examining the relative numbers listed in Appendix A, which show that faunal composition at this site is quite inconsistent. A somewhat different explanation seems likely for the stations from site 6. Station C had the lowest overall density recorded at any of the low pollution sites, and the Bray-Curtis measure is influenced by density differences. Application of Whittaker's (1952) sample size-independent measure of percent similarity (see Kohn and Riggs, 1982) showed that this station is indeed much more similar to the low pollution stations if relative percentages are used instead of densities. However, station A shows very strong affinities with several of the high pollution stations when compared using relative percentages. Whether this reflects some very localized disturbance is unclear, however it is evident that this station had the highest densities encountered at any site. It is unlikely that this site is highly stressed in view of the fact that one of the of the stations (station B of Fig. 5) showed very strong affinities with the less polluted stations. Secondly, the indicator species would

group stations A and C with the low pollution sites. Elaboration on this point is presented later.

An unfortunate disadvantage of clustering is that once a station is placed in a cluster it cannot be removed. Inspection of the original Bray-Curtis matrix shows that station C (Site 6) showed greater similarity to one of the stations from site 4 than to any of the other stations. As a result, the classification grouped them (at an similarity level of 50%), despite the dissimilarity station C showed with the other high-stress stations.

Multidimensional scaling has the capacity to compare all similarities simultaneously, and consequently did not intermix station C with the highly polluted sites. This flaw in clustering can result in the grouping of two stations that have several unique, but not indicative, species in common. This may explain why the classification dendrogram grouped station C (site 6) with the high stress stations. This problem was not observed with ordination.

It should be noted that minor changes in the raw data (e.g. lumping of congenerics) caused noticeable realignment in dendrogram clustering. The MDS mapping, however, did not appear to be nearly as sensitive, and produced a very similar configuration unless drastic changes were made to the data. This finding suggests it would be wise to avoid using dendrograms without accompanying ordinations.

The best "indicator species" (Table 3) were all species whose population size dropped considerably in number from low to high pollution sites. There was a noticeable absence of any species

that rapidly increased in response to stress. Some species must have increased in relative abundance in the stressed communities, but these were species that were already fairly abundant at low stress sites. In fact of the 8 possible indicator species, all showed a decrease in abundance at the high pollution stations. This is a direct contradiction of the suggestion by Gray (1979) that pollution response is most apparent in species that increase in abundance in reponse to pollution. In discussing the possibilities of log-normal analyses, he observed that species that are intermediate in numbers in a healthy community will be the best indicators of pollution because they respond quickly to pollution by either increasing or decreasing in abundance. He suggested that some of these species employ reproductive strategies and tolerance that permits increase under eutrophication conditions. It is interesting to note that one of the misclassified low pollution stations would classify correctly if the densities of the 5 best indicator species were used as the criteria for grouping. The second misclassified station would classify correctly using either the best indicator species (Minyanthura corallicola), or 4 of the top 6 indicator species.

Results of the comparison of densities show that mean density was lower at the highly polluted sites. It appears that the indicator species were being reduced without replacement, particularly in view of of the absence of high-stress indicator species. Therefore, the species that were less inhibited by eutrophication (or some negative influence associated with it), may have been unable to utilize the resources no longer consumed

by the sensitive species. Alternatively, competition may not have been an important factor, therefore a reduction in the indicator species would have had no effect on the more robust species. If little resource overlap existed before pollution became prevalent, then release of these resources by pollution intolerant species would be of no advantage to pollution tolerant organisms. This finding is somewhat surprising since it is common in eutrophied environments to find several very abundant (and dominant) species (e.g. Gray, 1979; Shaw et al.,1983; Grassle et al., 1985). A possible explanation for this finding is that some unmeasured toxic substance(s) in addition to eutrophication were involved, or that tropical communities are indeed very different in their response to pollution. Alternatively, this discrepancy may be attributed to the fact that these studies included algae, nematodes, and/or deposit feeding polychaetes that would likely benefit most from eutrophication (Grassle et al., 1985). Coles (1980) showed that two very different decapod faunas were found in healthy and recently killed Pocillopora meandrina, where environmental perturbation had led to the death of some isolated heads. He found that while some cryptofaunal species decreased in number as the percentage of live coral tissue decreased, a number of species increased in number as the percentage of dead coral increased. Therefore, there are crustacean species better adapted than others to deal with stress. In Barbados, however, these species appeared to respond to stress by maintaining rather than increasing their numbers, and there was a notable absence of pollution tolerant species that were able to effectively increase population size under high pollution conditions.

Both log-normal plotting and dominance indices were ineffective and are ill advised as a solitary means of tropical pollution detection. Classification gave reasonable results but tended to be somewhat erratic, therefore ordination is highly recommended as part of such an analysis. Eight possible indicator species were found, but because a reduction in their abundance was the only good indication of stress, a number of replicate samples would be advised before making decisions concerning the health of a Madracis mirabilis cryptofaunal community.

Obviously, generalizations concerning tropical ecosystems cannot be drawn from a single study, and studies of other communities are needed. It is evident, however, that temperate latitude monitoring schemes should not be readily applied to tropical systems without thorough testing.

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Chapter 2

Habitat Preference of Tropical Cryptofaunal Communities

ABSTRACT

The crustacean cryptofauna associated with two different growth forms of the coral Madracis mirabilis was sampled to establish how the physical structure of coral affects cryptofaunal species composition. Fifteen isolated heads of M. mirabilis were collected from a fringing reef on the west coast of Barbados, W.I., and 15 cores of the same coral were taken from each of 2 large adjacent stands. Coral in the isolated heads was observed to be covered largely with live tissue, while in the large beds only the tips were living. All motile crustacea, excluding brachyuran crabs, were removed, identified, and analysed. Analysis of variance performed to compare total densities as well as densities of decapods, amphipods, isopods, and copepods, revealed that isolated heads supported a higher total density and higher densities of decapods and amphipods. The abundance of large organisms in isolated heads may indicate a difference in food availability, and therefore in localized productivity. Further analysis of variance showed that abundance of all crustacea combined was significantly higher in the isolated heads, therefore comparisons of richness were made using analysis of covariance which corrected for differences in abundance. Species richness in decapods and amphipods was higher in isolated heads, but more species of isopods and copepods occurred in larger beds. It is suggested that the spatial heterogeneity of the dead coral base of large beds may allow greater resource partitioning of spatial habitat in smaller organisms such as copepods and isopods. Habitat heterogeneity may not be as beneficial to large amphipods and decapods, which may

be too large to utilize the variety of microhabitats available in dead coral. Furthermore, many of the decapods may be symbiotic, therefore requiring coral mucus for nutrition. The evenness of all species combined was lowest in the isolated heads, possibly a result of an "island size effect" in which the fauna of isolated heads would not migrate between heads, little variety of habitat would be available, and evenness would be reduced as a result of dominance of a few species. In large beds, however, organisms may migrate large distances without leaving the protection of the coral. This would mean more diverse habitats could be encountered and many species may be able to coexist.

INTRODUCTION

Biologists have long been interested in ecological diversity and the factors that contribute to it (e.g. Elton, 1927; Hutchinson, 1959; Connell, 1978). Habitat complexity has been proposed as one of the most important diversifying factors in a number of ecosystems, including coral reef communities (e.g. Kohn, 1968; Williams et al., 1983). Coral reefs are considered to be among the most diverse and complex marine ecosystems (e.g. Grassle, 1973; Connell, 1978). A current area of interest in coral reef ecology is the structure of the cryptic fauna and demersal zooplanton intimately associated with corals (e.g. Tsuchiya et al., 1986; Nakasone et al., 1986; Abele, 1984: Edwards and Emberton, 1980). Studies on reef associated zooplankton have shown habitat preference for physically different types of substrate (e.g. Alldredge and King, 1977; Porter and Porter, 1977; McWilliams et al., 1981), but most of these studies have dealt with either total biomass (e.g. Peyrot-Clausade, 1985) or density of major taxonomic groups (e.g. Alldredge and King, 1977; Ohlhorst, 1985). Aside from the work on decapods by Coles (1980) and Gotelli and Abele (1983), little effort has been directed toward relating density changes to species richness (number of species) and evenness (J) of different taxonomic groups. As a result, the only solid conclusion that has been drawn is that more physically complex reef substrates (i.e. many crevices and levels) support more individuals of many taxonomic groups (e.g. McWilliams et al., 1981). Coles (1980) was able to attach greater biological meaning

to this by showing that large symbiotic decapods dominate living coral but are replaced in dead coral by a more diverse community of small, non-symbiont decapods. He suggested that the reduction of living tissue has an inhibitory effect on symbiont decapods that require coral mucus as a source of nutrition, while the spatial heterogeneity created in dead coral (through the action of borers, invasion of sponges, etc.) may be advantageous to smaller decapods that may utilize the microhabitats. How growth form and coral composition relate to associated demersal zooplankton, however, remains unclear.

The subject of the present study is the cryptofauna associated with Madracis mirabilis (Duchassaing and Michelotti), an erect, branching coral that grows in two structurally different forms. In shallow water, isolated hemispherical heads approximately 10 to 20 cm in diameter are found growing on coral reef substrate. The branches are robust and consist of predominantly live tissue. M. mirabilis may also be found in deeper water of approximately 10 m, and this growth form is described in chapter 1.

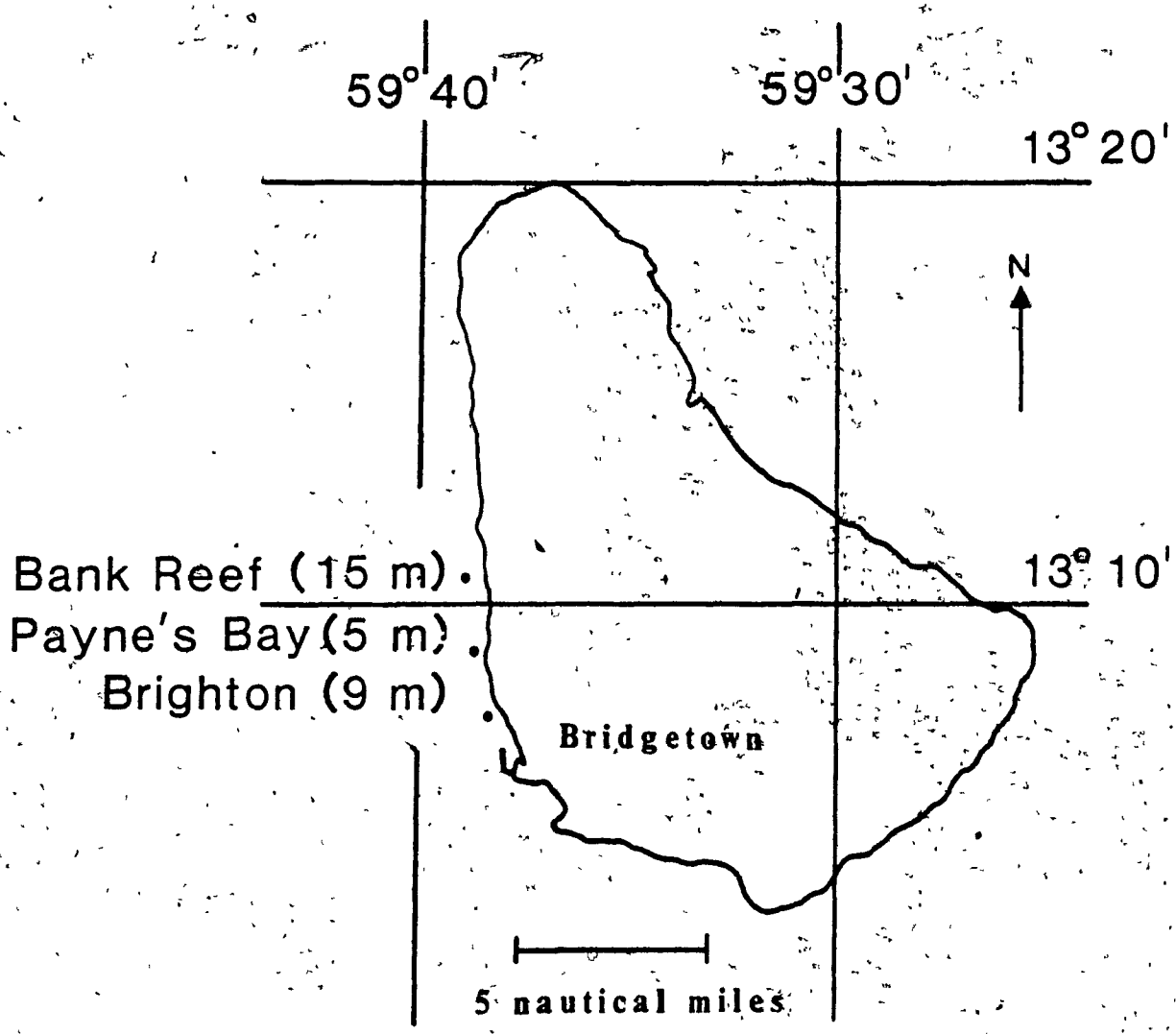
The availability of both of these growth forms in Barbados at the same approximate locality and depth makes possible the comparison of crustacean cryptofaunal communities in two habitats that differ in physical structure and in degree of live tissue. This may provide insight into habitat preference, and thereby community structure as a function of habitat type.

MATERIALS AND METHODS

Three sampling sites were selected along the west coast of Barbados on the basis of proximity and availability of Madracis mirabilis (Fig. 1). Tomascik and Sander (1985) demonstrated a pollution gradient along the coast, and in chapter 1 of the present study, a difference was shown in the cryptofaunal composition of highly polluted and less polluted reefs. Payne's Bay was found to have numerous isolated heads, and is situated at an intermediate pollution level. For this reason, large monospecific beds in a high pollution area (Brighton) and in a low pollution area (Bank Reef) were sampled for comparison with the isolated heads at Paynes Bay. These two sites were chosen not only because of their proximity to the Paynes Bay site but also because they represent extreme values of environmental quality. Of all of the sites monitored for environmental variables (see chapter 1), Brighton had the poorest water quality, while the Bank Reef site had the least nutrient loading and highest water clarity. Using samples from both sites to represent large bed cryptofauna ensured that any faunal differences between the two growth forms could not have been a function of the pollution gradient. Each of the three sites was visited three times between June and October, 1985. During each visit five replicate samples were taken, producing a total of 15 samples for each site.

