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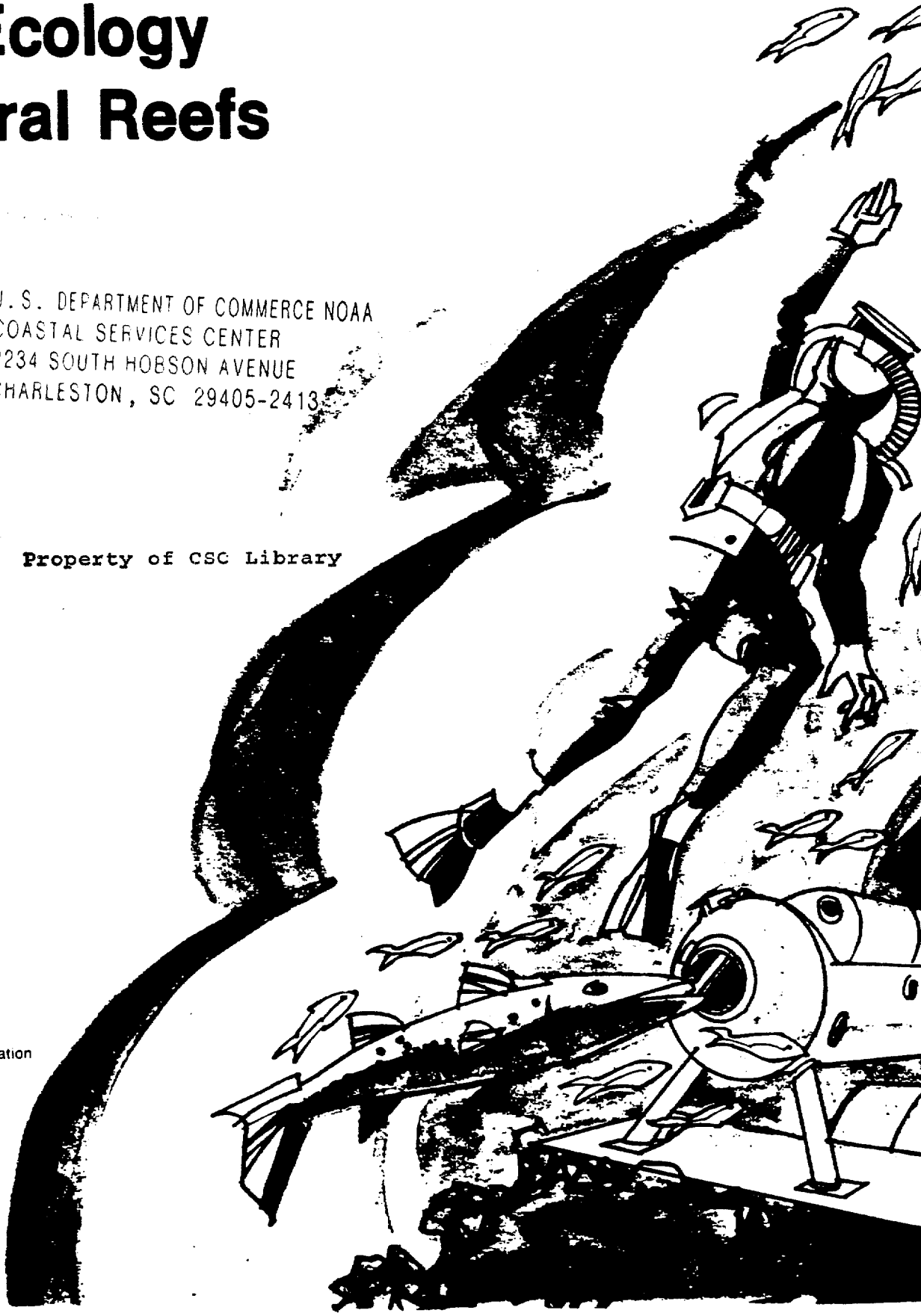

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SYMPOSIA SERIES FOR UNDERSEA RESEARCH
NOAA'S UNDERSEA RESEARCH PROGRAM, VOL. 3 NO. 1, 1985

The Ecology of Coral Reefs

Results of a Workshop on Coral Reef Ecology held by the American Society of Zoologists, Philadelphia, Pennsylvania, December 1983

Edited by
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Washington, D.C.
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CHAPTER I: INTRODUCTION

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This volume presents the results of a workshop on the ecology of coral reefs that was held at the American Society of Zoologists meetings in Philadelphia, December 1983. The workshop, which included four symposium presentations, four discussion sections, and presentations of undersea research facilities by NOAA's Office of Undersea Research, was sponsored by the Division of Ecology of the ASZ. The four symposium talks and discussion sections addressed the topics of growth and life history patterns, recruitment, community organization, and community metabolism in coral reef systems. The workshop was unusually well attended (attendance in the Ecology Division of the ASZ was 30% higher than in previous years and two additional contributed paper sessions in the Division of Ecology were devoted specifically to coral reef ecology), and vigorous group discussions continued well into the night. The objective of the workshop was to focus attention on what we do and do not know about the ecology of coral reefs, particularly along depth gradients, and to assess the most important directions for future research on coral reefs.

A previous volume in this series (Reaka, 1983), containing symposium presentations and contributed papers in each of the four topical areas, was made available at the Coral Reef Workshop. The present volume presents the main conclusions derived from the discussion sections (Chapter II) and additional contributed papers on the ecology of coral reefs (Chapter III).

In Chapter II, the discussion leaders summarize the topics discussed and the conclusions reached in each discussion section. William McFarland points out that astonishingly little is known about recruitment in coral reef species. He identifies some of the reasons for our lack of knowledge in this area, not the least of which is the prevalence of planktonic larvae in reef organisms. The production of hundreds to millions of tiny dispersing planktotrophic larvae distinguishes marine animals from those in every other major environment. Furthermore, the incidence of species with long-lived planktotrophic larvae is inversely related to latitude (Thorson, 1950; Mileikovsky, 1971), so that, in contrast to marine communities from high latitudes, the vast majority of coral reef species produce planktonic dispersing young. This phenomenon has profound implications for the population dynamics, community organization, and even evolutionary patterns of marine species compared to those in terrestrial or fresh water environments. In marine species thousands of recruits may occur in local areas in some years but not in others; planktonic larvae may settle in their parent population, may be carried to distant habitable sites, or even may be swept out to sea without any favorable substrate having been encountered. McFarland discusses several mechanisms that enhance the predictability of local recruitment on coral reefs, including the timing and dynamics of reproduction, currents or eddies that may return larvae to their parent populations, and behavioral patterns of the larvae and settling juveniles themselves. These

mechanisms, as well as fine scale observations of the larvae of species from different reef habitats, deserve extensive research before we will understand this critically important aspect of the biology of coral reef organisms.

Ronald Karlson summarizes the conclusions of his discussion section on a related topic, life history patterns. An emerging body of research demonstrates that the observed growth rates, form, and longevity of corals along depth gradients result from complex interactions between physical (e.g., light and wave disturbance) and biotic variables. Recent research shows that sublethal phenomena such as injuries due to physical and biotic agents have significant implications for growth and reproduction in many sessile reef organisms. These processes can vary significantly in different habitats. This discussion group also addressed the important topic of ecological and evolutionary patterns in solitary vs. colonial organisms on coral reefs. The importance of fission, fusion, and fragmentation (and thus of colony size) in both solitary and colonial species received particular attention as a productive avenue for future research.

Mark Hixon lead the discussion section on community structure and function. Coral reef ecologists have been in the forefront of the debate on whether communities are organized by stable predictable processes or whether they merely represent independent populations in shifting states of disequilibria. One of the reasons that disequilibrium and stochastic processes have been so apparent in coral reef communities may be because dispersing, feeding larvae engender unpredictable recruitment. However, recent research also has demonstrated the importance of irregular catastrophic perturbations, such as storms (e.g., Woodley, et al., 1981), population outbreaks (e.g., Birkeland, 1982), or diseases (e.g., Lessios, et al., 1984) in the organization of coral reef communities. One of these events, the mass mortality of Caribbean sea urchin populations, was ongoing at the time of the workshop and was a major topic of discussion. Although the causes and mechanisms of this outbreak still are not well understood, Hixon identifies the heuristic value of this "natural experiment" which has removed a major herbivore over large local and geographical areas of reefs. This discussion lead to an evaluation of a more deterministic process, herbivory by urchins vs. fishes, on reefs; this discussion centered on how human activities such as fishing in certain well studied localities can affect our interpretations of the past and present organization of reef communities. Although terrestrial and fresh water ecologists have been concerned about the effects of human intervention on natural communities for some time, the pervasiveness of this problem in coral reef communities has attracted attention only recently. Hixon argues that one of the most critical needs for future research is for experimental manipulations and long term comparative studies.

The discussion section on community metabolism was led by Stephen Smith. Smith shows how this field has developed from a focus on oxygen and carbon flux to studies of the physical, chemical, and biological variables that control metabolism of the reef ecosystem. The discussion addressed how the quantity and quality of available nutrients affect productivity, how nutrient flux between subcommunities can affect nutrient balance of the overall reef ecosystem, and how new technological approaches can improve our ability to measure community metabolism. Smith stresses that a holistic approach, including comparisons with other ecosystems, will represent important avenues for future research in this area.

Chapter III includes contributed papers whose topics span those covered in the four discussion groups. McFarland and Ogden provide a comprehensive review of recruitment in coral reef fishes and evaluate the various hypotheses advanced to account for the presence of planktonic larvae. They conclude that both reduced predation on young and enhanced dispersal favor the development of long-lived larvae which migrate offshore from local reefs. Due to the heterogeneity in patterns of larval development, however, these authors note that the relative importance of these selective factors must vary among different species of reef fishes. Brothers and Thresher evaluate the relationship between larval durations and the extent of the geographic distributions in 115 species of reef fishes. Their study yields the new and interesting result that, if larval durations are < about 45 days, the size of the geographic range (usually an indication of dispersal patterns) is not correlated with length of larval life. Larvae which have pelagic phases longer than 45 days, however, all have broad distributions and can transgress oceanic barriers at least occasionally. This work, then, has important implications for patterns of colonization and biogeography. Lobel and Neudecker analyze another aspect of reproductive biology of reef fishes that can influence dispersal of larvae on reefs: the timing and location of spawning. They describe and compare courtship in several species of hamlets. These fishes spawn at dusk over specific high reef structures, which may reduce predation and facilitate dispersal of eggs. The time and duration of spawning is influenced by depth and/or lunar phase as well as simulated attacks by predators. Emson, Mladenov, and Wilkie provide information on a different aspect of reproductive biology in a reef invertebrate. Various modes of asexual reproduction, including fission, are well known in a number of relatively sessile invertebrate phyla. However, these authors demonstrate that fission represents the major method of reproduction in many small species of motile brittle stars associated with algae and sea grass in lagoonal habitats. Many of these ophiuroids also apparently produce dispersing planktonic larvae, an unexpected phenomenon because small size usually is associated with brooding. These results again have implications for patterns of recruitment and maintenance of local populations.

Both meroplankton (the larvae of benthic reef organisms) and holoplankton (organisms that spend their entire life in the plankton) exhibit diel vertical migrations that are likely to influence their tendency to disperse in currents and their susceptibility to predation. The long term study reported by Ohlhorst also suggests that other factors, such as preceding rain and lunar effects, can influence abundance of zooplankton above the reef. Ohlhorst further demonstrates that numbers of zooplankton decline significantly with increased depth, and that even in the shallow areas these plankton can provide relatively little of the metabolic requirements for sessile reef organisms. Using frequent collections throughout the day and night, Ohlhorst and Liddell provide the first precise documentation of a predawn surge in abundance of plankton over the reef that complements the postsunset peak of emergence known for these organisms. A swarming holoplanktonic copepod usually was the most common zooplankter in both Jamaica and St. Croix, although other taxa, including meroplankters, became prominent during the hours around sunset. These papers therefore are related to the topics of dispersal and reproductive biology discussed above but also bear on community organization and energy flow among different components of the reef community.

The following three papers in the volume deal with damselfishes and/or urchins on reefs. The territorial activities of damselfishes are known to be significant for the structure and productivity of reef communities (e.g., Brawley and Adey, 1977; Hixon, 1983; and others). Sadovy studied the detailed dominance relations among individuals of bicolored damselfish in the field. Her results showed a linear, size-dependent dominance hierarchy in these fish and revealed some interesting similarities and differences between field and otherwise comparable laboratory studies. Robinson and Williams compare population characteristics of threespot damselfish and urchins (Diadema) in shallow back reef and fore reef environments. They found that urchins are larger, occur in lower densities, and are found higher in coral branches on the back reef than on the fore reef; in contrast, damselfish live at higher densities, have larger lawns, and exhibit less aggression toward urchins on the fore reef than on the back reef. Urchins may remain small and close to the substrate on the shallow fore reef because high wave action inhibits their grazing; thus interference between urchins and damselfish is less strong when mediated by disturbance on the fore reef than in more benign conditions on the back reef. Examining another species of urchin with a different but very significant impact on the structure of reefs, Hoskin and Reed use carefully controlled experimental methods to estimate the rates of bioerosion of carbonate substrates by urchins (Echinometra) and other burrowing infauna. These urchins excavate approximately 8.9 g substrate/m^2/day (9 tons/year for the population), while the remaining infauna produces about 5 g sediment/m^2/day (6.5 tons/year). This study illustrates the tremendous amount of sediment that is produced and transported in benthic reef communities. Scouring and burial by this sediment must represent one of the most important agents influencing the structure and dynamics of reef communities, yet the significance of these processes for community organization are almost unstudied. In addition, this study provides new data on the sources and rates of degradation of reef substrates, a significant aspect of long term morphogenesis and diagenesis of reefs. This paper therefore provides a link between the papers on community organization and those on community metabolism.

Adey and Steneck show how reef productivity is related to substrate complexity and surface area, light and water flow, and abundance of turf algae. They demonstrate that all of these factors can be understood in the context of geological development of the reefs. Using upstream/downstream flow respirometry techniques on reefs in three different stages of geological development in St. Croix, these authors provide good evidence for some of the highest rates of primary productivity reported for any marine environment. Dustan explores a different method of assessing primary productivity. He provides initial data on the spectral intensities of light impinging on, absorbed, and reflected by different substrates. Dustan suggests that much can be learned about the photobiology of reef organisms using these nondestructive bio-optical sampling techniques and indicates that we may be able to estimate primary productivity over vast tracts of previously inaccessible reefs if optical signals from these reefs can be detected from orbiting spacecraft. Although we are in the initial stages of interpreting these data, such new technological approaches offer the promise of measuring and understanding productivity on a global scale. Seitzinger and D'Elia present data on another new and potentially important aspect of community metabolism on reefs. While nitrogen fixation on reefs has received well deserved attention, Seitzinger and D'Elia show that some reef habitats, in particular dead coral heads and sediments, may be the sites of extensive denitri-

ERRATA

Several typographical errors were inadvertently included in our publication of The Ecology of Deep and Shallow Coral Reefs [Symp. Ser. Undersea Res., Vol. 1(1), 1983], and we would like to take this opportunity to correct them.

For Chornesky, E. A., and S. L. Williams, "Distribution of Sweeper Tentacles on Montastrea cavernosa, p. 61, par. 3, line 15 should read "or after contact and recognition;" p. 63, caption for figure 1 should read "For M. annularis, change in number of polyps."

For Wolf, N. G., E. B. Bermingham, and M. L. Reaka, "Relationships Between Fishes and Mobile Benthic Invertebrates on Coral Reefs," p. 69, the address of E. B. Bermingham should read "Department of Molecular and Population Genetics;" p. 72, line 3 should read "Although fewer planktivores were recorded on C than on A reefs."

For Hay, M. E., and T. Goertemiller, "Between-Habitat Differences in Herbivore Impact on Caribbean Coral Reefs," p. 100, par. 4, line 3 should read "and 12.8% versus 1% on Lighthouse (fig. 1);" p. 101, par. 2, lines 10-11 should read "or motility in sea urchin sperm (Norris and Fenical 1982, Paul and Fenical 1983). The polyphenolic compounds produced by Turbinaria."

For Szmant-Froelich, A., "Functional Aspects of Nutrient Cycling on Coral Reefs," p. 136, Table 1, DIN should be TDN.

fication, whereby NO_2^- and NO_3^- are lost from the system as atmospheric N_2. Such studies make important contributions to Smith's goal of understanding the overall balance of nutrient flow within and between major components of reef communities.

Many people have contributed to the successful completion of this volume. Thanks are especially extended to the authors for their fine contributions and cooperation throughout the editing process. In addition, the reviewers of these papers are gratefully acknowledged for contributing their time and criticisms, all of which improved the volume. Completion of this symposium volume would have been impossible without the expert typing and editorial assistance of Ms. Marcia Collie, Staff Assistant from NOAA's Office of Undersea Research; her cooperation, advice, and assistance through all the stages of publication are acknowledged with heartfelt thanks. Similarly, publication was made possible through NOAA's Office of Undersea Research, and the support of Mr. William Busch and Mr. Elliott Finkle throughout this endeavor are sincerely appreciated. Lastly, I thank my husband, Stephen, and our two little blonde boys, Alexei and Erik, for their sunshine and enthusiasm.

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CHAPTER II: RESULTS OF A WORKSHOP ON CORAL REEF ECOLOGY: SYNTHESES OF DISCUSSION SECTIONS

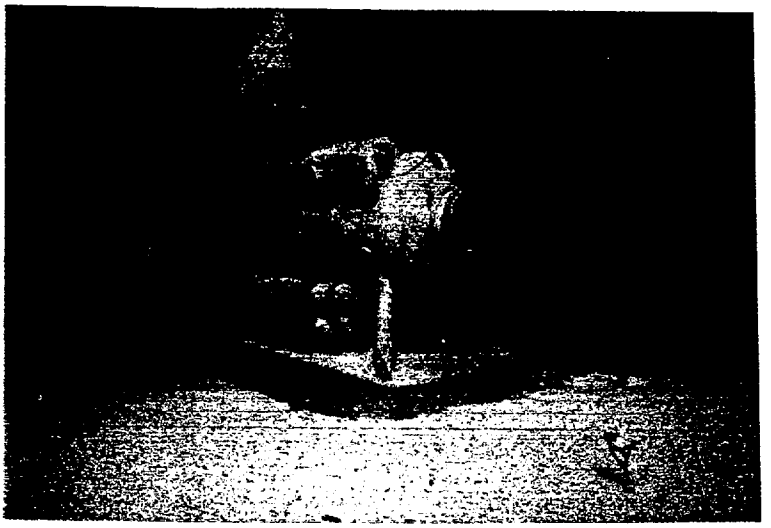

Figure 1

Coral reefs have been tremendously important in the history of human civilizations. Reefs support fisheries and provide protected embayments that are essential for food and commerce in coastal cultures. It is critical that we understand the biological dynamics responsible for the formation and degradation of these systems in order to preserve and manage their resources. NOAA's underwater habitat, HYDROLAB (fig. 1), has (continued on next page)

Figure 2

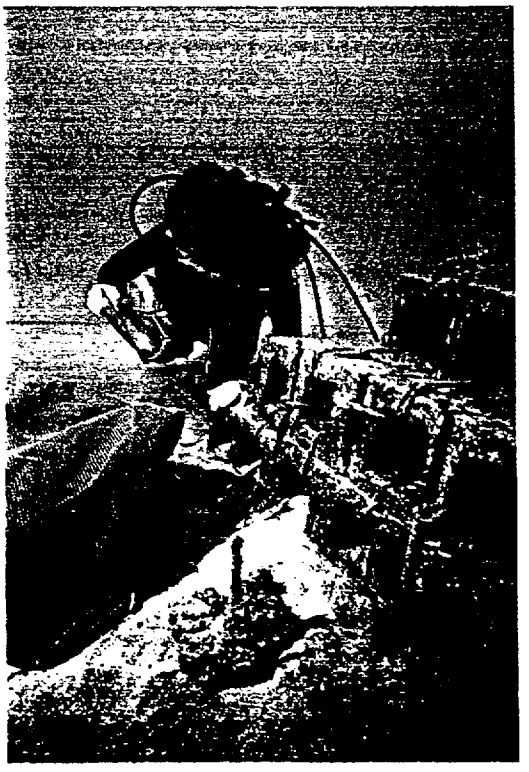

Figure 3

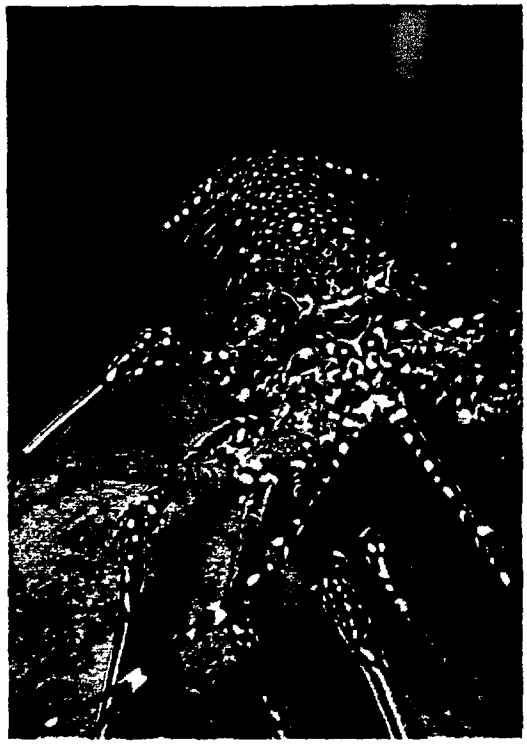

Figure 4

Figure 5

allowed scientists to conduct experimental field studies on reproduction, recruitment, population dynamics, and community organization of coral reef communities that would have been impossible without the extended diving time made possible through saturation techniques. Here divers study the factors that influence recruitment of fishes and invertebrates (figs. 2, 3, 4), many of them important fisheries and food stocks, on artificial reefs where large predators and grazers are excluded or allowed access. These facilities also have allowed extended study of the life histories, growth, and species interactions of the major structural agents on reefs, corals and sponges (fig. 5). The AEGIR, NOAA's mobile underwater habitat that will replace HYDROLAB in 1986, also is shown here (fig. 6).

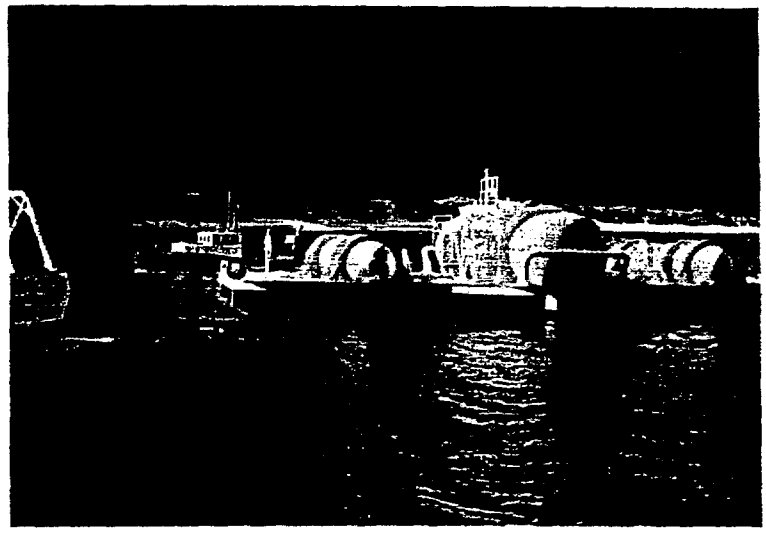

Figure 6

discussion section that spawning is a variable act within and between species and an activity that involves considerable behavioral plasticity. If the function of casting eggs into the plankton is to rapidly remove them from reef predators, then doing so at dusk (as many fish do) would seem safest. The fact that many fish do not spawn at dusk may relate to the presence of favorable currents that flush the eggs rapidly offshore and out of the reach of abundant small reef predators. Unfortunately, few papers deal simultaneously with spawning and local currents (McFarland and Ogden, 1985). As a result, it is rather difficult to resolve the differences that exist between species (see Robertson, 1983, for spawning variation in several acanthurids).

Although recruitment from the plankton occurs at the end of the larval stage, knowing how and when potential propagules are introduced into the plankton is essential for understanding recruitment because the spawning act initiates the recruitment process. The difficulties identified above could be partly resolved by an integrated study in a local area of the seasonal, monthly, and diel spawnings of many different species of coral reef fishes. Evaluating the function(s) of differential spawning amongst the various species will require that the observations be tightly coupled with analysis of local currents (for example, Robertson, 1983). If this is accomplished in several different areas, it should be possible to sort out the trade-offs that different species invoke in order to "safely" deliver young to the plankton.

Once spawned, the eggs of coral reef fishes usually hatch within a day (Thresher, 1984). Although most coral reef fish eggs and larvae are flushed offshore, in some circumstances the eggs and larvae are entrained within lagoons (apparently by local currents). Because eggs and very young larvae cannot swim and orient actively (Leis and Rennis, 1983), it is generally assumed that, when at sea, larvae are widely dispersed (through diffusional and other processes). As pointed out by Lobel during the discussion, similarly sized larvae of the same species often are taken in the same plankton hauls. In addition, newly recruited fish larvae often appear on reef sites in small groups of 3 or more fish (e.g., pempherids, high hats, grunts, etc.), but may also recruit as individuals, as noted by McFarland at the discussion. The question arose, therefore, as to how valid is the assumption of wide dispersion of individuals at sea? There was general agreement that little is really known about the distribution and dispersion of the eggs and larvae of individual species at sea (but see Leis and Goldman, 1984, for a beginning). Shapiro's paper in volume 1 of these proceedings develops a model which suggests that the dispersion of eggs resulting from a single spawning act will retain reasonable cohesiveness (after 24 hours of drift in a current; this varies depending on assumed conditions, but could yield as many as 1 post-hatchling in each adjacent m^3 of water). If newly hatched larvae can swim actively and are mutually attracted, it is at least possible that in the first few days they might form cohesive aggregations. Shapiro's thesis specifically suggests the possibility that young recruiting reef fishes may, in some instances, be kin. Tests of this hypothesis can involve electrophoretic analysis of recent recruits that occur in cohesive groups. A more immediate test involves the aging of all recruits in a group by use of the otolith aging technique (Brothers and Thresher, 1985; Victor, 1983). If spawned simultaneously and dispersed as a group, the cohesiveness of which is retained by active behaviors by individuals in the

OVERVIEW: THE DYNAMICS OF RECRUITMENT IN CORAL REEF ORGANISMS

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In her introduction to volume 1 of these proceedings, Marjorie Reaka states, "The second set of papers addresses the issue about which we probably know the least in coral reef ecology: what factors control recruitment?" One must conclude from the three contributed papers in volume 1 of these proceedings (Lobel and Robinson, 1983; Shapiro, 1983; Victor, 1983) and the papers in the present volume (Brothers and Thresher, 1985; Lobel and Neudecker, 1985; McFarland and Ogden, 1985) that data on reproduction, larval development, and recruitment are sparse. This is astonishing when we consider that almost all coral reef fishes, and a great majority of tropical invertebrates too, cast their eggs and larvae into the plankton where they must survive and grow before they can settle again to the reef as juveniles.

The discussion held on December 27, 1983, at the ASZ meeting in Philadelphia, dwelled on two aspects of recruitment, what we actually know and what we need to know to better understand the dynamics of reef recruitment. About 20 participants were involved in the discussion. Here I will summarize the more important trends of the discussion.

Given the ubiquity of a planktonic larval phase in so many coral reef organisms, why is so little known about recruitment? The answer is multiple. The eggs and larvae of most reef organisms are small, translucent, and difficult to identify to species. They are extremely hard to maintain and study in captivity because they are fragile and nutritional requirements often are either unknown or difficult to adequately provide. In addition, only over the last decade have newer techniques (e.g., otolith aging, increased use of SCUBA and saturation diving for observations, improved methods for measuring currents, etc.) become accessible to reef biologists. The paper by McFarland and Ogden (this proceeding) addresses what is known about why so many fishes cast their eggs and larvae into the plankton. They conclude that there is yet no definitive answer; that the function of a pelagic larval phase for one reef organism may not apply to another species; that in most species multiple functions prevail; and that avoiding predation and dispersal appear to be the most important factors that favor long-lived planktonic larvae. In addition, the times of spawning in most reef species are poorly known. In recent years, however, considerable effort has been placed on *in situ* observations of where and when reef fish spawn. Lobel and Neudecker's paper (this volume) describes spawning in a hamlet (*Hypoplectrus guttavarius*) and also reviews important papers on reproduction in other species of fishes. Although many reef species spawn at specific spawning sites and during a rush toward the surface, the time of spawning is variable, often occurring in the late afternoon and dusk (Lobel and Neudecker, 1985). However, spawning also often occurs during midday or midafternoon (Colin, 1982; Robertson, 1983). It was the general conclusion in the

group, then each recruit in the group should be of the same daily age. This specific experiment has not yet been performed.

As tantalizing as the possibility of kinship in recruits may be, a larger related question prevails. What do larval fishes do when at sea? It is axiomatic that they feed and grow, but beyond that the discussion group agreed that the behaviors of larval reef fishes remain virtually unknown. Quantitative data on the behaviors of a variety of species of reef fishes are crucial to understanding the recruitment process. Answers will not be easy nor rapidly forthcoming, for they must involve careful, stratified plankton sampling to determine vertical distributions (at different times of the day), and also must include specific experiments in the laboratory and on shipboard to assess the responses of fish larvae to various stimuli. The investigations are greatly complicated by larval growth. Because most reef fish larvae spend from 1 to 6 weeks and in some instances up to 15 weeks at sea (Brothers and Thresher, this volume), behaviors must change as the larvae grow. It is critical, therefore, to also evaluate the ontogeny of larval behaviors. The central importance of such studies to the overall process of tropical fish recruitment, however, should motivate investigators to overcome the difficulties that the study of larval fish behavior presents. Especially in this area will creative and imaginative investigations help, for they will provide short cuts to what otherwise would be a prolonged undertaking. The lead provided by researchers studying larval fish behaviors in temperate waters, fortunately, can be of great assistance in getting started (e.g., Blaxter and Hunter, 1982; Lasker, 1981; on clupeoid fishes).

Since the classic demonstrations of Johannes Schmidt (1922) that the leptocephalus larvae of the European eel can drift at sea for not only months but in some instances for more than a year, the duration of larval life of fishes has provoked constant interest. Knowing how long a larva can exist at sea has been particularly important in explaining long-distance transport of reef fishes, e.g., the presence of Indo-Pacific reef species in the eastern Pacific (Brothers and Thresher, this proceeding). The problem has been frustrating because of the lack of methods to age larvae. The "invention" of the daily otolith aging technique (Panella, 1971; Brothers, et al., 1976) and the "discovery" of a transitional check mark in the otolith increments that approximate settlement of the larvae from the plankton to the reef substrate (Brothers and McFarland, 1981; Brothers, et al., 1983; Victor, 1983) have revolutionized the aging of larval fishes and, as a consequence, estimating the duration of larval life of reef fishes. Brothers and Thresher's paper (this proceeding) examines 115 species of Pacific reef fishes. Interestingly, over 80% of these fishes have fairly short larval lives (< 45 days). All fishes with pelagic larval durations in excess of 45 days are widely distributed (as expected). We recognized that the use of otolith aging is an innovation that will assist in providing answers to many questions concerning recruitment. Already we have a better understanding of the lengths of larval life for a considerable number of species. In some species the length of larval life can be restricted to only a few days (e.g., French grunts, as noted by McFarland during the discussion) or can encompass a highly variable number of days (from a short number to many days and may show a strongly skewed distribution toward fewer days; Victor noted during the discussion that this is the case for some wrasses). Given the

novelty of the otolith aging technique, a general warning was sounded that care should be taken with generalizations. Nevertheless, it was agreed that few studies on fish recruitment could effectively proceed without the use of this revealing technique.