The isolated heads at Paynes Bay were sampled by wrapping a polyurethane bag tightly around the head and prying it from the substrate with a metal plate. As the head fell into the bag, the plate was gently withdrawn and the bag sealed. Sampling of the

Fig. 1. Map of Barbados, W.I. showing the three sites sampled for Madracis mirabilis cryptofauna. Approximate bottom depths are given in brackets.


59° 40'
59° 30'
13° 20'
N
Bank Reef (15 m)
13° 10'
Payne's Bay (5 m)
Brighton (9 m)
Bridgetown
5 nautical miles

large beds at the Brighton and Bank Reef sites was carried out in a slightly different manner. At these sites, cores of coral were taken as close in volume as possible to the isolated heads sampled at Paynes Bay. A complete description of coring methodology is found in chapter 1. At all three sites, every effort was made to sample 1 dm^3 of coral, the volume Clausade (1970) found adequate to obtain the majority of cryptofaunal species associated with a Pacific coral. However, variation in the depth of Madracis mirabilis beds and the diameter of the isolated heads made it impossible to maintain a constant volume, and some variation did occur.

Samples were transported to Bellairs Research Institute for processing, and complete details of this procedure are found in Chapter 1, along with a list of the taxonomic authorities who assisted in identification. Voucher specimens have been deposited with these authorities. Again, Brachyuran crabs were omitted from the study because they were numerically rare, and damage to many of the specimens made identification impossible.

Statistical analysis

To establish whether different faunas inhabited isolated Madracis mirabilis heads and large M. mirabilis stands, the same ordination and classification methods used in chapter 1 were applied. Density calculations, species reductions, and transformations necessary for clustering and multidimensional scaling were identical to those described in chapter. The only difference was that species reduction resulted in the retention of 36 species, rather than 33 species as in the previous chapter.

To determine how the sites differed in terms of species

composition, analyses of density and richness (species number) were necessary. Initially, analyses were performed on all taxa combined, but additional comparisons were made of isopods, amphipods, copepods and decapods. This division served as a means of breaking the organisms into four body size groupings, of which decapods were the largest, amphipods second largest, isopods third largest, and copepods smallest. For these analyses, tanaids were grouped with the isopods..

To establish whether any bias in sample volume was present, an analysis of variance was performed to compare the 3 sites. A further ANOVA was performed to compare the total number of individuals (abundance) collected at each site. In both instances, a Shapiro-Wilk, W, statistic was used to test normality and an F-max test used to test variance homogeneity. No violations of parametric assumptions were found. Because differences in abundance were found with the ANOVA, a correction was needed for this bias before richness at the 3 sites could be compared. Therefore, analysis of covariance (ANCOVA) was performed, in which the dependent variable (in this case richness) was adjusted for differences in the covariate (in this case abundance). An assumption of ANCOVA is that the dependent variable and covariate are linearly related, therefore transformed variables were used for the analyses. The best linear fits were established by taking the square root of species number and the $\log_{10}$ of abundance. ANCOVA also assumes that there is no difference in the slopes of the regression lines being compared. This was a problem with isopod richness, where slopes were not

homogeneous. As a result, a non-statistical comparison of the sites was necessary. It should be noted that comparison of amphipod richness violated the assumption of variance homogeneity, and therefore must be treated with caution.

Regression analysis was used to test whether volume of coral sampled could be used to statistically describe total species number. Analyses were performed on each site as well as on all sites combined.

The formulation used to determine evenness was that of Brillouin (1962):

$$J = \frac{\log(N!/n_1 n_2 \ldots n_s)/N!}{(\log N! - (s-r)\log c! - r(\log c+1)!)/N}$$

where N=total number of individuals in sample, n_1=individuals belonging to species i, s=number of species, c=integer portion of N/s, r=remainder of N/s and J=evenness. Composite indices of diversity were not used beyond the calculation of evenness because they combine information on evenness and richness, and are difficult to interpret without an understanding of the other two variables (Hurlbert, 1971; Pielou, 1975). It is important to realize that analysis of diversity (H) is problematic. Because evenness (J) is so closely related to diversity, the same problems exist in analysing evenness. Pielou (1974) pointed out that trying to estimate the diversity of a large community from smaller samples produces an underestimate of diversity and an overestimate of evenness. The present study, however, does not attempt to estimate the evenness of all isolated heads combined or the evenness of the entire large bed fauna. The evenness within each isolated head and within an equivalent volume of

coral from the large beds is being examined here. This means that the variance under investigation is not variance between subsamples of a larger community but replicates of similar communities that have been sampled in their entirety. Thus, the Brillouin index is most appropriate for the present study. Parametric statistics are inappropriate for derived variables such as diversity and evenness (Pielou, pers. comm.). Since no correction has been made for differences in abundance, non-parametric analysis would be deceptive. Therefore, only mean values are presented and the results must be interpreted with caution.

RESULTS

Fig. 2 shows the dendrogram produced by group average sorting. At an arbitrary similarity level of 60%, two large groupings are seen as well as one solitary sample. All of the 14 samples in the first grouping are from the Payne's Bay site while the 30 samples in the second grouping are from the Brighton and Bank Reef sites. Although some segregation of the highly polluted Brighton and low pollution Bank Reef samples did occur (at an arbitrary similarity level of 80%), the major faunal discontinuity appears to be between isolated heads (Payne's Bay) and large flat beds (Brighton and Bank Reef). The fauna of the isolated heads does not show a strong affinity with either the high pollution or the low pollution sites, and nor is it intermediate between the two.

The MDS plot (Fig. 3) provides the strongest evidence that a very distinct faunal discontinuity exists. The fit is very strong (X^2=3512.62, d.f.=87, $p<.001$) as is the correlation between the MDS mapping and the actual distribution of data points (r^2=.98, n=45, $p<.001$). Samples from Paynes Bay form a tight grouping separate from the group of large bed stations from the Brighton and Bank Reef sites. The groups are very distinct, and the distance between them suggests that the Paynes Bay site has no strong affinity with either of the other two sites. Furthermore, the spatial orientation of the plotted stations is conclusive evidence that Payne's Bay is not a faunal intermediate of the sites surrounding it.

Table 1 lists the 36 most common species and their densities

Fig. 2. Dendrogram showing classification of 45 samples along the west coast of Barbados based on the faunal densities of the 36 most common species. Densities were root-root transformed before comparison using group-average sorting of Bray-Curtis dissimilarities. Solid circles (•) represent isolated heads at Payne's Bay, heavy open circles (σ) represent large beds at Brighton, and thin open circles (o) represent large beds at the Bank Reef site.

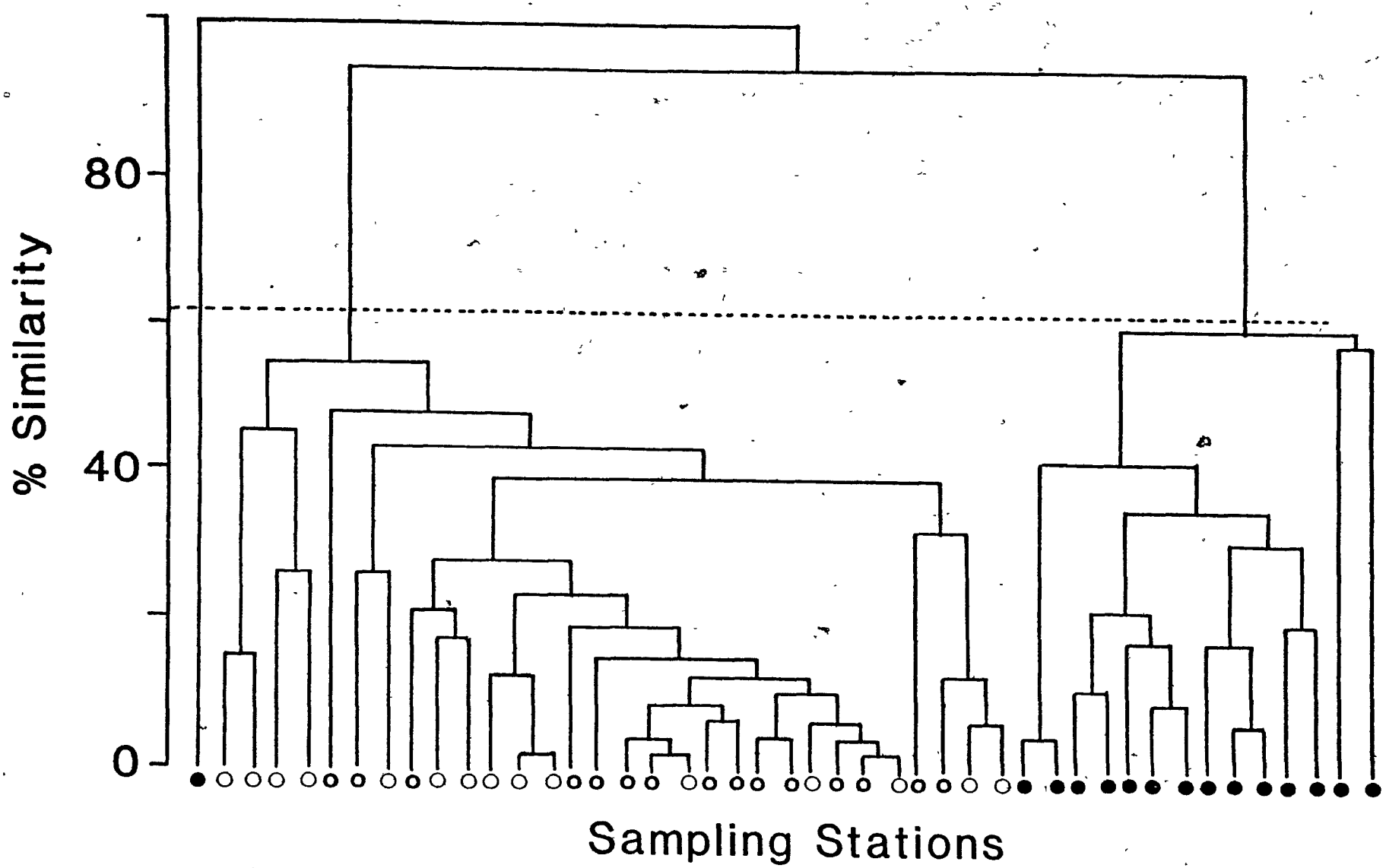

80
40
0
% Similarity
Sampling Stations

Fig. 3. MDS ordination of 45 samples based on faunal densities of the 36 most common species. Densities were root-root transformed before comparison of Bray-Curtis dissimilarities. Solid circles (•) represent isolated heads at Payne's Bay, heavy open circles (o) represent large beds at Brighton, and thin open circles (o) represent large beds at the Bank Reef site. Scales of axes are arbitrary and are therefore omitted.

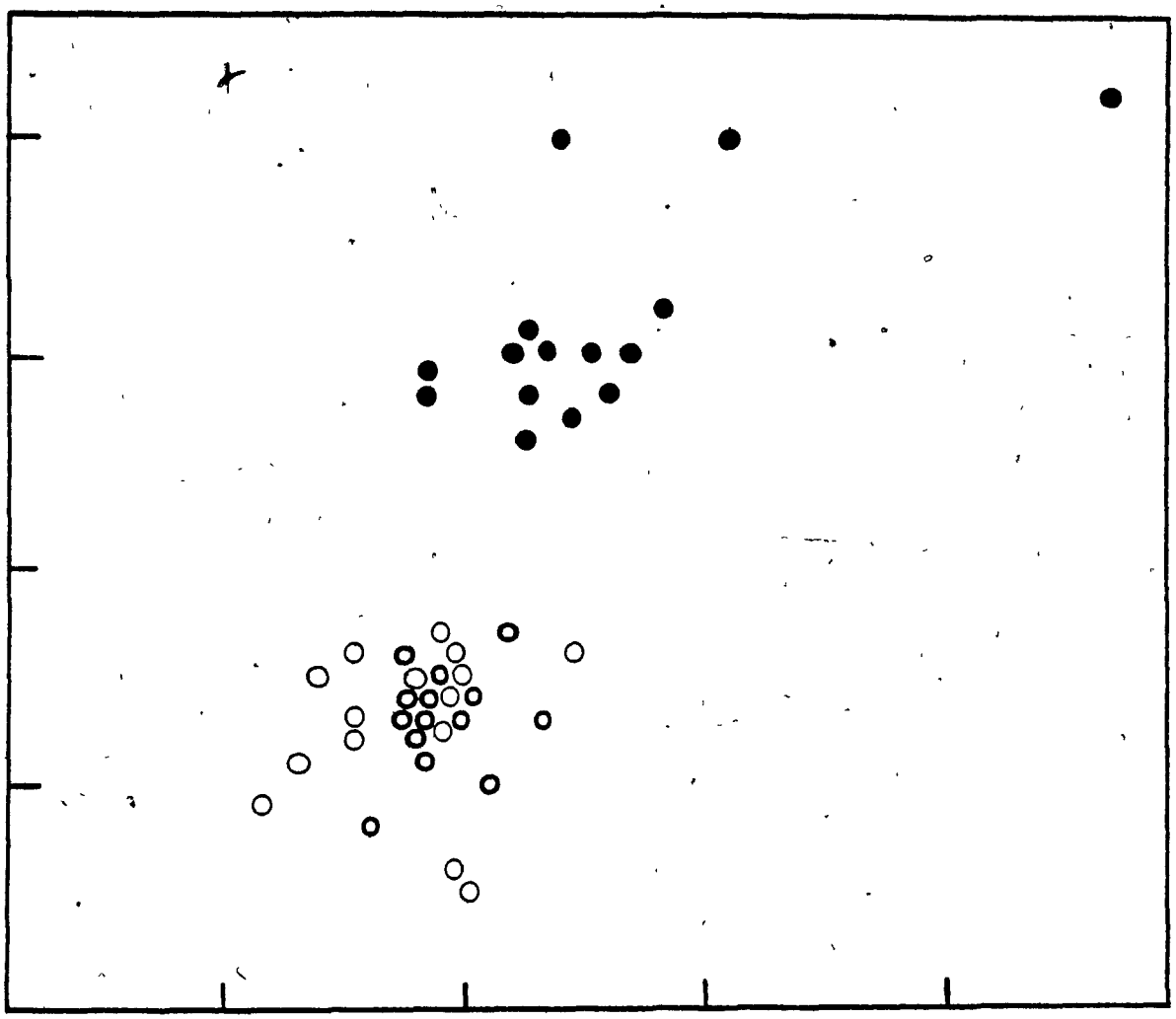


Table 1. Mean values for densities* of the 36 most common species encountered at the 3 sites.