The paper by Lobel and Robinson (1983) reviewed attempts to relate larval drift to mesoscale disturbances in the near surface waters, e.g., local current gyres. For many years various authors have invoked changes in local currents or even steady current conditions to explain how spawning, larval duration, and settlement are integrated to sustain local populations of fishes (Emery, 1972; Johannes, 1978, 1980; Sale, 1970). It is only over the last decade, however, that oceanographers have begun to develop instrumentation that allows ready determination of local current eddies, shears, etc., on a sufficiently small scale to be useful in biological investigations (see, for example, Robinson, 1983). Techniques include radio-tracked drogues, expendable rapid acting bathythermographs, current meters, and satellite infrared imagery. As deployed in Hawaii, the initial data appear to support the concept that larvae spawned at a particular site can drift in gyres (at certain times of the year only) and could be returned close to their point of departure in times coincident with the general length of larval life. We agreed that it was crucial that local current regimes in various areas of the tropics must be carefully measured at different times of the year and during all phases of the lunar month if the potential drift paths of eggs and larvae are to be ascertained. However, as indicated, daily changes in larval behaviors and the ability to swim and orient can place fishes in different local current regimes. It is possible, therefore, that active directed behaviors (such as vertical movements) could increase the chance(s) that fishes will be dispersed to suitable reef habitats for colonization. Thus, it is critical that subsurface currents as well as surface currents be measured.

As crucial as the measurements of currents are, they must be coupled to ongoing investigations of spawning, egg and larval distribution, and larval behaviors if they are to result in meaningful conclusions for understanding recruitment dynamics in the tropics.

As indicated by McFarland and Ogden (this proceeding) data on the actual settlement of reef fishes are sparse. Observations of settlement on a given day usually record the presence of recruits on a specific reef site, from which they were absent the previous day. Daily observations of this sort are useful in establishing recruitment cycles, but they reveal little about actual settlement behaviors of local reef fish. Do most reef fish larvae settle at night, or is there diel variation? And if so, are settlement behaviors species specific or plastic? What specific factors trigger settlement, and what attributes of a reef are attractive to each species? Answers to these questions will not yield to casual observation. As an example, during the discussion I indicated that newly recruited French grunts repeatedly established themselves on the same small coral heads and never recruited on closely adjacent heads that had similar configurations. Choice of a site might, thus, be resolved not only by appropriate substrate requirements but also by microscale differences in currents, as noted by Lobel. To know exactly what factors control site selection by new recruits will require carefully controlled manipulative experiments for a broad spectrum of reef species. Answers are critical before generalizations can be made: if

settlement is to a large degree passive and succeeds only because currents carry larvae over reefs, then the process can be considered somewhat stochastic; if, however, searching and testing behaviors, such as vertical movements in the water column (as observed in many invertebrate reef plankters; see McFarland and Ogden, this volume, for specific references), are widely utilized by larvae to identify suitable substrates on which to settle, then recruitment can be considered as an active determined process. However, even if fish larvae do actively 'search' for specific substrate as they settle from the plankton, or soon after, their success in establishing themselves can be negatively affected by the presence of previously settled juveniles (Shulman, et al., 1983). As a result, even if the act of settlement is deterministic for each larva, the overall success of individual recruits is infused with a large element of chance (e.g., being in a current that favors transport to native habitat, arriving in a region of native habitat at the appropriate time of day to avoid predation, actually finding an appropriate and 'empty' settlement site within the native habitat). In a very real sense, therefore, settlement can be viewed as partly determined and partly stochastic. Because we remain largely ignorant of the details of the settlement process, and because recruitment is central to understanding coral reef fish community structure (see Helfman, 1978, for review), generalizations about the proximal and ultimate causes of the high species diversity of fishes associated with coral reefs remain, at best, first approximations.

Although innumerable problems require solution to understand recruitment dynamics in coral reef organisms, it was generally concluded that rapid progress would result by focusing attention on four general areas: (1) the timing and dynamics of reproduction: where, when, and how often; (2) investigation of the fine scale horizontal, vertical, and diel distribution of larvae over a time frame that spans reproduction through recruitment; (3) coincident fine scale measures of local current regimes (at varied depths); and (4) descriptive and experimental investigations of the behaviors of larval coral reef organisms. Furthermore, it is not enough to study only one species, although individual researchers will be hard pressed to examine more than one at a time.

Because of the necessary broad scope of recruitment studies, the research will involve planktologists, fish biologists, invertebrate biologists, behaviorists, and physical oceanographers. As a result, interdisciplinary collaborations will be a requirement in understanding and solving tropical recruitment processes.

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GROWTH AND LIFE HISTORY PATTERNS OF CORAL REEF ORGANISMS: A DISCUSSION GROUP SUMMARY AND OVERVIEW

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I would like to take this opportunity to thank all who attended our late evening discussion group. Although it would have been impossible for us to deal with all major taxa of coral reef organisms, we discussed a reasonably diverse array of colonial organisms and a group of solitary echinoderms. Taxonomic areas of research and a partial list of participants include actinians (Sebens), bryozoans (Jackson), corals (Brakel, Highsmith, Hughes, Hunter, Jackson), echinoderms (Highsmith, Keller, Levitan, Mladenov), gorgonians (Harvell, Lasker, Wahle), sponges (Harvell, Pomponi, Suchanek), and zoanthids (Karlson, Sebens, Suchanek).

Six short presentations by Brakel, Hughes, Suchanek, Wahle, Karlson, and Mladenov were given in our discussion session. Each was followed by questions and/or discussion. Each presentation dealt with variability in one or more of the following: growth form, growth rate, overgrowth frequency, fecundity, survivorship, colonial integrity, or reproductive mode. We also discussed size-specific variation in life histories, fission, fusion, and brooding in coral reef invertebrates.

Brakel's presentation dealt with depth-related variation in the growth form of Porites astreoides (Brakel, 1983). He noted that much of the literature dealing with coral growth form suggests that there may be a simple monotonic relationship between colony shape and depth. Brakel's analysis indicates that flattened colonies are typical of high-energy, shallow water habitats and of low-light, deep water habitats. Between these two extremes, wave energy and light set upper limits on morphological variation and are not good predictors of mean morphological parameters.

Three additional citations to those given by Brakel (1983) on the general relationship between colony morphology and depth are Fricke and Schuhmacher (1983), Chappell (1980), and Stearn (1982). The first is an interesting paper on photoadaptations in deep hermatypic corals found down to 145 m. They noted the prevalence of flat hermatypes in deep water and a great diversity of growth forms in shallow water. This pattern was not observed for ahermatypic corals. Chappell (1980) discussed the effects of light and wave stress on coral growth form and rate and extended these effects to include the growth of coral reefs. Stearn (1982) critically reviewed the analysis of growth form in corals and stromatoporoids. He, like Brakel, concluded that the relationship between growth form and environmental variables is quite complex due to the influences of genetic and developmental processes.

The presentation by Hughes (1983) dealt with coral growth rates as well as life history variation over a depth range. The major point of this presentation

was that net coral growth rates do not vary much with depth. Although calcification rates decrease with increasing depth, rates of injury to colonies are much higher in shallow water. This results in several examples of deep corals at 35 or 55 m growing faster than corals of the same species at 10 or 20 m. These data suggest that we should exercise caution when using calcification rates to evaluate coral reef growth.

In our third presentation, Suchanek discussed the relative abundances and interaction frequencies of corals and demosponges over a 40 m depth range (Suchanek, et al., 1983). He emphasized the high frequency of demosponge-coral interactions at 40 m and the increasing prevalence of demosponges as aggressive spatial competitors with increasing depth. Aggressive interactions in shallow water involved encrusting gorgonians, hydrocorals, and zoanthids.

The effect of spatial competition on coral or demosponge growth, depth distribution, and life history variation remains to be determined. Even though deep hermatypic corals experience relatively low injury rates, a significant amount of this injury is caused by sponge overgrowth (Hughes, 1983; Suchanek, et al., 1983; Hughes and Jackson, in review). Lang (1974) has previously noted the prevalence of demosponges in deep fore-reef (below 55 m) and island slope zones off Discovery Bay, Jamaica. Hermatypic corals growing under light-limited conditions near their lower distributional limit may be more susceptible to overgrowth by demosponges than corals growing at shallower depths.

Wahle presented his data on the relationship between injury, colony size, and life history variation in the gorgonian Plexaura homomalla (Wahle, 1983). Between-colony analysis of variation in fecundity indicated that only colonies taller than 20 cm contained eggs. Natural and experimentally induced injuries to large female colonies resulted in physiologically isolated colony branches which exhibited size-related variation in fecundity. This work demonstrates that: 1) "colony size and not age controls both onset and continuation of gametogenesis"; 2) "injury can subtly reduce fecundity without noticeably affecting (colony) size"; and 3) injuries can alter the level of colony integrity and "create mosaics of different life history stages coexisting within the same colony."

My own presentation dealt with an analysis of divergent life history patterns in Zoanthus sociatus and Z. solanderi. Since these data do not appear elsewhere, I present them here in more detail than that given to the other five presentations. Both of these zoanthids are very common at several locations throughout the Caribbean Sea. These sessile colonial organisms generally inhabit shallow subtidal and lower intertidal zones where they occasionally are exposed to extreme wave action (e.g., Hurricane Allen, see Woodley, et al., 1981) or to desiccation (Sebens, 1982a; Fadallah, et al., 1984). Both species may successfully escape from such extremes by dispersing gametes and/or fragmented clusters of adult polyps.

Highsmith (1982) has suggested that fragmentation is an important part of the life history of many corals, and that one characteristic typical of fragmenting species is delayed sexual reproduction. The data in table 1 were collected from 101 zoanthid colonies to determine if either Z. sociatus, Z. solanderi, or both species delay sexual reproduction. Both species have been

Table 1.--The frequency of fertile polyps in four colony size classes of *Z. sociatus* and *Z. solanderi*. Colonies were collected in June, 1983, at Discovery Bay, Jamaica. Numbers of colonies are given in parentheses.

Colony size class	Polyp condition	*Z. sociatus*	*Z. solanderi*	χ^2
A. < 20 polyps	fertile	0	8	9.44
	nonfertile	227 (N=31)	188 (N=40)	$p < 0.005$
B. 20 < 40 polyps	fertile	0	22	22.12
	nonfertile	103 (N=4)	92 (N=4)	$p < 0.001$
C. 40 < 60 polyps	fertile	0	9	11.63
	nonfertile	58 (N=1)	40 (N=1)	$p < 0.001$
D. very large (subsamples = 50 polyps per colony)	fertile	105	179	26.93
	nonfertile	395 (N=10)	321 (N=10)	$p < 0.001$
E. < 60 polyps	fertile	0 (N=36)	39 (N=45)	21.36
very large	fertile	105 (N=10)	179 (N=10)	$p < 0.001$

observed to fragment either as clusters of loose polyps, analogous to the "polyp balls" reported by Rosen and Taylor (1969), or as polyps attached to shifting rubble. The fact that fragmentation occurs, however, does not demonstrate that it is adaptive or an important life history characteristic.

The frequency of fertile polyps in ten extremely large colonies of *Z. sociatus* and *Z. solanderi* was 21% and 36%, respectively (table 1D). These were sampled during their peak reproductive season, as indicated by Karlson (1981, and unpub. data). None of the polyps in 36 small colonies (< 60 polyps) of *Z. sociatus* were fertile; 11% of the polyps in 45 small colonies of *Z. solanderi* were fertile (table 1E). All three small colony size classes exhibited significantly higher frequencies of fertile polyps for *Z. solanderi* than for *Z. sociatus* (table 1A, B, and C). The absence of fertile polyps in small *Z. sociatus* colonies suggests that this species delays sexual reproduction while *Z. solanderi* does not.

Further examination of the 81 small zoanthid colonies (< 60 polyps) revealed another significant difference between these two species. Colonial growth in zoanthids commonly occurs by the budding of new individuals from stolons. These stolonal connections can degenerate over time (West, 1979), resulting in very loosely organized colonies with extremely low levels of integration and asynchronous sexual reproduction (e.g., table 1D). As a measure

Table 2.--Group size as a measure of colonial integrity

Colony size class	Group size		t-test
	Z. sociatus	Z. solanderi	
< 20 polyps	$\bar{X}$ = 3.6 polyps per group Range = 1 - 13 n = 63 groups in 31 colonies	2.3 polyps per group 1 - 8 84 groups in 40 colonies	3.68 p < 0.001
20 < 40 polyps	$\bar{X}$ = 6.9 Range = 1 - 27 n = 15 in 4 colonies	2.3 1 - 5 49 in 4 colonies	4.40 p < 0.001
40 < 60 polyps	$\bar{X}$ = 5.3 Range = 1 - 30 n = 11 in 1 colony	2.7 1 - 5 18 in 1 colony	1.25 N.S.

of colonial integrity, I have counted the number of unconnected polyp groups and the number of polyps within each group. There were a total of 89 polyp groups within 36 colonies of Z. sociatus and 151 polyp groups within 45 colonies of Z. solanderi (table 2). Zoanthus solanderi had significantly fewer polyps per group than did Z. sociatus in the two smallest colony size classes. The maximum number of polyps per group was also much higher in Z. sociatus than Z. solanderi.

These significant differences in polyps per group may have important life history implications. Variation at this low level of colonial integrity is likely to influence the size of colony fragments and the size frequency distribution of zoanthid colonies. Among colonial species, survivorship, fecundity, fragmentation, and fusion are highly dependent on colony size (e.g., Hughes and Jackson, 1980, and ms. in review; Buss, 1980, 1981; Sebens, 1982b; Hughes, 1984). Small fragments of Z. sociatus colonies have higher mortality rates than do fragments of the same size for Z. solanderi (Sebens, 1982a; Karlson, in preparation). In addition, small colonies of Z. sociatus are nonreproductive (table 1). The high level of colonial integrity in Z. sociatus suggests a benefit to large group (and colony) size in this species and, conversely, a cost (e.g., lower survivorship) associated with small size. There appears to be little cost to small size in Z. solanderi. This zoanthid is more resistant to predation than Z. sociatus (Sebens, 1982a) and does not delay sexual reproduction. Low colonial integrity in Z. solanderi is likely to enhance fragmentation of small clusters of polyps. Higher colonial integrity in Z. sociatus may enhance production of larger clusters by fragmentation or, alternatively, it may enhance resistance to fragmentation.

In our last presentation, Mladenov briefly reviewed some of the life history characteristics of seven shallow-water Jamaican ophiuroids. All of the

species studied were small cryptic forms. Three species were fissiparous (see also Mladenov, et al., 1983) and produced relatively small eggs; two of these broadcast "exceedingly small numbers of larvae." Two non-fissiparous species produce and brood a small number of relatively large eggs which undergo direct development.

Mladenov noted that of approximately 2,000 extant ophiuroid species, only 57 are known brooders (Hendler, 1979) and 37 undergo fission (Emson and Wilkie, 1980; Emson, et al., 1985). While 65% of those exhibiting fissiparity and 12% of the brooders are found in the tropics, brooders like Amphipholis squamata and fissiparous species like Ophiactis savignyi are among the "most widespread and abundant" tropical ophiuroids. At Discovery Bay, the three fissiparous ophiuroid species were numerically dominant. Emson, et al. (1985) speculate that populations of these species have been "maintained almost solely by asexual reproduction."

Among colonial species, growth, fission, fusion, and fragmentation are important asexual life history processes (e.g., Bak and Engel, 1979; Hughes and Jackson, 1980; Karlson, 1980, 1983; Bothwell, 1981; Tunnicliffe, 1981; Lasker, 1983; Rylaarsdam, 1983; Hughes, 1984). More critical evaluation of the importance of sexual reproduction to these colonial species is currently underway. There has been a relatively recent increase in this particular research area. At the Third International Coral Reef Symposium held in 1977, there were no presentations on this topic. Four years later at the Fourth International Coral Reef Symposium, there were six such presentations (Bothwell, unpub. data; Karlson, 1981; Kojis and Quinn, 1981; Richmond, 1981; Van Moorsel, 1981; Yamazato, et al., 1981). Data from the Van Moorsel presentation have now been published (Van Moorsel, 1983). An excellent review of this subject dealing with over 100 scleractinian coral species has also just been published by Fadallah (1983); also see Harrison, et al. (1984). Fadalallah (1983) and Szmant-Froelich, et al. (1983) suggest the need for further work on reproductive cycles, reproductive modes, relative fecundity, and reproductive effort in order to satisfactorily evaluate the importance of sex to coral reef organisms. At this point we know virtually nothing about the relationship between reproductive effort and the actual input of settled larvae into adult populations; this point also is stressed by McFarland (1985).

The original purpose of this discussion group was to compare growth and life history patterns of solitary and colonial organisms on shallow and deep reefs. We did, in part, deal with depth-related variation in coral growth form, growth rate, and life history patterns. Furthermore, we briefly discussed some general differences and similarities between colonial and solitary species (see Jackson, 1977). The remarkable success of fissiparous echinoderms and colonial corals, sponges, gorgonians, and zoanthids has been noted. This is suggestive of some level of evolutionary convergence favoring asexual strategies even in solitary organisms. My own work with zoanthids emphasized low colonial integrity in two very successful species. These species may be more similar to aggregating solitary organisms (e.g., barnacles, anemones, polychaetes, and mussels) than to more highly organized colonial forms. One curious and potentially significant difference between solitary and colonial organisms is the ability of colonial species to fuse (Teissier, 1929; Stephenson, 1931; Schijfsma, 1939; Ivker, 1972; Hughes and Jackson, 1980; Buss, 1982). It is

generally thought that fusion, whether it occurs between clonemates or non-clonemates, results in the formation of a larger colony with higher survivorship and/or fecundity (Hughes and Jackson, in review). It also results in a level of physiological continuity which even aggregating solitary organisms cannot mimic. Variation in colonial integrity and the adaptive significance of fragmentation and fusion among colonial species would appear, then, to be an interesting new direction for future exploration.

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OVERVIEW: CORAL REEF COMMUNITY STRUCTURE AND FUNCTION

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This paper summarizes an open discussion session which took place during the "Coral Reef Ecology Workshop" held at the annual meeting of the American Society of Zoologists in Philadelphia on December 27, 1983. Due to either sampling error or a genuine bias in current research emphasis, most of the participants in this session studied herbivory and grazing patterns on reefs. Consequently, most of the discussion centered around two related topics: (1) the recently discovered mass mortality of urchins in the Caribbean and (2) the relative importance of urchins vs. fishes in structuring benthic reef communities in areas facing different fishing pressures. A third more general topic was discussed briefly toward the end of the session: approaches to research on the community structure of reef systems. I will cover each of these topies in turn, extending discussion on the final topic with an overview of future needs in the study of coral reef communities.

MASS MORTALITY OF CARIBBEAN URCHINS

One of the major herbivores on Caribbean reefs is the long-spined urchin Diadema antillarum. In November 1983, a letter published in Science reported unprecedented mass mortalities of this species that were sweeping the Caribbean (Lessios, et al., 1983). Haris Lessios (Smithsonian Tropical Research Institute) attended the session and provided both a description of the effects of the apparent pathogen (the origin or nature of which was currently unknown) and an updated account of the spread of the calamity.

The apparent disease runs a 4- to 5-day course, beginning with the urchins emerging from coral cover and climbing up any available substrate. The urchins then discolor, gradually lose their attachment capabilities, and ultimately lose their spines and die. Up to 98% mortality has been reported in some populations, with apparently resistant individuals remaining. Curiously, no other species of urchin has been affected.

The outbreak was first noted near the Caribbean entrance of the Panama Canal in January 1983. Urchin mortalities were observed subsequently in Colombia, Costa Rica, and Grand Cayman by June; in Jamaica, Belize, Cancun (Mexico), and Key Largo (Florida) by July; in the Bahamas by August; in the Dry Tortugas and Bermuda by September; in Grand Turk and Haiti by October; and throughout the Greater and Lesser Antilles, including Curacao, Bonnaire, and part of the coast of Venezuela, between November 1983 and January 1984.

Initially, the spread of the die-off appeared to follow prevailing ocean currents. However, certain exceptions, such as the outbreak in Barbados in October (a full month or two before the remainder of the Antilles), suggested a

more complex situation. At present, Lessios reports that the entire Caribbean except for much of Venezuela, Tobago, and the area between Guadaloupe and the British Virgin Islands, has been affected, although these areas could be affected by the time this report is published.

Mark Hay (University of North Carolina at Chapel Hill) noted that, despite the die-off of Diadema in the Florida Keys, algal abundance on reefs there was not unusually high 2 months after the die-off. He suggested that either herbivorou fishes were sufficiently abundant to check algal growth or 2 months may not have been enough time to detect a noticeable change.

Douglas Morrison (University of Georgia) summarized his quantitative data on the effects of the die-off on a Jamaican reef. Mean densities of urchins 1 year before the die-off were about 15 per m^2 at 5 m depth and about 2 per m^2 at 16 m. Several months after the die-off, mean densities had declined to about 1 per m^2 at 5 m depth, and no urchins were apparent at 16 m. After the urchin die-off at the shallow site, the coverage of crustose coralline algae (an indicator of high grazing intensity) declined from 45% to about 18%. Replacing the coral-lines, coverage by fleshy macroalgae quadrupled (from 7% to about 28%) and coverage by filamentous algae nearly tripled. These patterns were corroborated by earlier urchin-removal experiments conducted before the die-off; in the experimental absence of grazing, crustose corallines were replaced by upright macroalgae. In contrast, the die-off had little apparent effect upon algal growth at the deep site, where urchin densities were normally low, and macroalgal abundance remained relatively high (73% cover). The macroalgae that increased in abundance at the shallow site are known to be resistant to fish grazing but not to urchi grazing. These included members of the genera Lobophora, Caulerpa, and Dictyo

Whatever its cause, the mass mortality of Diadema throughout the Caribbean provides an excellent (although uncontrolled) "natural experiment" for determining the impact of urchins on entire reef systems. Where adequate baseline data are available, observations following the die-off will test the widespread applicabilit of previous experimental analyses of small patch-reef systems (e.g., Ogden, et al., 1973) and help to resolve the controversy discussed in the next section.

ARE URCHINS IMPORTANT GRAZERS ON UNFISHED REEFS?

Hay summarized a study that was in press at the time of the workshop (Hay, 1984). He noted that most of the studies of the impact of urchin grazing on reef benthos have occurred at two sites: Teague Bay, St. Croix (e.g., Ogden, et al., 1973) and Discovery Bay, Jamaica (e.g., Sammarco, 1980). Such studies have led some to believe that urchins are the most important grazers on "typical" coral reefs. However, Hay suggested that these particular sites are atypical in that they have been heavily fished, indirectly resulting in unusually high densities of urchins which have been freed from predation by (and perhaps competition with) fishes. Using pieces of the seagrass Thalassia testudinum as a field bioassay for the intensity of herbivory on macrophytes, he found that eight lightly fished sites scattered throughout the Caribbean (including Salt River on St. Croix) showed decreasing grazing intensity with increasing depth and that almost all herbivory was due to fishes. Moreover, urchin abundances were low at these sites. In contrast, Haiti and Teague Bay on St. Croix, both

heavily fished areas, showed the traditional opposite patterns. Hixon added that Hay's general observation that urchins are often rare where large urchin-eating fishes are abundant is evident on Hawaiian reefs. Where fishing is prohibited on marine reserves, such as Hanauma Bay and Coconut Island on Oahu, urchins appear to be relatively rare.

Hay stressed that his major point was that many patterns documented on human-impacted reefs may be recent, having prevailed only for the past few hundred years. Because herbivory by fishes may select for different evolutionary responses in algae than herbivory by urchins, attempts to extract evolutionary implications from ecological data gathered on heavily fished reefs is not justified.

Les Kaufman (New England Aquarium) objected to a number of Hay's assertions, particularly the idea that urchins on heavily fished reefs necessarily are freed from predation by fishes. He took issue with Hay's data which indicated, on one hand, a decrease in grazing intensity with increased depth at Salt River on St. Croix but, on the other hand, an increase in grazing intensity with increased depth at nearby Teague Bay on the same island. Based on his diving experience at these sites, Kaufman felt that both areas supported fishes capable of eating urchins. Thus, other factors besides the overall abundance of fishes may explain the patterns that Hay attributed to fishing pressure. Further, Kaufman felt that Hay failed to consider the importance of juvenile mortality in urchin populations. He suggested that predation by wrasses on juvenile urchins may be considerable on heavily fished reefs, such as Teague Bay (St. Croix) and Discovery Bay (Jamaica), so that fishing pressure on larger fish species may not ultimately affect urchin densities.

Substantial discussion centered on the adequacy of Thalassia as a bioassay of grazing intensity. Robert Carpenter (University of Georgia) suggested that different measures of grazing could produce different depth profiles of grazing intensity (see also Steneck, 1983). Carpenter felt that the Thalassia technique measured mostly parrotfish grazing and that a more general measure of grazing is provided by counting the number of herbivore bites per unit reef area. Hixon agreed, noting that bite marks by fishes from different families (e.g., parrotfishes vs. surgeonfishes) can be individually identified and counted on flat substrates (e.g., Hixon and Brostoff, 1983). Morrison also concurred and suggested that, instead of Thalassia, a food readily consumed by all herbivores should be used to measure overall grazing intensity. Based on his own and other's work, Morrison indicated that filamentous algae seem to be preferred by urchins and nearly all herbivorous fishes (especially parrotfishes and damselfishes).

Sara Lewis (Duke University) noted that some algal species (e.g., Lobophora variegata) are differentially susceptible to grazing on different reefs. She suggested that these within-species differences may represent geographical variation in the development of plant defensive compounds. Hay agreed, noting that herbivory on a local level possibly could induce the production of chemical defenses. He went on to stress the problem of interpreting data from herbivore food-preference observations. Data on food preferences provide information on the responses of herbivores to different plants, but not necessarily on the selective pressure that herbivores impose upon the plants. Clearly, more information will be required to elucidate the reciprocal interactions between reef herbivores and algae.

STUDYING COMMUNITY STRUCTURE IN REEF SYSTEMS

Eldredge Bermingham (University of Georgia) introduced this general topic toward the end of the session by suggesting what he believed to be a major problem with coral reef community ecology. He felt that reef ecologists were often academic descendants of bird ecologists, but failed to follow their ornithological forefathers' passion for detailed natural history data. He stressed that lack of solid baseline data on coral reefs inhibits our ability to understand these systems.

Both John Ebersole (University of Massachusetts at Boston) and Hixon agreed in turn that detailed observational data are essential for any convincing ecological study. In particular, long-term baseline data illustrating the constancy or variability of observed patterns are needed. However, Hixon questioned whether most (or even many) reef ecologists were academic descendants of bird ecologists and, more importantly, noted that reef ecologists have conducted far more rigorous experimental studies than most bird ecologists. This disparity is understandable. On one hand, many terrestrial systems (especially many avian communities) are amenable to long-term observation but not to experimental manipulation. On the other hand, most coral reefs are both geographically distant from most research institutions and difficult to observe for long periods due to diving constraints. However, some reef systems are small enough or the associated organisms sedentary enough to allow direct experimentation, as evidenced by the papers in this symposium. Moreover, artificial reefs constructed from either natural or manmade materials allow researchers to rigidly control the age and structure of reef habitats, allowing powerful experimental designs (e.g., Shulman, et al., 1983; Fitz, et al., 1983; Wolf, et al., 1983).

SYNTHESIS AND PROSPECTUS

It seems appropriate to close this paper with an overview of our future needs in the study of coral reef communities. It is clear that, despite the knowledge that has accrued since the first professional ecologists donned SCUBA gear in the 1950's, we have only begun to scratch the surface of the complexities of coral reef systems. The number of research possibilities is infinite; the field is wide open. Thus, rather than suggesting what we need to study in particular, I would like to review the ideas suggested during this workshop on how we might improve future studies.

Based on criticisms leveled at current studies and pleas for future changes aired at various times during this workshop, three basic needs are evident. First, the complexities of coral-reef community structure cannot be elucidated without more extensive use of properly controlled field experiments. This suggestion is not new (e.g., Connell, 1974), and many reef ecologists have embraced experimentation enthusiastically. However, any experiment, no matter how elegantly designed and executed, cannot stand alone. As discussed above, detailed observational knowledge of a system is essential before field experiments can be properly interpreted.

This brings us to a second need: long-term field studies. Because (1) most coral reefs are located far from universities and other research

institutions, (2) most researchers cannot spend large blocks of time away from home, and (3) travel costs are becoming prohibitive, few current studies have followed long-term variations in reef systems. Moreover, current policy dictates that most research grants are limited to durations of several years at most. The net result is that most ecological studies are relatively static "snapshots" of intrinsically dynamic systems. Thus, our ability to understand the long-range consequences of various ecological interactions, and especially major environmental events (such as the urchin die-off discussed above), becomes severely limited. Likens (1983) recently has characterized the establishment and funding of long-term ecological studies in general to be a major priority for the future. Perhaps reef systems will one day be included in the National Science Foundation's Long-Term Ecological Research Program. In any event, the establishment and funding of facilities for detailed studies in prescribed local areas (such as NOAA's HYDROLAB in Salt River Canyon, St. Croix) or in local regions (such as NOAA's MAKALI'I submersible program in Hawaii and Johnston Island, the JOHNSON SEA-LINK submersible program in Florida and the Bahamas, and the submersible now available at the Discovery Bay Marine Laboratory, Jamaica) represent important first steps toward obtaining long-term data on deep reef systems.

The third need is for future studies to include several study areas in order to determine the ubiquity of observed patterns. Most present studies occur at single sites, making widespread generalizations about coral reefs based on a single study tenuous at best (although this fact rarely stops us). This problem can be rectified by a single project being conducted at a number of locations, either sequentially by a single research team or simultaneously by several teams using standardized methods. Present controversies, such as the importance of urchins as grazers discussed above, could be resolved by such an approach. NOAA's proposal to establish a saturation facility which can be moved among different geographical locations for comparative surveys of reef biota and processes should facilitate standardized studies.

Unfortunately, enacting these last two proposals may require changes in the current policies of granting agencies. The present system seems geared toward a fast-turnover "results-now" policy. While programs such as HYDROLAB provide the potential for long-term studies of reef systems, few such facilities exist presently, precluding detailed comparative studies among a number of study sites. In any case, should the majority of reef ecologists concur that these needs are important, long-term observational and experimental studies over wide areas will be realized eventually.

ACKNOWLEDGMENTS

Many thanks to the U.C. Irvine Committee on Faculty Travel (especially Peter Dixon) for funding my participation in the workshop; to the discussion participants for providing written summaries of their contributions (my sincere apologies for any misquotes); to Marjorie Reaka and John Ebersole for constructive comments on my manuscripts; and, especially, to Marjorie Reaka for bringing us all together.