Family	Species	Bank Reef	Payne's Bay	Brighton
Amphipods				
Amphilochidae	Amphilochus sp.	10.9	8.5	2.2
Aoridae	Microdeutopsis sp.	0.0	73.4	0.5
Gammaridae	Maera sp.	0.0	44.7	0.0
Isaeidae	?Megamphopus sp.	33.1	7.8	22.5
Leucothoidae	Leucothoe sp.	6.3	18.3	2.2
Leucothoidae	Leucothoella sp.	17.2	44.5	5.7
Decapods				
Alpheidae	Synalpheus paraneptunus	15.8	0.0	6.3
Alpheidae	Synalpheus townsendi	0.0	16.6	0.5
Hippolytidae	Lysmata rathbunae	2.8	0.6	0.9
Hippolytidae	Thor sp. a	0.9	8.6	0.2
Hippolytidae	Undetermined a	0.6	8.9	0.0
Undetermined	Decapod a	0.4	15.8	0.2
Isopods				
Anthuridae	Chalixanthura lewisi	6.6	16.4	8.6
Anthuridae	Eisothistos teri	15.5	0.3	10.5
Anthuridae	Minyanthura corallicola	46.2	0.5	0.6
Gnathiidae	Gnathia rathi	9.3	3.2	2.9
Janiridae(I)	Carpias minutus	32.3	0.5	40.2
Sphyraepidae	Undetermined	29.6	21.2	32.9
Stenetriidae	Stenetrium patulipalma	25.9	1.6	15.0
Stenetriidae	Stenetrium spathulicarpus	9.9	96.4	9.8
Tanaids				
Apseudidae	Apseudomorpha sp.	2.5	2.7	4.0
Paratanaidae	?Heterotanais sp. a	21.6	30.9	19.1
Paratanaidae	?Heterotanais sp. b	5.6	0.7	5.6
Paratanaidae	?Heterotanais sp. c	4.7	1.3	5.5
Copepods				
Artotrigidae	Acontiphorus sp. nov.	8.1	0.0	3.5
Asterocheridae	Asterocheres sp. nov.	16.2	40.6	43.0
Asterocheridae	Scottocheres elongatus	2.4	8.4	2.1
Diosaccidae	Amphiascus sp.	28.4	9.5	20.3
Diosaccidae	Amphioscopsis sp.	7.2	2.1	1.6
Diosaccidae	Undetermined	12.8	1.4	14.2
Tetragonoceptidae	Phyllopodopsyllus sp.	6.0	2.1	5.8
Laophontidae	Laophonte bulbifera?	3.2	4.9	4.45
Laophontidae	Paralaophonte sp.	5.2	1.6	1.3
Lichomoglidae	Undetermined sp. a	6.9	3.0	8.5
Peltidae	Peltidinum perturbatum	9.1	0.0	2.2
Tisbidae	Tisbe sp. a.	2.2	1.2	3.0

*individuals/dm^3 of coral sampled.

at the 3 sites. A number of species differ greatly in density, particularly in comparing isolated heads to the monospecific beds. A complete species list is given in Appendix A.

Regression analysis failed to show any discernible relationship between coral volume and total species number over all sites combined (r^2=0.01, n=45, p>0.236), or within the Payne's Bay (r^2=0.01, n=15, p>0.84), Bank Reef (r^2=0.06, n=15, p>0.19), or Brighton sites (r^2=0.05, n=15, p>0.43). However, analysis of variance on mean total abundance showed that the sites did differ (F=4.73, n=45, p<0.01), and the Tukey multiple mean comparison showed that discernibly more individuals were collected at Payne's Bay than at Brighton.

Mean densities at the three sites are illustrated in figure 4 and summarized in Table 2. No discernible differences are seen in overall mean density (Table 3), but several differences are apparent within the taxonomic subgroups. Payne's Bay shows a statistically higher decapod density than either of the other two sites, and a higher density of amphipods in comparison with Brighton. The Bank reef site is highest in copepod and isopod density (Table 2), but the densities are not statistically higher than the Payne's Bay or Brighton sites (Table 3). In fact, the Payne's Bay data indicate that this site has significantly higher densities (decapods and amphipods) or densities that are not statistically different from the highest values at the Brighton and Bank Reef sites (isopods and copepods).

Richness shows a number of differences between the 3 sites (Table 3). Payne's Bay has the lowest overall richness (Table 2), although the difference is not significant. Of the taxonomic

Table 2. Mean values for richness, evenness (J) and density in each taxon examined. Richness has been root transformed and corrected for abundance differences by the ANCOVA model, therefore values cannot be extrapolated beyond comparisons within the study and comparisons between taxa are meaningless. Furthermore, this correction renders the sum of the richness of taxonomic subgroups numerically unequal to the total.

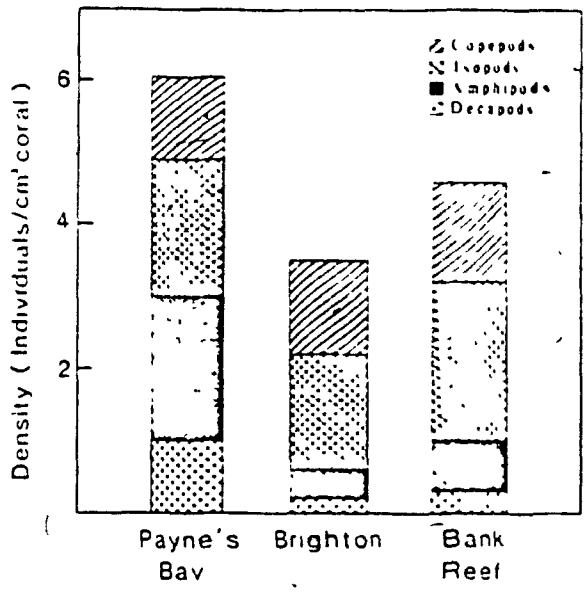
Site	Variable	Decapods	Amphipods	Isopods	Copepods	Total
Payne's Bay	Richness	2.25	2.08	2.24	3.05	5.04
	Evenness	0.86	0.76	0.54	0.75	0.78
	Density*	0.10	0.20	0.19	0.12	0.61
Brighton	Richness	1.92	1.84	2.88	3.20	5.15
	Evenness	0.89	0.84	0.84	0.85	0.34
	Density*	0.02	0.04	0.16	0.14	0.36
Bank Reef	Richness	1.88	1.80	3.02	3.37	5.32
	Evenness	0.83	0.81	0.81	0.87	0.85
	Density*	0.03	0.07	0.22	0.14	0.46

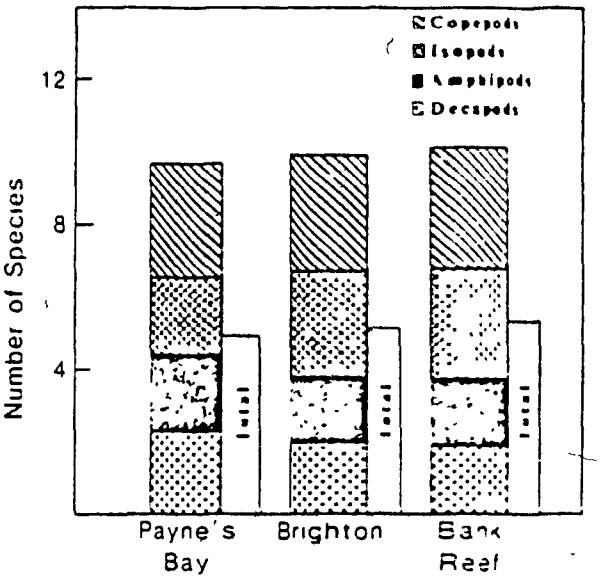
*Number of individuals per cm^3 of coral sampled

Table 3. Statistical differences (α=.05) in decapod, amphipod, isopod, copepod, and total crustacea richness, and density. (x) indicates discernible differences, (o) indicates non-discernible differences, and (-) indicates comparisons that could not be made as a result of problems with the assumptions of the ANCOVA model. Richness, and density are shown in the same sequence in each box. ANOVA was used to show density differences and ANCOVA was used to show differences in richness.

		Payne's Bay	Brighton	Bank Reef
Payne's Bay	Decapods	---	x x	x x
	Amphipods	---	o x	x o
	Isopods	---	- o	- o
	Copepods	---	o o	x o
	Total	---	o o	o o
Brighton	Decapods		---	o o
	Amphipods		---	o o
	Isopods		---	o o
	Copepods		---	o o
	Total		---	o o
Bank Reef	Decapods			---
	Amphipods			---
	Isopods			---
	Copepods			---
	Total			

Fig. 4. Bar chart showing mean values for richness and density in each taxon examined. Richness (number of species) has been corrected for differences in abundance, therefore comparisons between different faunal groups are meaningless as are comparisons outside the present study. Total in second chart refers to mean number of species of all taxa combined. Again the ANCOVA model has been used to correct for differences in abundance and the taxa are therefore non-additive.


Copepods
Isopods
Amphipods
Decapods
Density (Individuals/cm² coral)
6
4
2
Payne's Bay
Brighton
Bank Reef

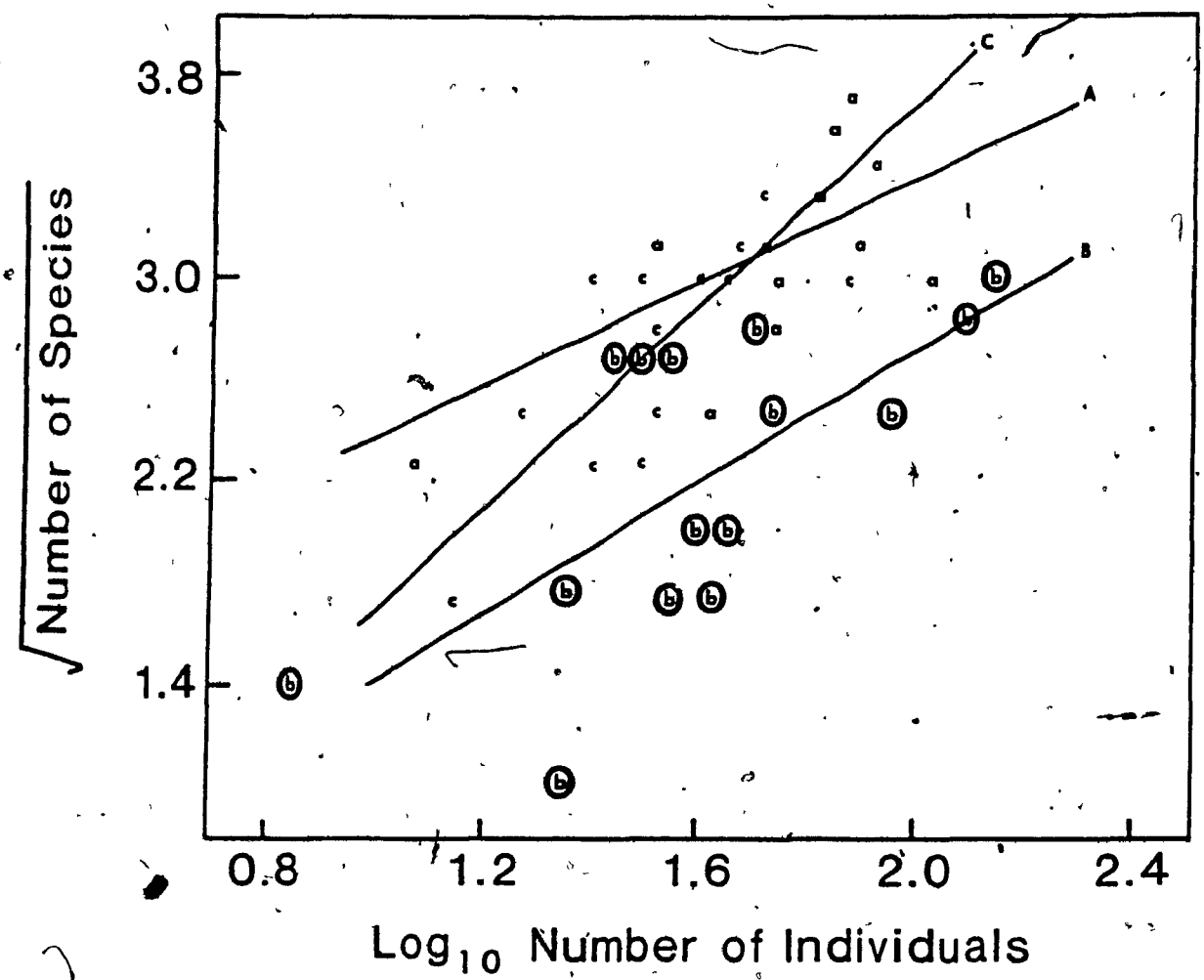

Copepods
Isopods
Amphipods
Decapods
Number of Species
12
8
4
Total
Total
Total
Payne's Bay
Brighton
Bank Reef

subgroups, copepods display the same trend, with the lowest value at Payne's Bay statistically differing from the highest value at the Bank Reef site. Table 2 and figure 4 summarize trends in species richness. The relationship between number of isopod species and number of individuals is illustrated in figure 5. Over the range of abundances sampled, the number of species present at Payne's Bay, for a given abundance, consistently falls below that observed at either of the other sites. However, with amphipods and decapods the trend is reversed (Table 2). Values of amphipod and decapod richness at Payne's Bay are both statistically higher than those at the Bank Reef site, and decapods are also richer in species at Payne's Bay than at Brighton (Table 3).