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Note added in proof: A recent update on the mass mortality of urchins can be found in:

Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. "Spread of Diadema Mass Mortality Through the Caribbean." Science 226:335-337.

SOME THOUGHTS ON THE PAST, PRESENT, AND FUTURE OF STUDIES ON CORAL REEF COMMUNITY METABOLISM

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Marjorie Reaka, as editor of these two volumes on The Ecology of Deep and Shallow Coral Reefs, has kindly offered me the opportunity to comment on where I see studies of reef community metabolism to be coming from--and going to. The following thoughts arise as I consider, in particular, the seven papers loosely grouped in "The Organization of Reef Ecosystems" in these proceedings.

These papers have some aspect of the metabolic performance of coral reef communities or systems as a broad common theme. Within the context of that theme, all of the papers can trace their ancestry back to the "foundation studies" by Sargent and Austin (1949) at Rongelap Atoll and Odum and Odum (1955) at Enewetak Atoll. Earlier papers in the field of reef community metabolism can, of course, be identified. They have tended to remain lost in obscurity compared to the two I have cited. Over the intervening years, the field has matured and expanded sufficiently that citation of these important papers is beginning to drop off. Instead, I recognize increasing proportions of second (or third) generation citations, both in the papers on reef metabolism in these volumes and in the general literature.

These early papers dealt primarily with oxygen and carbon flux of reef-flat communities. Several of the papers in the present volumes and a survey of the literature suggest that we can move beyond a direct concern with average rates of oxygen and carbon fluxes in studies of reef metabolism. We now can speak with some confidence about the typical oxygen and carbon metabolic performance of reef-flat communities. It is, however, worth noting that we remain without a comparable large data base for other parts of coral-reef ecosystems.

We are beginning to gain an appreciation for the relationships between variation in reef metabolism and the controlling roles of external physical, chemical, and biological variables. Many casual observations about reef metabolic response to external controls have led to erroneous or trivial conclusions. Clearly, controlled experiments and carefully designed field surveys need to be conducted in order to test hypotheses about metabolic responses to controlling variables.

The study of nutrient fluxes in relation to community metabolism has, perhaps, been more extensive than other aspects of controls on community metabolism. This work became prominent during the Symbios Expedition to Enewetak Atoll (Johannes, et al., 1972). Studies of nutrient flux continue, and most of the papers on reef metabolism in these volumes at least touch on this subject. In particular, there is an interest in the effects of both quantity and quality of nutrient supply on reef metabolism and in the interactive roles of various communities (especially macrofauna/meiofauna/microfauna in interreef soft-

sediment communities) in nutrient processing of the total system. From my own bias, I perceive the need to "balance the books" of nutrient fluxes in entire reef systems as a recurrent--and important--theme.

Solar radiation is clearly fundamental to the community metabolism of reefs, yet our understanding of metabolic responses to light remains poor. Traditionally, most studies of coral reef metabolism have not adequately considered either the quantity or the quality of incident solar radiation, light attenuation through the water column, or loss of radiant energy through back-scattering. This situation is beginning to change. We see among the papers in these volumes several attempts to evaluate the metabolic response of reefs to light. More work is needed.

Finally, I observe that students of coral reefs tend to emphasize the unique characteristics which make reefs such pleasurable places to work. I suggest that we have a great deal more to learn, as ecologists, by considering coral reefs within the spectrum of other ecosystems than we will ever learn by treating reefs as unique.

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Figure 1

Further studies of deep coral reefs and sea mounts have been possible through the use of submersibles such as NOAA's MAKALI'I, which is shown while in transit on its launch, retrieval, and transport (LRT) vehicle (fig. 1). During launch, the LRT is submerged with the submersible; at 50 feet the submersible is released to continue its descent for research (fig. 2).

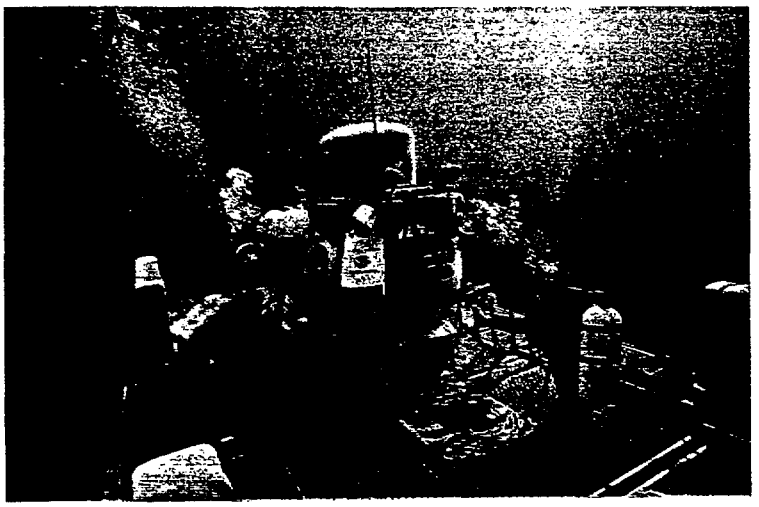

Figure 2

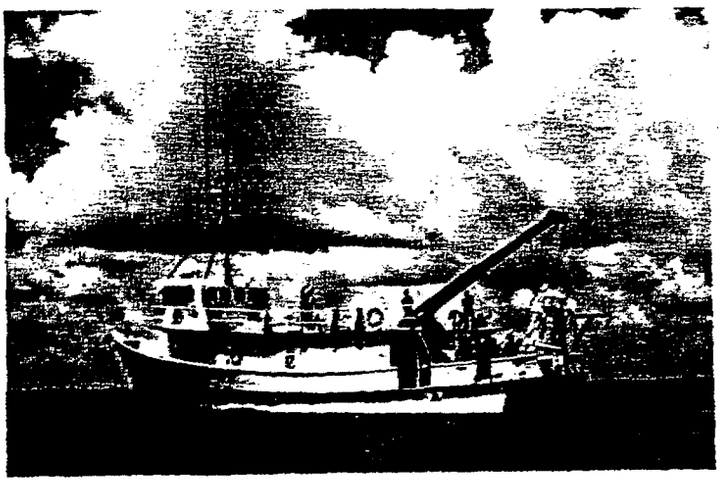

Figure 3

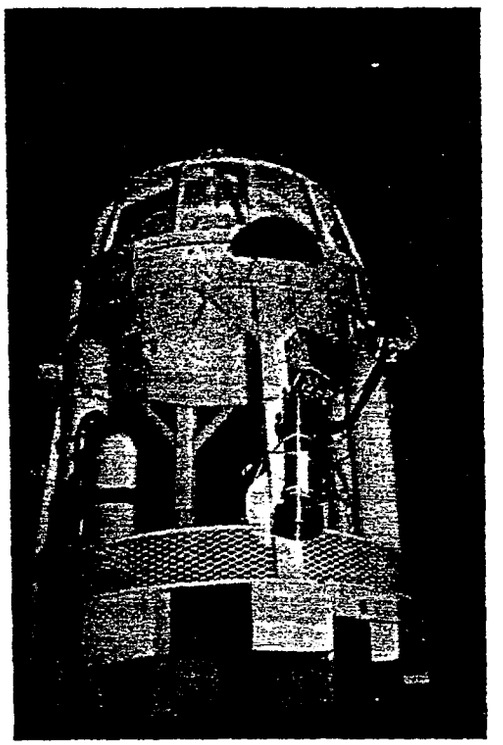

Figure 4

NOAA also supports research on the biology of deep water communities in various localities through the deep diving bell facilities operated off the R/V SEAHAWK (figs. 3, 4) which is based at the University of North Carolina at Wilmington. An additional habitat is being constructed for use in research on marine communities off the southern California coast (fig. 5).

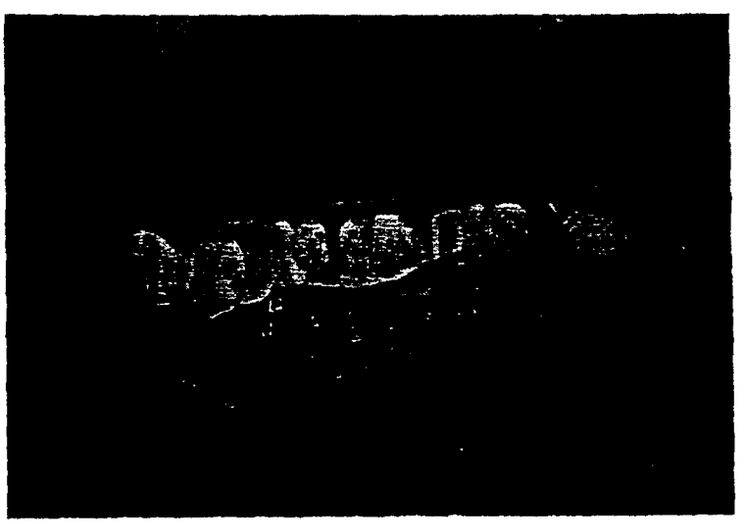

Figure 5

RECRUITMENT OF YOUNG CORAL REEF FISHES FROM THE PLANKTON

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ABSTRACT

This paper examines the widely held view that the planktonic eggs and/or larvae of most coral reef fishes represent mechanisms that reduce predation and/or serve for dispersal of the young. Data on spawning, the pelagic phase, and recruitment of coral reef fishes are examined. Recruitment represents the successful end product of a complex suite of adult and larval behaviors and physical conditions that directly affect survival of offspring. Although considerable data are available, in no single species has the cycle from spawning to recruitment been clearly documented. As a result, assessing the various hypotheses that attempt to explain the almost universal presence of a pelagic larval phase in coral reef fishes remains tenuous.

Predation on young and ultimate dispersal are both potent selective factors. The high degree of variation in reproduction, larval characteristics, and recruitment amongst coral reef species implies, however, that these two selective factors undoubtedly vary in importance among species.

INTRODUCTION

Virtually all coral reef fishes produce numerous offspring and release either their eggs or larvae into the offshore plankton (Breder and Rosen, 1966; Ehrlich, 1975; Goldman and Talbot, 1976; Sale, 1977, 1978a; Johannes, 1978; Barlow, 1981). There is one known exception, the pomacentrid Acanthochromis polyacanthus; members of this species brood their young and disperse them directly onto the reef (Robertson, 1973). Also, some apogonids (mouth brooders) and some brotulids (live bearers) have completely eliminated the planktonic larval phase.

Considering the high diversity of reef fishes (Connell, 1978; Sale, 1980) and their numerous ecological roles (Hobson, 1974; Sale, 1978b; Smith, 1978), it is astonishing that so many species use the same reproductive strategy. Indeed, the central position of a larval pelagic existence in coral reef fishes led Helfman (1978) to wonder whether answers to the high species diversity of coral reef fish assemblages "lie in the plankton." One major hypothesis favors the view that community composition is dependent on the chance recruitment of each species from the plankton when space becomes available (Russell, et al.,

1974; Sale and Dybdahl, 1975, 1978; Sale, 1977, 1978a). Thus, species composition on a reef should change through time, but over years as opposed to centuries or longer. A contrasting hypothesis suggests that species composition is more deterministic and dependent on competition between adults for resources (Smith, 1973, 1978; Smith and Tyler, 1973). Recruitment from the plankton, therefore, would not primarily affect diversity but the abundance of each species over time. No doubt there is truth in each view, but the controversy continues with additional participants (Gladfelter and Gladfelter, 1978; Holles, 1978; Talbot, et al., 1978; Gladfelter, et al., 1980; Ogden and Ebersole, 1981; Shulman, 1983; Abrams, 1984).

Given the virtually universal use of a pelagic egg and/or larval phase and its potential significance to explanations of the high diversity amongst assemblages of coral reef fishes, investigations of the reproductive activities of adults, the disposition of their eggs and larvae at sea, and the effect(s) of currents on the dispersal of these propagules are, therefore, not inconsequential. If, for example, the recruitment of each species is not consistent over a reasonable time scale, then the high diversity of coral reef fishes could not be maintained.

In general, data about recruitment processes in coral reef fishes are sparse and must often be gleaned from literature that primarily deals with other aspects of coral reef fish biology. Over the last few years, however, efforts have been directed toward recruitment in particular species. Given the central importance of recruitment to coral reef fish community structure, we expect that larval biology at sea will be explored in great detail over the coming decade. Here we summarize what is presently known about recruitment and closely related processes in coral reef fishes.

REPRODUCTION

Spawning activities in coral reef fishes vary considerably. Only over the last 10 years have sufficient direct observations accumulated to provide a basis for understanding how the spawning act might be adaptive. Many reef species spawn over long periods of each year, but they usually show maximum reproduction in either spring and/or fall (Munro, et al., 1973). In Munro's study, which examined the state of the gonad as an index of reproductive potential, over half of the species were active for longer than 6 months. Labrids (Warner, et al., 1975) and some haemulids (McFarland, 1980, 1982) spawn over the entire year, but many species have highly restricted spawning seasons. Between these extremes, however, some species produce all of their eggs in a single or in very few reproductive acts, while others rely on a more consistent release which involves the release of fewer eggs during each reproductive bout. It is difficult to generalize with certainty how these highly varied spawning tactics relate to dispersal and recruitment. This is further complicated by the fact that virtually every assemblage of coral reef fishes contains species that utilize each reproductive tactic.

Many species tend to show periodicity of spawning over a season or even longer. In a survey of reproduction in 52 tropical fishes, Johannes (1978)

found that 20 tended to spawn near or at new moon, 8 at full moon, 13 at times of both new and full moon, and the remaining 11 during quarter moons.

Several direct observations have related the timing of spawning to specific phases of the moon (e.g., quarter moons, Polydactylus sexfilis, May, et al., 1979; Centropyge potteri, Lobel, 1978). The periodicity in spawning has been interpreted as an adaptation to enhance the chance that the eggs will be flushed by tidal currents away from the reef, and therefore reduce mortality by egg predators, which is commonly observed (Randall and Randall, 1963; Moyer, 1974; Meyer, 1977; Robertson and Hoffman, 1979; Colin, 1978; Robertson, 1983).

Mortality among the pelagic eggs and larvae is high when compared to the adults (Sale, 1980). Very likely as a response to this high mortality (but perhaps also to increase the probability that some propagules will be dispersed) the fecundity of reef fishes is high, usually in excess of 50,000 eggs per year per female in pelagic spawners (Randall, 1961; Bryan, et al., 1975; Thompson and Munro, 1978), and greater than 8,000 eggs in demersal spawners (Warner, et al., 1975; Bell, 1976).

In addition to varied lunar periodicities, many reef fishes migrate to the deeper areas of the reefs and/or to pinnacles and reef extensions to spawn, and there usually invoke discrete behaviors when spawning (e.g., a rush to the surface to spawn the eggs as far from the reef as possible; Lobel, 1978; Colin, 1982). In addition, spawning often shows a daily cycle (e.g., occurring at dusk; Lobel, 1978). These behaviors have been interpreted as acts to reduce egg predation and may be particularly effective because eggs are small, transparent, and therefore difficult to detect, especially at dusk (Hobson and Chess, 1976). Many species, however, spawn during midday or the afternoon (Colin, 1982; Robertson, 1983).

Although the observations on spawning behavior suggest tactics that can reduce mortality of eggs and improve dispersal away from the reef, few observations are supported by direct measurements of prevailing tides, currents, and other conditions to verify that this is what actually happens. A recent paper by Robertson (1983) combines careful field observations of spawning in seven species of surgeonfishes at four different localities in the Pacific and Indian Oceans. Readers are referred to the original for the wealth of observations detailed by Robertson. Several general conclusions, however, are important. (1) The various species spawned over different intervals of the day (a few in the morning; most from midday until dusk). (2) Both paired spawnings and group spawnings occurred in several of the species. (3) Except where territorial harems were established, most individuals migrated toward outer and deeper portions of the reefs to spawn. (4) In almost all instances, spawning fishes rose toward the surface to spawn. (5) The most common feature among the seven species was a strong tendency to spawn during ebb tides, as water was flushed off the reef. All of these behaviors would minimize the chance that freshly fertilized eggs would be exposed to planktivorous reef fishes. Spawning as tides flush water off reefs also was indicated by Randall (1961), Robertson and Choat (1974), Lobel (1978), and Thresher (1979). In contrast, Robertson (1983) found no distinct tidal rhythms in surgeonfish spawnings at Lizard Island where the currents flow parallel to the reef rather than on and off the reef. This

finding suggests that spawning in a species is strongly influenced by local conditions. Thus, behaviors that in one location may reduce egg mortality might increase egg mortality if repeated precisely at another site.

In summary, reproductive efforts in a species often can be shown to diminish predation on spawned eggs and enhance the chance of their dispersal. But, many species show variable spawning behavior. It is therefore uncertain that all reproductive behaviors are selected to reduce egg predation and/or assure dispersal.

DISPERSAL -- THE PELAGIC PHASE

Hypotheses to Explain the Pelagic Larval Phase

Why should almost all coral reef fishes cast their eggs and/or larvae offshore? Three primary hypotheses have been suggested: (1) the antipredator hypothesis, (2) the food hypothesis, and (3) the dispersal hypothesis (see Johannes, 1978, for review). Johannes, who favors the antipredation hypothesis, argues that if the eggs and larvae were left on the reef unprotected, they would be subject to an excessive mortality by reef predators (see also Smith, 1978). Although it is certain that predation on eggs and larvae is very high by reef planktivorous fishes (Hobson and Chess, 1978) and by sessile filter feeders (Johannes, 1978), it is not clear how much predation is reduced when eggs and larvae are offshore (Barlow, 1981). Egg mortality offshore can approach 30% per day (Jones and Hall, 1974; Ware, 1975). Considering the relative merit of these factors and others led Barlow (1981) to postulate that the reduction in predation achieved from a pelagic phase was of less significance to survival than the advantages that are derived from dispersal (over both short and long distances). Barlow sees dispersal as a means to ensure survival of a species by reducing inbreeding (Bengtsson, 1978), and, particularly, as an adaptation to the instability of reef communities (Connell, 1978; Sale, 1978a). He argues that the longer an egg or larvae travels, the less its chance of survival (Thorson, 1946; Gadgil, 1971). For long-range dispersal to succeed, reef fishes must produce numerous offspring, which they do, and larvae must be adapted for a lengthened pelagic life, which in many species is true (e.g., in surgeonfishes, butterflyfishes, wrasses, and in eels; Barlow, 1981). The possibility exists, nevertheless, that cohorts from a single spawning may remain together as eggs and larvae in the plankton, and thus maintain genetic relatedness among recruits (see Shapiro, 1983). This interesting possibility, which would increase inbreeding success, remains to be documented.

The food hypothesis is dismissed by both Johannes (1978) and Barlow (1981) because in general planktonic food is less available offshore than inshore; thus, the advantage of offshore disperal must find another explanation, such as a reduction in predation or enhanced dispersal.

Although Johannes and Barlow are aware that both recolonization and long-range dispersal occur, their respective arguments favor different views of the role of dispersal in larval recruitment from the plankton. Barlow (1981) views the long-range transport of larvae to other localities than the parent reef (island, etc.) as the essential selective force that has operated. In contrast

Johannes (1978) emphasizes avoiding predation and invokes data (largely anecdotal) to suggest that eggs are cast into local current gyres that often return to the same island or, at least, to the same general locality and not necessarily to far distant shores. There were some data to suggest that this was so when Johannes (1978) postulated the role of local currents in recolonization (Jones, 1968; Sale, 1970; Watson and Leis, 1974; Lobel and Reaka, 1977; and since then Leis, 1982). More convincing data have now been provided by Lobel and Robinson (1983) that current gyres do develop off the big island of Hawaii twice each year and, importantly, coincide with the two major seasonal spawning peaks for many of the coral reef fishes in Hawaii (Jones, 1968; Sale, 1970). Lobel and Robinson, using radio-tracked drogues, found circulation times of 7-14 days (offshore and return inshore) and evidence for at least two cycles. Thus, there would be time for eggs and larvae to develop to a sufficient size to settle onto the reef after initially being advected away from the reef. However, it should be emphasized that in multiple releases of drogues, some returned close to the inshore release site, but others drifted off and even headed toward the island of Molokai. Furthermore, as Barlow (1981) emphasizes, even if major seasonal spawnings at Hawaii do coincide with the weakest offshore currents and the presence of local gyres (Watson and Leis, 1974) which might favor recolonization, spawning nevertheless continues in many species at other times of the year when currents would not favor recolonization, but rather long-range dispersal.

Duration of Larval Life

Certainly if long-range dispersal is to be invoked, as for example Barlow (1981) suggests occurs for those coral reef species that have managed to cross the Indo-Pacific barrier (see Rosenblatt and Walker, 1963), then the length of larval life must be long. An alternative tactic for long-range dispersal would invoke rafting of juveniles or adults, a requirement if the larval phase is of short duration (< 20-30 days). How long, then, are larvae advected at sea?

By comparing spawning dates with recruitment dates, larval duration has been estimated to vary among coral reef species from a week to several months (Randall, 1961; Moran and Sale, 1977; Johannes, 1980). Over the last few years, the otolith daily aging technique has allowed direct estimation of the age of individual larvae (Brothers and McFarland, 1981). The results to date indicate that larval duration does vary from weeks to months in different species (Ralston, 1976; Brothers, et al., 1983; Victor, 1983a; and Brothers and Thresher, 1985). The duration within a species is often variable, as it is in marine invertebrates (Scheltema, 1968, 1971), but some species have very restricted lengths of larval life, the cause of which is unknown (Brothers and McFarland, 1981). For the 115 species of Pacific coral reef fishes studied, Brothers and Thresher (1985) obtained otolith ages for settlement (the so-called settlement check mark; see Brothers and McFarland, 1981; Brothers, et al., 1983; Victor, 1983b) that range from 15 to 82 days. In some labrids, it can be a week (Victor, 1983b), and in grunts settlement always occurs at about 15 days (McFarland, 1982). These pelagic periods favor only short-range dispersal. But, some labrids can have larval durations up to 50 days (Brothers, et al., 1983), which would allow for long-range dispersal.

Larval Behavior

Another factor that can affect larval mortality and dispersal is the behavior of fish larvae at sea. It is generally conceded (although with little direct evidence) that fish larvae disperse passively in offshore currents (Sale, 1970; Leis and Miller, 1976) and, therefore, that their final destinations are subject to hydrographic conditions. Alternatively, it has been argued that larval drift is not passive (Sale, 1980). In Hawaii, larvae from species with pelagic eggs (labrids, chaetodontids, acanthurids) are more common offshore than species with demersal eggs (pomacentrids and gobies), which are more common inshore (Miller, 1974; Leis and Miller, 1976; Watson and Leis, 1974). This is explained by invoking active larval mechanisms. However, it may also be explained merely by initial passive drift of pelagic eggs. Nevertheless, once fish larvae begin to swim, vertical movements could place them in currents that would hold them inshore or advect them away. Unfortunately very little is known about larval behaviors. Several investigations have established that many pelagic invertebrates undertake marked diel vertical migrations, ascending toward the surface at night and to deeper depths during the daytime (see Segal, 1970, for overview). Recent investigations also have revealed that reef meroplankton emerge high into the water column at night, especially during the dark phase of the moon (Porter, et al., 1977; Porter and Porter, 1977; Alldredge and King, 1977, 1980; Hobson and Chess, 1979; Robichaux, et al., 1981; Ohlhorst, 1982, 1985). These vertical movements take place over a few meters. Similar vertical distributions seem to occur in coral reef fish larvae, at least nearshore (Hobson and McFarland, preliminary unpubl. data). It is known, however, that reverse tidal currents can occur over shallow depths, as they do at St. Croix (Lee, et al., 1977), and it is possible, even likely, that fish and invertebrate larvae use these currents, in combination with vertical migratory behavior, in their dispersal.

Certainly broad parallels occur between benthic marine invertebrates and fishes. In tropical regions, 80-85% of the invertebrates produce long lived, planktotrophic larvae that will hatch, as in fishes, from relatively small eggs (Thorson, 1950). In general, larval pelagic existence is longer in tropical invertebrates than in species from higher latitudes (see Thorson, 1950; Mileikovsky, 1971; and Jablonski and Lutz, 1983, for review). Extended larval periods appear to enhance dispersion and are associated with broad geographic distributions in tropical invertebrates (Scheltema, 1968, 1971), and this pattern seems, at least tentatively, to also hold for coral reef fishes (Brothers and Thresher, 1985).

In summation, there is no simple explanation in terms of dispersal versus antipredatory mechanisms that resolves what major selective processes have caused virtually all coral reef fishes to produce pelagic propagules. In fact the data cited show such wide variation that it is likely that in some species dispersal was the preeminent selective factor, while in other species antipredation was the most important. In any case, dispersal and antipredation are not mutually exclusive selective factors, and certainly both act to increase survival. Nevertheless, it is difficult not to wonder, as Barlow (1981) has, why more coral reef fishes do not invest in postzygotic activities to reduce the duration of the larval pelagic phase, or even eliminate it.

Barlow suggests that postzygotic activity leads to a reduction in lifetime fecundity in part because of the parental investment required. Most coral reef fishes that spawn demersal eggs tend to be small, a circumstance that in itself limits egg production. In addition, most coral reef species are strongly site-attached and spend their adult lives in a relatively small local area (Sale, 1980). Pelagic dispersal thus can be considered a necessary consequence of their restricted mobility. If, for example, specific reef habitats tend to be unstable over time, a circumstance that recent events document (e.g., severe hurricane damage of reef habitat at Jamaica, Woodley, et al., 1981; Kaufman, 1983; storm effects at Lizard Island, Lassig, 1983; coral blight in the Caribbean and Pacific, Lessios, et al., 1983), then dispersal to colonize adjacent or distant habitats is an essential element in each species' survival.

RECRUITMENT--HOW DO FISHES SETTLE ON REEFS?

In a review of coral reef fish ecology, Sale (1980) stated, "The mechanisms whereby larval fishes make their return to the reef are totally unknown." In addition, it is only over the last few years that more systematic observations of recruitment in reef fish larvae have begun to appear in the literature. For most of the observations, maximum recruitment occurs over a single season and often is episodic; it may follow a lunar periodicity (Johannes, 1978); it may be monthly but not coupled to a particular phase of the moon (mixed guilds of pomacentrids; Williams, 1983), or a rhythm may not be conspicuous (Thalassoma bifasciatum; Victor, 1982, 1983a).

Larval French grunts (Haemulon flavolineatum) settle from the offshore plankton following a semi-lunar timetable. This periodicity is most closely correlated with the quarter moons and/or daily intermediate tidal excursions that fall between the spring and neap tides (McFarland, et al., 1985; also see McFarland, 1982). Furthermore, although seasonal, some recruitment continues throughout the year. Larval life is short (ca. 15 days; Brothers and McFarland, 1981), which implies that spawning also must occur throughout the year; also ripe eggs are present in adult French grunts at all times of the year (Munro, et al., 1973).

The extreme variations seen in the spawning periodicities of reef fishes (see earlier section) are reflected in the variable periodicity in recruitment. What do larvae select when they settle from the plankton to the reef? Here we are almost totally in ignorance. Most larval (or postlarval) recruits are first observed on substrate (coral patches, seagrass beds, sand, etc.). Usually, it is not possible to state that they have just settled. In a study of recruiting pomacentrids, Williams and Sale (1981) found that different species tended to prefer different species of corals. Earlier Sale (1969) found that young surgeonfish preferred reefs with shaded overhangs. It is generally understood that each species has certain needs for settlement, but determination of these needs has barely been initiated. In addition, settlement to a specific site can be dramatically influenced by resident competitors (Shulman, et al., 1983).

Actual settlement has seldom been observed. During observations of the acronurus larvae of Acanthurus triostegus in Hawaii, Randall (1961) concluded

that they settle at night. We have observed the same nocturnal timing for acronurus larvae on settlement reefs at St. Croix. Recruiting young pomacentrids also seem to appear overnight (Doherty, 1981). But daytime settlement is not precluded. Given the present status of our knowledge of larval fish behaviors, it is difficult to envision how a larval fish avoids settling if by chance it is carried across suitable substrate during the daytime; but, in contrast, how does a larval fish "know" that it should settle at night? Are cues visible, olfactory, or, perhaps, sonic? Certainly, planktivorous reef fishes are less active at night (Hobson, 1974; Hobson, et al., 1981; Gladfelter and Johnson, 1983), but filter-feeding sessile invertebrates are most active at night (Sebens and DeReimer, 1977). Obviously, more precise studies are required to evaluate just how important nocturnal settlement is to survival.

It should be emphasized that recruitment of larvae varies considerably from year to year (Williams and Sale, 1981; Williams, 1983). As Williams states, "One large pulse alone is sufficient to make total recruitment in a year unusually successful." He reminds us as well that a large recruitment of one species does not mean the same for another species, even in the same guild.

Finally, it has been implicit in the various arguments of recent fish biologists interested in explaining the diversity in coral reef fish assemblages that the offshore plankton provides a huge, although variable, reservoir of potential recruits which is drawn upon when appropriate space opens on the reef (Dale, 1978; Sale, 1978a; Smith, 1978). Perhaps this is so, but Doherty (1981) suggests that at least at certain times the larval pool may not be endless and can be limiting to the maintenance of reef populations. His theoretical model assumes that larval existence for most species is "precarious" at best (see also Johannes, 1978), and this limiting function introduces a high degree of chance into the recruitment process.

CONCLUSIONS

From what is currently known about the recruitment of coral reef fishes from the plankton, it seems likely that strong interactions between local currents and the times of spawning exist. The function(s) of this interaction is best explained as a mechanism to both remove eggs and larvae from the vicinity of the reef to reduce predation and to disperse the young to other localities. The possibility of seasonally developed recirculating eddies could lead to local recolonization. Even totally isolated islands could sustain their fish populations by holding larvae in downstream eddies (Emery, 1972), especially if discrete larval behaviors are used to remain in the eddies. What is missing is an unambiguous case that this routinely occurs.

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PELAGIC DURATION, DISPERSAL, AND THE DISTRIBUTION OF INDO-PACIFIC CORAL-REEF FISHES

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ABSTRACT

The breadth of distribution of most Indo-Pacific coral-reef fishes does not clearly correlate with the duration of their pelagic developmental stages. Rather, there is a threshold effect at approximately 45 days, above which species tend to be broadly distributed, but below which pelagic duration and distribution appear unrelated. Long larval durations also characterize species that have colonized geographically isolated areas, such as the Hawaiian Islands and the Eastern Pacific. Comparison of larval durations with estimates of time required to cross the "East Pacific Barrier" further suggests colonization of the New World to be an infrequent event, most likely associated with unusually strong development of the Equatorial Countercurrent.

INTRODUCTION

The pelagic larval stage characteristic of many invertebrates and fishes is widely assumed to serve as a dispersal mechanism (Scheltema, 1971, 1978; Crisp, 1976; Barlow, 1981; Smith, 1982). A logical corollary of this assumption, also widely accepted, is that long larval duration correlates with broad dispersal and consequent broad distribution (Shuto, 1974; Strathmann, 1974; Zinsmeister and Emerson, 1979; Reaka, 1980; Ayal and Safriel, 1982; Jablonski and Lutz, 1983). We tested this hypothesis by comparing the distributions of 115 species of Indo-Pacific coral-reef fishes, in 22 families, with the duration of their pelagic developmental stages, determined by examination of otolith microstructure. The data suggest a threshold effect, with long pelagic durations correlating with broad distributions only above a species mean value of approximately 45 days. Only 20% of the species we examined have pelagic durations this long, a value in surprisingly close agreement with independent estimates of the frequency of "true long-distance" pelagic larvae of marine invertebrates (Thorson, 1961). We also examine the question of whether long pelagic durations are typical of those species that have colonized geographically isolated areas, such as the Hawaiian Islands, and, particularly, the Eastern Pacific.

METHODS

Duration of the pelagic larval stages was determined either by aging of individuals newly recruited to the reef (Brothers, et al., 1983) or by examination

of otolith "settlement marks" in juveniles and adults, the latter involving techniques similar to those used in other studies (Brothers and McFarland, 1981; Victor, 1982; Thresher and Brothers, in press). Total duration of the pelagic stages was assumed to be equal to calculated otolith ages for most demersal spawning fishes. This assumption is based on limited data (Brothers, unpublished data) which suggests that daily growth increments in most demersal spawning fishes begin forming shortly after hatching. The only demersal spawning families for which this is not likely to be true are Balistidae and Siganidae, both of which hatch as relatively undeveloped prolarvae (see review in Thresher, 1984). For these two families, 2 days were added to calculated pelagic durations to account for the likely duration of pelagic pre-feeding stages. For pelagic spawning fishes, total duration of the pelagic stages was estimated by adding 3 days to otolith ages. This was based on a mean incubation time of 43.1 hours for pelagic eggs of such fishes (Thresher, 1984), plus limited data suggesting that another 24 hours may pass before the first growth increment forms (Brothers, unpublished data).

Species distributions were based on taxonomic reviews and comparison of faunal lists for different areas. The extent of distribution was quantified by dividing the tropical Indo-Pacific into 29 "bio-geographical areas" and counting the number of areas inhabited by each species. Division of the Indo-Pacific follows Allen (1979). The rationale behind this approach is discussed in Thresher and Brothers (in press).

Data were obtained for 115 species (see table 1) in 22 families, essentially all those we had available to us. The taxonomic distribution is not intended to be qualitatively or quantitatively representative of typical reef ichthyofaunas, although effort was made to include representatives of as many families as possible. The only fishes specifically excluded from the analysis were Hawaiian endemics and a few families, such as kyphosids and carangids, that are known or strongly suspected to raft as juveniles or adults under floating objects. The few Hawaiian endemics we had available were excluded because of difficulty in discerning a single or discrete "settlement mark" (see Thresher and Brothers, in press, for further discussion of this problem). Some material was obtained for us directly in the field (the Philippines, Japan, the Marshall Islands, and Australia), but the majority were obtained as juveniles and small adults from the aquarium. As such, most were probably collected in the Philippines, the Hawaiian Islands, or off the Australian Great Barrier Reef. Specimens maintained in captivity for a variable period were suitable for our study since they were initially captured as settled juveniles or adults (rather than being reared in captivity) and because there are no indications, nor expectations, that conditions in captivity affect structures already laid down in the otoliths.

Specific samples sizes were typically small (range 1 - 15, $\bar{X}$ = 2.62, mode = 1), but intraspecific variation in most species examined was also small (see results; also Thresher and Brothers, in press). Calculated durations, therefore, are likely to be robust for most species examined. Results of our analysis are also sufficiently broadly based that minor adjustments of a few species are likely to have little or no impact on the conclusions drawn.

RESULTS

Table 1 summarizes our data for mean pelagic duration and geographic distribution for the 115 species examined. Intraspecific variation appears to be low for most species. Of 57 species with $N > 2$, this variation ranged from 0 to 25 days, with a mode of 3 days, a mean of 5.0 days, and a standard deviation of 4.97 days. Only seven species (5 broadly distributed) varied intraspecifically by more than 10 days, and only three, Coris gamaird and Gomphosus varius (Labridae) and Rhinomuraena amboinensis (Muraenidae), varied by more than 20 days. Based on observations of specimens collected in other areas, large intraspecific variation appears to be more common in these families and also the Gobiidae and Scaridae (Brothers, et al., 1983; and Brothers, unpublished data) than in the remaining families. As yet, we have no data on geographical or environmental effects on intraspecific variability in larval duration, if any.

Based on species mean values, there is a conspicuous threshold effect in the relationship between pelagic duration and species distribution at approximately 45 days total pelagic duration (fig. 1). Below this threshold, duration of the pelagic stage does not correlate with breadth of distribution (Spearman Rank Correlation = 0.12, $N = 92$, $p > 0.2$), suggesting that for most Indo-Pacific coral-reef fishes (79.3% of species examined, and all representatives in 14 of the families), the length of time that pelagic eggs and/or larvae disperse is not the principal determinant of the extent of species distributions. In contrast, of the 23 species that have mean pelagic durations longer than 45 days, all but three are broadly distributed in the Indo-Pacific, with more than half (14 of 23) inhabiting 25 or more biogeographic areas (as compared with 3 out of 92 subthreshold species; this difference is significant at $p < 0.001$; $\chi^2 = 53.7$, $df = 2$). The exceptions to the above are Chaetodon collare (total duration 46 days), Neocirrhites armatus (51 days), and Rhinomuraena amboinesis (74 days). Of these, the first two are close to the threshold value. We are unable, however, to account for the limited distribution of the muraenid, R. amboinesis. The two specimens examined differed markedly in apparent larval duration (63 and 85 days), but both are well above the threshold and are consistent with our data for other muraenid species.

The data also suggest that unusually long pelagic durations are critical for colonization of geographically isolated areas. The average pelagic duration for Central Pacific species that also are found in the Hawaiian Islands, widely considered an isolated out-lier of the Indo-Pacific faunal province (Ekman, 1953; Briggs, 1974), is 68.4% longer than those that are not found in Hawaii (Central Pacific only, $\bar{X} = 49.1$ days, S.D. = 9.5, $N = 91$; species also in Hawaii, $\bar{X} = 49.1$ days, S.D. = 10.3; $N = 15$; difference significant at $p < 0.001$, Kolmolgorov-Smirnov test for unequal sample sizes; fig. 2). The minimum observed duration of Hawaiian-inclusive species, 35 days, is longer than the mean durations of 59.5% of the species examined, suggesting that most Central Pacific species may be incapable of colonizing Hawaiian reefs under normal circumstances. The pattern for colonizing Eastern Pacific reefs by Indo-West Pacific species is similar (fig. 2). Trans-Pacific species examined have a mean pelagic duration 25.6% longer than even Hawaiian-inclusive species, and a minimum duration (48 days) that is longer than mean durations of 81.0% of the species we examined.

Table 1.--Duration of pelagic larval stage (in days, as number of pre-transition otolith increments, age of new recruits, or both) and extent of geographical distribution (number of biogeographic areas occupied) for 115 species of Indo-Pacific coral reef fish. Location: AT = Aquarium Trade, AUS = Australia, JA = Japan, MI = Marshall Islands, OT = One Tree Island, PH = Philippines.

Family and species	No. of specimens	Source	$\bar{X}$ Otolith increments		Larval duration (Range)	Size of geographic distribution
			Pre-transition	Total for new recruits		
ACANTHURIDAE						
Acanthurus glaucopareius	3	AT	59.7		56-62	18
A. lineatus	2	AT	39.5		38-41	21
A. triostegus	1	AT	51		—	28
Naso lituratus	1	AT	69		—	27
Paracanthurus hepatus	1	AT	37		—	17
Zebrasoma veliferum	1	AT	36		—	26
APOGONIDAE						
Apogon cyanosoma	5	OTI		18.2	18-19	20
A. doderleini	5	OTI		22.6	16-27	8
Cheilodipterus quinquelineata	4	OTI	18.8		17-20	24
	25	OTI		23.1	17-21	
Siphamia orbicularis	1	AT	17		—	13
BALISTIDAE						
Balistoides conspiculatum	3	AT	36.0		35-38	18
Rhineacanthus rectangulatus	6	AT	43.5		39-46	24
R. aculeatus	1	AT	48		—	25
Palaluteres prionurus	1	OTI		28		21

Table 1.--Continued

Family and species	No. of specimens	Source	$\bar{X}$ Otolith increments		Larval duration (Range)	Size of geographic distribution
			Pre-transition	Total for new recruits		
BLENNIIDAE						
Petroscirtes mitratus	2	OTI	24.5		24-25	19
CALLIONYMIDAE						
Synchiropus splendens	2	AT	36		33-39	4
CHAETODONTIDAE						
Forcipiger flavissimus	3	AT	50.7		41-57	28
Heniochus diphreutes	2	AT	32.0		30-34	8
Chelmon rostratus	2	AT	27.0		26-28	11
	2	OTI		25.5	25-26	
Chaetodon lineolatus	1	AT	54		—	22
C. kleini	1	AT	56		—	22
C. speculum	1	AT	26		—	10
C. trifascialis	2	AT	32		30-34	24
C. baronessa	2	AT	38		38	8
C. auriga	2	AT	46.5		40-53	26
C. unimaculatus	2	AT	35.0		35	24
C. collare	1	AT	43		—	6
C. rainfordi	1	OTI		35		3
C. plebius	1	OTI		39		13
CIRRHITIDAE						
Cirrhitichthys oxycephalus	1	AT	51		—	27

Table 1.--Continued

Family and species	No. of specimens	Source	X̄ Otolith increments		Larval duration (Range)	Size of geographic distribution
			Pre-transition	Total for new recruits		
CIRRHITIDAE (continued)						
Neocirrhites armatus	1	AT	48		—	10
Oxycirrhites typus	3	AT	69.0		62-73	20
EPHIPPIDAE						
Platax pinnatus	1	AT	25		—	21
GOBIIDAE						
Amblygobius rainfordi	4	OTI		40.3	40-41	4
Paragobiodon echinocephala	1	OTI		36	—	19
P. melanosoma	3	OTI		42.3	39-47	11
LABRIDAE						
Anampses coeruleopunctatus	1	AT	25		—	20
Coris aygula	1	AT	51		—	26
C. gamaird	1	AT	51.3		35-60	26
C. variegata	3	OTI		29.7	28-30	5
Cirrhilabrus temminkii	1	OTI	24		—	23
	1	OTI		30	—	
C. cyanopleura	1	AT	30		—	10
Gomphosus varius	5	AT	52.8		42-75	26
Halichoeres biocellatus	1	OTI	21		—	10
	1	OTI		27	—	
Hemipteronotus taeniurus	2	AT	45.0		43-48	27

Table 1.--Continued

Family and species	No. of specimens	Source	$\bar{X}$ Otolith increments		Larval duration (Range)	Size of geographic distribution
			Pre-transition	Total for new recruits		
LABRIDAE (continued)						
Labroides dimidiatus	6	AT, OTI	23.2		22-24	23
L. bicolor	1	AT	24		—	23
Lierdenella fasciata	2	AT	20.0		19-21	16
Macropharygodon meleagris	1	AT	30		—	24
Stethosulis axilaris	1	PH	35		—	24
Thalassoma hardwicki	6	PH	45.7		44-47	16
T. lunare	4	AT, OTI	47.0		42-50	26
LETHRINIDAE						
Lethrinus nebulosus	1	OTI	37		—	20
LUTJANIDAE						
Lutjanus sebae	1	AT	40		—	17
MALCANTHIDAE						
Hoplolatilus purpureus	3	AT	34.0		33-36	4
MURAENIDAE						
Echidna nebulosus	1	AT	80		—	27
Rhinomuraena amboinensis	2	AT	71		60-82	9
OSTRACIIDAE						
Ostracion meleagris	2	AT	69.0		68-70	25

Table 1.--Continued

Family and species	No. of specimens	Source	X̄ Otolith increments: Pre-transition	X̄ Otolith increments: Total for new recruits	Larval duration (Range)	Size of geographic distribution
POMACANTHIDAE						
Apolemichthys trimaculatus	3	AT	24.2		22-26	17
Centropyge acanthops	1	AT	34		—	3
C. bicolor	3	AT	32.0		29-34	11
C. bispinosus	3	AT	32.0		31-33	17
C. eibli	6	AT	25.3		24-27	7
C. ferrugatus	1	AT	38		—	3
C. flavissimus	3	MI, AT	30.3		28-32	7
C. heraldi	4	AT	32.0		32	7
C. interruptus	2	JA	31.5		29-34	2
C. loriculus	1	AT	38		—	6
C. multifasciatus	3	AT	26.2		25-28	7
C. nox	2	AT	31.5		28-33	5
C. tibicen	3	AT	30.0		27-34	10
C. vroliki	1	AT	29		—	10
Chaetodontoplus melanosoma	3	AT	22.2		20-23	6
C. mesoleucas	5	AT	19.9		18-22	7
C. personifer	4	AT, AUS	23.25		23-24	3
C. septemtrionalis	1	AT	23		—	5
Genicanthus bellus	1	AT	25		—	9
G. melanospilos	1	AT	25		—	6
Holacanthus venustus	1	AT	25		—	3
Pomacanthus annularis	2	AT	21.0		20-22	6

Table 1.--Continued

Family and species	No. of specimens	Source	$\bar{X}$ Otolith increments		Larval duration (Range)	Size of geographic distribution
			Pre-transition	Total for new recruits		
POMACANTHIDAE (continued)						
P. imperator	2	AT	22		22	25
P. navarchus	3	AT	22.8		22-24	3
P. semicirculatus	4	AT	19.5		19-20	21
P. sexstriatus	2	AT, AUS	18.0		17-19	8
P. xanthometopon	4	AT	20.4		19-22	5
Pygoplites diacanthus	2	AT	24.5		23-26	25
POMACENTRIDAE						
Chromis caeruleus	5	PH	25.0		23-26	21
C. atripectoralis (probably)	1	AT	19		—	11
	2	OTI		23.0	20-26	
Dascyllus aruanus	5	AT	22.4		20-26	25
	4	OTI		22.0	20-23	
D. melanurus	3	AT	23.3		22-24	5
D. reticulatus	1	AT	23		—	23
D. trimaculatus	5	AT	24.2		21-25	23
Abudefduf saxatilis	1	OTI	23		—	22
Glyphidodontops cyaneus	6	AT	19.5		17-21	7
G. biocellatus	1	AT	19		—	8
G. hemicyaneus	5	AT	19.25		18-21	4
G. rex	3	AT	22.0		19-25	8
	3	OTI	19.7		19-20	

Table 1.--Continued

Family and species	No. of specimens	Source	$\bar{X}$ Otolith increments		Larval duration (Range)	Size of geographic distribution
			Pre-transition	Total for new recruits		
POMACENTRIDAE (continued)						
G. rollandi	3	OTI		23.0	23	2
G. talboti	1	OTI		22		
Dischistodus pseudochrysopoecilus	1	OTI		23	—	3
Neopomacentrus azysron	1	OTI		24	—	3
Paraglyphidodon behni	4	AT	17.75		15-21	6
Pomacentrus amboinensis	8	OTI	19.6		19-20	6
	18	OTI		22.5	18-26	
P. australis	4	OTI	25.0		23-26	1
	2	OTI	85.0		85	
P. coelestis	1	AT	20		—	13
P. popei	10	OTI	19.1		18-21	8
	4	OTI		24.0	23-25	
P. wardi	7	OTI	20.0		20	1
	4	OTI		24.25	23-25	
P. vaiuli	6	OTI	24.2		23-26	10
P. sp.	15	OTI		22.9	20-24	4
SCARIDAE						
Bulbometopon muricatum	1	AT	31		—	21
SCOLOPSIDAE						
Scolopsis dubiosus	3	OTI		19.0	15-23	8

Table 1.--Concluded

Family and species	No. of specimens	Source	$\bar{X}$ Otolith increments		Larval duration (Range)	Size of geographic distribution
			Pre-transition	Total for new recruits		
SERRANIDAE						
Anthias pascalus	1	AT	26		—	7
Cromileptis altivelis	1	AT	24		—	9
SIGANIDAE						
Siganus (Lo) *vulpinus*	2	AT	23.5		23-24	8
ZANCLIDAE						
Zanclus cornuta	1	AT	57		—	28

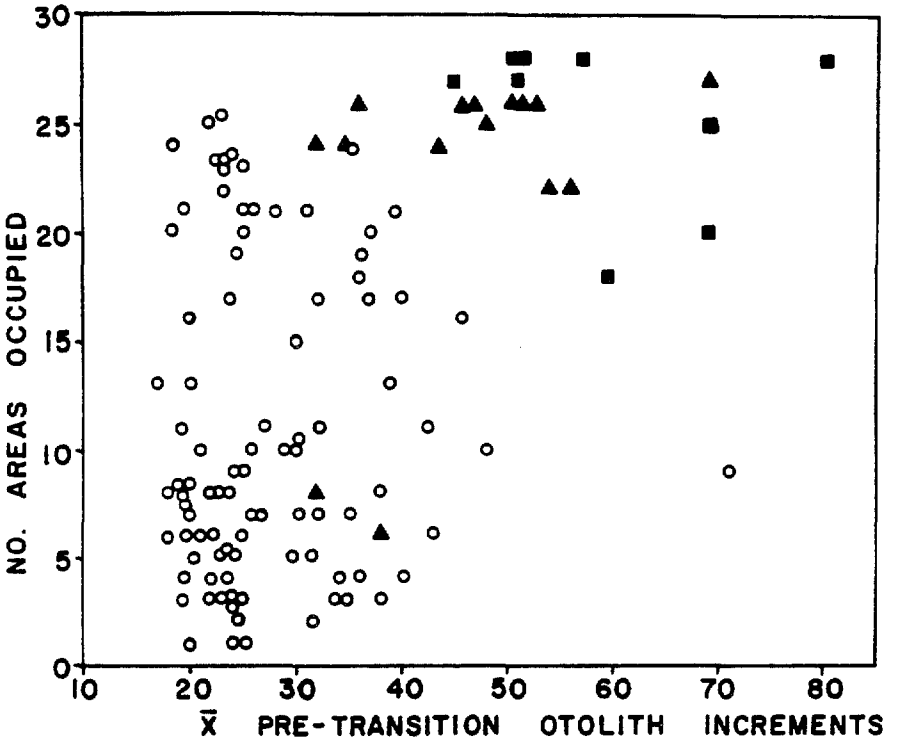

Figure 1.--The relationship between species mean pelagic larval duration, as indicated by the number of pre-transition daily growth increments, and the breadth of distribution of 115 species of Indo-Pacific coral-reef fishes. Total pelagic durations are 0-3 days longer than increment counts, depending on the family.

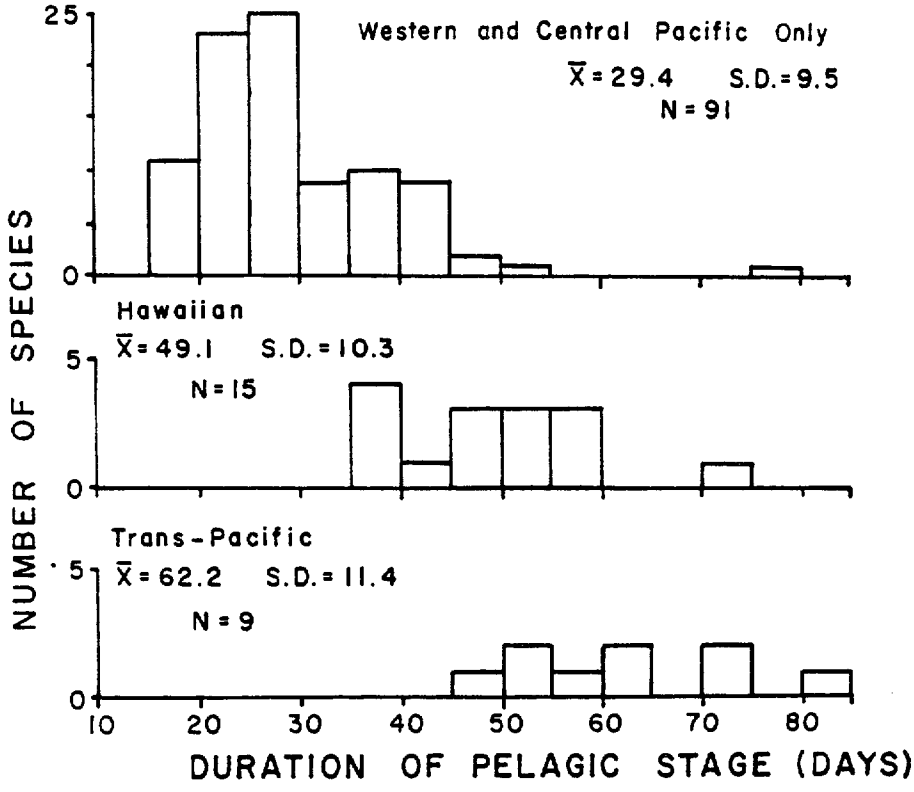

Figure 2.--Comparison of the duration of the pelagic stages for species showing different zoogeographic distributional patterns. Values on the abscissa are adjusted (see text) to convert pre-transition increment counts to pelagic duration. Open circles = means for species occurring in the Western and Central Pacific only; solid triangles = species whose range includes the Hawaiian Islands; solid squares = species distributed trans-Pacifically. All but one trans-Pacific species are found also in the Hawaiian Islands.

The mean duration for trans-Pacific species is 62.2 days (S.D. = 11.4, N = 9). The difference between these and the Hawaiian-inclusive species is not significant ($p = 0.13$; Kolmolgorov-Smirnov test, two-tailed), although the trend in the data is both evident and consistent with predictions made elsewhere in the literature (e.g., Rosenblatt and Walker, 1963). All but one trans-Pacific species also is found in Hawaii.

DISCUSSION

Our results suggest that a general correlation between long pelagic larval durations and broad geographic distributions is a valid assumption only when applied to a relatively few species with exceptionally long-lived pelagic stages (see also Thresher and Brothers, in press). In this respect, our conclusions are strikingly similar to those of Thorson (1961), who surveyed the pelagic durations and distributions of marine invertebrates. Thorson concluded that only 20% of all bottom invertebrates with pelagic larvae have "true long-distance larvae." These he defined as those with a planktonic life longer than 6 weeks. Both of these figures are strikingly close to those we calculate for Indo-Pacific coral-reef fishes, i.e., a threshold value of about 45 days, with 20.7% of the species examined exceeding this value. The latter figure obviously could be manipulated by adding species with high or low pelagic durations. We strongly suspect, however, that this threshold value will remain robust as more data are added. It is premature to draw strong conclusions without additional, detailed work for other families of fishes and other phyla, but the surprisingly close quantitative agreement between the current study and Thorson (1961) suggests that some fundamental principle that applies across phyla may be involved.

Our data are also in substantial agreement with suggestions that geographically isolated regions of the Indo-Pacific are colonized primarily by species with longer than average pelagic developmental stages. This point has previously been raised, particularly with respect to colonization of the Eastern Pacific Faunal Province by Indo-West Pacific species, both for marine invertebrates (e.g., Thorson, 1961; Dana, 1975; Zinsmeister and Emerson, 1979; Reaka, 1980) and coral-reef fishes (Briggs, 1961, 1974; Rosenblatt and Walker, 1963; Rosenblatt, 1967). Comparison of the minimum observed pelagic durations of species that occur in Hawaiian waters and in the Eastern Pacific with the large majority of species found only in the Central Pacific suggests that, although an element of chance certainly is involved, under normal circumstances the majority of Central Pacific species may not be capable of colonizing these outlying areas. Moreover, even for those species that have colonized the Eastern Pacific, such colonization may well be intermittent rather than continuous, and dependent on the occurrence of unusual oceanographic conditions. The minimum time required to cross the "Eastern Pacific Faunal Barrier" (see Ekman, 1953) can be estimated from the distance between the likely source of colonists, the Line Islands, and the westernmost point of the Eastern Pacific faunal province, Clipperton Island, and peak reported values for the Equatorial Countercurrent, the presumed route of colonization (e.g., Leis, 1983; Reaka and Manning, 1980). The distance involved is approximately 5250 km, and normal peak current velocities are in the range of 0.46 to 0.7 m sec^{-1} (Wyrtki, 1965; Tsuchiya, 1974). Consequently, normal transit time of the Eastern Pacific

Barrier by a passively drifting object will be at least 87 days; given that currents vary temporally and also decline as the near-shore environment is reached, a minimum estimate of 100 days is probably more realistic. Yet, apparent pelagic durations of nine trans-Pacific species examined range from 48 to only 83 days, averaging 24.8 days less than a reasonable minimum. None of the 302 specimens we examined had a larval duration longer than 87 days, suggesting that, even if one includes individual variation in larval competance, few if any species are likely to cross the barrier under normal circumstances. Our tentative conclusion, therefore, is that such colonization takes place only during periods when the countercurrent is unusually strong, i.e., during El Niño-type events (Wyrtki, 1965). If so, then we would predict that, following the recent very strong El Niño event in 1982-83 (see Gill and Rasmussen, 1983; Philander, 1983), unusually large numbers of new recruits of Indo-West Pacific species should be present on Eastern Pacific reefs.

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DIURNAL PERIODICITY OF SPAWNING ACTIVITY BY THE HAMLET FISH, HYPOPLECTRUS GUTTAVARIUS (SERRANIDAE)

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ABSTRACT

Many coral reef fishes spawn during the afternoon crepuscular period, a time of increased predatory activity by piscivores. We document the diel timing and spawning behavior of the hamlet fish, Hypoplectrus guttavarius, at St. Croix, U.S.V.I. This fish spawns daily during dusk in the water column above specific reef sites.

The time of spawning relative to sunset was quantified at two sites at different depths. Spawning commenced earlier at the deep reef site and continued later at the shallow reef site. A field manipulation evaluated how this species responded to disburbances during reproduction. When scuba divers attempted to alter the fish's behavior by swimming vigorously toward mating pairs, the hamlets did not abort spawning. The pair responded (1) by continuing to spawn later into the night than those not disturbed and (2) by spawning progressively nearer the substratum.

INTRODUCTION

Until the 1970s, the reproductive behavior of most tropical coastal marine fishes eluded observation. This has changed recently with the discovery that many species spawn during restricted times of ebb tide, off-reef current flow, or crepuscular periods. A majority of coral reef fishes spawn eggs that are bouyant and are advected by ocean currents. Having planktonic propagules is thought to facilitate both rapid advection/dispersal in currents and reduced predation by other reef fishes (Johannes, 1978; Lobel, 1978; Barlow, 1981). In general, fishes seek out specific reef localities and/or pinnacles over which they ascend and spawn. This behavior is particularly interesting for fishes spawning shortly before and during dusk because crepuscular periods are generally believed to be times of increased predator activity and success (e.g., Hobson, 1968, 1972, 1974). Also, to witness

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natural predation on spawning fishes or their eggs is not rare (Randall and Randall, 1963; Hobson, 1965; Moyer, 1974, 1975; Meyer, 1977; Colin, 1976, 1978; Robertson and Hoffman, 1977; Jones, 1981; Robertson, 1983). Some species gather in spawning aggregations and apparently are oblivious to human or natural piscivore predators even when disturbed or attacked (Johannes, 1978, 1981; Robertson, 1983). In contrast, the mere presence of a diver-observer will interrupt the mating of some smaller species unless the fish are approached and observed with stealth (Johannes, 1978; Lobel, 1978).

To date, studies on the reproductive behavior of tropical coastal marine fishes in the field have been primarily observational. The emphasis has been on documenting where, when, and how various species spawn. Herein we report the spawning behavior, diel timing, and a manipulation that attempted to disturb the behavior of a fish during reproduction. Our goal was to see whether and how the spawning behavior of the Caribbean hamlet, Hypoplectrus guttavarius, might be altered. Because hamlets and many other fishes spawn during the evening crepuscular period when predation by piscivores is most likely, we wanted to determine whether fish that were disturbed by scuba divers during the spawning act would cease all activity, move sites, depart and seek other mates, or merely continue despite the disturbance.

The Caribbean hamlet, Hypoplectrus guttavarius (fig. 1) was selected for study because it maintained stable, identifiable pairs which spawned almost every evening at specific sites during February 1980, at St. Croix. It was common, easily observed, and the spawning act was unmistakable and easily quantified. The diel timing of spawning is compared with that of H. chlorurus, H. nigricans, H. puella, and H. unicolor.

The reproductive ecology of hamlets is somewhat enigmatic. It has been suggested that Hypoplectrus nigricans and other hamlets are simultaneous hermaphrodites, and that individuals alternate sexual roles between spawning clasps (Barlow, 1975; Fischer, 1980a, 1980b, 1981). It is also controversial whether different morphological variants of hamlets represent aggressive-mimetic morphs of the single species, Hypoplectrus unicolor, or are reproductively isolated incipient species (Thresher, 1978; Graves and Rosenblatt, 1980; Fischer, 1980b). Hamlets usually mate assortatively by color patterns, although mixed pairs have been observed, and individuals which exhibit color markings characteristic of two or more color forms are known (Barlow, 1975; Thresher, 1978; Graves and Rosenblatt, 1980; Fischer, 1980a). Thus, the reproductive behavior of hamlets is interesting from several perspectives. To maintain simplicity and clarity, we refer to the various hamlets by their established species names (cf. Randall, 1968).

STUDY SITES

Fish were examined at two locations on St. Croix, U.S. Virgin Islands (64°35'W, 17°45'N). The first site was the east slope of Salt River canyon within the excursion limits of the NOAA National Undersea Laboratory System habitat (HYDROLAB). Since we were saturated, we spent approximately 53 hours per person observing fish at 20-30 m depths from February 11 to 15, 1980. The second site was located on several patch reefs at about 10 m depths in

Figure 1.--Adult Hypoplectrus guttavarius (the shy hamlet) approximately 11 cm in length.

the Buck Island Channel outside Teague Bay Reef on the northeast coast of St. Croix. Observations were made from February 20 to March 3, 1980. Further site descriptions are given by Neudecker and Lobel, 1982.

METHODS

Specific pairs of H. guttavarius were identified and details of their spawning behavior were recorded before, during, and after the manipulation. Observers selected one pair each evening and positioned themselves unobtrusively on site at least 15 min before the fish initiated courtship. The baseline spawning behavior of each pair was determined during one or two evenings prior to the disturbance manipulation (3 of 7 pairs were observed for 2 consecutive days before the manipulations; the other 4 pairs were observed the day before the manipulations). In cases where sites lacked distinguishing natural features, the specific site at which each pair spawned was marked with small floats. We spent several days diving at all hours, including sunrise, and saw hamlets spawn only during dusk (total observation 158.7 man-hours during the 7 days in HYDROLAB). Data recorded each time a pair spawned included the time, height in the water relative to the bottom and the coral/gorgonian structure over which spawning took place, approximate distance moved between spawning sites, and general notes on the pair's response to observers and other species.