The differences in evenness are very similar to those in richness (Table 2). Overall evenness is lowest at Payne's Bay, and within the subgroups, copepods, amphipods, and isopods are all less evenly distributed at Payne's Bay compared to the other two sites. Because evenness decreases with abundance (see chapter 3) these values must be interpreted carefully. However, at Payne's Bay, density of copepods is lowest and density of isopods second lowest. Despite this, Payne's Bay still shows the lowest values for evenness. This indicates that the reduced evenness at Payne's Bay is not merely a function of sampling bias.

Comparisons between the Brighton and Bank Reef sites are not mentioned above because within the subgroups, as well as with all groups combined, richness and density do not show ~~any~~ statistical differences between the sites, and numerical differences in

Fig. 5. Plot of square root transformed number of isopod species versus log transformed number of individuals for each of the 3 sites being compared. (b) represents isolated heads at Payne's Bay ($r^2=0.42$, $p<.005$, $n=15$), (a) represents large beds at the Bank Reef site ($r^2=0.30$, $p<.02$, $n=15$), and (c) represents large beds at Brighton ($r^2=0.61$, $p<.0004$, $n=15$).


3.8
3.0
2.2
1.4
√Number of Species
0.8
1.2
1.6
2.0
2.4
Log10 Number of Individuals
A
B
C

evenness are extremely small. A list of raw data on evenness, abundance, and richness is found in Appendix B.

DISCUSSION

The faunas associated with isolated coral heads and large beds of Madracis mirabilis are markedly different. Although some segregation of polluted and unpolluted samples was also evident, the separation of the two coral growth forms was much more distinct (Figs. 2 and 3). None of the isolated heads showed affinities with samples from either of the other sites, despite the fact that the Brighton and Bank Reef sites represent extremes of environmental quality. The MDS mapping of the samples (Fig. 3) also showed that the Paynes Bay fauna is not intermediate between the faunas of the surrounding stations. Clearly, isolated M. mirabilis heads harbour a very different cryptic fauna than large beds. This difference was not likely just a function of depth since the known depth ranges of many of the decapods (Dardeau, 1984) and isopods (Kensley, 1984a;1984b) extend beyond that of the three sites sampled. Nor was sampling bias likely to have been a problem, since no differences were found in the volumes of coral sampled at the 3 sites. The absence of any relationship between volume (roughly equivalent to area) and species number further supports this argument. Species number is generally known to increase with area sampled (e.g. Coles, 1980; Gotelli and Abele, 1983; Tsuchiya et al., 1986). The absence of such a relationship in the present study indicates that efforts to keep sample volume constant were successful, therefore the range in "area" was not wide enough to show any relationship.

A number of differences were found between the results of the present study and those of McWilliams et al. (1981) and Alldredge and King (1977). In these studies, the relative abundance of

isopods, tanaids and harpacticoids was extremely low, while in the present study these groups were far more abundant than either cyclopoids or calanoids. This is likely a result of the different sampling techniques used in the different studies. McWilliams et al. (1981) and Alldredge and King (1977) both sampled emerging zooplankton, while the present study sampled all fauna living within the coral. McCloskey (1970) and Grassle (1973) both sampled all of the coral associated fauna, and obtained relative proportions of organisms similar to those found in the present study.

Because of these differences in sampling method, it has been impossible to evaluate the relative numerical importance of different taxonomic groups, and how richness, abundance, and evenness are related to substrate. Alldredge and King (1977) examined several types of substrate, but their comparison of dead and living coral is the most relevant to the present study. The major difference between isolated Madracis mirabilis heads and the large flat beds is the relatively high proportion of living tissue on the branches in the isolated heads. Thus, in comparing the results of the present study to those of Alldredge and King (1977) and Porter and Porter (1977), the isolated heads correspond to their "living coral" and the large flat beds with "coral rubble". In this context, the results are comparable. For example, total zooplankton densities associated with live coral were higher than those associated with predominantly non-living coral (Table 1). Shrimp densities showed the same trend, both in the present study and in that of Alldredge and King (1977).

Amphipod densities were also discernibly higher in live coral in the present study, and although Aldredge and King (1977) did not find a statistical difference, the same trend was evident. Such elevated density in the isolated ("live") coral reef cryptofauna was likely related to localized differences in food availability, particularly since organisms with a larger biomass (decapods and amphipods) were more abundant in this habitat. However, data on localized productivity and food availability would be required to clarify this.

Elevated biomass and abundance are not necessarily indicative of high species richness. In this case high numbers of large individuals are inversely proportional to community richness (Table 3). The heterogeneity of dead coral has been described by Grassle (1973) and this may explain the high overall species richness in the dead coral studied by Coles (1980) and the flat beds of the present study. When coral dies, boring organisms invade the skeletons. Their boring action creates a heterogeneous habitat with many more crevices and contours, while their mere presence diversifies available food resources. Therefore, interference competition for habitat space (e.g. Buss and Jackson, 1975) and exploitative competition for available food (see Marcotte, 1984) may be reduced in dead coral. This spatial and nutritional heterogeneity may allow finer resource partitioning and the coexistence of more species with fewer individuals per unit area. Competition may be alleviated as organisms specialize to utilize these available resources.

Coles (1980) sampled entire heads of Pocillopora meandrina and found a shift from large symbiont decapods in live heads to

smaller non-symbiont decapods in dead coral heads. He suggested that dead coral offers a much more heterogeneous habitat than live coral, and will therefore support a richer fauna which does not depend on living tissue. Even those species that are symbiotic with live coral tend to be confined to the dead, basal area rather than the more homogeneous area of live tissue.

A similar but broader interpretation may be applied to the results of the present study. Decapod and amphipod species richness is extremely high in predominantly live isolated heads, while isopod and copepod richness is comparatively low. The reverse is true of largely non-living coral in flat beds, where isopod and copepod species richness is much higher than in the isolated heads and decapod and amphipod richness much lower. A possible explanation for the high species richness of harpacticoids and isopods in large stands is that being small, they may be able to utilize the microhabitats within dead coral. Because the isolated heads offer a habitat of living tissue with reduced microhabitat variability, smaller organisms would not find the many refuges necessary to maintain high diversity. This may be further compounded by coral polyp predation, which would be far more detrimental to smaller organisms than larger ones. Predation would intensify competition for the few available microhabitats, particularly if the predation was non-selective. This could accelerate elimination of weaker competitors. Because of their large size, decapods and amphipods would not be subject to predation by such small polyps. Large size would also prevent amphipods and decapods from taking

advantage of large bed microhabitats, therefore less spatial resource partitioning and species packing would be possible. Large symbiotic decapods require an abundance of living coral tissue, and their nutritional needs may not be met by the small proportion of living coral in the flat beds. In the isolated heads, however, the living tissue would be beneficial to the symbiotic decapods in terms of mucus production by the coral.

This explanation assumes that intense spatial competition exists in the isolated heads, therefore few refuges for subordinate competitors has lead to elimination of weaker species and a reduction in species number (see Marcotte, 1984). The large beds, however, offer more numerous and heterogeneous spatial refuges for smaller organisms, and therefore the coexistence of more species

A similar interpretation may explain the observed differences in evenness. Overall evenness was lowest at the Payne's Bay site. Of the taxonomic groups, copepods, amphipods and isopods all followed this pattern. The same trend was not evident with decapod evenness, which was intermediate in value at the Payne's Bay site. However, the very low density of decapods at sites other than Payne's Bay meant that evenness was generally calculated on only a few individuals. It is therefore pointless to attach any importance to the differences observed. However, evenness in copepods, amphipods, isopods, and all taxa combined is lower in the isolated heads than in the large beds. A possible explanation for this trend in evenness is found in Preston (1962) and reiterated by Gotelli and Abele (1983). Because there is spatial separation of the isolated heads, migration between the

heads might be expected to be very low. As a result, species within a coral head would reproduce without dispersal, little variety of microhabitat would be available, and dominance of a few competitively superior species would occur. In large, flat beds, however, individuals could migrate tens of metres without leaving the protection of the coral. They would encounter a far greater variety of microhabitats and a much more evenly distributed community would be expected. It should be noted that Coles (1980) suggested that coral heads less than 1000 cm^3 cannot support a predictable symbiont decapod community. Unpredictable biological communities are often characterized by dominance, so the small size of the isolated heads sampled in the present study may be as important as distance between colonies. Whether this estimate may be extended beyond the decapods of Coles' study, however, is unclear.

Clearly, the two growth forms of Madracis mirabilis support very different faunas. Both coral predation and environmental heterogeneity may play an important role in structuring these faunas, but the relative importance of each cannot be determined from the present study. However, the difference in fauna in the two growth forms shows that the physical structure of the coral substrate is important. Thus, coral growth form and the resulting habitat heterogeneity may potentially alter the demersal zooplankton community. If this is the case, it is possible that the major determinant of cryptofaunal composition is physical structure rather than the taxonomic identity of the coral species alone. The most important question may

therefore not be "who" you are but "what" you are (i.e. the physical heterogeneity of the coral substrate). Such a possibility must be considered in any future study of demersal zooplankton substrate preference.

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Chapter 3

Potential Bias in the Analysis of Diversity, Richness and Evenness with an Example from a Tropical Benthic Cryptofaunal Community

ABSTRACT

Although warnings have appeared in the literature on problems associated with evaluating composite diversity, richness and evenness, many marine researchers continue to use these parameters and ignore possible bias that may result from differences in absolute abundance or density. Regression analysis showed a strong, statistically discernible positive relationship between number of individuals sampled and species richness and a strong negative relationship between number of individuals sampled and evenness. By comparing the results obtained from an analysis that did not correct for differences in abundance to an analysis that did correct (using analysis of covariance), the seriousness of the problem is demonstrated. A theoretical explanation is provided to clarify why this is so and provide an intuitive understanding of why greater discretion is needed.

INTRODUCTION

In 1971, Stuart Hurlbert published a paper that should have ended the use of composite indices of diversity in community analyses. He pointed out that composite indices, such as those proposed by Shannon and Weaver (1963), Margalef (1958) and MacArthur and Wilson (1967), are influenced by both species richness (number of species collected from a community) and species evenness (distribution of individuals among species), and cannot be interpreted without an understanding of both of these variables. In proposing an alternative approach to analysis of community structure , he also criticised richness and evenness on the grounds that richness increases and evenness decreases with abundance (number of individuals sampled), and may give spurious results when communities with different numbers of individuals are compared. Further criticism and warnings have come from other sources (e.g. Goodman, 1975; Pielou, 1977; Frontier, 1985). Despite this, marine ecologists continue to use diversity indices indiscriminantly, and publications of analyses of composite diversity, richness, and/or evenness in marine communities remain common (e.g. Tsuchiya et al., 1986; Swartz et al., 1986; Ansari et al., 1986; Morin et al., 1985; Stoner and Lewis, 1985) In short, Hurlbert's warning has gone unheeded.

Some studies necessarily employ unequal sampling effort (e.g. Coles, 1980). Almost every study will sample different numbers of individuals in comparing quadrats, habitats, or sites. Differences in abundance are biologically important and must be considered. However, differences in both sampling effort and

numbers of individuals collected can bias calculations of richness and evenness, and division by total area or total individuals collected is not a suitable correction. Although the results and interpretations of the studies listed above may be correct, analysis with correction for any possible sampling bias would be required to determine this. To illustrate this point, the present study uses the community analyses commonly employed in marine work and compares it with the corrected analysis used in chapter 2. By demonstrating that the analyses produce different results, and offering an intuitive explanation of why this is so, it is possible to demonstrate how misleading these parameters can be if abused.

MATERIALS AND METHODS

A complete description of the sampling sites and methodology is found in chapter 2. For the purposes of this chapter it is sufficient to understand that Madracis mirabilis coral samples of approximately the same volume were collected using similar methods at 3 sites along the west coast of Barbados, W.I. The purpose of the collections (see Chapter 2) was to demonstrate whether the different growth forms at the sites influenced community structure of associated crustaceans. The present chapter is merely a reanalysis of the data presented there, and represents an example of the analyses used in many recent studies.

Analysis of variance (ANOVA) was performed to compare abundance, species richness, and species evenness. Initially the crustacean fauna was treated as a single taxon. Subsequent ANOVAs were calculated to compare isopods, copepods, decapods, and amphipods at the three sites. This provided a convenient means of dividing the organisms into 4 size groupings of which decapods were the largest, amphipods second largest, isopods third largest, and copepods smallest.

For each of these tests, normality of the raw data was tested using the Shapiro-Wilk, W, statistic and an F-max test (Zar, 1984) was used to examine homogeneity of variance. Violations of parametric analyses were found with richness and evenness, neither of which was normally distributed. Attempts to normalize these variables using the transformations suggested by Sokal and Rohlf (1981) were unsuccessful. As a result, it was necessary to

convert the data to ranks and normalize using Blom's (1958) method. The assumptions of parametric analysis were then met, and analysis of variance was performed. The means of variables that were found to be statistically different with ANOVA were then tested using a Tukey multiple comparison test (SAS Institute Inc., 1982) to determine which of the sites differed. It should be noted that the results obtained using the ranked data showed the same differences between sites as the unranked data, but had the advantage of also meeting the assumptions of parametric analysis.

Richness and evenness were also compared using analysis of covariance (ANCOVA) in which abundance was introduced as a covariate. This allowed correction for differences in abundance that existed between the sites. A more detailed explanation of ANCOVA is given in chaper 2. It is critical to realize that both ANOVA and ANCOVA are parametric tests, and are therefore inappropriate for analysis of evenness (Pielou, pers. comm.). They are therefore used only to illustrate how differences in ecological interpretation may arise if no correction is made for abundance differences.

Further ANOVA was performed to compare volumes of coral sampled at the three sites. No violations of parametric analyses were found using the Shapiro-Wilk and F-max tests. Although no significant differences were found among mean volumes sampled, some standardization of species number was needed to correct for the minor differences in volume of coral collected. Species richness was therefore calculated by dividing the number of species by the volume of coral sampled. This reduced species

number to a common unit (species/cm^3). The formulation used to determine evenness was that of Pielou (1966):

$$J' = -\sum p_i \log p_i / \log s$$

where p_i=proportion of total individuals belonging to species i, s=number of species, and J'=evenness. Although this index is less appropriate for the present data than Brillouin's index (see chapter 2), Pielou's index is much more commonly seen in current studies (where it is often equally inappropriate). Since the purpose of this comparison is to examine current methods of analysis, the more common index of Pielou was chosen. Composite indices of diversity were not used for reasons which will be clarified later.