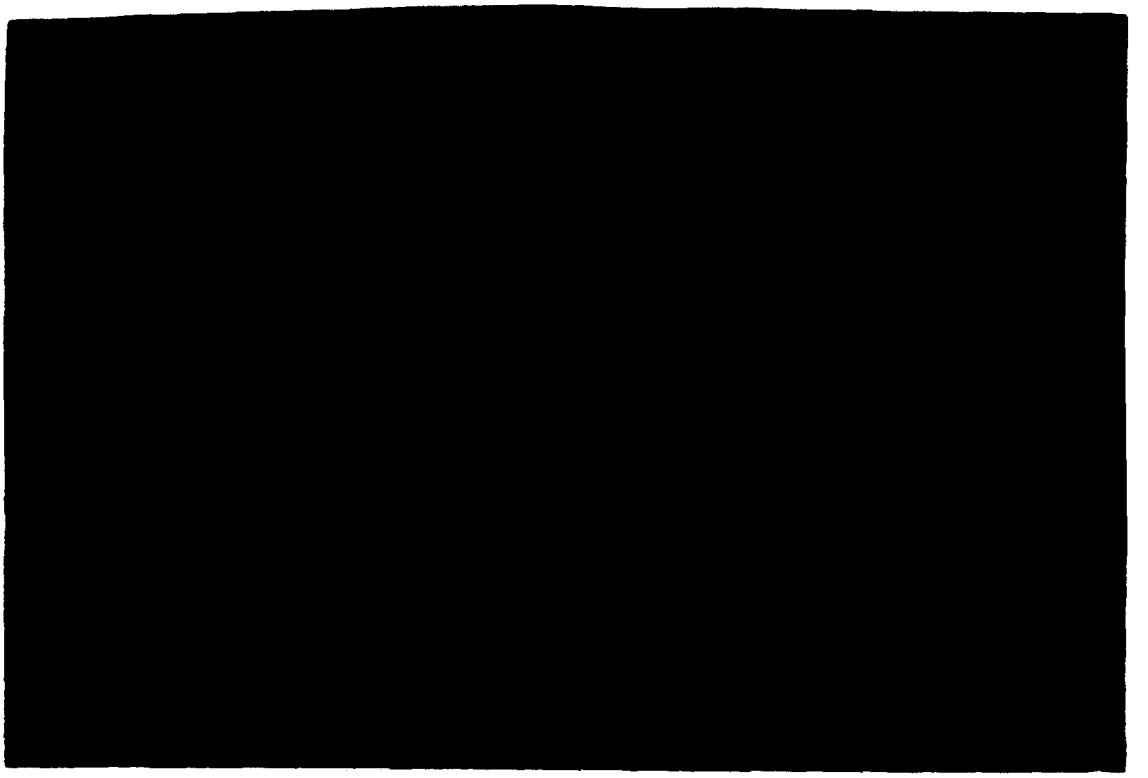

Figure 2.--A pair of Hypoplectrus guttavarius engaged in courtship at a typical spawning site (Deep Reef at East Wall of Salt River Canyon, HYDROLAB site).

The disturbance manipulations were conducted the day after baseline spawning behavior was determined. The manipulation was to disrupt the spawning act each time the fish attempted it. As the pair began to enter the spawning clasp, the observer swam rapidly toward the pair (in an attempt to mimic a predator's behavior). The pair was harassed repeatedly this way for as long as spawning was attempted. When mates parted, close watch was maintained until it was certain that spawning had ceased for the night. Occasionally, a pair would separate, swim several meters apart, return several minutes later, rejoin and attempt to spawn again. Follow-up observations were made on the same pair the day after the manipulation. Data analysis of treatments used the nonparametric Mann-Whitney U test statistic.

On any given day, at least three diver/observers were engaged in various phases of the manipulation. To provide control observations, a diver watched a spawning pair without interfering while other divers were either harassing a spawning pair or conducting follow-up observations.

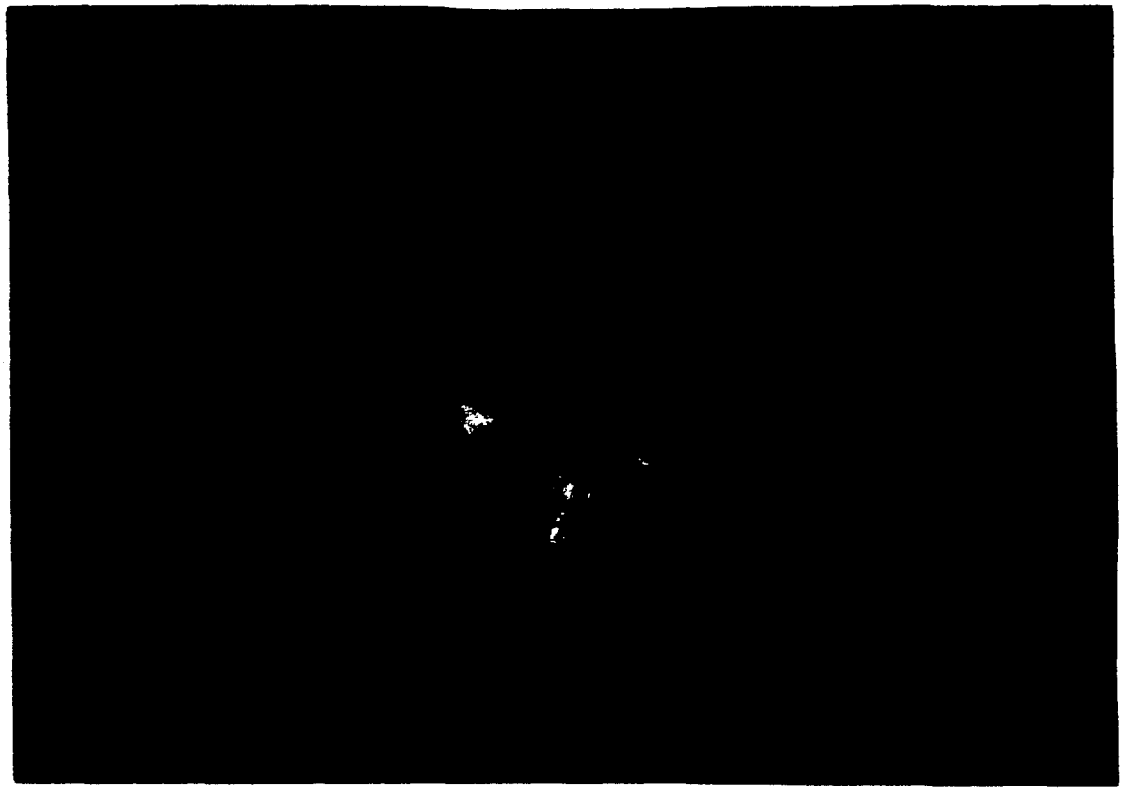

Figure 3.--Hypoplectrus guttavarius embraced in the spawning clasp. The individual facing head-down has bent body in an S-shape.

RESULTS

Typical Spawning Behavior

Our observations provided the following general picture of spawning in H. guttavarius. Hamlets mate only in pairs. Fertilization is external and zygotes are planktonic. During the daytime, mates appear loosely associated in adjacent or nearby home ranges. They begin to interact within 2 hr of sunset. They first rendezvous, remain close together, and engage in occasional short chases. The spawning act begins when one fish presents a lateral display while flicking its pelvic fins (fig. 2). The displaying individual slowly rises while continuing its display. The bright blue flank of this individual fades to a pastel shade. The other fish follows. The two then rise together about 1 m above some towering reef structure. At St. Croix, these structures were vertical colonies of the gorgonian, Pseudoplexaura sp., or the coral, Acropora cervicornis.

Once the proper height (about 1-2 m) is attained over a tall reef structure, the following fish folds around the pale colored leader, who poses head down in an S-shaped position (fig. 3). Release of eggs and sperm occurs

Figure 4.--Hypoplectrus guttavarius embraced in the spawning clasp. The individual folded around the other one facing head-down opens its mouth while quivering and spawning.

as both fish quiver. Quivering lasts for 2-3 sec. The individual folded around the other often opens its mouth while quivering (fig. 4). Following consummation, the fish cease embracing and quickly descend to the bottom. The embracing behavior of hamlets when spawning has been termed the spawning clasp (Fischer, 1980a) and occurs many times throughout an evening. Infrequently, fish would embrace but not quiver, and the release of gametes was not evident. Fischer (1980a) has described the similar spawning behavior and sexual role of H. nigricans.

Each pair of hamlets initiated spawning at a specific reef location each evening. Pairs showed strong spawning site specificity. They moved between a few (from 1 to 4) particular sites each evening, and frequently a pair returned to their original site. When some pairs moved between spawning sites, other individuals occasionally interfered and attempted to steal a mate. These 'floater' individuals were seldom successful. Out of all hamlet spawnings observed (N = 314 of 5 spp.), only once was a floater successful in stealing a mate by breaking up an existing pair (the pair and floater species was H. unicolor).

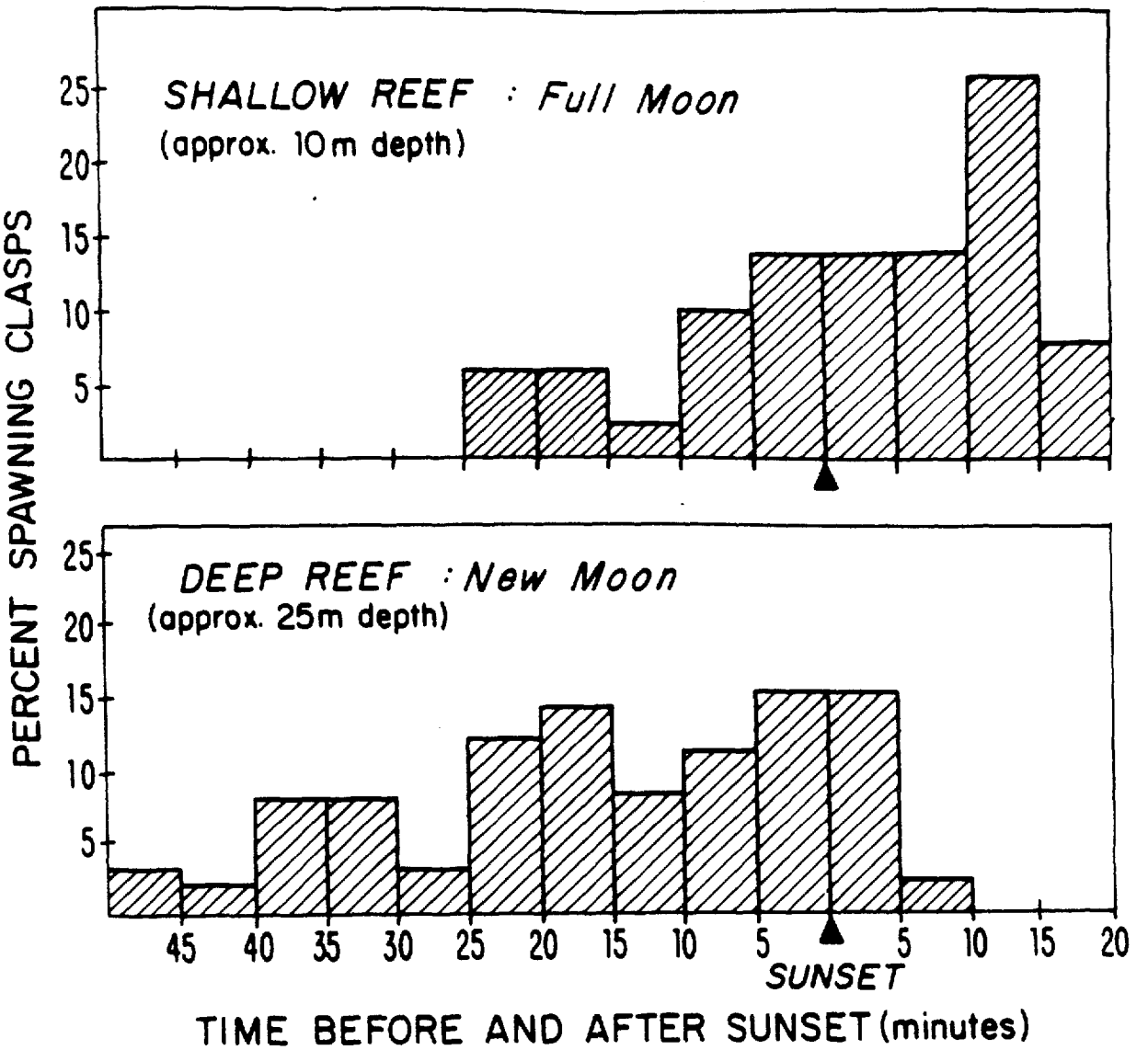

Figure 5.--Diel reproductive timing of Hypoplectrus guttavarius at two depths. The shallow site (10 m depth) was occupied during the full moon phase (Feb. 24-27, 1980), while the deep site (22-30 m depth) was occupied during the new moon (Feb. 11-13, 1980). The shallow group consisted of 4 pairs observed over 4 days for a total of 67 spawning clasps. The deep group consisted of 7 pairs observed over 4 days for a total of 210 spawning clasps. Time is in minutes before and after sunset. See text for discussion.

Diel Reproductive Timing

Hypoplectrus guttavarius spawned almost every evening during the study period. Fish were studied at two sites which differed in depth. The deep reef site (20-30 m depth) was occupied by us February 11-15, and the shallow site (10 m depth) from February 20-March 3. We did not see hamlets spawn on two evenings, February 21-22. Observations at the deep site corresponded to the presence of a new moon (February 15). We were at the shallow site during the full moon (March 1). The dates on which hamlets were not seen spawning coincided with the last quarter moon phase (February 22).

The diel timing of reproduction, relative to sunset, differed for *H. guttavarius* at the two sites (depths) and lunar phases. The first spawnings at the deep reef site began 50 min before sunset (with a mean, $\bar{X}$, and standard deviation, S.D., of 33 $\pm$ 1 min) and the last spawnings ended 10 min ($\bar{X} \pm$ S.D. = 2 $\pm$ 9 min) after sunset; most spawnings occurred just prior to sunset. Spawning at the shallow reef site commenced later, 25 min ($\bar{X} \pm$ S.D. = 16 $\pm$ 7 min) before sunset, and ended later, 20 min ($\bar{X} \pm$ S.D. = 3 $\pm$ 6 min) after sunset; here most spawnings occurred just past sunset (fig. 5). Reproduction by fish at the two sites did not differ in any other aspect.

We did not observe any strong lunar periodicity in the daily spawning behavior of *H. guttavarius*. However, our data do not allow distinguishing between the possible effects of 1) different phases of the moon during the times that each group was observed vs. 2) the difference in depth and corresponding changes in light levels during dusk.

Effects of Disturbance on Spawning Behavior

All *H. guttavarius* persisted in spawning in spite of overt and constant harassment. Harassed pairs attempted twice as many spawning clasps and continued for about 25 min later than nonharassed (day before and day after) pairs (tables 1, 2). However, the frequency of spawning clasps attempted per 5 min remained the same (about 2 $\pm$ 1 clasps; tables 1b, 2b). The number of times a pair changed spawning sites relative to the number of spawning clasps also did not vary significantly (tables 1c, 2c). One particularly striking effect of disturbance on these spawning fish was that, as spawning was continuously disrupted, a pair attempted to spawn progressively nearer the substratum (based on our qualitative observations). At the end of the disturbance period, several pairs were trying to spawn next to the bottom while hidden among coral/gorgonian branches. This result simply may indicate that once ovulation has begun, the fish must spawn.

Overall, the fish persisted in spawning despite the aggressive behavior of the scuba divers. However, we have no estimate of the fate of zygotes when released next to the bottom and in between coral/gorgonian branches as compared to those normally dispersed about a meter above reef structures. The experience of the disturbance had no apparent lasting effects on the fish. The fish's behavior did not differ markedly on the day after compared to the day before the disturbance (tables 1, 2).

Table 1.--Effect of disturbance on the spawning behavior of Hypoplectrus guttavarius. Data for shallow and deep water groups were pooled except when related to sunset time. In addition to the above changes, when fish were disturbed, they would attempt to spawn closer to the substrate until they were on the bottom. Notations in last rows (e, f) indicate before (-) or after (+) sunset.

	Baseline before disturbed (7 pairs; 10 observations)	During disturbance (6 pairs; 6 observations)	Day after disturbed (5 pairs; 5 observations)
a. $\bar{X}$ ± S.D. (range) no. spawning clasps per pair	12 ± 3 (7 to 16)	25 ± 9 (10 to 33)	12 ± 2 (9 to 15)
b. $\bar{X}$ ± S.D. (range) no. spawning clasps per 5 min	2 ± 1(0.6 to 3.6)	2 ± 1 (1.5 to 3.1)	2 ± 1 (1.5 to 3.2)
c. $\bar{X}$ ± S.D. (range) ratio of no. moves pair made between spawning sites to total no. spawning clasps	0.23 ± 0.16 (0 to 0.5)	0.48 ± 0.30 (0.06 to 0.86)	0.26 ± 0.19 (0 to 0.46)
d. $\bar{X}$ ± S.D. min. (range) duration of spawning period per day	31 ± 8 (11 to 91)	57 ± 21 (33 to 69)	28 ± 8 (21 to 38)
e. Time ($\bar{X}$, range) relative to sunset that spawning commenced (min)			
shallow group (full moon)	-16 (-22 to -6) (N = 4)	-24 (-44 to -8) (N = 3)	-11 (-19 to -2) (N = 3)
deep group (new moon)	-33 (-50 to -19) (N = 6)	-50 (-71 to -35) (N = 3)	-40 (-44 to -35) (N = 2)
f. Time ($\bar{X}$, range) relative to sunset that spawning ceased (min)			
shallow group (full moon)	+13 (+ 5 to +18) (N = 4)	+30 (+20 to +38) (N = 3)	+12 (+ 2 to +24) (N = 3)
deep group (new moon)	- 2 (-19 to + 5) (N = 6)	+10 (- 2 to +21) (N = 3)	- 4 (- 6 to - 1) (N = 2)

Table 2.--Statistical comparison of data from table 1. Values listed are calculated values of Z using the Mann-Whitney U test. Values marked by * are statistically different at p = 0.05 (critical value for Z = 1.960.)

	Before vs. During Disturbance	After vs. During Disturbance	Before vs. After Disturbance
a. No. spawning clasps per pair	*2.490	*2.008	0.245
b. No. spawning clasps per pair per 5 min.	1.844	0.548	1.347
c. No. moves pair made between spawning sites per total no. spawning clasps	1.627	1.278	0.367
d. Duration of spawning period	*2.169	*2.373	0.857

Spawning of Other Hamlets

Four other hamlets also were observed spawning at the shallow reef site: H. puella, H. unicolor, H. chlorurus, and H. nigricans. We did not see mixed mating among hamlets. Data contrasting aspects of reproduction in these fishes and of H. guttavarius are presented in table 3. However, the data set lacks sufficient detail to allow more than a general indication of how the pattern and timing of reproduction might vary among congeners of hamlets.

DISCUSSION

Many diurnal tropical marine fishes that remain active during the evening crepuscular period may risk being eated by piscivores, whose feeding activities generally are believed to increase at this time (Hobson, 1968, 1972, 1974; Domm and Domm, 1973; Major, 1977). This increased threat of predation is reflected in the potential prey's behavior, and most species retreat to shelter, aggregate, or forage closer to the reef (Hobson, 19783, 1978; Robertson and Sheldon, 1979). However, many species also periodically spawn during dusk (e.g., Randall, 1961; Lobel, 1978; Moyer and Nakazano, 1978; Moyer, 1979; Moyer and Zaiser, 1981; Zaiser and Moyer, 1981; Neudecker and Lobel, 1982; Moyer, et al., 1983). Spawning during the evening crepuscular period is thought to reduce the likelihood of predation on planktonic eggs, since most planktivorous fishes that select such small prey are inactive by this time. It is noteworthy that the eggs of nestbuilding, demersal-spawning balistid and pomacentrid fishes hatch after dark, whereupon the larvae become planktonic (Allen, 1972; Moyer and Bell, 1976; Ross, 1978; Fricke, 1980; Lobel and Johannes, 1980; Doherty, 1983). Diurnal planktivores consume smaller prey, including eggs, than nocturnal planktivores which infrequently

Table 3.--Reproductive behavior by other hamlets (*Hypoplectrus* spp.). These fish were observed at 25-30 ft. depth, February 25-March 2, 1980. For *H. nigricans* (*), see Fischer, 1980, for comprehensive spawning data.

	H. puella (N = 2 pairs)	*H. unicolor* (N = 2 pairs)	*H. chlorurus* (N = 2 pairs)	*H. nigricans** (N = 1 pair)
$\bar{X}$ (range) no. spawning clasps per day	10 (8-12)	12 (6-17)	17 (16-18)	27
$\bar{X}$ (range) no. spawning clasps per 5 min.	3 (3-4)	2 (2-2)	2 (-2-2)	1
$\bar{X}$ (range) no. moves pair made between spawning sites per 10 spawns	5 (4-6)	7 (7-7)	7 (7-7)	7
$\bar{X}$ (range) min. duration of spawning per day	15 (14-16)	27 (16-38)	42 (38-45)	101
Minutes before sunset that spawning commenced	5 + 6	13 + 16	28 + 39	87
Minutes after sunset that spawning ceased	8 + 11	1 + 24	8 + 11	14

eat eggs (Hobson and Chess, 1978). Most egg-eating fishes cease foraging as light levels diminish, since low light levels make visual orientation difficult and also predation by piscine predators generally increases at this time (Hobson, 1972, 1974: Hobson and Chess, 1978). Additionally, any planktivores still actively feeding through dusk may be quickly satiated by the simultaneous spawning of many fishes.

Spawning during dusk may reduce mortality of fish eggs by predation, but it also may increase the potential risk of predation for adult fishes. Hobson (1968, 1972, 1974, 1978; Hobson, et al., 1981) has documented extensive evidence suggesting increased predation by fish predators on tropical reef fishes exposed or otherwise vulnerable during the crepuscular periods. Fishes also are thought to be more vulnerable to predation when preoccupied with mating (Johannes, 1978, 1981; Robertson, 1983). Furthermore, it must be noted that there are many fishes, particularly labrids and scarids, which spawn throughout the day, appearing more in phase with tidal currents than crepuscular periods (Barlow, 1981; Kuwamura, 1981; Robertson, 1983).

In this study, we wanted to evaluate how a fish would alter its mating pattern when disturbed or attacked. The results might then provide some insight into the selective pressures molding the reproductive tactics of coastal marine species in the tropics. At the time, the best arrangement we could devise to test the possible effect of predation was by simulating predator behavior using scuba divers. Other studies also have considered a fish's response to a human diver as indicative of reaction to a piscine predator (e.g., Coates, 1980). Nevertheless, results of this manipulation should be related only tenuously to how the hamlet might respond to a fish predator. A fish predator probably would not continue to attack the same prey throughout dusk.

The hamlet, Hypoplectrus guttavarius, altered its normal mating behavior when harassed by 1) attempting more clasps longer into the night and 2) spawning progressively nearer to the bottom in and among shelter. In no case was spawning terminated early; in fact, the opposite occurred, and fish prolonged spawning attempts. This result simply may indicate that once ovulation has begun, the fish must spawn. The spawning sites were all reef structures (gorgonian and coral) taller than the surrounding terrain. Only after a pair had shifted sites repeatedly did they commence spawning nearer the bottom or in shelter. Difference in survivorship of the free-floating zygotes when released high above the reef vs. near the bottom was not determinable. Fish which were attacked and harassed one day showed no indication of lasting behavioral affects the next day.

The importance attributed to spawning above a tall reef structure is that it provides a degree of safety for the adults. It allows the fish to mate relatively high in the water column while remaining as close as possible to shelter. Spawning high in the water places the free-floating eggs beyond the grasp of benthic planktivores and in a position most favorable to advection by currents.

Hobson (1972, 1974) has suggested that the well defined twilight activities of tropical reef fishes have been shaped by the threat of crepuscular predators (Hobson, et al., 1981). If this hypothesis is correct, then it would seem that

fishes spawning during evening crepuscular periods have not been overtly deterred by the potential threat of predation. Alternatively, the adaptive pressures favoring zygote survival may have been more influential in molding the diel timing of reproduction than factors affecting survival of the parents (e.g., predation) while spawning during the evening crepuscular period.

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PATTERNS OF REPRODUCTION IN SMALL JAMAICAN BRITTLE STARS: FISSION AND BROODING PREDOMINATE

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ABSTRACT

Brittle stars were collected from coralline algae and from an adjacent turtle grass bed in the back reef lagoon at Discovery Bay, Jamaica. Fissiparous species are numerically predominant in both habitats. These species, although systematically diverse, share strikingly similar life history characteristics, including small adult size (< 4.5 mm disc diameter), low fecundity, yet probable planktotrophic development and asexual propagation. Brooding species are also well represented. They too are small in adult size (< 4.0 mm disc diameter) but are hermaphroditic direct developers, brooding small numbers of young in the bursae. There appears to be selection for small adult size in brittle stars in the habitats studied here. Small size in turn is correlated with modified reproductive patterns like fissiparity and brooding. The relative importance of these patterns in reef habitats is considered and the frequency and geographic distribution of fissiparity and brooding in brittle stars briefly discussed.

INTRODUCTION

Coral reefs present many microhabitats which may provide refuges from the pressures of predation generally considered to exist on open surfaces in such areas. Coralline algae, sponges, and coral boulder scree all offer cryptic spaces exploitable by certain species. Such crevices potentially provide both a refuge for juveniles of large species and a habitat in which small species can complete their entire life history.

During studies on the reproductive biology of the small fissiparous brittle star Ophiocomella ophiactoides (H. L. Clark) at Discovery Bay, Jamaica, W.I. (Mladenov, et al., 1983; Mladenov and Emson, 1984), we became aware that in the

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[1] Contribution number 343 of the Discovery Bay Marine Laboratory of the University of the West Indies.

coralline algal habitat occupied by O. ophiactoides and adjacent turtle grass, a number of other small brittle stars were present, some in abundance. Of these species, some showed evidence of fissiparity; others, however, were nonfissiparous brooding species which nevertheless shared certain characteristics with the fissiparous forms. In this paper, we present data on the relative abundance of brittle stars in these microhabitats, briefly review some of the life history characteristics of these brittle stars, discuss the similarities and differences between them, speculate on the reasons for the abundance of small brittle stars in these habitats, and comment on the association of small size with fissiparity and brooding in brittle stars.

STUDY SITES AND METHODS

The study sites consisted of (1) a shallow, sheltered cove (known locally as Maze Cove or the Blue Maze) located in a part of the back reef just west of the dive locker of the Discovery Bay Marine Laboratory, Jamaica, and (2) a closely adjacent bed of turtle grass.

The rocky walls of the cove are covered with a deep carpet of coralline and other red algae in which Amphiroa rigida and A. fragillisima are most prominent. These algae are all dark in color and, except at the bases of the fronds, relatively free of detritus. During August 1981 and July 1984, clumps of algae were carefully transferred to polythene bags underwater, removed to the laboratory, and searched for brittle stars and other fauna. The brittle stars were identified, examined for evidence of cross-disc division (three long arms and three shorter regenerating arms on the disc), counted, and measured (the parameters noted were the greatest dimension of the disc and, in the case of the fissiparous species, the length of the arms). The sexual condition of the animals was later examined by dissection. In the case of Ophiocomella ophiactoides, egg size was obtained by measuring the diameter of spawned, fertilized eggs. For the other species studied, the diameter of the largest oocytes present in histological sections of ripe females was measured. For estimation of total egg number, the ovaries were removed, blotted free of excess moisture, and weighed. A small fraction was then separated, weighed, and the number of eggs counted. Total egg number was obtained by multiplication.

The site adjacent to the cove has a sand and silt substratum that supports an abundance of turtle grass, Thalassia testudinum, as well as a variety of algae. The bases of the Thalassia are uniformly pale, due to attached detritus and the presence of dead decaying leaf bases on the outsides of the plants. Detritus is abundant around and between the plants. Thalassia shoots were pulled from the substratum and placed in polythene bags underwater along with samples of the surface of the substratum from immediately around the base of the plants. This material subsequently was treated similarly to that obtained from the algal clumps.

RESULTS

The Species and Their General Characteristics

The brittle stars found in the algal turf are listed in table 1A. This table also shows their relative abundances in these microhabitats and gives

Table 1.--Characteristics of the brittle stars from two adjacent habitats at Discovery Bay, Jamaica, in 1981. A. Coralline algal turf (N = 195); B. *Thalassia* bed (N = 75). Algal volume 1.5 l. *Thalassia* volume approximately 6 l.

	Species	Family	Relative Abundance (% of specimens in sample)	Maximum disc size (mm)	Appearance	Mode of Reproduction
A.	*Ophiocomella ophiactoides*	Ophiocomidae	69	4.5	Dark green, arms banded	Fissiparous and broadcasts planktotrophic larvae (Mladenov, *et al.*, 1983; Mladenov and Emson, 1984)
	Amphipholis squamata	Amphiuridae	21	3.0	Brown disc, arms paler and often banded	Brooder (Fell, 1946)
	Ophiactis savignyi	Ophiactidae	9	3.0	Brown or mottled disc, banded brown and white arms	Fissiparous and broadcasts larvae; probably planktotrophic (Mortensen, 1931)
	Ophiostigma isacanthum	Amphiuridae	1	4.0	Sand colored	Fissiparous; mode of sexual reproduction unknown

Table 1.--Continued

	Species	Family	Relative Abundance (% of specimens in sample)	Maximum disc size (mm)	Appearance	Mode of Reproduction
B.	Ophiostigma isacanthum	Amphiuridae	52	4.0	As in A above	As in A above
	Ophiolepis paucispina	Ophiolepidae	21	4.0	Sand colored	Brooder (Hendler, 1979)
	Amphipholis squamata	Amphiuridae	15	3.0	As in A above	As in A above
	Ophiocomella ophiactoides	Ophiocomidae	5	4.5	As in A above	As in A above
	Ophioderma cinereum	Ophiodermatidae	4	4.5	Sand colored	Only juveniles in this habitat. Mode of reproduction unknown.
	Ophiactis savignyi	Ophiactidae	1	3.0	As in A above	As in A above
	Ophiothrix oerstedi	Ophiothricidae	1	-	-	Only juveniles in this habitat. Adults broadcast lecithotrophic larvae (Mladenov, 1979)

Table 2.--Relative abundance (% of specimens) in samples from the coralline algal turf habitat in 1984. * = all juveniles with disc diameter less than 5 cm.

	A	B	C	D
Total number recovered	N = 115	N = 164	N = 50	N = 183
Algal volume (ml)	1,505	1,390	345	1,260
Ophiocomella ophiactoides	76.5	61.0	58	75.4
Amphipholis squamata	10.4	12.2	34	14.2
Amphiura stimpsoni	5.2	16.4	2	9.9
Ophiactis savignyi	3.4	3.0	0	0
Ophiostigma isacanthum	0.9	5.5	4.4	0
Ophiactis algicola	-	0.6	2	0.5
Ophiocoma pumila*	0.9	-	-	-
Ophiothrix oerstedi*	0.9	-	-	-
Ophioderma appressum*	1.8	0.6	-	-
Ophiolepis paucispina	-	0.6	-	-

details of their sizes, appearances, and reproductive modes. Of the four species present in 1981, Ophiocomella ophiactoides was the most abundant and Ophiostigma isacanthum, the least. Further samples from this habitat in 1984 (table 2) show that the pattern is consistent over time, although in these later samples rather more occasional species were taken and Amphiura stimpsoni was moderately abundant. Four of the six most common species (O. ophiactoides, Ophiactis savignyi, Ophiactis algicola, and O. isacanthum) in the latter collections are fissiparous, able to reproduce asexually by cross-disc division, and two (Amphipholis squamata and A. stimpsoni) are brooders. The fissiparous species are members of three different families (Ophiocomidae, Ophiactidae, Amphiuridae). The species represented as juveniles may be found in abundance as adults elsewhere in Discovery Bay.