To demonstrate how abundance of individuals is related to richness and evenness, regression analyses were performed in which evenness and richness were independently regressed against abundance. To eliminate problems of variance heteroscedasticity, a square root transformation of richness was regressed on $\log_{10}$ transformed abundance and root transformed evenness was regressed on root-root transformed abundance.

RESULTS

Table 1 lists mean values of richness, evenness, and abundance for each taxon examined. Table 2 illustrates how the biased analyses (ANOVA) compare to the unbiased analyses (ANCOVA) Comparisons of richness or evenness that changed in acceptance or rejection of the null hypothesis that there were no differences among means are circled (note that 6 comparisons were not possible using ANCOVA because of failure to meet certain assumptions of the model). In total, 3 of 24 possible comparisons became statistically different when bias was eliminated, and 1 of 24 comparisons became statistically indiscernible. All of the differences are confined to comparisons with Payne's Bay, which was the "isolated head" site of chapter 2. Thus, these 4 changes were all within the 14 most critical comparisons of the previous chapter, since they were confined to comparisons of two different growth forms and not just two different sites.

A number of statistically significant differences are also seen in mean abundance (Table 2), and this is probably a result of density differences as shown in Table 2 of Chapter 2. The most important result, however, is that 3 of the 4 changes found in richness or evenness correspond to discernible differences in mean abundance. The only change that does not correspond to an abundance difference is also the only comparison that became non-discernible as a result of bias removal. Therefore, all 3 of the mean values of richness and evenness that became statistically different once bias was removed correspond to comparisons in which mean abundance was also statistically discernible.

Table 1. Mean values for richness*, evenness and abundance** in each taxon examined at each of the sites sampled. Each mean is based on 15 replicate samples.

Site	Variable	Decapods	Amphipods	Isopods	Copepods	Total
Payne's Bay	Richness	0.025	0.018	0.019	0.033	0.098
	Evenness	0.849	0.765	0.559	0.806	0.784
	Abundance	27.9	58.9	49.9	32.2	168.9
Brighton	Richness	0.009	0.013	0.033	0.043	0.098
	Evenness	0.900	0.842	0.841	0.845	0.844
	Abundance	5.2	9.5	39.4	32.6	86.9
Bank Reef	Richness	0.011	0.013	0.039	0.049	0.113
	Evenness	0.804	0.820	0.809	0.868	0.852
	Abundance	8.8	18.2	58.5	36.9	122.4

*Richness refers to number of species per cm^3 of coral sampled.
**Abundance refers to number of individuals per sample without correction for minor differences in volume of coral sampled.

Table 2. Discernible differences (α=.05) in decapod, amphipod, isopod, copepod, and total crustacea richness, evenness and abundance. x indicates statistically discernible differences, and o indicates non-discernible differences. - indicates that comparison could not be made due to problems with ANCOVA assumptions. Richness, evenness and abundance are shown in the same sequence in each box. Circled letters are those that have changed in acceptance or rejection using biased ANOVA in comparison with the unbiased analyses (ANCOVA). Note that parametric analysis of evenness is problematic, and is presented here merely to illustrate how misleading comparison of evenness can be if no correction for abundance differences is made.

		Payne's Bay	Brighton	Bank Reef
Payne's Bay	Decapods	---	(o) - x	x - x
	Amphipods	---	o o x	(o) o x
	Isopods	---	- - o	- - o
	Copepods	---	o o o	x o o
	Total	---	o (x) o	o (o) x
Brighton	Decapods		---	o - o
	Amphipods		---	o o o
	Isopods		---	- - o
	Copepods		---	o o o
	Total		---	o o o
Bank Reef	Decapods			---
	Amphipods			---
	Isopods			---
	Copepods			---
	Total			---

ANOVA indicated that the volumes of coral collected were not statistically different at the 3 sites ($F=2.15$, $n=45$, $p>0.13$). Linear regression analysis showed a positive relationship ($r^2=0.61$, $p<.0001$, $n=45$) between richness and abundance (Fig. 1) and a negative relationship ($r^2=0.26$, $p<.0002$, $n=45$) between evenness and abundance (Fig. 2).

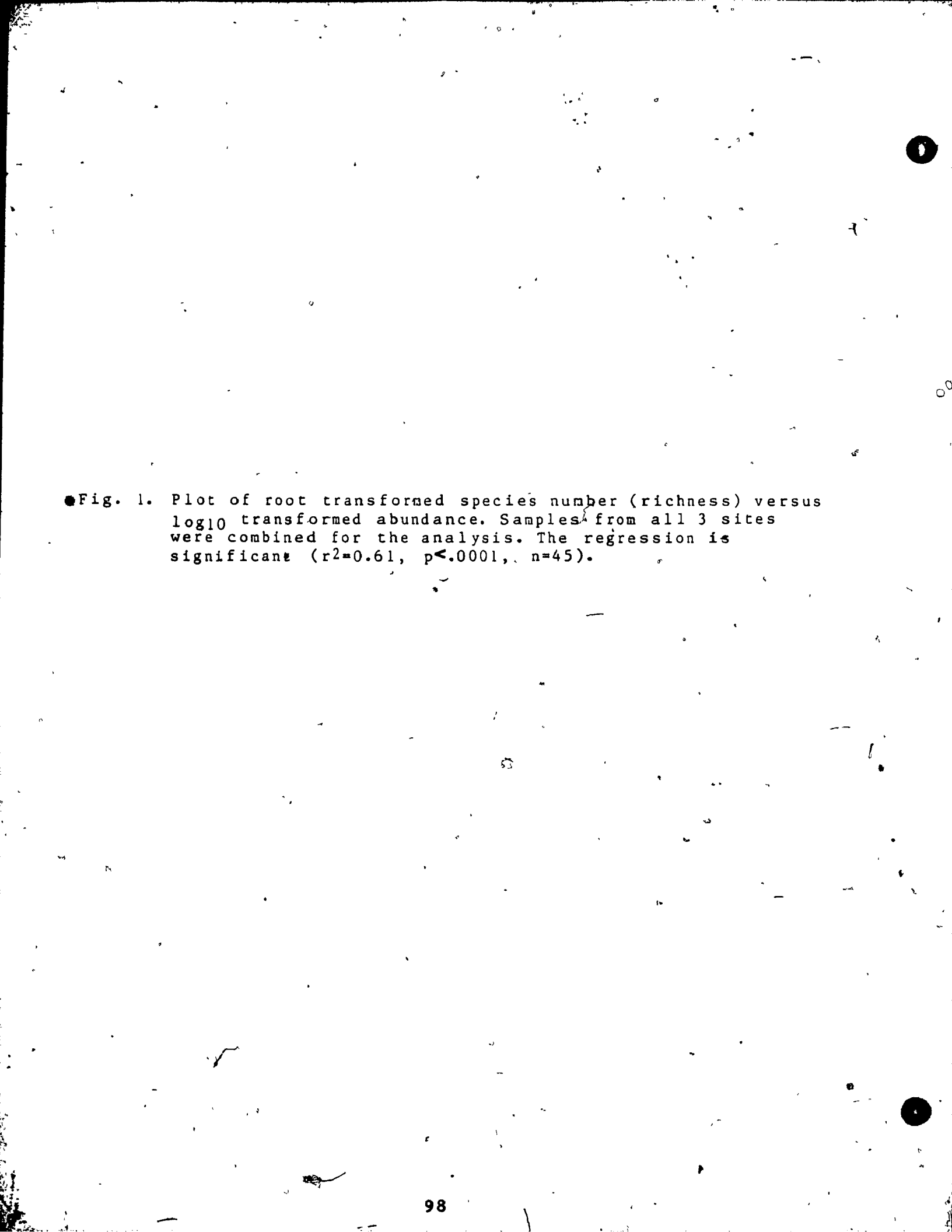


Fig. 1. Plot of root transformed species number (richness) versus $\log_{10}$ transformed abundance. Samples from all 3 sites were combined for the analysis. The regression is significant ($r^2=0.61$, $p<.0001$, $n=45$).

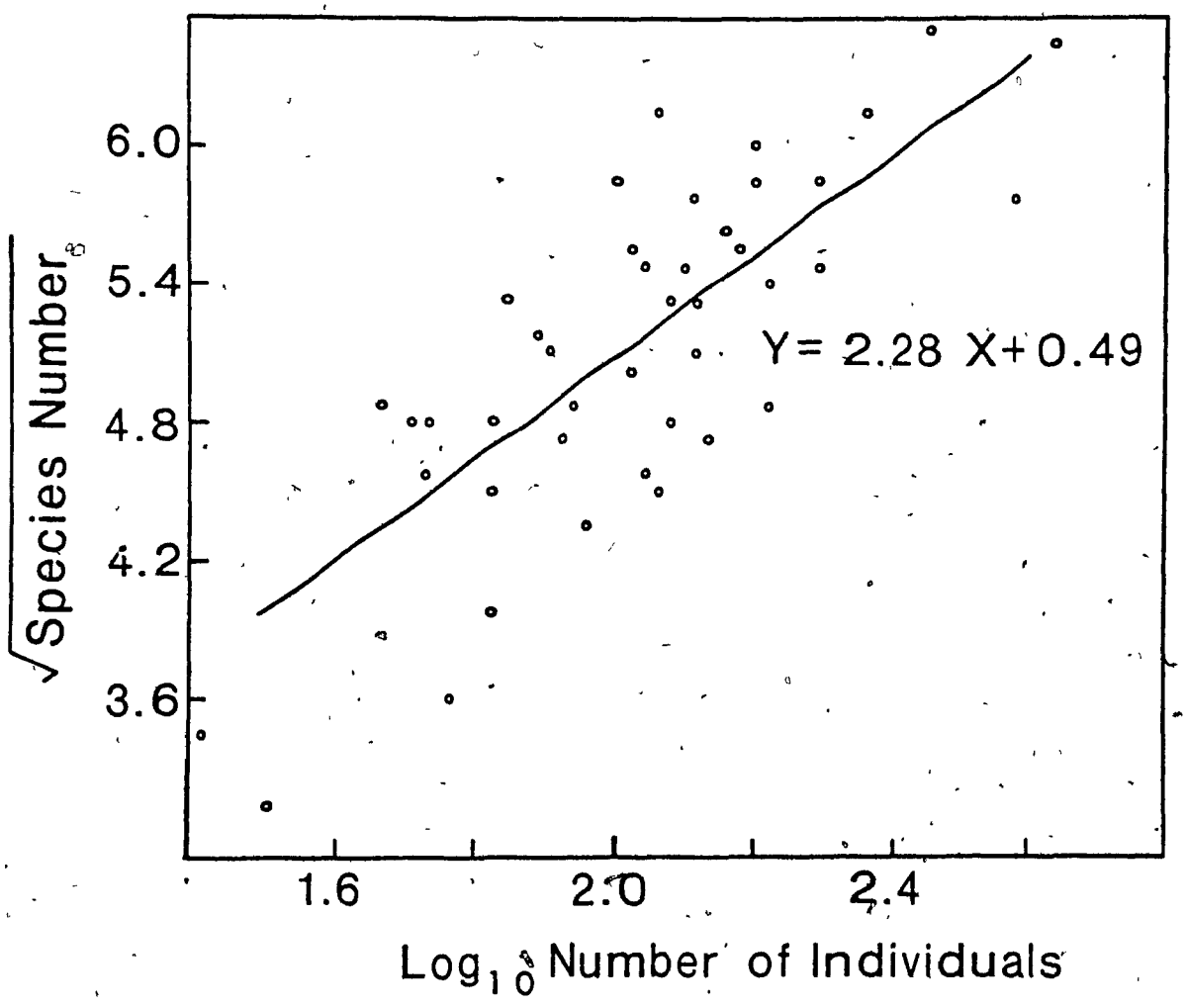
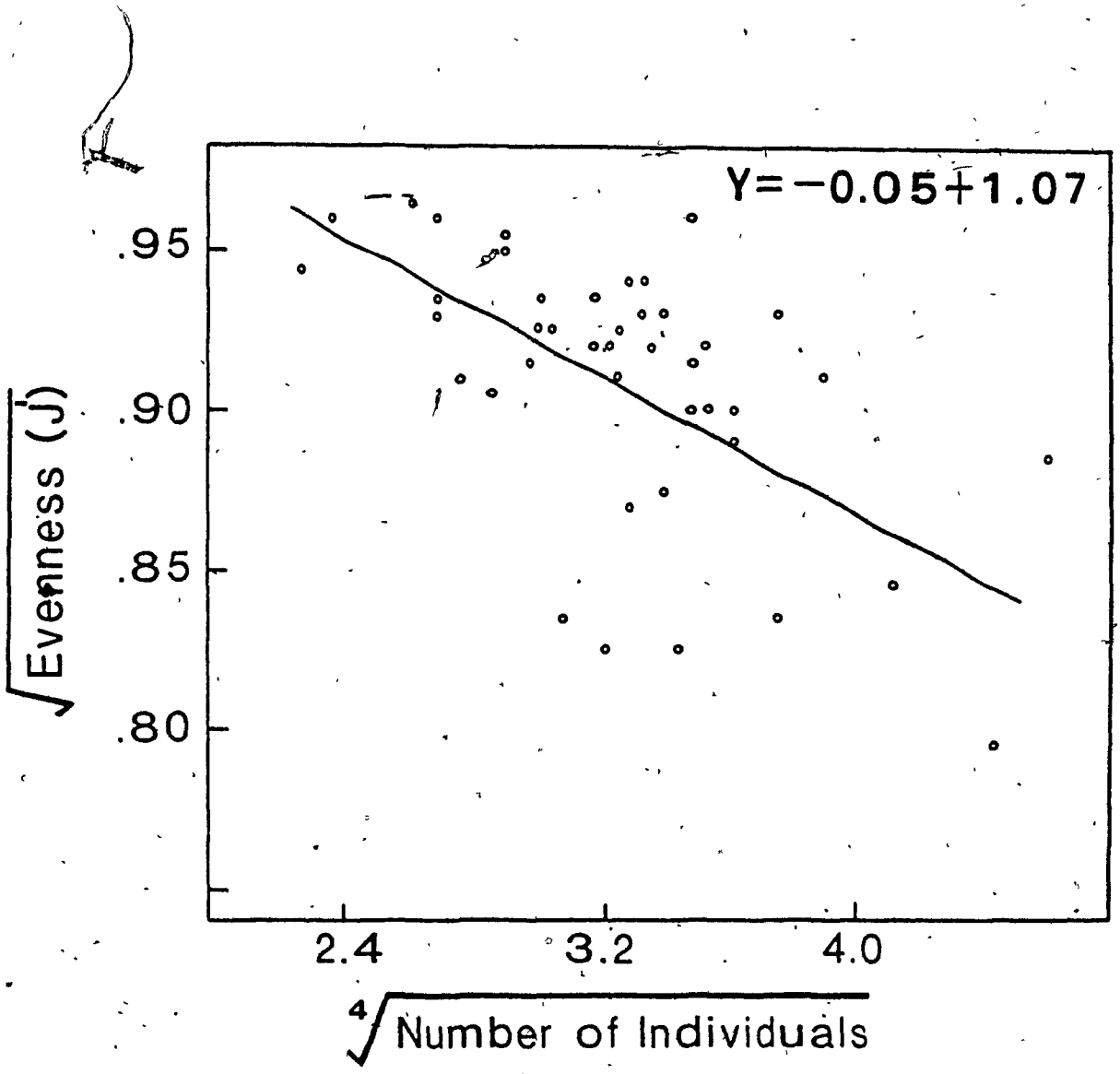

6.0
5.4
4.8
4.2
3.6
√Species Number
Y= 2.28 X+0.49
1.6
2.0
2.4
Log10 Number of Individuals

Fig. 2. Plot of root transformed evenness versus root-root transformed abundance. Samples from all 3 sites were combined for the analysis. The regression is statistically significant (r^2=0.26, $p<.0002$, n=45).