A rather similar group of species of brittle stars was found in the samples taken (in 1981 only) from the detritus surrounding the Thalassia testudinum shoots and, to a small extent, the axils of Thalassia leaves (table 1B). Of the seven species found, all except Ophioderma cinereum were also in the algal turf. However, the relative abundances of these species are very different in

the two habitats, since O. isacanthum, Ophiolepis paucispina, and A. squamata are the prominent species in this habitat. Only A. squamata achieves a similar abundance in both habitats, and fissiparous species are numerically predominant in both habitats.

Two features were common to all the species in these habitats. One is small body size. No species exceeds 4.5 mm maximum disc diameter, and most species are smaller than this. All species except O. cinereum and Ophiothrix oerstedi included reproductively active adult individuals. The second feature common to these species is the color pattern of the brittle stars. All are very difficult to see in the natural habitat because of their size and because the coloration of the animals renders them cryptic; the banded arms of several species are particularly concealing. Even when the algae were dissected in the laboratory, many brittle stars were detected only when they moved. Furthermore, for those residing in coralline algae, the arms were similar in diameter to the algal strands. It was noticeable that other fauna found within the algal clumps, notably the small (2-5 cm) holothuroid Synaptula hydriformis and some unidentified amphipods, also were cryptically patterned. A dark green with paler blotches, S. hydriformis is very similar to O. ophiactoides in color.

Asexual Reproduction in the Fissiparous Species

The overall percentage of individuals showing evidence of fission in each of the three common fissiparous species is very high (table 3) and is clearly an important means of population increase in all three. This similarity is only one of several that can be discerned. For instance, the range of disc size was very similar (table 3), and the size frequency histograms (fig. 1) were virtually identical in pattern, each population being dominated by individuals with disc diameters of 1.0-2.5 mm. Few animals of larger disc size were evident, and very small animals also were missing. Data were available only for August 1981 and July 1984 for O. savignyi and O. isacanthum, but for O. ophiactoides data were also available for June, July, and December of 1981 (Mladenov, et al., 1983) and July of 1984; the size frequency patterns were identical at all times. No evidence of larval recruitment was apparent in that species at any time. While it remains possible that larval recruitment occurred in intervening months, we suspect that the populations of all three species are, at these sites, maintained almost solely by asexual reproduction.

Another similarity between the species is in the relationship between disc size and evidence of recent fission. Table 4 shows the proportion of animals with different disc sizes found in each of four regeneration categories. In all three species, there is a clear trend: most small animals show evidence of recent splitting (i.e., a low ratio for length of short/long arms), while a high proportion of large animals do not.

Sexual Reproduction in the Fissiparous Species

Larger individuals in all three fissiparous species may contain mature functional gonads (table 3 and below). Mladenov and Emson (1984) already have reported that O. ophiactoides with disc diameters greater than 2.2 mm can

Table 3.--Some features of fissiparous brittle stars from Discovery Bay, Jamaica. [1] = Diameter of spawned fertilized eggs; [2] = largest oocytes present in mature females.

Species	Range of disc size (mm)	% fission apparent in population	Minimum disc size of mature females	Egg diameter	Egg number of largest specimen sampled
Ophiocomella ophiactoides (N = 359)	1.0-4.5	90	2.2 mm	0.08 mm[1]	7,400
Ophiostigma isacanthum (N = 56)	1.0-4.0	80	3.3 mm	0.12 mm[2]	5,000
Ophiactis savignyi (N = 65)	1.0-3.0	67	None of the specimens contained gonads	-	-

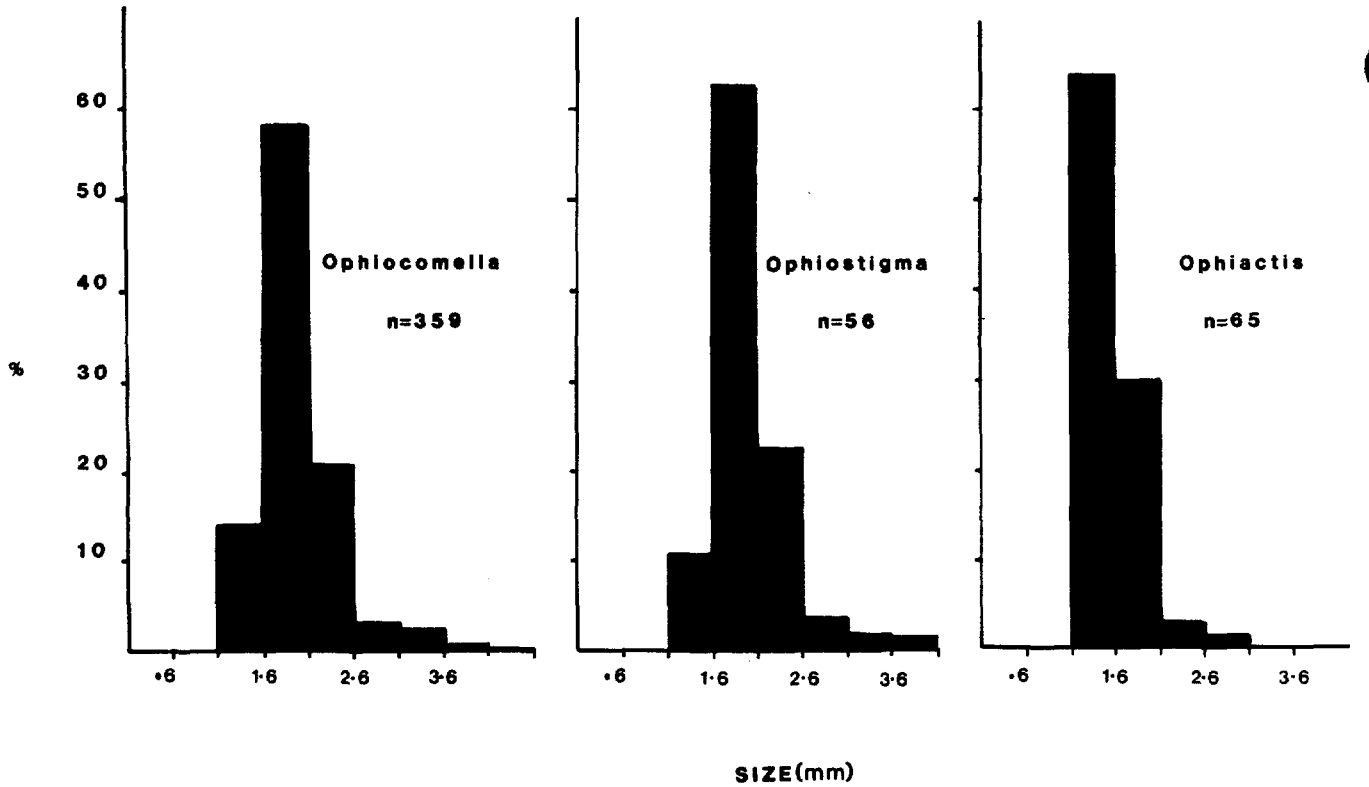

Figure 1.--Size frequency distributions of discs of the three fissiparous brittle stars at Discovery Bay (August 1981).

contain ripe gonads, and of 246 animals with disc diameters greater than 2.0 mm, 57 were female (23%). Of the 56 specimens of O. isacanthum examined during this study, 11 with disc diameters greater than 2.7 mm had recognizable gonads. Of the 11, 2 with disc diameters of 3.6 and 3.3 mm were mature females, 3 with disc diameters of 3.5 and 2.8 mm were mature males, and the remaining 6 were unsexable. None of the O. savignyi examined from the Discovery Bay sites contained gonads (table 3), but Emson and Wilkie (1984) have shown that at the Bogue Islands in Montego Bay on the Jamaican north coast, O. savignyi achieved a larger size (up to 5.5 mm) and specimens with disc diameters greater than 4.0 mm may contain ripe ova and achieve successful sexual reproduction. The largest oocytes in these specimens measured 0.10 mm in diameter, and the largest individual (5.5 mm disc diameter) contained roughly 10,000 eggs.

The three fissiparous species are similar in producing small eggs within the size range (0.07-0.20 mm) regarded as resulting in planktotrophic larvae (Hendler, 1975; Mladenov, 1979).

Since disc size and egg size are similar in the three species, it is not surprising that reproductive output, as measured by maximum number of eggs produced, is roughly equivalent (table 3). The maximum egg number for these species is two to three orders of magnitude lower than that recorded for nonfissiparous brittle stars with planktotrophic development (Hendler, 1975; Mladenov, 1979; Mladenov and Emson, 1984). Compared to their nonfissiparous planktotrophic

Table 4.--Comparison of the regeneration patterns of the three fissiparous brittle stars found at Discovery Bay, Jamaica. Regeneration category refers to the ratio of length of short arms to length of long arms. Data are given as percent of all individuals with a given disc diameter.

Species		*Ophiocomella ophiactoides* (N = 359)				*Ophiactis savignyi* (N = 65)				*Ophiostigma isacanthum* (N = 56)			
Regeneration category (%)		0-25	26-50	51-75	75+	0-25	26-50	51-75	75+	0-25	26-50	51-75	75+
Disc Diameter (mm)	0-0.5	0	0	0	0	0	0	0	0	0	0	0	0
	0.6-1.0	63	37	0	0	42	12	21	25	75	0	0	25
	1.1-1.5	55	28	14	3	21	35	13	31	53	18	19	10
	1.6-2.0	51	28	17	4	0	0	33	67	20	20	27	33
	2.1-2.5	45	16	26	13	0	0	0	100	40	0	20	40
	2.6-3.0	14	42	15	29					0	0	0	0
	3.1-3.5	0	28	14	58					0	0	0	100
	3.6-4.0	0	0	0	100					0	0	0	0
	4.1-4.5	0	0	0	100								

counterparts, therefore, these fissiparous brittle stars broadcast exceedingly small numbers of larvae at each spawning, with important potential consequences for recruitment. Even if these species spawned 10 times a year, their output would be low. As only a small proportion of the population is sexually mature, the output of larvae must be very small.

The three nonfissiparous species present as adults (A. squamata, A. stimpsoni, and O. paucispina) share similar reproductive methods. They are hermaphroditic species which produce a small number of relatively large yolky eggs. These are brooded within the genital bursae and released, quite possibly throughout the year, as competent juveniles (although Hendler, 1975, and Emson, unpub. obs., have noted that release is reduced at some seasons).

Observations of Potential Predators

Many species of fishes live in the water adjacent to the algal carpets. During our collections, fish were observed picking at the surface of the algae on several occasions. Blue Tangs (Acanthurus coeruleus), Surgeon Fish (Acanthurus chirurgus), and, in particular, Slippery Dicks (Halichoeres bivittatus) were observed darting at and pushing into the algal clumps. The latter species is known to eat invertebrates (Randall, 1967).

DISCUSSION

Throughout the Discovery Bay area, brittle stars are an abundant and obvious component of the benthic macrofauna. In most areas, large species predominate, although crevices and algae such as Halimeda sp. harbor both juveniles of large species and individuals of small species. The algal turf and turtle grass habitats studied here, however, were unusual in having a large number of very small, inconspicuous species of brittle stars occurring in abundance. Large species were extremely rare at these sites and, when present, were represented only by small juvenile forms. It appears that these microhabitats are particularly favorable for small species and not suitable for large species. Brittle stars are considered to be subject to considerable predation pressure in Discovery Bay (Sides, 1982) and our observations suggest that fish may pose a threat to brittle stars easily visible in the algal clumps. It seems possible that a similar situation exists around the bases of Thalassia.

Larger brittle stars survive by concealment beneath rocks, within rubble, or in crevices, and by burying within the sediment; many also are nocturnal in activity. They are probably absent from algal turf because it would be difficult for them to move through, would offer inadequate concealment, and perhaps would not provide suitable feeding opportunities. Conversely, the stiff, narrowly spaced strands of the algal turf provide an ideal microhabitat for the small species which dominate it, a microhabitat that allows movement, provides concealment, and, if abundance is a guide, offers good feeding conditions. The juveniles of large species that settle in this microhabitat presumably emigrate when they "outgrow" it or become victims of predation.

The axils and detrital layer around the bases of Thalassia are also inaccessible to large brittle stars. There appears, however, to be no reason why the equally cryptically colored adults of, for example, the species of Ophioderma should not be successful in the sandy areas between Thalassia plants.

It seems reasonable to suppose that similar sized crevices elsewhere on the reef would also be populated by small species, providing that food is available, and evidence for this has recently been obtained by Hotchkiss (1982, who found many of the species considered here living in empty conch shells), Hendler (in press), and the present authors.

The two microhabitats considered in this study, coralline algal turf and Thalassia beds, are sufficiently different that no single species is predominant in both. This has several potential causes. Feeding opportunities will likely be different in the algal turf and around Thalassia beds. Apparent detritus feeders such as O. isacanthum are favored in Thalassia, whereas the scavenging and apparently predatory O. ophiactoides (Emson and Mladenov, in prep.) is favored in algal turf. It is interesting that the highly adaptable onmivorous detritivore A. squamata achieves moderate abundance in both habitats. Perhaps reflecting predation pressures, body coloration is also probably important, since the algal turf generally hosts dark colored species and the Thalassia paler species.

Small size in brittle stars clearly has resulted in reproductive constraints. Small size inevitably means that small numbers of eggs can be produced. Thus the production of long lived, planktotrophic larvae is unlikely to be a successful mode of reproduction for small species, unless perhaps gametes are shed several times a year. Several alternatives appear to be open to small species. Two are alternative means of sexual reproduction. One is abbreviated development (Hendler, 1975) in which rapid development results in a post larva. The other involves direct development, often with associated viviparity or brooding. A third alternative is to supplement sexual reproduction with asexual multiplication.

All the brittle stars in this sample of small adult size either reproduce asexually or brood the young. The similarity in life history traits among the three abundant fissiparous species is remarkable. Despite the fact that they are from three different families, they are small in size, they reproduce asexually by fission, and they can produce only a very small number of small eggs which apparently develop into planktotrophic larvae. Rearing experiments already have demonstrated that fertilized eggs of O. ophiactoides develop into typical planktotrophic ophioplutei (Mladenov and Emson, 1984), and the egg sizes suggest that this is probably the case for the other species as well.

Asexual reproduction appears to be the dominant mode of propagation in all three fissiparous species. It is probably responsible for reliable local recruitment, whereas sexual reproduction may result in dispersal of small numbers of larvae which, on occasion, found new populations or recruit into existing populations maintained mainly by asexual reproduction.

Brooding is the other reproductive pattern exhibited by the small adult brittle stars of this study. This reproductive mode appears to be a clear adaptation to low fecundity resulting from small size. Hendler (1979) noted an association between size and brooding in ophiolepid brittle stars and suggested that there was selective pressure for brooding because of low fecundity. Also, Menge (1975) and Emson and Crump (1979) found similar associations between size and brooding in the sea stars and suggested the same cause.

A general relationship between small adult size and brooding has been documented for many groups of invertebrates including echinoderms, and hypotheses explaining the association have been advanced by Strathmann and Strathmann (1982). However, brooding is rare among brittle stars, although it is obvious in the present study. Hendler (1979) noted that only 57 of all known brittle stars brood, and of these only 7 are tropical. It seems that, although the particular conditions of the habitats sampled here favor this life history pattern, elsewhere other methods are selected.

The alternative to brooding, abbreviated development (Hendler, 1975), is also characteristic of species with relatively small disks that are capable of producing eggs in numbers of the same order of magnitude as fissiparous species (e.g., Amphiura chiajei; Hendler, 1975). Species with this reproductive pattern are present on coral reefs but were not found in our study.

Fission is also uncommon in brittle stars. Emson and Wilkie (1980) reported that only 34 species possess this habitat, although they failed to record O. isacanthum as fissiparous (Hotchkiss, 1982). By contrast with brooding, however, fissiparity is largely a warm water phenomenon. Emson and Wilkie (1980) recorded that 24 of the 34 fissiparous species were tropical in distribution. The reasons for these patterns are unknown and would bear further investigation.

The similarity of these results to the situation described by Boffi (1972) for Brazil is considerable. Not only are the fissiparous ophiactids Ophiactis lymani and Amphipholis squamata the predominant species in the algal turfs examined by Boffi, but the other species in which adults were present were Amphipholis januarii and Ophiactis savignyi. The remaining four species were represented by juveniles and uncommon.

It thus seems possible that these reproductive patterns may prevail among small brittle stars inhabiting algae throughout the tropical and subtropical Atlantic, since the present authors have established that similar reproductive patterns are characteristic of small brittle stars from Bermuda and Carrie Bow Cay, Belize. Hotchkiss (1982) observed many of the same species in discarded conch shells, demonstrating that these reproductive patterns probably are adaptive for many cryptic habitats in sheltered areas of coral reefs.

Evolution to a small size is infrequent in brittle stars, but those species which achieve it may become very successful. The brooding Amphipholis squamata and the fissiparous Ophiactis savignyi are among the most abundant brittle stars. Their size apparently allows them access to an underexploited

microhabitat, and their biological characteristics, particularly their reproductive patterns, enable them to achieve remarkable success in this environment. Much of contemporary life history theory is concerned with trade-offs between dispersal ability, fecundity, reproductive effort, and body size (e.g., Stearns, 1984; Olive, et al., 1984). The situation briefly examined here illustrates two examples of successful trading and probably deserves more detailed study.

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REEF ZOOPLANKTON COLLECTED ALONG A DEPTH GRADIENT AT DISCOVERY BAY, JAMAICA

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ABSTRACT

Reef zooplankton from three sites in the vicinity of Discovery Bay, Jamaica, were sampled on 29 nights during 1976-77 to determine their abundance and species composition. Depth was inversely correlated with zooplankton volume; 10.2 ml of zooplankton/m^2/night were collected at 6 m, 5.3 ml at 15 m, and 3.2 ml at 24 m. No seasonality in volume of zooplankton was observed. Variability in volume both within and between nights at any one site was high, but never were enough zooplankton collected to meet more than an estimated 12% of the metabolic requirements of the sessile reef dwellers.

Volume of zooplankton was positively correlated with the number of individuals in the sample. The unpredictability of zooplankton abundance is at least partially explained by the swarming behavior of the dominant (usually > 95% of individuals) copepod, the holoplanktonic Oithona colcarva Bowman. Because of this variability, it is unlikely that local zooplankton abundance and distribution has any causal effect upon reef species diversity. In addition to many groups of holoplanktonic copepods, ostracods, isopods, and decapods were among the most numerous taxa represented. The 6 m site differed from the sites at 15 m and 24 m in the relative abundance of noncopepod groups.

INTRODUCTION

Zooplankton are an important component of food webs in coral reef communities. They provide nutrients to corals (Goreau, et al., 1971; Johannes, et al., 1970; Porter, 1974) and to other benthic suspension feeders such as zoanthids (Sebens, 1977), crinoids (Liddell, 1980; 1982) and ophiuroids (Macurda, 1976), and they form a major part of the diet of many reef fish (Hobson, 1974; Gerber and Marshall, 1974; Hobson and Chess, 1978). Emery (1968) first reported that many zooplankton reside within coral reefs and, more recently, researchers using light (Sale, et al., 1976) and emergence traps (e.g., Alldredge and King, 1977, 1980; Hobson and Chess, 1979; McWilliam, et al., 1981; Porter and Porter, 1977; Porter, et al., 1977; Walter, et al., 1982) have characterized certain aspects of the resident zooplankton of shallow reefs and lagoons in the Pacific. Few studies have examined reef-associated zooplankton in the Caribbean; Robichaux, et al. (1981) and Youngbluth (1982) placed traps over sand and/or seagrass beds, while Ohlhorst (1982) reported on diel patterns over reef substrata at one depth. Only one study (McWilliam, et al., 1981) has addressed the question of seasonality in zooplankton (from the Pacific), and none have sampled along a depth gradient on a reef. Further information on the abundance and behavioral patterns of these zooplankton, especially in the Caribbean, is necessary to the

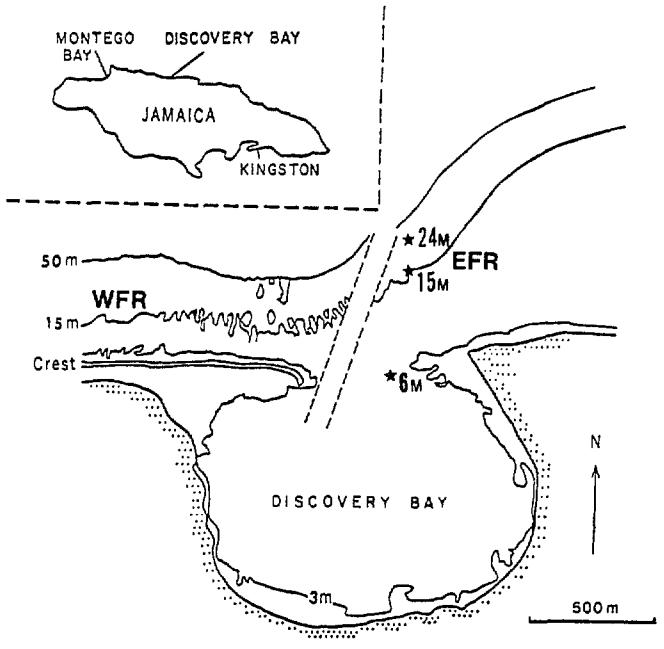

Figure 1.--Map of Discovery Bay, Jamaica, and adjacent fore reef showing the three sites sampled in this study. EFR = East Fore Reef; WFR = West Fore Reef.

development of realistic models of reef energetics and an understanding of the behavioral and feeding strategies of many reef organisms.

This study was undertaken to examine patterns of abundance and distribution among reef zooplankton at three depths on a Caribbean reef. In this study, reef zooplankton are those zooplankton [holoplanktonic, meroplanktonic, and demersal forms (Robichaux, et al., 1981)] which reside for some period in or near the reef substratum and at some time migrate at least 1 m into the water column. Most planktivory by the sessile reef community should be upon this group of zooplankton during their vertical migration. Zooplankton were collected with emergence traps in a collection program designed to answer the following questions about the quantity and predictability of zooplankton available as a potential food source for reef organisms: (1) What quantity of zooplankton is available to the reef community, especially to sessile reef-dwelling organisms? (2) How variable is the amount of zooplankton on different nights? (3) Do reef sites at different depths differ in a predictable way with respect to abundance of zooplankton? (4) Do reef sites at different depths differ in species composition of zooplankton? (5) Is there any predictable cycling of zooplankton abundance?

MATERIALS AND METHODS

A total of 392 zooplankton samples were collected over 29 new and full moon nights during 1976-77 using a modified version (Ohlhorst, 1980, 1982) of the demersal trap described by Porter and Porter (1977). Traps were placed prior to sunset, and collection bottles were removed the following morning.

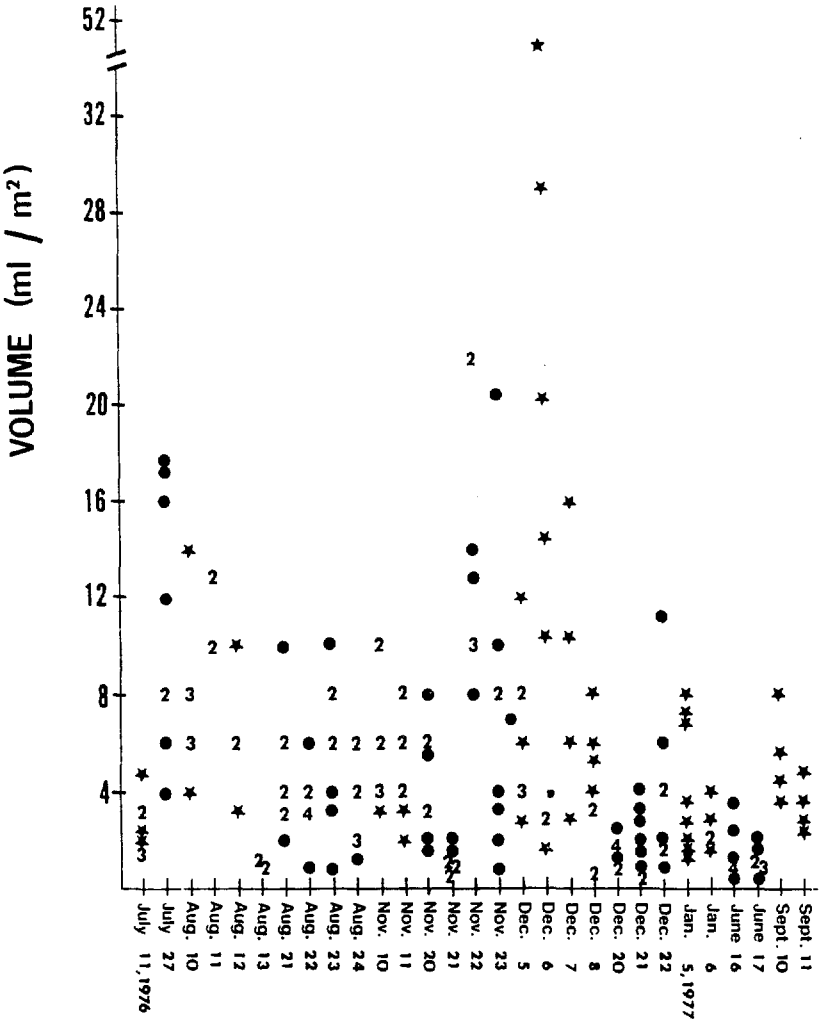

Figure 2.--Volumes of zooplankton (ml/m^2) from the 15 m site are plotted for the 29 nights sampled. Stars indicate full moon nights, and circles indicate new moon nights.

Samples were preserved in 5-10% formalin immediately upon return to the surface. Each sample was concentrated over a 90 m mesh sieve, resuspended in formalin solution and allowed to settle in graduated centrifuge tubes until a constant volume was reached (usually after 48 hr) (Porter, et al., 1978).

Zooplankton were collected from three reef sites at Discovery Bay, Jamaica (fig. 1): a shallow site (6 m) immediately behind the reef crest to the east of the Discovery Bay ship channel; a 15 m site on a broad, shallow sloping fore reef plain to the east of the boat channel; and a 24 m site on this same plain (see Ohlhorst, 1980, and Liddell, et al., 1984, for site descriptions). Because of the variability in abundance of zooplankton from different locations at any one reef site on a single night (fig. 2), traps were placed over the same permanently marked reef locations at each sampling to eliminate substrata induced variation when comparing one night with the next.

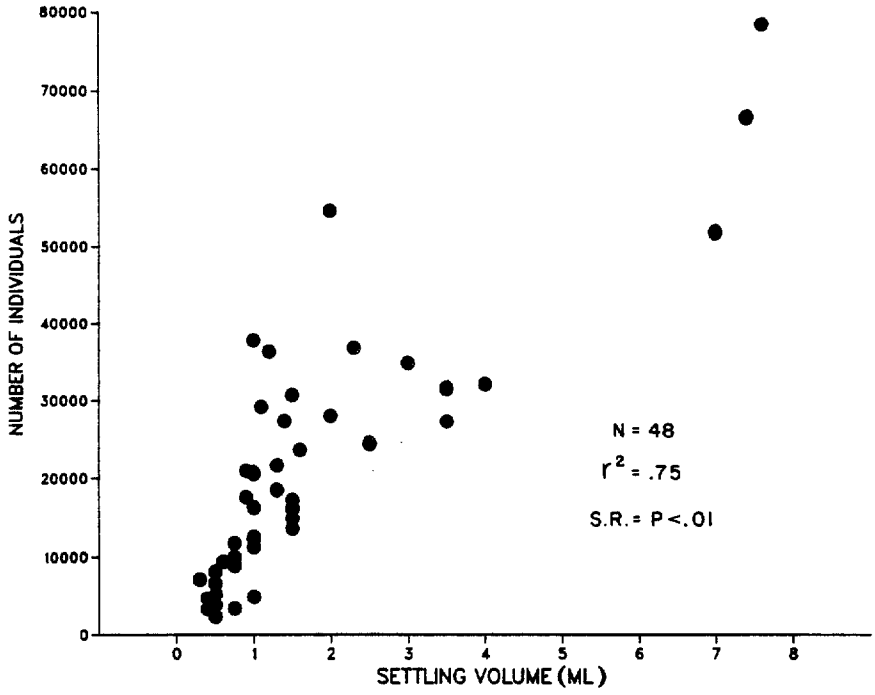

Figure 3.--Correlation of zooplankton settling volume with the number of individuals counted in the sample. Results are given for regression analysis (r^2) and Spearman Rank Correlation (S.R.).

Caloric determinations were made on six freeze-dried (10.5-15.5 mg) samples of zooplankton (all dominated by copepods) using a microbomb calorimeter (Tinkle and Hadley, 1973). Samples of known volume were ashed at 450°C for 5 hr for ash weight determination. Samples of known settling volume were freeze dried, weighed, and the weight/individual calculated using the mean value of 1.6×10^{-4} individuals/ml settling volume determined from a count of individuals from 30 samples of known settling volume. Samples consisting of 20-30 individuals were removed and weighed on a Cahn Electro-balance for an independent estimate of individual weight.

In addition to volumetric determinations on all 392 samples, 56 of the zooplankton samples from 7 nights at the 3 reef sites were enumerated.

RESULTS

Differences in the "packability" of species may result in difficulties in interpreting settling volume data. However, the dominance of a single species and the general similarity in morphology, size, and composition of species in these samples made volume determinations a relatively easy method by which to compare sites. As illustrated in figure 3, the number of zooplankton is positively correlated (Spearman Rank Correlation, $p < 0.01$) with the settling volume of zooplankton.

Variability in Volume of Zooplankton Within Reef Sites

Volumes of zooplankton from the 15 m site ranged from 0.4-50.8 ml/m^2 ($\bar{X}$ = 5.3 ml/m^2) (figs. 2, 4) and, on any one night, differed among sites by 0.4-49.2 ml/m^2 ($\bar{X}$ difference in volume/night = 8.0 ml/m^2). The variability occurring between consecutive nights was as great as that between randomly paired nights (Mann Whitney U Test, $p > 0.05$). This wide range in volumes was found for all three sites, with samples from 24 m showing the least variation (fig. 4).

Differences in Abundance of Zooplankton Between Reef Sites

The results of the zooplankton sampling from all three sites are presented in figure 4. Volume of zooplankton is inversely correlated with depth (Spearman Rank Correlation, $p < 0.01$). The shallow (6 m) site yielded the greatest volume ($\bar{X}$ = 10.2 ml/m^2), while the 24 m site yielded the least ($\bar{X}$ = 3.2 ml/m^2). Pairwise comparison of volumes from all nights shows that volumes from 6 m vs. 24 m and 15 m vs. 24 m are significantly different (Mann-Whitney U Test, $p < 0.01$), but not 6 m vs. 15 m. However, these relationships do not hold for every night considered separately. When the sites are paired night by night, the volume at 6 m is greater than at 24 m only 45% of the nights (N = 11), and the volume at 15 m is greater than at 24 m only 57% of the nights (N = 14). While overall the volumes from 6 m and 15 m do not differ significantly, volumes from 6 m are greater than those from 15 m on 45% of the nights.