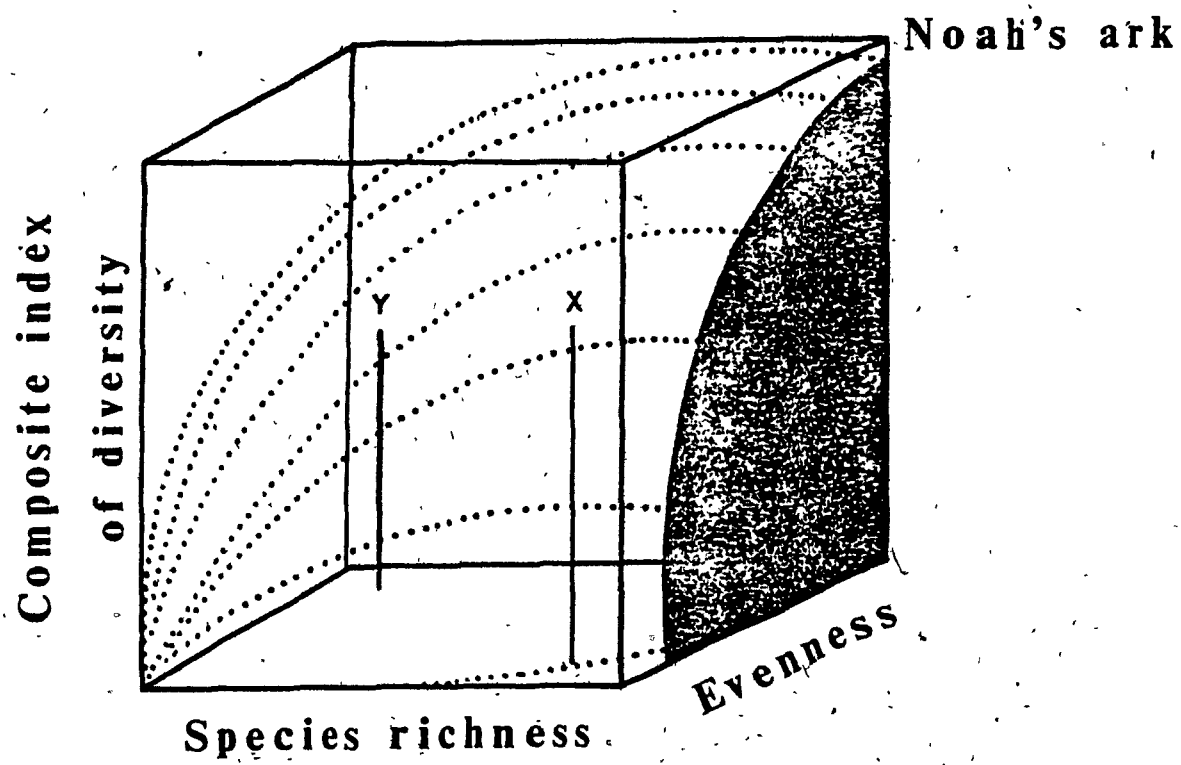

Y=−0.05+1.07
.95
.90
.85
.80
√Evenness (J)
2.4
3.2
4.0
⁴√Number of Individuals

DISCUSSION

Two objects may be be most easily compared if each can be represented by a single descriptive number. This is probably why composite indices of diversity have achieved such tremendous popularity, and are now commonplace in marine ecological literature. Unfortunately, composite indices are just that - a composite of evenness and richness. Figure 3 is a 3-dimensional representation of the relationship between a composite diversity index, species richness, and evenness. The relationship resembles the topography of one-eighth of a sphere. All communities will lie somewhere on the outer surface of the partial sphere, and will therefore correspond to some combination of values of richness, evenness and composite diversity. Communities X and Y both have similar values of a composite index of diversity, however X is much more species rich. Community Y, because it is located further back on the surface of the partial sphere, is more evenly distributed. It is apparent that community X has many species, but many of them are rare. Numerous rare species correspond to low community evenness, therefore it is possible to have two communities with identical composite diversity values but very different community structure. Researchers have attempted to circumvent this by including values of richness and/or evenness, without considering possible sample bias in their measure. The analysis in the present study shows that richness and evenness are biased, and the aim of this discussion is to explain why.

Problems with richness and evenness may arise not only when comparing samples collected with different sampling effort, but

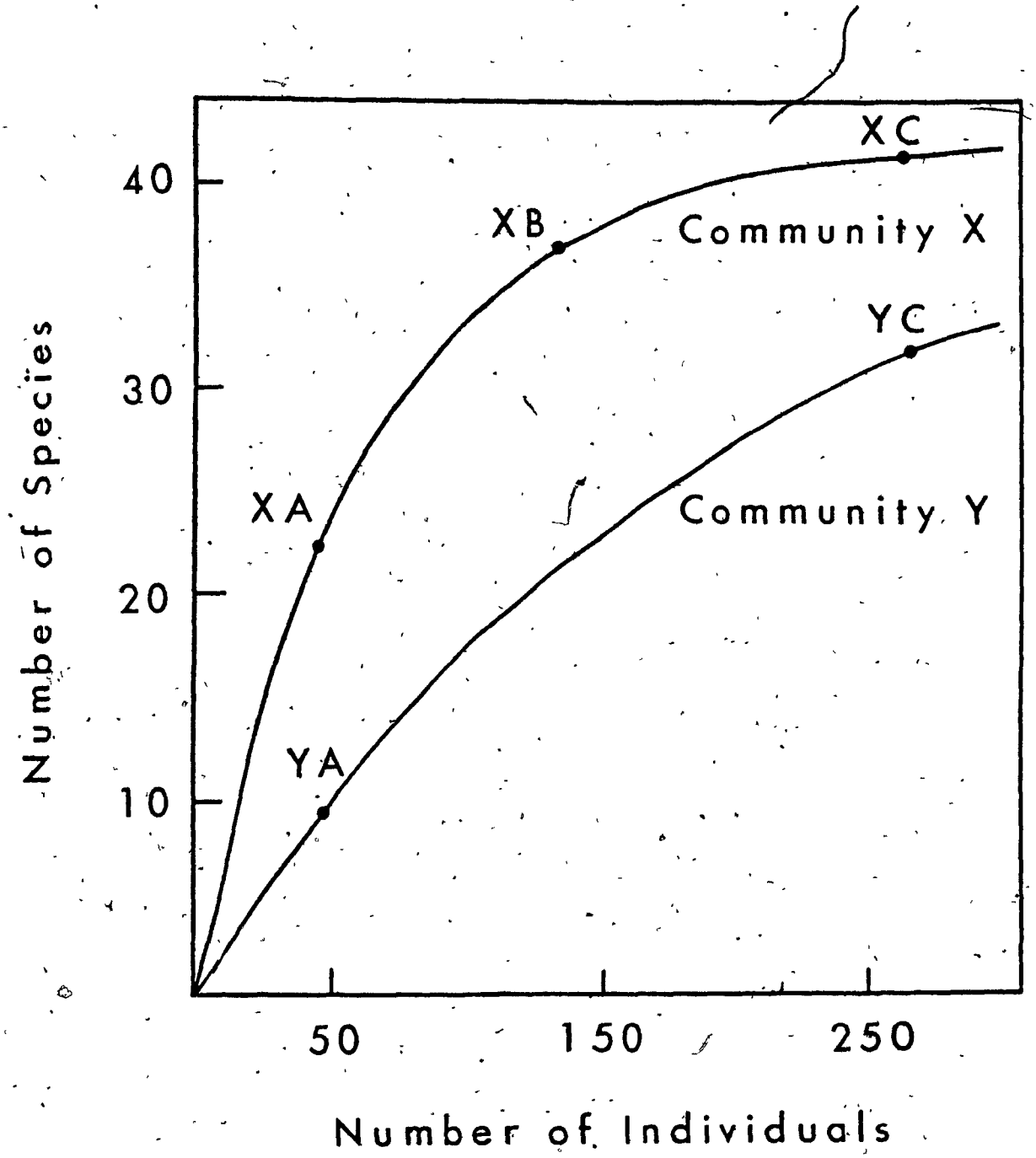
Fig. 3. Theoretical relationship between composite diversity, richness, and evenness for biological communities. The figure represents 1/8 of a sphere, which is turned slightly into the page. All communities will lie somewhere on the surface of the sphere, and maximum values for the 3 variables will occur at the front right corner of the cube (For example Noah's Ark would have had this value since all species were supposedly present and represented by exactly two individuals). Minimum values (0 or abiotic) will occur in the front lower left corner.


Noah's ark
Composite index of diversity
Y
X
Species richness
Evenness

also when the numbers of individuals in the samples are very different. Because the volume of coral collected in the present study did not differ between the sites, the inconsistent results cannot be the product of biased sampling effort. However, the effect of number of individuals collected is evident. Total abundance was statistically higher at Payne's Bay than at the Bank reef site, and this was also the only comparison of total taxa that produced different results in richness and evenness after correction for bias. A similar situation was seen with decapods, where abundance at the Bank Reef and Brighton sites was statistically lower than at Payne's Bay. A further finding that supports the importance of abundance differences is the absence of change in copepod evenness or richness after correction of bias. The abundance of copepods was not discernably different at the 3 sites and this taxon did not show changes in richness or evenness comparisons between sites after correction for abundance differences.

Why such a correction is needed is most easily explained using a comparison of two very different communities. Figure 4 is a theoretical plot of two communities that differ in richness and evenness. The forms of the curves are identical to the rarefaction curves proposed by Sanders (1968). The distributions represent extreme examples, and most communities will lie somewhere between the two lines. All communities will conform to these curves in some way, although precise distribution may differ between communities. In fact rarefaction curves have been proposed as a possible alternative to diversity indices (Simberloff, 1978), and the analysis suggested by Hurlbert (1971)

Fig. 4. Theoretical plot of two communities showing how species number will increase with number of individuals sampled. Numerical values placed on the axes represent possible scales though the choice of numbers is arbitrary.


XC
40
XB
Community X
YC
30
XA
Community Y
20
YA
10
Number of Species
50
150
250
Number of Individuals

is a modified version of the technique. It is easy to appreciate that collecting more individuals from a community will generate more species. However, as the more common species are all collected, return in species per unit effort becomes less and less since many individuals must be collected before any new species are added.

Community X has more species than community Y when the samples contain equivalent numbers of individuals. Community X is also more evenly distributed than Y, since fewer individuals (about 125 in this example) need to be sampled to include most species (point XB along the curve for community X). With community Y, on the other hand, many more individuals (250) must be collected before most species are included (point YC).

By examining species richness or evenness at any equivalent number of individuals (at A for example), a meaningful comparison can be made between the communities. However, if the numbers of individuals in the samples being compared are very different, misleading results may occur. For example, if the number of individuals collected in a sample from community X falls on point XC (250 individuals) and community Y sample falls on point YA (50 individuals), then the researcher would incorrectly conclude that community X is less evenly distributed. This would be so because a number of rare species would be included in sample X, whereas most of the species in the sample from community Y would be very common. Alternatively, if sample X was sampled at point XA (50 individuals) and community Y at point YC (250 individuals), more species would be attributed to community Y (31 species as opposed to 22). If an attempt was made to

correct for number of individuals by calculating number of species per unit number of individuals, further problems would be encountered. For example, samples XA and XC from the same community might produce very different results, with sample XC appearing less "species rich" (.164 species/individual) than sample XA (.440 species/individual). Table 3 summarizes how these community descriptors vary with number of individuls sampled. The main point, however, is that samples with different numbers of individuals may give rise to erroneous interpretations if no correction is employed.

Obviously, differences in density (individuals per unit volume or area) may be of great interest per se. A study of community structure that corrects for density differences without considering why the differences exist will not likely produce a clear explanation of what ecological mechanisms are at work. Richness, evenness, and density are all intimately related, and must be considered together in understanding how communities differ. But if one is a direct mathematical function of the other, as will be the case when bias is not removed, then little is gained by looking at any of them.