When the total numbers of individuals captured at each site (table 1) are compared, similar patterns are observed as for volume. More individuals occurred at 6 m than at 24 m (Mann Whitney U Test, $p < 0.0006$) and more at 15 m than at 24 m (Mann Whitney U Test, $p < 0.002$), but there was no difference between 6 m and 15 m. However, the pattern changes when the dominant copepod is removed from calculations. With Oithona colcarva Bowman removed, the site at 6 m does not have significantly more individuals than 15 m or 24 m (Mann Whitney U Test, $p > 0.05$), and, curiously, the 24 m site has significantly more than the 15 m site (Mann Whitney U Test, $p < 0.002$).

The Effect of Lunar Phase on Abundance of Zooplankton

The phase of the moon appears to influence volumes of zooplankton, although the results from different depths are conflicting. The 6 m site yielded a significantly greater volume on nights of the new moon than full moon, while the 15 m site yielded a greater volume on nights of the full moon than new moon (Mann Whitney U Tests, $p < 0.01$).

The lunar effect on numbers of zooplankton was significant only at the 6 m site, where significantly greater numbers (Mann Whitney U Test, $p < 0.03$) were captured on nights of the new moon than full moon, both for total plankton and for plankton without O. colcarva. However, with only 7 nights (2 full moon, 5 new moon) sampled, this deserves further investigation.

When numbers of zooplankton captured in different phases of the moon are compared among sites, collections at 6 m did not differ from those at 15 m or

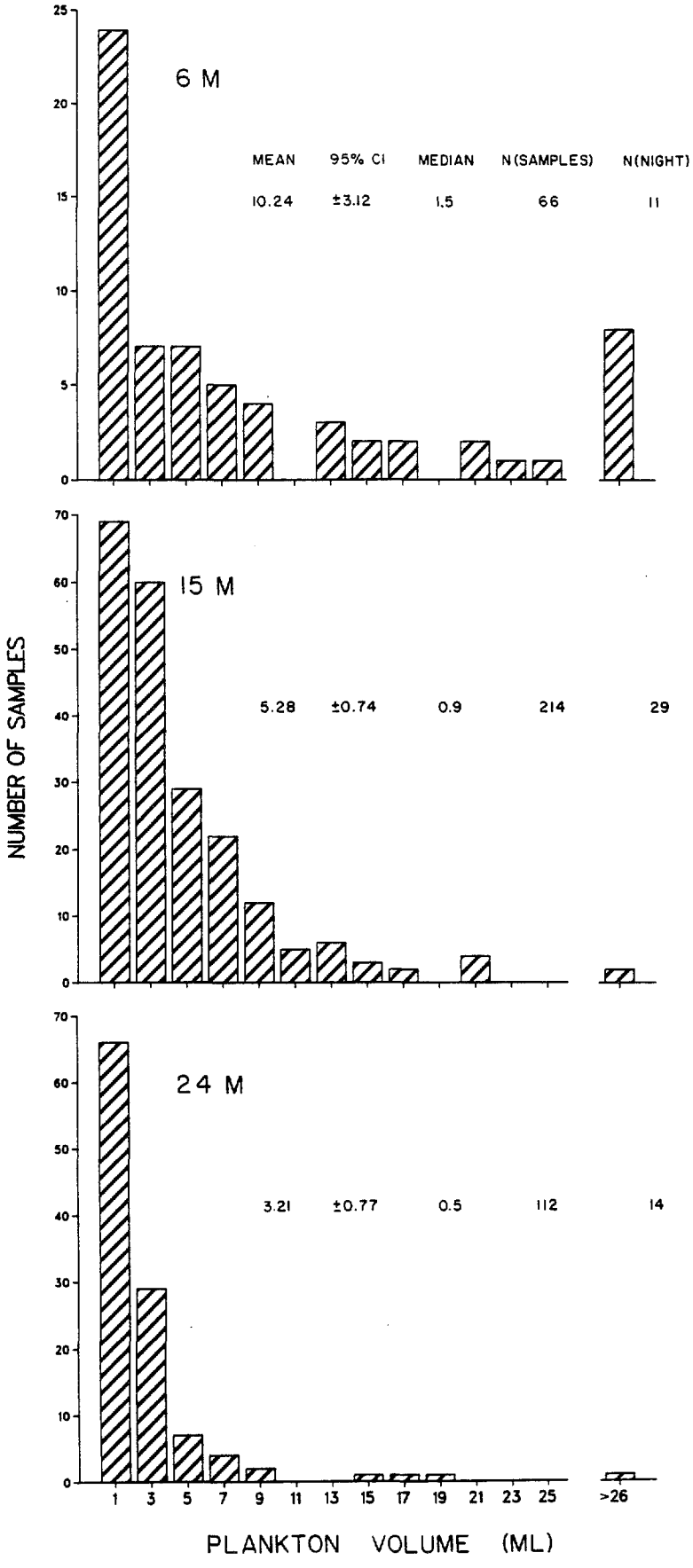
6 M
MEAN 95% CI MEDIAN N(SAMPLES) N(NIGHT)
10.24 ±3.12 1.5 66 11
15 M
5.28 ±0.74 0.9 214 29
24 M
3.21 ±0.77 0.5 112 14
NUMBER OF SAMPLES
PLANKTON VOLUME (ML)
1 3 5 7 9 11 13 15 17 19 21 23 25 >26

Table 1.--Zooplankton collected over 1 m^2 of reef substrata at three depths. Mean, standard deviation and percent of samples containing each organism are given for the common categories of organisms. Samples from 6 m included 8 samples from 3 nights; those from 15 m included 27 samples from 7 nights; and those from 24 m included 21 samples from 7 nights.

	6 M			15 M			24 M		
Zooplankton	Mean number	(St.Dev.)	%	Mean number	(St.Dev.)	%	Mean number	(St.Dev.)	%
Oithona colcarva	124396	(83206)	100	79307	(51392)	100	54381	(118901)	100
Cyclopoid #1			0	32	(64)	27	492	(617)	71
Cyclopoid #2	27	(50)	88	55	(100)	54	87	(116)	52
Cyclopoid #3	26	(74)	38	47	(85)	63	41	(85)	43
Corycaeus sp.	1832	(2215)	100	690	(771)	85	876	(839)	100
Misc. cyclopoids	136	(277)	38	130	(199)	59	243	(346)	81
Harpacticoid #1	26	(74)	63	281	(333)	93	226	(265)	90
Harpacticoid #2			0	15	(40)	52	32	(70)	48
Misc. harpacticoids	68	(148)	38	501	(336)	93	760	(512)	100
Calanoid #1	3046	(5877)	63	177	(319)	52	47	(76)	33
Misc. calanoids	12649	(17242)	88	477	(539)	89	1820	(2280)	100
Copepod nauplii	21	(58)	13	35	(79)	22	110	(140)	52
Barnacle nauplii	74	(85)	75	42	(88)	56	65	(105)	52
Ostracods			0	87	(196)	89	404	(929)	95
Amphipod #1			0	53	(84)	63	21	(37)	43
Amphipod #2			0	8	(29)	30	20	(46)	29
Misc. amphipods	78	(156)	38	62	(107)	89	61	(66)	86
Isopod #1	322	(430)	75	154	(218)	52	324	(376)	71
Isopod #2	84	(162)	75	243	(264)	89	148	(222)	71
Tanaids	53	(107)	38	112	(165)	89	93	(125)	95
Cumaceans	93	(151)	88	23	(60)	70	9	(22)	57
Mysids	53	(148)	88	85	(131)	74	80	(78)	90
Lucifer sp.	1560	(2413)	75			0			0
Misc. decapods	132	(226)	100	88	(381)	70	43	(55)	81
Polychaetes	148	(161)	100	98	(125)	93	126	(142)	86
Appendicularians			0	15	(49)	15	87	(138)	52
Chaetognaths			0	172	(178)	93	105	(113)	95
Gastropods	77	(106)	50	83	(144)	56	94	(90)	38
Total (includes uncommon species not included above)	146056	(102924)		83244	(51216)		60904	(118592)	

Figure 4 (opposite page).--Volume frequency histogram for the three reef sites. The number of samples of differing volumes (converted to volume/m^2) is plotted. Volume is plotted in 2 ml increments with the midpoint volume indicated for each.

24 m on new moon nights (Mann Whitney U Test, $p > 0.05$) but did have greater numbers than samples from 15 m or 24 m on new moon nights. This holds for counts both with and without O. colcarva, except that samples from 6 m have more individuals than those from 24 m on full moon nights when O. colcarva is included.

Composition of Zooplankton

The mean, standard deviation, and percent occurrence for 29 categories of organisms are presented in table 1. No statistically significant differences between sites in occurrence of taxa were noted across all nights, with the exception of the absence of several organisms and the exceptional abundance of a holoplanktonic decapod, Lucifer sp., at 6 m. The relative abundance of copepod groups was similar (Spearman Rank Correlation, $p < 0.01$) at all sites, but the ranking of noncopepod groups differed between 6 m and both 15 m and 24 m (Spearman Rank Correlations, $p > 0.05$). The 24 m site possessed a significantly greater number of organism categories [17.9 $\pm$ 6.2 (S.D.)] than did the sites at either 6 m (10 $\pm$ 3.2) or 15 m (12.5 $\pm$ 5.9). Evenness and species diversity were consistently higher at 15 m and 24 m than at 6 m ($\bar{X}$ H' at 6 m = 1.35, 15 m = 2.11, 24 m = 2.46).

Bomb Calorimetry and Biomass Determination

The results of caloric and biomass determinations are presented in table 2. Bomb calorimetry produced caloric values of 5.6 [$\pm$ 0.05(S.D.)] calories/mg dry weight, a figure which agrees well with published values (Cummins and Wuycheck, 1971). Only 6% of the freeze dried weight was inorganic ash material. The weighing of a known number of Oithona colcarva individuals (the dominant organism; Ohlhorst, 1980, 1982) produced weights averaging 2.5 µg/individual, while the weighing of a known volume with a calculated number of individuals produced weights averaging 1.6 µg/individual.

DISCUSSION

The highly three-dimensional nature of the reefs in this study made it impossible to place traps completely flush with the reef floor, and thus some zooplankton movement undoubtedly occurred both into and out of the traps. A number of workers have addressed the problems related to demersal trap design (Robichaux, et al., 1981; Youngbluth, 1982), and their results should be taken into account when evaluating the results of work based on demersal emergence traps. Caution is necessary in interpreting the origin of the zooplankton ["demersal traps" catch more than demersal plankton (Robichaux, et al., 1981)] and their relative abundances due to differing plankton behavior (Robichaux, et al., 1981; Youngbluth, 1982). Nonetheless, studies such as this, with one method used throughout, provide data by which different sites can be compared. The volumes of zooplankton obtained in this study give an indication of the amount and types of zooplankton available for capture by the sessile inhabitants of the reef, and serve as a useful basis for comparison of different reef sites.

Table 2.--Biomass and caloric value determinations of zooplankton samples (mean ± standard deviation). a: The value of 5.584 calories/mg dry weight agrees well with similar determinations by other workers (Cummins and Wuycheck, 1971). b: The mean values from weight determinations by two independent methods (see text). c: Values calculated by Johannes, et al. (1970) for 1 m^2 living coral.

	Dry Weight (mg)	Ash Free Dry Weight (mg)	Calories
1 ml settling volume	31.5 (±8.1)	29.6 (±7.5)	175.9 (±45)[a]
1 Oithona colcarva (0.5 mm)[b]	0.002 ($\pm 4 \times 10^{-4}$)	0.0019 ($\pm 4 \times 10^{-4}$)	0.012 ($\pm 3 \times 10^{-3}$)
Zooplankton over 1 m^2 reef at 15 m	167 (±35)	157 (±33)	928 (±176)
Metabolic requirements of 1 m^2 of reef[c]	6000		33,600

Abundance of Zooplankton

The average volume of 5.3 ml of zooplankton per 1 m^2 reef substratum at 15 m depth on the East Fore Reef indicates that only 3-4% of the reef energy needs, as determined by Johannes, et al. (1970) for an area of high coral cover, could be met by the capture of all of the demersal zooplankton (table 2). While the 6 m site yielded more zooplankton, it was rarely more than 12% of the amount necessary to sustain the corals. Gut analyses of various reef planktivores, such as corals (Porter, 1974) and crinoids (Liddell, 1980, 1982), and observations of feeding by corals (Johannes and Tepley, 1974) confirm that inadequate numbers of zooplankton are caught to meet the estimated energy needs of these reef inhabitants.

A comparison of results from this study with those of Alldredge and King (1977); Porter and Porter (1977); Porter, et al. (1977); McWilliam, et al. (1981); and Walter, et al. (1982) is presented in table 3. Volume and numbers of zooplankton collected over Jamaican reefs were larger than those of the other studies. This difference may reflect either real differences in the biology of the reefs studied or merely differences in the amount of swarming copepods captured because of imperfect fit of the traps to the substrata. Nonetheless, these studies together indicate the range of values for the amount of demersal zooplankton to be found over coral reefs. Further study using identical collection methods, including sealing efficiency and plankton mesh size, is necessary to determine the differences betwen the Caribbean reef studied in this work and the Pacific reefs studied by others.

Variability in Abundance of Zooplankton

The high degree of spatial and temporal heterogeneity in zooplankton volume (figs. 2, 4) is probably attributable to the swarming behavior of the dominant copepod, Oithona colcarva. Although swarms of this species were not observed by the author at Jamaica, other members of this genus are known to swarm in large numbers (Emery, 1968; Hamner and Carleton, 1979).

One result of this variability was that patterns of differences in zooplankton volume between sites varied from night to night, although certain statistically significant trends were discernible when data from all nights were pooled. This illustrates how sampling frequency might influence conclusions about the presence or absence of differences between collection sites; depending on which nights were sampled, contrary conclusions could be drawn. McWilliam, et al. (1981) also reported on the variability of zooplankton abundance from consecutive nights.

Factors Affecting Abundance of Zooplankton

This study indicates that zooplankton volumes for fore reef sites are negatively correlated with depth within the range of 6-24 m. This is, therefore, a very important consideration when extrapolating from studies done over shallow reefs (all of the previous work) to those which may be deeper.

Table 3.--Comparative abundances of zooplankton over coral substrata on eight reefs. a: This study. b: Samples collected as in this study, August 8-9, 1976; N = 24. c: Samples collected as in this study, July 2-3, 1976; N = 12. d: Samples collected as in this study, July 26-27, 1976; N = 24. e: Alldredge and King (1977). f: Porter and Porter (1977) and Porter, et al. (1977). g: Walter, et al. (1982). h: McWilliam, et al. (1981).

Reef location	Volume/m^2/night (ml)	Number/m^2/night	Ash free dry weight/ m^2/night (mg)
Jamaica[a]	6m: 10 15m: 5.3 24m: 3.2	6m: 1.6×10^5 15m: 8.5×10^4 24m: 5.3×10^4	6m: 296 15m: 167 24m: 101
Barbados[b]	20m: 3.5	20m: 1.3×10^4	
Colombia[c]	15m: 3.4	15m: 1.9×10^4	
Curacao[d]	15m: 4.8	15m: 1.4×10^4	
Lizard Island Lagoon[e]		2-5m: 1.1×10^4	2-5m: 95
Philippines[f]	10m: 9.5	10m: 2.0×10^4	
Philippines[g]		3m: 5.4×10^4	
Great Barrier Reef[h]		4-5m: 3.7×10^3	

The apparent correlation between high zooplankton volume and full moon periods for collections at 15 m probably reflects the fact that a much higher proportion of the full moon nights were also "rain" nights (Fisher Exact Probability Test, $p < 0.01$). The correlation of volume with "rain" [volumes correlated only to rainfall (> 0.6 cm) within the 48 hr prior to collection] is found during both phases of the moon, and in this study it appears that lunar phase had no effect on the volume of vertically migrating zooplankton on the East Fore Reef (Ohlhorst, 1980). The implication of rain as a factor affecting zooplankton volume also has been reported for zooplankton collected over Puerto Rican reefs (Glynn, 1973) and in Kingston Harbor, Jamaica (Grahame, 1973), where volumes of plankton from surface net samples correlated with monthly rainfall. It is not clear why rainfall should have the immediate effect found in this study, unless an increase in floculation of organic matter or land runoff occurred and produced an immediate increase in the foraging activity

of the zooplankton. There was no measurable change in salinity at any site during rain periods (Ohlhorst, 1980).

Interpretation is further complicated because no correlation between volume of zooplankton and lunar phase or rainfall was found at the 24 m site, and the 6 m site yielded results opposite to those at 15 m, with more zooplankton captured on new moon (= "nonrain" in this study) than full moon nights. At the 6 m site, there is an obvious advantage for zooplankton that do not enter the water column on full moon evenings, as visual predators should be more active on these nights. It is, therefore, surprising that yields of zooplankton at 15 m were the reverse (highest on full moon evenings), since the reefs at 15 m were well illuminated on these nights also.

Although Glynn's (1973) collections of plankton from the surface water in Puerto Rico sampled a different component of the reef zooplankton, his collections over a shallow reef (< 5 m) through one lunar cycle yielded a pattern consistent with that found for the shallow (6 m) site in this study; more zooplankton were collected on the new moon nights than on the full moon nights. In the study by Alldredge and King (1980) in the Pacific, abundance of zooplankton was not correlated with lunar phase.

There was no seasonality observed in zooplankton volumes in this study, although some periods of the year were less intensively sampled (fig. 2). Periods of high zooplankton yields reflected the occurrence of rain within 48 hr of sampling; however, collections of very low volumes were interspersed with these high volumes, casting doubt on any real causative effect (such variation also is found in other reports of seasonality; Glynn, 1973). It appears, therefore, that zooplankton volumes are indicative of previous rainfall, but rainfall is not necessarily predictive of high zooplankton yields. Moore (1967) and Grahame (1976) found no patterns of seasonality in their collections of surface zooplankton from the south coast of Jamaica. In contrast, McWilliam, et al. (1981) did find seasonality on a Pacific reef, with more zooplankton in the summer.

With the exception of the trend for greater abundance of zooplankton on "rain" nights at the 15 m site and for lower yields on full moon ("rain") nights at the 6 m site, there was no indication that certain of the nights were more conducive than others for zooplankton migration. Neither the pairing of collections on the same night from the 15 m and 24 m sites nor the pairing of collections on the same night from the eight 15 m trap locations produced a significant correlation (Spearman Rank Correlation, $p > 0.05$). It appears, therefore, that abundance of zooplankton cannot be predicted on the basis of any environmental parameter which would be experienced throughout the reef.

Composition of Zooplankton

As reported earlier for Jamaican reefs (Ohlhorst, 1980, 1982), copepods are the dominant organism collected in demersal emergence traps placed over the reef. Because of the great variance, the sites rarely differed significantly and the ranks of abundances for copepod taxa were correlated between sites.

Due to the absence from the 6 m site of a number of categories of organisms and the presence of Lucifer sp. which was rare elsewhere, the rankings of

abundances for noncopepod categories differed at 6 m from those at either 15 m or 24 m. These data indicate differences between shallow and deeper reef sites which should be investigated further. They also indicate that caution should be used when extrapolating data from shallow reefs to other reef sites.

Robichaux, et al. (1981) and Youngbluth (1982) discuss the effect of differing collection methodology on zooplankton species composition. In light of the many confounding variables, comparisons between this study and others will be brief and restricted to shallow reef sites. The data from the 6 m site in this study compare most closely with those from 3 m in the Philippines (Walter, et al., 1982). The relative abundance of most plankton groups and the absolute abundance of certain groups are comparable. Lucifer, for example, is an important component of the fauna in both shallow reef collections; however, amphipods are more important in their study than in this study. Although the abundant taxa from this study are not the same as those from the sealed traps of Hobson and Chess (1979) and Robichaux, et al. (1981), the values for certain of the taxa are comparable. Robichaux, et al. (1981), for example, collecting over a Thalassia bed (3 m), recovered an average of 56 tanaids and 54 amphipods/m^2, while this study produced an average of 53 tanaids and 78 amphipods/m^2 at the 6 m reef site.

CONCLUSIONS

This study indicates that reef-associated zooplankton can only be of minor caloric value to sessile reef organisms. While there is a negative correlation between abundance of zooplankton and depth of the reef site, local abundance is highly unpredictable. It would appear difficult for planktivores to choose areas of maximum food potential and unlikely that local zooplankton abundance has any causal effect upon patterns of species diversity. The polytrophic habit of many of the reef dwelling invertebrates (Trench, 1974) may reflect the unpredictability of this food source.

It should be noted that the significance of zooplankton may lie not in their role as a major caloric source, but in their critical role in the cycling of nutrients in the reef environment. Zooplankton are able to feed on the very abundant mucus and organic particles in the water (Johannes, 1967; Gerber and Marshall, 1979; Richman, et al., 1975; Gerber and Gerber, 1979), much of which is generated by reef organisms themselves (Lewis, 1973; Coles and Strathmann, 1973). Zooplankton also feed on the bacteria on these organic aggregates (Sorokin, 1973) and on the phytoplankton. Thus, the zooplankton prevent the nutrients from all of these sources from being lost from the reef ecosystem. Not only do these nutrients pass along the food chain through predation upon zooplankton, but the production of fecal pellets, often composed of only partially digested material, provides an important food source for certain benthic invertebrates (Frankenberg and Smith, 1967; Turner and Ferrante, 1979) and also serves to keep the important nutrients within the reef ecosystem.

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TEMPORAL PATTERNS OF ZOOPLANKTON MIGRATION

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ABSTRACT

The NOAA/NULS-1 underwater habitat facility at St. Croix was utilized during July 1982 for a study of the temporal patterns of migration into the water column by reef zooplankton. Samples were collected for 6 days at 9 daily time intervals using mesh emergence traps, diver pushed plankton nets, and surface plankton net tows. This is the first study to sample such finely spaced time intervals. Preliminary analysis from 2 days indicated that there was migration throughout the night, with increased activity found prior to sunrise as well as following sunset. This is the first time a predawn rise of zooplankton has been documented.

The cyclopoid copepod, Oithona colcarva, dominated most time intervals, although it was not nearly as abundant as in an earlier Caribbean reef zooplankton study. Most zooplankton taxa followed the same general pattern of activity, and the relative abundance of the common taxa generally remained the same throughout the 24 hours. The time intervals around sunset were an exception, however. For example, during the hour following sunset, calanoids, harpacticoids, polychaetes, and pagurid larvae were relatively more abundant than during the hour prior to sunset, while copepod nauplii and amphipods were less abundant during this postsunset time interval. Significantly more taxa were captured during the first hour of darkness than during any other time interval.

The effects of different trap designs and types of reef substrata on zooplankton samples also were examined. There was no significant difference in the number of individuals collected between treatments using sealed and unsealed traps or between those using unsealed traps over coral and sand substrata. This is in contrast to other studies; two possible explanations for these discrepancies relate to the types of substrata over which sealed and unsealed traps are compared and to differences in trap sealing efficiency when different substrata types are being compared.

INTRODUCTION

The zooplankton that reside within or near coral reef ecosystems have only recently begun to receive the attention of researchers. Zooplankton have been studied from various Pacific reef communities primarily by using various modifications of emergence traps (Alldredge and King, 1977, 1980; Porter and Porter, 1977; Porter, et al., 1977; Hobson and Chess, 1979; Birkeland and

Smalley, 1981; McWilliam, et al., 1981; and Walter, et al., 1982). Fewer studies of reef zooplankton from the Caribbean have been conducted (Ohlhorst, 1980, 1982, 1985; Robichaux, et al., 1981; and Youngbluth, 1982). While the diel migration patterns of these zooplankton have been shown to influence the behavior of nocturnal planktivorous fish (Hobson, 1974; Hobson and Chess, 1978; Robertson and Howard, 1978) and might affect the behavior of other reef planktivores (Porter, 1974; Sebens, 1977; Liddell, 1982), few studies have investigated the diel migration patterns of reef zooplankton in detail (Alldredge and King, 1980; Ohlhorst, 1982; Walter, et al., 1982). The only study of migration by Caribbean reef zooplankton (conducted at Jamaica by Ohlhorst, 1982) suggests that there is no single pulse of migratory activity; rather zooplankton rise into the water column at variable rates throughout the night with a peak of activity during the second hour after sunset. Also, different taxa were shown to exhibit differing migratory patterns. While these observations are consistent with those from the Pacific, it is important to determine whether or not such patterns occur elsewhere in the Caribbean. Additionally, more frequent sampling than previously conducted would be of value in refining the patterns of zooplankton migration.

One of the reasons for the paucity of detailed studies addressing this question is the physiological limitation placed upon safely conducting the repeated sampling dives which are necessary for such studies. Previous studies which have addressed the question of migratory patterns of reef zooplankton have been restricted to sampling widely spaced time intervals or sampling very shallow (< 5 m) sites. Data from Ohlhorst (1985) suggests that caution should be used when extrapolating data from shallow sites to greater depths. The present study examines the migratory patterns of reef zooplankton at an intermediate (15 m) depth at St. Croix through repeated sampling of finely spaced time intervals. This sampling was made possible by saturation diving from the NOAA/NULS-1 Underwater Habitat, HYDROLAB.

METHODS

Sampling of reef zooplankton was conducted from the NOAA/NULS-1 HYDROLAB located at 15 m depth in the Salt River submarine canyon on the north coast of St. Croix, U.S. Virgin Islands (17°45' N, 64°45' W) during July 1982. Samples were collected from both reef and sand areas located approximately 15 m east of the Habitat. To eliminate biases caused by the proximity of the study sites to the Habitat, all of the external lights of the HYDROLAB remained off for the duration of the study. Saturation diving from the HYDROLAB enabled two teams of divers to collect plankton samples at closely spaced intervals over a 6-day period.

Zooplankton were sampled by three methods: (1) Emergence traps, which covered 0.5 m^2, were placed over various types of reef substrata to capture zooplankton moving from the reef site into the water column. Certain of these traps were sealed over their substrata by a skirt (Robichaux, et al., 1981), while others were affixed more loosely over their substrata. (2) Diver pushed

Table 1. *Number of zooplankton captured/m^2/hour*, beginning with 0030 on July 16 and continuing through 2300 on July 17, 1982. ST= Students' T test at $p \leq 0.05$, 0 = no significant difference between this and the previous time interval, + = a significant increase, - = a significant decrease; MWU = Mann Whitney U test at $p \leq 0.05$, symbols are the same as for ST.

Time Interval	#Samples	Mean (Std. Dev.)	Median	ST	MWU
0030	8	139.2 (78.0)	136.6		
0230	8	109.4 (52.0)	100.0	0	0
0500	8	176.0 (97.8)	168.0	0	0
0600	4	26.6 (20.2)	20.0	-	-
1200	8	10.6 (9.0)	8.0	0	0
1830	8	40.0 (21.8)	39.0	+	+
1930	8	246.8 (103.8)	256.0	+	+
2230	8	99.6 (60.0)	92.0	-	-
0030	8	348.0 (376.0)	202.0	0	0
0230	8	702.0 (662.0)	54.6	0	0
0500	8	306.0 (364.0)	140.8	0	0
0600	8	55.8 (22.2)	60.0	0	0
1200	8	6.2 (2.0)	6.0	-	-
1800	4	92.6 (24.2)	90.0	+	+
1930	4	399.2 (199.0)	341.4	+	0
2030	4	189.6 (144.2)	133.0	0	0
2300	4	51.0 (26.0)	40.4	-	0

zooplankton net samples were collected 1 m and 5 m above the reef. (3) A plankton net was towed at the surface from a boat to sample zooplankton just below the surface, and vertical net hauls from 15 m to the surface also were made from the boat. The emergence traps and zooplankton nets were made with 90 micron meshes. Two additional emergence traps were constructed with clear polyvinyl. The traps were modified (Ohlhorst, 1980, 1982) from those used by Porter and Porter (1977).

Five hundred and eighty samples were collected over 6 days and 9 time intervals each day (table 1). Samples were preserved in 5-10% buffered formalin immediately after collection and counted as in Ohlhorst (1982). Preliminary

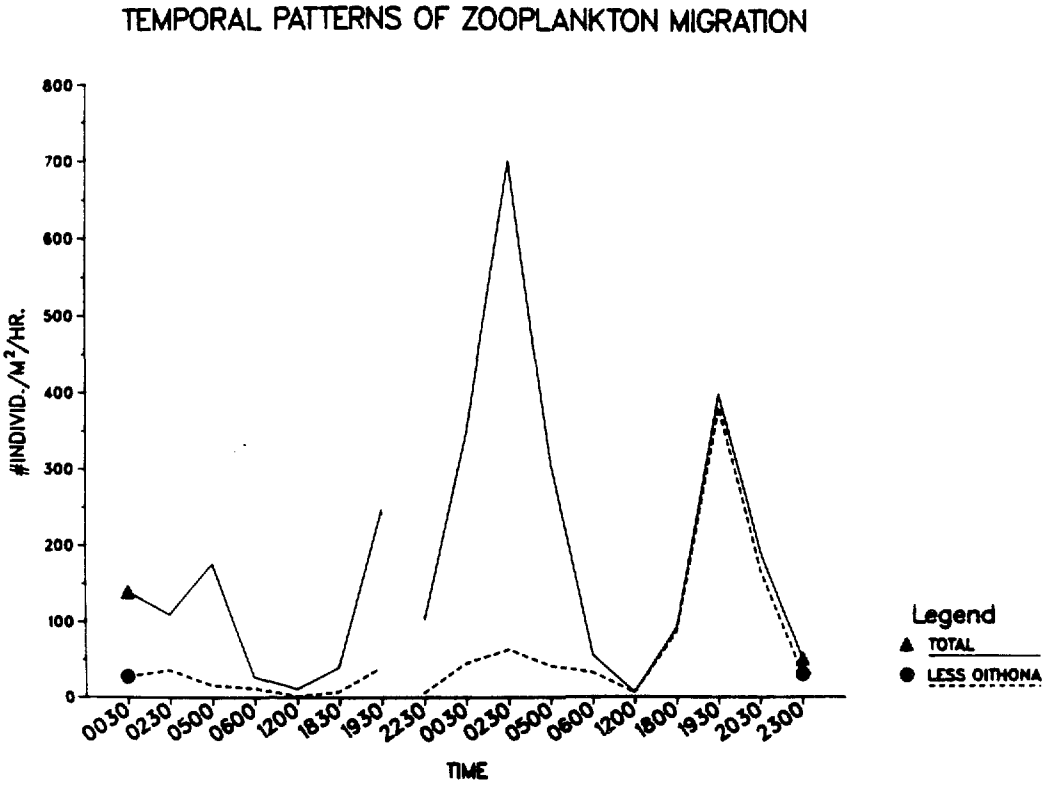

Figure 1.--The number of individuals captured per hour during the different time intervals are plotted, both with and without the copepod Oithona colcarva. Samples from 2030 on July 16 have not been counted. Refer to table 1 for the means, medians, and standard deviations. Note that units of time along the x axis are unequal.

results from 148 samples from mesh emergence traps from 2 days (July 16-17) will be presented herein. During the collection period sunrise was at 0600, sunset at 1800, and the lunar phase was new moon.

RESULTS

Effects of Traps and Substrata

No significant differences [$p \leq 0.05$; Mann Whitney U (MWU), Students' T (ST) tests] in the number of individuals captured per hour were observed between mesh traps with sealed vs. unsealed bottoms over coral substrata. Additionally, no significant differences ($p \leq 0.05$) in the number of individuals captured per hour occurred between traps positioned over sand vs. those positioned over coral or rubble. For all subsequent tests, data from sealed and unsealed traps and traps located over sand and over coral or rubble were pooled. The polyvinyl traps tended to capture more zooplankton than mesh traps. Although the difference between types of trap was not significant, most of the data presented herein are from mesh traps only.