The regressions shown in figures 1 and 2 further illustrate the problem. Both richness and evenness are closely related to abundance, with richness increasing and evenness decreasing as numbers of individuals increase. Evenness is calculated by dividing a composite index of diversity (H') by maximum possible value for the same number of species (H'_{max}). As shown in Pielou (1977), H'_{max} is equivalent to $\log_{10}$ of species number. Therefore,

Table 3. Example of how species richness and evenness change as a function of number of individuals. Values are taken from the theoretical plot shown in Fig. 4. J' refers to Pielou's index (see page 92) and J refers to Brillouin's index (see page 63)

Community	Number of individuals	Number of species	species/ individ	rare species	J or J'_{max}	J'_{max}	J'_{min} (J_{min})	$J'_{max}-J'_{min}$ ($J_{max}-J_{min}$)
Y	50	9	0.180	some	moderate	1.00	0.35 (0.32)	0.65 (0.68)
	150	20	0.133	more	low	1.00	0.25 (0.23)	0.75 (0.77)
	250	32	0.128	many	very low	1.00	0.23 (0.21)	0.77 (0.79)
X	50	22	0.440	few	high	1.00	0.63 (0.61)	0.36 (0.39)
	150	37	0.246	some	moderate	1.00	0.39 (0.36)	0.61 (0.64)
	250	41	0.164	many	low	1.00	0.24 (0.25)	0.76 (0.75)

as species number in samples from the same community increases, calculated evenness for that community will generally decrease. This is biologically meaningful if similar abundances are being compared, but if samples with very different abundances are being examined, analysis of richness and evenness may really be a reexamination of abundance in a different form.

If the communities in Fig. 2 plotted as a straight line, then evenness would not change as sample size increased. Such a plot is unlikely, however, since all communities possess at least a few rare species. Thus, although maximum possible evenness at any point along the curve is very close to 1, this value will usually only be attained very close to the base of the curve. Minimal evenness, however, necessarily decreases as number of individuals increases since more and more rare species will be included. In comparing the two theoretical communities X and Y (Table 3), community X will always have more species than community Y at an equivalent number of individuals. Because X contains more species, minimal possible evenness will be numerically larger in X than in Y. The range of maximum and minimum evenness will be less for community X, since minimum evenness is much lower in Y (except at very large numbers of individuals, where the difference becomes much less pronounced). In Fig. 4, it is possible that with 50 individuals, community Y may be found to be more evenly distributed than community X. However, in view of the overall shapes of the curves, such samples would not be representative of the communities and obtaining such a result would therefore be improbable. Thus, it is conceivable that evenness could be higher in a sample from Y, but this would be

the exception rather than the rule.

Researchers select sample size either by logistic constraints or by finding a sample size (volume or area) that will include "most species". In some instances it is impossible to take samples large enough to include most species in the entire community (e.g. organisms found in isolated or discrete habitats such as coral heads, communities distributed over a vast area such as pelagic fish or zooplankton). A researcher seldom can sample in such a manner that most species will be included at all sites (at least not consistently so) while maintaining a constant sampling effort. Seasonal and spatial variation may further complicate this. Obviously any number of factors can result in comparisons that need correction for bias, but few studies consider this.

In most instances rare species are of less interest than species that are common or intermediate in abundance. From the explanation above, however, it is apparent that rare species may strongly influence richness and evenness. One method of avoiding this problem is the covaraince analysis shown in chapter 2. This is similar to a technique used by Gotelli and Abele (1983) in looking at effects of area on species richness. Note that similar problems can arise with species-area relationships if corrections are not made for abundance differences. Hurlbert (1971) proposed a method based on expected number of species (E(s)) which is similar to rarefaction, as explained by Simberloff (1978). All of these methods can be used to get around the problem of abundance and density differences, and allow a very useful description of

community structure in terms of richness. Problems with analysis of evenness are less easily resolved, and therefore ecological interpretation of evenness remains somewhat subjective when density differences exist. Richness and evenness are among the most interesting and enlightening concepts in community ecology, but their potential in describing and interpreting community patterns will only be realized if they are used with discretion.

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Appendix A: A list of all species collected, and the number of individuals taken at each site.

Family	Species	Sites 1	2	3	4	5	6
(Amphipods)							
Amphilochidae	*Amphilochus* sp. a	8	39	40	28	27	31
Amphilochidae	*Amphilochus* sp. b	8	3	2	6	1	5
Aoridae	*Microdeutopsis* sp.	2	370	0	1	1	2
Cerotidae	Undetermined sp.	0	1	0	0	0	1
Colomastigidae	*Colomastix* sp.	7	12	2	2	2	4
Isaeidae	?*Megamphopus* sp.	86	41	138	90	203	153
Leucothoidae	*Leucothoe* sp.	7	71	25	4	2	15
Leucothoidae	*Leucothoella* sp.	24	188	65	48	43	25
Leucothoidae	*Leucothoides* sp.	0	0	0	3	0	0
Phoxocephalidae	*Phoxocephalus* sp.	0	0	1	5	0	2
Gammaridae	*Maera* sp.	0	157	0	1	0	3
Undetermined	Amphipod a	0	1	0	0	1	0
Undetermined	Amphipod b	1	0	0	0	0	0
Undetermined	Amphipod c	0	0	0	0	0	1
(Decapods)							
Alpheidae	*Alpheopsis* sp.	2	3	0	2	2	0
Alpheidae	*Alpheus amplyonyx*	0	0	0	3	0	0
Alpheidae	*Alpheus cristulifrons*	2	20	2	5	0	1
Alpheidae	*Alpheus formosus*	1	12	6	4	2	6
Alpheidae	*Synalpheus brevifrons*	0	5	0	0	0	0
Alpheidae	*Synalpheus obtusifrons*	0	17	7	2	1	3
Alpheidae	*Synalpheus pandionis*	3	6	0	6	0	4
Alpheidae	*Synalpheus paraneptunus*	25	0	74	1	1	39
Alpheidae	*Synalpheus sanctithomae*	0	11	0	0	0	0

Appendix A (cont.): A list of all species collected, and the number of individuals taken at each site.

Family	Species	Sites 1	2	3	4	5	6
(Decapods cont.)							
Alpheidae	*Synalpheus townsendi*	2	81	0	4	0	1
Alpheidae	Undetermined sp.	1	5	4	4	9	2
Gnathophyllidae	*Gnathophyllum* sp.	2	0	0	0	1	0
Hippolytidae	*Lysmata rathbunae*	4	3	12	15	5	3
Hippolytidae	*Thor* sp. a	0	68	5	6	3	2
Hippolytidae	*Thor* sp. b.	1	31	4	4	3	0
Hippolytidae	Undetermined a	0	34	2	1	0	0
Hippolytidae	Undetermined b	0	3	0	0	2	0
Palaemonidae	*Brachycarpus biungiculus*	5	5	1	8	1	2
Palaemonidae	*Neopondites* sp.	0	0	0	0	1	0
Palaemonidae	*Periclimenaeus schmidti*?	0	7	0	0	2	1
Palaemonidae	*Periclimenaeus* sp. a	1	9	0	1	1	1
Palaemonidae	*Periclimenaeus* sp. b	0	2	0	0	0	1
Palaemonidae	*Periclimenes americanus*?	0	0	0	2	1	0
Undetermined	Decapod a	1	58	2	2	6	10
Undetermined	Decapod b	0	1	0	0	0	0
Undetermined	Decapod c	0	8	0	0	0	0
Undetermined	Decapod d	0	0	0	0	1	0
Undetermined	Decapod e	0	0	2	0	0	0
(Euphausiid)							
Undetermined	Euphausiid a	1	0	0	0	0	0
(Mysids)							
Mysidae	*Heteromysis dispar*?	0	2	1	2	0	1
Mysidae	*Heteromysis formosa*?	4	0	0	0	2	0
Undetermined	Mysid a	0	0	1	0	0	0

Appendix A (cont.): A list of all species collected, and the number of individuals taken at each site.

Family	Species	Sites 1	2	3	4	5	6
(Ostracods)							
Undetermined	Ostracod a	14	46	17	6	27	58
	Nebalia sp.	8	9	0	1	0	0
(Isopods)							
Anthuridae	*Chalixanthura lewisi*	30	44	28	27	22	51
Anthuridae	*Eisothistos teri*	39	1	55	1	43	46
Anthuridae	*Minyanthura corallicola*	2	2	198	9	545	206
Anthuridae	Undetermined sp.	0	0	1	0	0	0
Apanthuridae	*Apanthura* sp.	0	0	1	7	1	3
Apanthuridae	*Mesanthura paucidens*	0	1	0	0	1	0
Apanthuridae	*Mesanthura pulchra*	0	3	2	1	0	4
Cirolanidae	*Cirolana minuta*	3	3	3	0	8	4
Cryptoniscid larva		0	1	0	1	1	1
Gnathiidae	*Gnathia rathi*	11	12	38	27	57	102
Janiridae	*Carpias minutus*	147	3	125	108	152	126
Joeropsidae	*Joeropsis personatus*	0	0	16	0	0	0
Stenetriidae	*Stenetrium patulipalma*	49	7	102	27	43	56
Stenetriidae	*Stenetrium spathulicarpus*	32	0	0	0	0	0
Undetermined	Isopod a	0	0	0	0	2	0
Undetermined	Isopod b	0	2	0	1	0	1
Undetermined	Isopod c	0	0	0	1	0	0
Undetermined	Isopod d	0	1	2	1	0	0
Undetermined	Isopod e	1	0	0	0	1	2
Undetermined	Isopod f	0	0	0	0	2	3

Appendix A (cont.): A list of all species collected, and the number of individuals taken at each site.

Family	Species	Sites 1	2	3	4	5	6
(Tanaids)							
Apseudidae	Apseudomorpha sp.	14	11	6	109	83	32
	Cycloapseudes indecorus?	0	9	0	0	0	0
Paratanaidae	?Heterotanais sp. a	74	133	99	25	57	47
Paratanaidae	?Heterotanais sp. b	21	4	23	26	52	46
Paratanaidae	?Heterotanais sp. c	21	5	21	11	26	6
Paratanaidae	?Heterotanais sp. d	0	0	0	1	0	0
Paratanaidae	Leptochelia savigni	0	2	0	0	0	0
Paratanaidae	Tanaid a	0	0	0	1	0	2
Sphyrapidae	Undetermined	146	70	120	118	74	121
(Caprellid)							
Undetermined	Caprellid a	0	2	2	0	3	10
(Cumacean)							
Undetermined	Cumacean a	1	4	1	2	1	0
(Copepods)							
Artotrigidae	Acontiphorus sp. nov.	11	0	31	4	24	11
Asterocheridae	Asterocheres sp.	146	179	70	32	59	197
Asterocheridae	Scottocheres elongatus	7	43	1	5	4	6
	Pteropontius sp. nov.	0	4	7	0	0	2
Diosaccidae	Amphiascus paracaudespinosis	74	33	120	69	127	61
Diosaccidae	Amphioscopsis sp.	6	11	28	24	37	18
Diosaccidae	Undetermined sp.	55	5	52	22	57	10

Appendix A (cont.): A list of all species collected, and the number of individuals taken at each site.

Family	Species	Sites 1	2	3	4	5	6
(Copepods cont.)							
Ectinosomatidae	Pseudobradya sp.	18	20	13	29	14	3
Ectinosomatidae	Undetermined sp.	12	11	4	3	7	13
Ectinosomatidae	Undetermined sp.	6	6	9	4	5	6
Laophontidae	Laophonte bulbifera?	13	8	14	5	6	9
Laophontidae	Paralaophonte adriatic?	4	8	23	7	23	16
Laophontidae	Phyllopodopsyllus sp.	20	10	25	6	24	13
Lichomoglidae	Undetermined sp. b	3	0	0	2	1	11
Lichomoglidae	Undetermined sp. c	0	1	5	0	6	0
Peltidae	Pertidinum perturbatum	9	0	29	7	131	26
Peltidae	Undetermined sp.	1	10	11	6	58	31
Porcellidium	Porcellidium trisetosum	1	9	11	0	9	32
Siphonostomatoid	Undetermined sp.	2	3	0	0	6	0
Tetragonoceptidae	Undetermined sp. a	2	6	5	3	4	3
Thalestridae	Dactylopusia platysoma	0	0	1	0	2	0
Thalestridae	Phyllothalestris mysis?	0	1	0	1	0	0
Tisbidae	Tisbe sp. a	12	7	8	20	12	9
Tisbidae	?Tisbe sp. b	10	12	14	10	21	15
Undetermined	Copepod a	2	1	12	4	11	1
Undetermined	Copepod b	2	1	3	3	5	2
Undetermined	Copepod c	0	0	1	0	0	0
Undetermined	Copepod d	2	1	4	2	5	1
Undetermined	Copepod e	11	18	0	0	0	0

Appendix A (cont.): A list of all species collected, and the number of individuals taken at each site.

Family	Species	Sites 1	2	3	4	5	6
(Copepods cont.)							
Undetermined	Copepod f	0	4	3	1	2	9
Undetermined	Copepod g	1	1	1	3	4	4
Undetermined	Copepod h	0	6	0	0	0	0
Undetermined	Copepod i	0	0	1	0	0	1
Undetermined	Copepod j	1	0	1	0	2	1
Undetermined	Copepod k	1	16	0	1	0	0
Undetermined	Copepod l	1	11	2	2	1	0
Undetermined	Copepod m	2	7	0	1	3	0
Undetermined	Copepod n	3	1	1	0	1	0
Undetermined	Copepod o	0	0	0	2	1	0
Undetermined	Copepod p	0	0	0	0	2	0
Undetermined	Copepod q	2	0	1	6	0	0
Undetermined	Copepod r	0	0	1	0	0	0
Undetermined	Copepod s	1	0	0	0	0	0
Undetermined	Copepod t	1	0	0	1	1	0
Undetermined	Copepod u	0	0	0	0	1	0
Undetermined	Copepod v	0	0	0	0	5	0
Undetermined	Copepod w	0	0	0	1	0	0

Appendix B: Values of H, H_{max}, J, total individuals, and species count for the 3 sites examined in Chapter 2.

Site	Sample Number	Species Number	H	H_{max}	J	Number of individuals
(All taxa combined)						
Bank Reef	01	31	1.131	1.344	0.842	148
Bank Reef	02	28	0.988	1.299	0.761	132
Bank Reef	03	29	1.052	1.335	0.788	169
Bank Reef	04	24	1.032	1.271	0.812	168
Bank Reef	05	24	1.028	1.203	0.855	87
Bank Reef	06	24	1.041	1.106	0.941	45
Bank Reef	07	23	0.973	1.118	0.870	52
Bank Reef	08	22	1.002	1.172	0.855	83
Bank Reef	09	30	1.108	1.316	0.842	126
Bank Reef	10	34	1.160	1.377	0.842	155
Bank Reef	11	32	1.243	1.349	0.921	143
Bank Reef	12	34	1.162	1.327	0.876	101
Bank Reef	13	30	1.092	1.405	0.791	103
Bank Reef	14	33	1.213	1.394	0.870	198
Bank Reef	15	33	1.166	1.353	0.862	133
Payne's Bay	01	22	0.822	1.225	0.671	140
Payne's Bay	02	10*	0.757	1.824	0.919	31
Payne's Bay	03	43	1.077	1.515	0.711	284
Payne's Bay	04	19	0.782	1.138	0.687	92
Payne's Bay	05	26	1.105	1.277	0.865	133
Payne's Bay	06	32	0.898	1.431	0.628	383
Payne's Bay	07	27	1.024	1.217	0.841	75
Payne's Bay	08	32	0.949	1.385	0.685	203
Payne's Bay	09	21	0.981	1.188	0.826	111
Payne's Bay	10	31	1.092	1.345	0.812	150
Payne's Bay	11	20	0.888	1.178	0.754	117
Payne's Bay	12	38	1.204	1.453	0.829	225
Payne's Bay	13	37	1.207	1.368	0.882	115
Payne's Bay	14	20	0.908	1.113	0.816	65
Payne's Bay	15	42	1.202	1.540	0.781	440
Brighton	01	25	0.817	1.238	0.660	104
Brighton	02	28	1.107	1.214	0.912	70
Brighton	03	24	0.720	1.242	0.580	122
Brighton	04	26	1.049	1.243	0.844	99
Brighton	05	23	1.064	1.159	0.918	67
Brighton	06	23	0.981	1.115	0.880	51
Brighton	07	28	1.121	1.288	0.870	120
Brighton	08	36	1.122	1.395	0.804	154
Brighton	09	12	0.755	0.844	0.895	25
Brighton	10	21	1.015	1.248	0.813	52
Brighton	11	29	1.100	1.288	0.854	109
Brighton	12	27	1.133	1.276	0.888	120
Brighton	13	25	1.057	1.204	0.878	79
Brighton	14	13	0.802	0.970	0.827	58
Brighton	15	16	0.948	1.051	0.902	67

*Outlier omitted from ANCOVA

Appendix B (cont.): Values of H, H_{max}, J, total individuals and species count for the 3 sites examined in Chapter 2.

Site	Sample Number	Species Number	H	H_{max}	J	Number of individuals
(Isopods)						
Bank Reef	01	11	0.773	0.930	0.831	67
Bank Reef	02	12	0.616	0.976	0.631	83
Bank Reef	03	10	0.675	0.910	0.742	81
Bank Reef	04	9	0.717	0.889	0.807	109
Bank Reef	05	10	0.749	0.829	0.903	33
Bank Reef	06	5	0.504	0.518	0.973	12
Bank Reef	07	10	0.676	0.787	0.859	33
Bank Reef	08	6	0.564	0.689	0.819	42
Bank Reef	09	10	0.661	0.879	0.752	54
Bank Reef	10	14	0.705	1.018	0.693	74
Bank Reef	11	8	0.724	0.804	0.900	54
Bank Reef	12	13	0.768	0.936	0.821	43
Bank Reef	13	9	0.648	0.847	0.765	56
Bank Reef	14	11	0.742	0.930	0.798	67
Bank Reef	15	13	0.808	0.987	0.819	69
Payne's Bay	01	3	0.123	0.430	0.286	35
Payne's Bay	02	2	0.121	0.221	0.548	7
Payne's Bay	03	9	0.496	0.901	0.550	142
Payne's Bay	04	6	0.298	0.625	0.477	55
Payne's Bay	05	3	0.167	0.411	0.406	22
Payne's Bay	06	6	0.534	0.668	0.799	32
Payne's Bay	07	7	0.423	0.715	0.592	31
Payne's Bay	08	6	0.289	0.726	0.398	88
Payne's Bay	09	4	0.412	0.540	0.763	39
Payne's Bay	10	4	0.229	0.543	0.422	41
Payne's Bay	11	3	0.268	0.435	0.616	41
Payne's Bay	12	8	0.427	0.799	0.534	50
Payne's Bay	13	6	0.425	0.651	0.653	26
Payne's Bay	14	1	0.000	0.000	.	22
Payne's Bay	15	8	0.449	0.845	0.531	113
Brighton	01	9	0.471	0.868	0.543	76
Brighton	02	9	0.691	0.766	0.902	25
Brighton	03	8	0.561	0.766	0.732	34
Brighton	04	6	0.573	0.671	0.854	33
Brighton	05	9	0.742	0.815	0.910	39
Brighton	06	9	0.655	0.794	0.825	32
Brighton	07	10	0.743	0.877	0.847	53
Brighton	08	11	0.749	0.927	0.808	65
Brighton	09	3	0.373	0.386	0.966	14
Brighton	10	6	0.576	0.622	0.926	19
Brighton	11	10	0.721	0.864	0.834	46
Brighton	12	9	0.701	0.828	0.847	44
Brighton	13	11	0.783	0.909	0.861	53
Brighton	14	5	0.512	0.608	0.842	32
Brighton	15	5	0.503	0.592	0.850	25

Appendix B (cont.): Values of H, H_{max}, J, total individuals and species count for the 3 sites examined in Chapter 2.

Site	Sample Number	Species Number	H	Hmax	J	Number of individuals
(Amphipods)						
Bank Reef	01	3	0.336	0.432	0.778	37
Bank Reef	02	3	0.309	0.406	0.761	20
Bank Reef	03	4	0.396	0.538	0.736	37
Bank Reef	04	1	0.000	0.000	.	1
Bank Reef	05	3	0.296	0.410	0.722	21
Bank Reef	06	4	0.365	0.464	0.787	12
Bank Reef	07	3	0.232	0.332	0.699	7
Bank Reef	08	3	0.349	0.369	0.946	11
Bank Reef	09	3	0.280	0.417	0.671	25
Bank Reef	10	3	0.362	0.417	0.868	25
Bank Reef	11	5	0.447	0.562	0.795	18
Bank Reef	12	3	0.259	0.259	1.000	3
Bank Reef	13	4	0.402	0.480	0.838	15
Bank Reef	14	3	0.368	0.381	0.966	13
Bank Reef	15	3	0.329	0.422	0.780	28
Payne's Bay	01	4	0.284	0.563	0.504	71
Payne's Bay	02	4	0.404	0.468	0.863	13
Payne's Bay	03	7	0.483	0.716	0.675	49
Payne's Bay	04	2	0.140	0.200	0.700	5
Payne's Bay	05	5	0.569	0.606	0.939	31
Payne's Bay	06	6	0.317	0.755	0.420	239
Payne's Bay	07	3	0.296	0.326	0.908	6
Payne's Bay	08	5	0.431	0.635	0.679	52
Payne's Bay	09	3	0.307	0.427	0.719	32
Payne's Bay	10	7	0.602	0.754	0.798	51
Payne's Bay	11	5	0.440	0.634	0.694	51
Payne's Bay	12	6	0.697	0.732	0.952	101
Payne's Bay	13	9	0.691	0.779	0.887	27
Payne's Bay	14	6	0.552	0.592	0.932	15
Payne's Bay	15	7	0.609	0.803	0.758	139
Brighton	01	3	0.306	0.369	0.829	11
Brighton	02	4	0.366	0.425	0.861	8
Brighton	03	4	0.356	0.356	1.000	5
Brighton	04	4	0.403	0.425	0.948	8
Brighton	05	3	0.278	0.344	0.808	8
Brighton	06	2	0.159	0.159	1.000	3
Brighton	07	3	0.264	0.422	0.626	28
Brighton	08	8	0.576	0.686	0.840	17
Brighton	09	2	0.151	0.151	1.000	2
Brighton	10	2	0.106	0.233	0.455	9
Brighton	11	2	0.189	0.221	0.855	7
Brighton	12	4	0.440	0.451	0.976	11
Brighton	13	3	0.232	0.332	0.699	7
Brighton	14	1	0.000	0.000	.	14
Brighton	15	1	0.000	0.000	.	4

Appendix B (cont.): Values of H, H_{max}, J, individuals and species count for the 3 sites examined in Chapter 2.

Site	Sample Number	Species Number	H	H_{max}	J	Number of individuals
(Decapods)						
Bank Reef	01	4	0.375	0.443	0.847	7
Bank Reef	02	3	0.259	0.259	1.000	3
Bank Reef	03	6	0.311	0.676	0.460	35
Bank Reef	04	2	0.151	0.151	1.000	2
Bank Reef	05	3	0.270	0.270	1.000	4
Bank Reef	06	4	0.356	0.356	1.000	5
Bank Reef	07	1	0.000	0.000	.	1
Bank Reef	08	3	0.260	0.295	0.881	5
Bank Reef	09	2	0.159	0.159	1.000	3
Bank Reef	10	6	0.461	0.626	0.736	20
Bank Reef	11	4	0.381	0.425	0.896	8
Bank Reef	12	2	0.121	0.221	0.548	7
Bank Reef	13	1	0.000	0.000	.	3
Bank Reef	14	3	0.231	0.426	0.542	31
Bank Reef	15	3	0.260	0.295	0.881	5
Payne's Bay	01	8	0.690	0.759	0.909	24
Payne's Bay	02	3	0.350	0.362	0.967	10
Payne's Bay	03	9	0.703	0.795	0.884	21
Payne's Bay	04	5	0.503	0.580	0.867	22
Payne's Bay	05	8	0.735	0.794	0.926	47
Payne's Bay	06	9	0.731	0.914	0.800	56
Payne's Bay	07	4	0.418	0.506	0.826	10
Payne's Bay	08	9	0.762	0.838	0.909	29
Payne's Bay	09	7	0.567	0.631	0.899	14
Payne's Bay	10	11	0.771	0.912	0.845	43
Payne's Bay	11	3	0.361	0.451	0.800	11
Payne's Bay	12	8	0.668	0.766	0.872	25
Payne's Bay	13	9	0.667	0.832	0.802	34
Payne's Bay	14	8	0.654	0.736	0.889	20
Payne's Bay	15	9	0.626	0.951	0.658	89
Brighton	01	4	0.345	0.345	1.000	4
Brighton	02	6	0.464	0.517	0.897	9
Brighton	03	1	0.000	0.000	.	4
Brighton	04	5	0.317	0.608	0.521	32
Brighton	05	2	0.151	0.151	1.000	2
Brighton	06	1	0.000	0.000	.	1
Brighton	07	3	0.295	0.295	1.000	5
Brighton	08	6	0.518	0.536	0.966	10
Brighton	09	0	0.000	0.000	.	0
Brightin	10	2	0.159	0.159	1.000	3
Brighton	11	1	0.000	0.000	.	1
Brighton	12	2	0.140	0.200	0.700	5
Brighton	13	0	0.000	0.000	.	0
Brighton	14	0	0.000	0.000	.	0
Brighton	15	0	0.000	0.000	.	0

Appendix B (cont.): Values of H, H_{max}, J, total individuals and species count for the 3 sites examined in Chapter 2.

Site	Sample Number	Species Number	H	H_{max}	J	Number of individuals
(Copepods)						
Bank Reef	01	13	0.722	0.918	0.786	37
Bank Reef	02	10	0.717	0.797	0.900	26
Bank Reef	03	9	0.641	0.701	0.914	16
Bank Reef	04	12	0.782	0.941	0.831	56
Bank Reef	05	8	0.483	0.749	0.645	29
Bank Reef	06	11	0.709	0.739	0.959	16
Bank Reef	07	9	0.636	0.636	1.000	11
Bank Reef	08	10	0.629	0.792	0.794	25
Bank Reef	09	15	0.835	0.983	0.849	44
Bank Reef	10	11	0.788	0.867	0.909	36
Bank Reef	11	15	0.937	1.023	0.916	63
Bank Reef	12	16	0.858	1.013	0.847	48
Bank Reef	13	16	0.855	0.932	0.917	29
Bank Reef	14	16	0.906	1.076	0.842	87
Bank Reef	15	14	0.849	0.912	0.931	31
Payne's Bay	01	6	0.518	0.536	0.966	10
Payne's Bay	02	1	0.000	0.000	0.000	1
Payne's Bay	03	16	0.746	0.057	0.706	72
Payne's Bay	04	6	0.448	0.536	0.836	10
Payne's Bay	05	10	0.495	0.829	0.597	33
Payne's Bay	06	9	0.655	0.847	0.773	56
Payne's Bay	07	12	0.754	0.856	0.881	28
Payne's Bay	08	8	0.368	0.766	0.480	34
Payne's Bay	09	7	0.540	0.698	0.774	26
Payne's Bay	10	8	0.612	0.667	0.918	15
Payne's Bay	11	8	0.584	0.652	0.896	14
Payne's Bay	12	15	0.893	0.994	0.898	49
Payne's Bay	13	12	0.759	0.856	0.887	28
Payne's Bay	14	4	0.366	0.425	0.861	8
Payne's Bay	15	16	0.804	1.088	0.739	99
Brighton	01	9	0.647	0.661	0.979	13
Brighton	02	9	0.639	0.781	0.818	28
Brighton	03	11	0.289	0.942	0.307	79
Brighton	04	11	0.739	0.823	0.898	26
Brighton	05	9	0.682	0.728	0.937	18
Brighton	06	11	0.716	0.727	0.985	15
Brighton	07	12	0.796	0.885	0.899	34
Brighton	08	11	0.567	0.922	0.615	62
Brighton	09	7	0.551	0.551	1.000	9
Brighton	10	11	0.745	0.795	0.937	21
Brighton	11	16	0.783	1.026	0.763	55
Brighton	12	12	0.779	0.950	0.820	60
Brighton	13	11	0.729	0.772	0.944	19
Brighton	14	7	0.569	0.600	0.948	12
Brighton	15	10	0.728	0.845	0.862	38