Table 2. Percent occurrence of phyla in demersal traps. Samples were collected on July 16-17, 1982 and are from both mesh and polyvinyl traps. The taxonomy is according to Barnes (1980).

time:	0030	0230	0500	0600	1200	1830	1930	2030	2230
# traps :	(20)	(20)	(20)	(14)	(20)	(16)	(16)	(6)	(16)
Phyla									
ANNELIDA	30	65	35	21	20	6	100	67	56
ARTHROPODA	100	100	100	100	100	100	100	100	100
CHAETOGNATHA	25	30	15	14	5	19	13	0	25
CHORDATA	15	15	25	7	20	19	25	33	31
COELENTERATA	0	25	25	21	25	38	56	67	44
ECHINODERMATA	0	0	0	0	5	0	0	0	0
MOLLUSCA	40	35	35	29	60	94	81	50	38
NEMATODA	0	0	0	0	5	0	13	0	0
PLATYHELMINTHES	0	5	0	0	5	0	19	0	0
SARCODINA	35	80	45	29	80	94	81	67	31
SIPUNCULIDA	25	15	10	21	40	25	63	67	25

Temporal Patterns

The number of zooplankters migrating per hour for the various sampling intervals is presented in table 1 and figure 1. Data from July 16-17 displayed significant decreases ($p \leq 0.05$; MWU, ST tests) in the total number of individuals captured per hour between 0500 or 0600 and 1200 hours, and significant ($p \leq 0.05$) increases between 1200 and 1800/1830 hours and between 1800/1830 and 1930 hours, followed by a significant ($p \leq 0.05$) decrease after 1930 hours. The pattern differed somewhat when the cyclopoid copepod Oithona colcarva (Bowman) was removed from analysis (fig. 1).

There was no significant ($p \leq 0.05$; MWU, ST tests) difference between the 2 days in the number of individuals migrating per hour for most time intervals (fig. 1, table 1). Significantly more individuals ($p \leq 0.05$; MWU, ST tests) were captured on July 17 than on July 16 in both the intervals from 0030-0230 and 1200-1800/1830. When the samples were considered without O. colcarva, numbers of zooplankters differed between days both in the intervals mentioned above and at 0500-0600.

Crustaceans made up the majority of the zooplankters captured by the traps, although representatives of 11 phyla, including foraminifera, echinoderm larvae, sipunculids, Amphioxus, and appendicularians also were collected (table 2). A

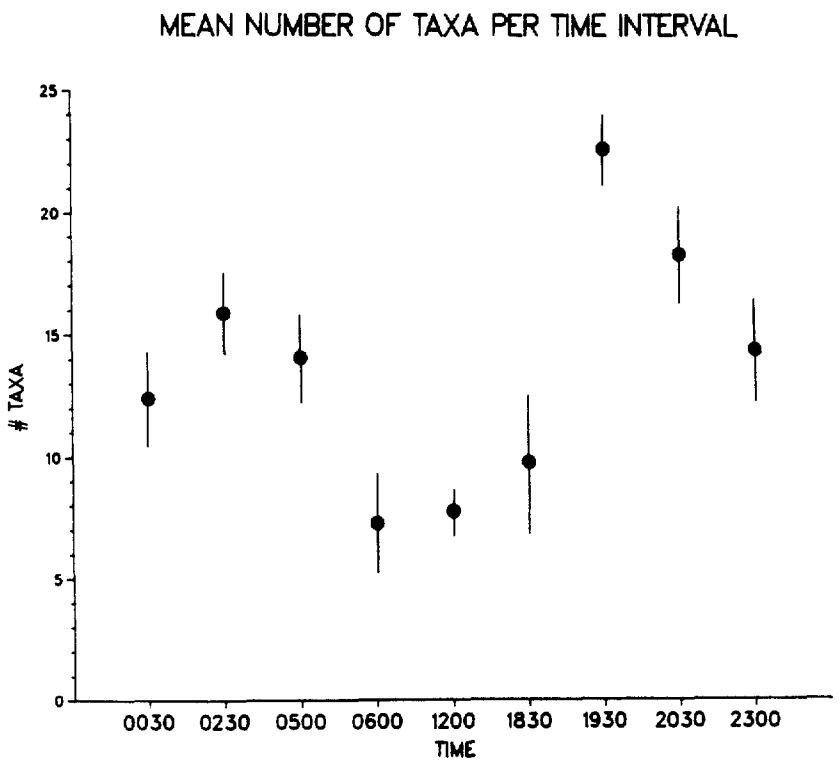

Figure 2.--The mean number of taxa captured during the various time intervals (days combined) is plotted. Vertical bars represent 95% confidence intervals. Units of time along the x axis are unequal.

total of 73 taxa were identified from these samples. Many were rarely encountered, and 27 taxa was the maximum found in a single sample (July 17, 1982). Figure 2 shows the pattern for the mean number of taxa captured during each time interval for the 2 days pooled. The only significant differences ($p \leq 0.05$, MWU, ST tests) between the 2 days in the number of taxa captured occurred at 0030 and 0600, when significantly fewer were captured on July 16. When the days were pooled, there were significant increases ($p \leq 0.05$; MWU, ST tests) in number of taxa in samples collected at 0030 vs. 0230 and in those collected at 1830 vs. 1930; in addition, significant decreases in number of taxa were observed between 0500 and 0600, 1930 and 2030, and 2030 and 2300. In general, the fewest taxa were captured during the day, the most during the first hour after sunset, and intermediate numbers during the rest of the night.

The mean and standard deviation for the abundance of the more common taxa are presented for the different time intervals in table 3. The cyclopoid copepod Oithona colcarva (Bowman) was the most abundant of the organisms captured at all time intervals except those between 1200-2030, although there was some variation in this pattern when the days were considered separately (fig. 1). During the morning interval (0600-1200), O. colcarva, foraminifera, and certain calanoid and harpacticoid species were the most abundant organisms; however, all occurred in relatively low numbers. In the afternoon (1200-1830), foraminifera

Table 3. Organisms captured at various time intervals ($\bar{x}$ = mean, SD = standard deviation, * = present in 50-75% of samples, ** = present in 75-100% of samples). Only the 29 most common of the 73 taxa recorded are presented here.

Time:	0030		0230		0500		0600		1200		1830		1930		2030		2230	
#Samples:	16		16		16		12		16		12		12		4		12	
Taxa	$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)
Oithona colvarva	200	(272)**	354	(538)**	186	(260)**	20.2	(18.2)**	2.8	(6.6)**	3.7	(3.1)**	33.0	(38.8)**	24.0	(36.0)**	45.8	(47.4)**
Corycaeus spp.	0.5	(0.6)*	0.9	(1.0)*	1.9	(3.5)*	3.8	(4.3)**	0.1	(0.2)	0.7	(0.7)*	1.8	(2.6)*	0		0.1	(0.3)
Calanoid "A"	5.8	(9.8)**	4.1	(4.3)**	9.8	(21.4)**	2.5	(2.3)*	0.7	(0.6)**	0.5	(0.5)*	12.5	(9.9)**	4.5	(7.7)*	4.1	(5.0)**
Calanoid "B"	5.6	(9.1)*	4.5	(6.3)*	9.0	(21.8)**	0.5	(0.9)	0.1	(0.2)	0.1	(0.1)	8.8	(9.2)**	7.5	(3.0)**	0.8	(1.5)
Microsetella spp.	2.3	(2.7)*	8.2	(7.2)**	2.5	(3.5)	5.8	(11.2)*	0.4	(0.7)	5.0	(13.3)*	22.4	(37.2)	43.6	(50.2)**	0.2	(0.4)
Harpacticoid "A"	1.4	(2.4)*	2.7	(2.8)*	5.1	(5.4)*	2.2	(2.3)*	0.7	(0.9)*	1.3	(3.7)	42.8	(52.4)**	22.6	(25.2)**	5.8	(8.1)**
Harpacticoid "B"	0.2	(0.7)	0.4	(1.0)	2.0	(2.8)	0		0.3	(0.4)*	1.2	(1.5)*	4.5	(6.5)*	0		2.8	(5.3)*
Harpacticoid "C"	0.4	(0.9)	1.2	(2.2)	0.3	(1.0)	0.5	(1.2)	0		0		0.1	(0.4)	3.0	(3.5)**	0	
Copepod "A"	0.6	(0.8)	1.2	(1.3)*	0.8	(1.0)	0.7	(1.3)	0.1	(0.1)	0.1	(0.3)	5.7	(7.0)*	7.5	(4.4)**	0.4	(0.6)
Copepod nauplii	0.2	(0.4)	0.5	(0.9)	3.1	(6.9)*	0.7	(1.0)	0.1	(0.2)	0.8	(1.7)	9.1	(16.1)	5.0	(7.6)*	0.3	(0.7)
Barnacle nauplii	0		0.6	(1.0)	0.2	(0.6)	0		0.1	(0.1)	0.1	(0.2)	1.3	(1.3)*	0		0.1	(0.3)
Ostracods	0.4	(0.8)	0.3	(0.6)	0.5	(1.0)	0.3	(1.2)	0.1	(0.3)	0.1	(0.2)	3.6	(3.6)**	0		0.4	(0.8)
Amphipod "A"	4.2	(4.0)**	4.2	(4.8)**	2.9	(4.9)*	3.0	(7.9)	0.1	(0.2)	0		6.9	(6.7)**	3.0	(1.1)**	1.9	(2.0)**
Amphipod "B"	0.1	(0.2)	1.3	(1.3)**	0.2	(0.5)	0.7	(1.8)	0.3	(0.4)	0.7	(1.4)	8.0	(13.1)*	7.0	(10.1)**	0	
Isopods	0.3	(0.6)	0.2	(0.4)	0.5	(0.7)	0		0.1	(0.1)	0.2	(0.2)	2.4	(1.4)**	1.0	(1.2)*	1.4	(1.9)*
Cumacean "A"	4.8	(4.3)**	4.8	(4.0)**	4.9	(4.7)**	0		0.1	(0.1)	0.1	(0.5)	10.6	(16.2)**	24.6	(33.2)**	4.1	(4.8)**
Cumacean "B"	0.7	(1.0)	0.2	(0.5)	0.2	(0.4)	0		0		0		1.4	(2.8)	1.0	(2.0)	0.1	(0.3)
Tanaids	0.3	(0.6)	0.4	(0.8)	0.8	(1.1)*	0.2	(0.6)	0		0		1.3	(2.7)	0.5	(1.0)	0.3	(0.6)
Mysids	0.1	(0.5)	0.6	(0.9)	0.7	(1.2)	0.2	(0.6)	0		0.1	(0.1)	1.5	(2.4)	0		2.4	(4.4)**
Shrimp	0.7	(1.0)	1.1	(1.2)*	0.3	(0.7)	0		0.1	(0.2)	0.1	(0.1)	0.7	(1.6)	3.0	(2.6)**	2.0	(2.6)*
Shrimp larvae	0.5	(1.2)	0.1	(0.3)	0.4	(0.9)	0		0		0		7.9	(6.9)**	0		0.5	(0.9)
Pagurid larvae	7.0	(15.0)**	2.4	(4.1)*	1.8	(2.7)*	0.3	(0.8)	0.1	(0.1)	0.1	(0.1)	19.4	(33.2)	5.0	(5.0)**	2.5	(4.2)*
Decapod zoea	0.1	(0.3)	1.2	(1.5)*	1.8	(3.2)	0.2	(0.6)	0		0.1	(0.1)	0.7	(1.4)	0.5	(1.0)	0.1	(0.3)
Miscellaneous crustaceans	0.7	(1.3)	3.2	(3.5)**	0.4	(1.2)	0.2	(0.6)	0.1	(0.2)	0.6	(0.8)*	15.1	(18.3)**	5.5	(4.1)**	0.7	(0.8)*
Chaetognaths	0.5	(1.7)	0.4	(0.7)	0.1	(0.4)	0.3	(0.8)	0		0.1	(0.1)	0.2	(0.6)	0		0.6	(1.4)
Polychaetes	0.2	(0.4)	0.7	(0.8)*	0.3	(0.6)	0.3	(0.8)	0.1	(0.1)	0.1	(0.1)	17.7	(15.5)**	7.0	(6.6)**	0.8	(0.7)*
Gastropods	0.4	(0.6)	0.4	(0.7)	0.6	(1.0)	0.7	(1.0)	0.5	(0.7)*	18.8	(23.2)**	30.2	(27.8)**	3.0	(3.8)*	0.5	(0.7)
Sipunculids	0.3	(0.6)	0.1	(0.3)	0.2	(0.6)	0.3	(0.8)	0.2	(0.5)	0.1	(0.2)	4.8	(11.2)*	2.5	(2.5)**	0.2	(0.4)
Foraminifera	1.2	(2.0)	2.2	(2.4)**	1.9	(3.2)*	0.8	(1.6)	1.1	(1.2)**	22.8	(14.7)**	8.5	(8.1)**	3.0	(2.6)**	1.2	(2.1)

and gastropods dominated the samples. Samples collected in the hour following sunset were dominated by harpacticoids, with a variety of other organisms (including O. colcarva and gastropods) occurring abundantly. Samples taken during the second hour after sunset again were dominated by harpacticoids, although the relative abundance of the different harpacticoid species switched (table 3). Oithona colcarva and a species of cumacean were the other most abundant taxa during this second hour. Oithona colcarva dominated the other night time intervals from 2030-0500.

The relative abundance of nine common taxa (O. colcarva, calanoid copepods, harpacticoid copepods, copepod nauplii, amphipods, cumaceans, pagurid larvae, polychaetes and gastropods; table 3) were compared using Spearman Rank Correlations (SRC). Although the abundances were greater at night, the relative abundances (% total sample) of these taxa were correlated ($p \leq 0.05$) between pooled day samples and pooled night samples. When samples from consecutive time intervals were compared, the relative abundances of taxa in all such pairs were correlated ($p \leq 0.05$) except those from 1800/1830 vs. 1930, and 1930 vs. 2030. For example, harpacticoids, pagurid larvae, calanoids, and polychaetes were relatively more important, while copepod nauplii, amphipods, and gastropods were relatively less abundant, at 1930 than at 1800/1830. Cumaceans and amphipods increased in relative abundance between 1930 and 2030, while gastropods and pagurid larvae decreased in relative numbers over this interval. Therefore, the hours around dusk were the only ones where the relative abundance of captured organisms differed.

Differences in the relative abundances of certain taxa reflect their different temporal behavior patterns. Sixty-two percent of the 29 common taxa (table 3) were captured in greatest numbers during the first hour after sunset (1830-1930), while 17% were captured in greatest abundance during the second hour after sunset. The only taxon showing peak abundance during the day was foraminifera. Many of the taxa exhibit sustained vertical migration throughout the night following the post-sunset pulse (e.g., calanoid "A," amphipod "A," cumacean "A," pagurid larvae in table 3). A few taxa (calanoid "B," decapod zoea) were captured most frequently during the last interval of night (0230-0500), and many (28%) exhibited a pulse of migration at this time. Only the cyclopoid Corycaeus spp. peaked in abundance during the hour prior to sunrise (0500-0600); the harpacticoid Microsetella spp. also exhibited a pulse of vertical migration at this time. The behavior of O. colcarva was variable throughout the various time intervals (fig. 1). The mean number of this species captured for both nights combined was greatest at 0230; however, that peak reflects an especially high number captured on July 17 ($\bar{X} = 638$) and a similar pattern was not observed on July 16 (fig. 1). Migration rates for this species were high during all night hours.

DISCUSSION

The zooplankton captured by emergence traps in this study do not solely represent, either in numbers or composition, the demersal zooplankton (Hobson and Chess, 1979; Robichaux, et al., 1981) living within the reef substrata over which the traps are placed. These data do, however, provide information on the temporal patterns of migration by the total reef zooplankton which is of value to studies of reef energetics and the behavior of reef planktivores.

Both Robichaux, et al. (1981) and Youngbluth (1982) addressed the question of trap design and both found differences in number and composition of zooplankton between sealed and unsealed traps. Both of these studies, however, were conducted over sandy bottoms where a complete seal was possible and zooplankton movement through the underlying substrata unlikely. In this study, both sealed and unsealed traps were placed over reef substrata; the former were sealed as well as possible through the use of sand and rubble placed over the trap skirts. No differences were observed in the numbers of zooplankton captured between the two treatments, possibly suggesting that there is more movement by zooplankton through interstices of the reef than previously thought. Analysis of differences in species composition between the two treatments is currently underway.

While Alldredge and King (1977) and Porter and Porter (1977) found the most zooplankton over structurally complex coral substrata, this was not found by Ohlhorst (1980) or Birkeland and Smalley (1981). In the present study, there also was no difference in the number of individuals captured over different substrata. One contributing factor may be the differential ability to seal traps over sand and coral substrata. Robichaux, et al. (1981) and Youngbluth (1982) both found that more zooplankton were captured by unsealed traps than by sealed traps when both were placed over sand substrata. Youngbluth (1982) observed that a gap of 1 cm between trap and substratum resulted in capture of significantly greater numbers of zooplankton than a total seal, while there was no difference between samples from traps with gaps of 1 and 10 cm. Therefore, differences in number of zooplankton collected over different types of substrata might be expected when certain treatments are well sealed and others not. If the sand traps of Alldredge and King (1977) and Porter and Porter (1977) were well sealed in contrast to those over coral substrata, it may be difficult for these researchers to compare their substratum treatments. Birkeland and Smalley (1981) compared coral substrata to algal turf pavement and probably were able to sample both treatments similarly, since in either habitat a total seal is unlikely. Ohlhorst (1980) and this study used unsealed traps to sample both coral and sand substrata. These traps captured the zooplankton moving along the reef bottom over both types of substrata, and the data indicated that the numbers of zooplankton available to planktivores were comparable in both habitats. Analysis of the species composition of zooplankton over various reef substrata is in progress.

Fewer zooplankton were captured per hour in this study than in previous Caribbean studies by one of the authors (Ohlhorst, 1980, 1982, 1985). The most probable explanation lies in the sole use of polyvinyl traps in the previous studies. In this study, two polyvinyl traps were used in addition to mesh traps (details will be discussed elsewhere); and, while no statistically significant differences were found in abundance of plankton between these treatments (due to high variance and small sample size of polyvinyl traps), the polyvinyl traps usually captured considerably more zooplankton. Both this study and the earlier work by Ohlhorst (1980, 1982, 1985) found considerable variability between nights sampled.

The bimodal emergence pattern (post-sunset, pre-sunrise) suggested by Glynn's (1973) data from plankton tow nets appears to be supported by this study (fig. 1), although more complete information will be available when all the samples have been analyzed. The present study provides the first documentation

of a presunrise emergence of zooplankton and has considerable implications for reef bioenergetics and planktivore feeding behavior.

As in the previous work where plankton were collected over Caribbean reef substrata at different time intervals (Ohlhorst 1982), Oithona colcarva, various calanoids and harpacticoids, copepod nauplii, amphipods, and polychaetes were important components of the fauna. The relative abundances of these organisms from the two studies are correlated ($p \leq 0.05$, SRC). There are, however, differences in the behavior of certain taxa between these studies. In Jamaica, for example, the harpacticoid Microsetella spp. migrated in greater numbers during the day than at night, while at St. Croix the peak migration was during the first and second hour after sunset. Also, isopods were an important component of the Jamaican fauna but were relatively rare at St. Croix. Oithona colcarva was less abundant at St. Croix than in Jamaica, and its activity pattern differed. At Jamaica O. colcarva was captured in the greatest numbers during the second hour after sunset, while at St. Croix the capture rate of this copepod was highest from midnight to just prior to sunrise. The sample size needs to be increased at both reef locations to determine if these differences are real.

The differences between this study and those over primarily sand substrata in the Caribbean (Robichaux, et al., 1981; Youngbluth, 1982) may be related to habitat differences and/or trap design. The relative abundance of nine common taxa from this study and the unskirted traps of Robichaux, et al. (1981) were positively correlated ($p \leq 0.05$, SRC). There was no correlation, however, between the relative abundance of taxa in this study and that from any of the treatments of Youngbluth (1982). While harpacticoids were a very important component of the reef zooplankton in St. Croix, they did not dominate to the degree reported by Robichaux, et al. (1981) and Youngbluth (1982) in the Bahama Islands. The St. Croix samples usually were dominated by the cyclopoid Oithona colcarva. This is a swarming meroplanktonic species unlikely to be captured in traps sealed over sand. Cumaceans and calanoids were important over St. Croix reefs, as was found with certain trap designs over sand by Youngbluth (1982) but not by Robichaux, et al. (1981).

This preliminary analysis of data collected from St. Croix is consistent with earlier diel studies (Walter, et al., 1981; Ohlhorst 1982) which indicated that zooplankton move up into the water column throughout the night with a pulse in activity following sunset. Although zooplankton are therefore available to planktivores throughout the night, the indication that there are predawn (this study) and postdusk peaks of migration is consistent with the hypothesis that fish predation is an important selective factor upon zooplankton behavior since these dawn and dusk peaks of emergence coincide with periods when there are few fish predators (Hobson, 1975).

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FIELD ANALYSIS OF THE DOMINANCE HIERARCHY OF THE BICOLOR DAMSELFISH STEGASTES PARTITUS (POEY) (PISCES: POMACENTRIDAE)

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ABSTRACT

The dominance relations of the damselfish Stegastes partitus were examined in the field. The dominance hierarchy, based on aggressive interactions, was linear and size-dependent, with most aggression between individuals most similar in size and least between those most dissimilar in size. These results show both similarities to and differences from results obtained in a very similar earlier study on the same species but conducted entirely in the laboratory. The importance of field studies in assessing the degree of reliability of results obtained under artificial conditions is emphasized.

INTRODUCTION

Many species of animals display a dominance hierarchy among members of social units. A group of animals may be said to have a dominance hierarchy if the interactions between individuals allow some to have priority over others under certain circumstances. The most simple hierarchy is defined as follows: individual A dominates all members of a group; another animal B dominates all members except A, and so on to the last member, omega, which dominates no other individuals. If this relationship holds, then the hierarchy is said to be linear (Chase, 1974).

Considerable research has examined the dominance relations of a wide variety of animal species. However, the majority of studies have been conducted in the laboratory or under other artificial conditions. In studies carried out both in the field and in the laboratory on the same species, there often have been discrepancies in the conclusions. Thompson (1960) found that laboratory populations of house finches had a hierarchy dominated by females, but that field populations did not show this pattern. In some primates, a different form of social structure was evident between captive animals and the same species in the field (Rowell, 1967; Hinde, 1974). In the baboon, Papio anubis, interactions were about four times as frequent among captive animals as among individuals observed in the field (Rowell, 1967). Among the fishes, Myrberg (1972a) conducted a field and laboratory study of territoriality and social hierarchy in the bicolor damselfish (Pomacentridae), Stegastes (= Eupomacentrus)

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partitus. However, limitations of resolution in the underwater camera used for field observations precluded analyses as detailed as those obtained during the laboratory section of the work. Therefore, the two parts of the study were not strictly comparable.

Many damselfish are territorial, and the bicolor, like several other closely related species, defends a territory which it infrequently leaves. In the field, several or many such territories may be found in close proximity, forming colonies on suitable substrate. Reproduction usually occurs within colonies, which consist of both males and females. Colony members frequently interact with each other close to territory borders. In small colonies, all colony members may interact with one another, whereas in very large colonies many individuals rarely come into contact. Small colonies are, therefore, particularly useful for studies on intracolony social relationships.

The aims of the present study were: (a) to examine in detail the aggressive social interactions of small colonies of the bicolor damselfish in the field and (b) to compare the dominance system of these colonies with hierarchies found in the laboratory (Myrberg, 1972a).

METHODS

The study was conducted from October 9-16, 1980, from the NOAA underwater facility, HYDROLAB, situated in 50 feet of water off the north coast of St. Croix in the U.S. Virgin Islands.

Seven small damselfish colonies, each confined to a patch of coral rubble and separated from each other by clear areas of sand, were selected. The colonies were small enough to permit interactions between all colony members. Aggressive social interactions ("chases") were recorded between all individuals in each colony, where both the giver and receiver of each "chase" were noted. A chase is defined as a rapid swim towards a fish that is moving away or that starts to move away from the chaser (Myrberg, 1972b).

Each colony contained six to eight individuals, most of which were distinguishable on the basis of size. However, very small fish ("tinies") were difficult to identify individually. Consequently, in the colonies containing more than one "tiny," i.e., in colonies larger than six fish, the number of interactions per tiny was determined by dividing the sum of chases given or received by all tinies of a particular colony by the number of tinies in that colony. Therefore, in each colony larger than six individuals, the rank (see below) of six consisted of an average interaction rate per tiny.

Data were taken during both the morning and afternoon over a period of 3-6 days and until at least 65 interactions had been noted for each colony (average observation time per colony = 131 minutes; range = 85-240 minutes). Since colonies were monitored for varying lengths of time, the observations were standardized to give the number of chases per 100 minutes per colony so that the colonies could be compared directly.

Matrices were constructed for the chase data from each colony by assigning dominance ranks to every colony member. For example, rank 1 chased each other

colony member more than any member chased it; rank 2 chased each colony member more than any other member chased it, except for rank 1.

For analysis, data on chases were ordered by rank, and all data for each rank were summed across all 7 groups. The data were then divided into three categories: (a) the number of chases received by each rank; (b) the number of chases given by each rank; and (c) the number of chases given by each rank to each other rank. Each of these categories was analyzed using the Kruskal-Wallis one-way ANOVA to determine whether or not there was a significant difference among ranks, i.e., an H-value giving $p < 0.05$. If so, then the data were subjected to a nonparametric version of the Newman-Keuls Multiple Range test (Zar, 1974) to determine how the distribution of chases varied among ranks (significance level, $p < 0.05$).

RESULTS

For each colony, a distinct size-dependent social hierarchy was apparent; it was highly linear with proportionally very few reversals (4.5%). A reversal is a chase directed at an individual higher in the hierarchy than the chaser.

Figure 1 shows the distribution of chases received by each rank (category a). This distribution is not homogeneous (Kruskal-Wallis, $p < 0.001$). The nonparametric Multiple Range test showed that ranks 3 and 4 received the most chases; ranks 2, 5, and 6 received less than 3 and 4 but more than rank 1 ($p < 0.05$ in each case).

Figure 2 shows the distribution of chases given by each rank (category b). This distribution is not homogeneous (Kruskal-Wallis, $p < 0.001$). The nonparametric Multiple Range test showed that ranks 1, 2, and 3 gave the most chases; rank 4 gave fewer chases but more than ranks 5 and 6 ($p < 0.05$ in each case).

Figure 3 shows the distribution of chases from each rank to each rank below it in the hierarchy (category c). The distribution is not homogeneous for ranks 1 to 4 (Kruskal-Wallis, $p < 0.01$). In most cases, each rank directed most chases to its closest ranking subordinate and least to the individual ranked farthest from itself. See figure 3 for the significant differences shown by the nonparametric Multiple Range test ($p < 0.05$ in each case).

CONCLUSIONS

The analyses of the distribution of chases given and received show that there is a distinct pattern to intracolony aggression:

(a) there is a strong size-dependent social hierarchy which is linear with few reversals;

(b) individuals chase those closest to and just below themselves in rank most frequently and those furthest in rank least frequently;

(c) the highest ranking individuals (1, 2, and 3) chase more than other ranks. Lower ranking individuals chase progressively less the lower their rank;

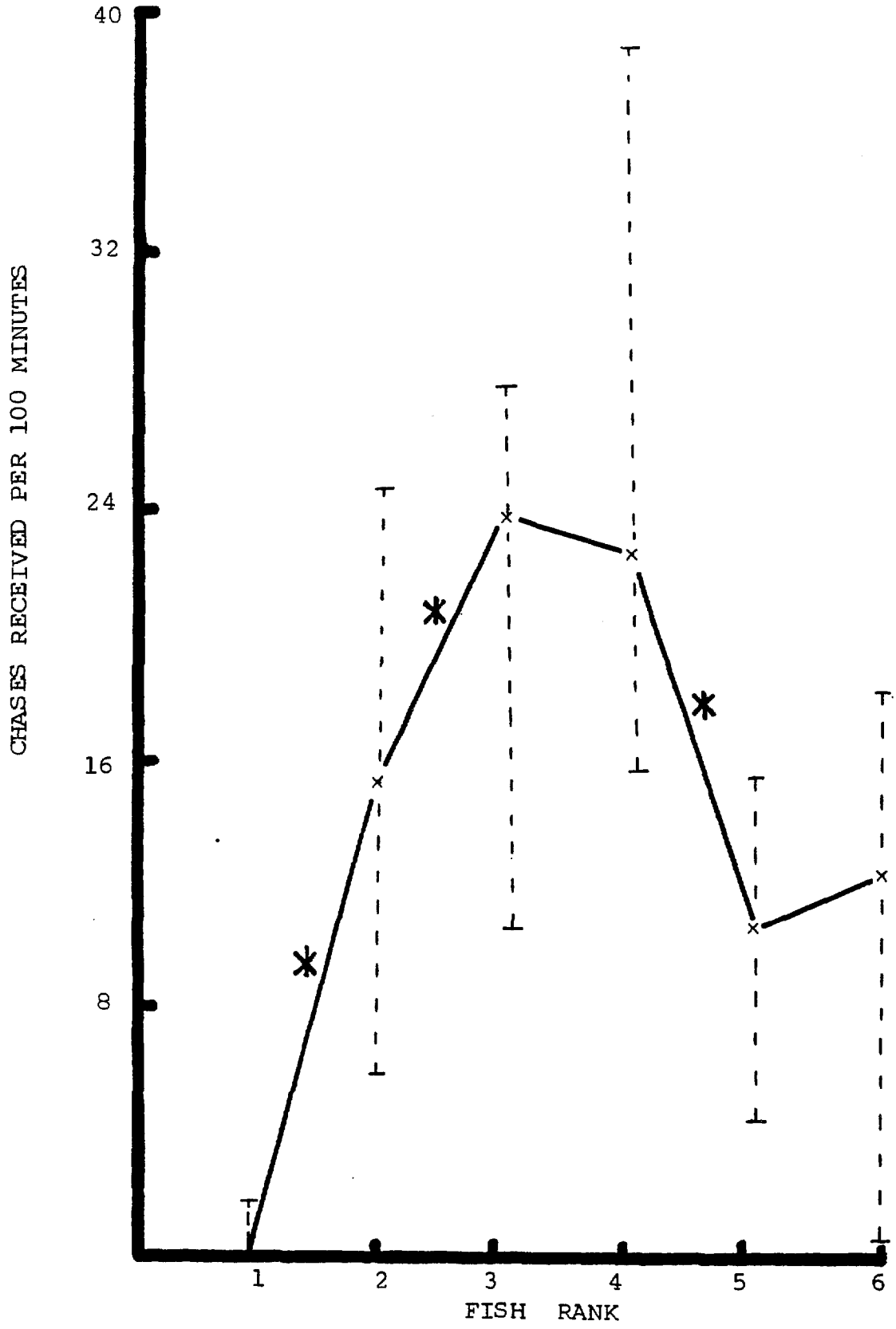

Figure 1.--Chases received by each rank plotted as medians and interquartile ranges. The asterisks denote significant differences between adjacent points ($p < 0.05$); e.g., rank 2 received more chases than rank 1.

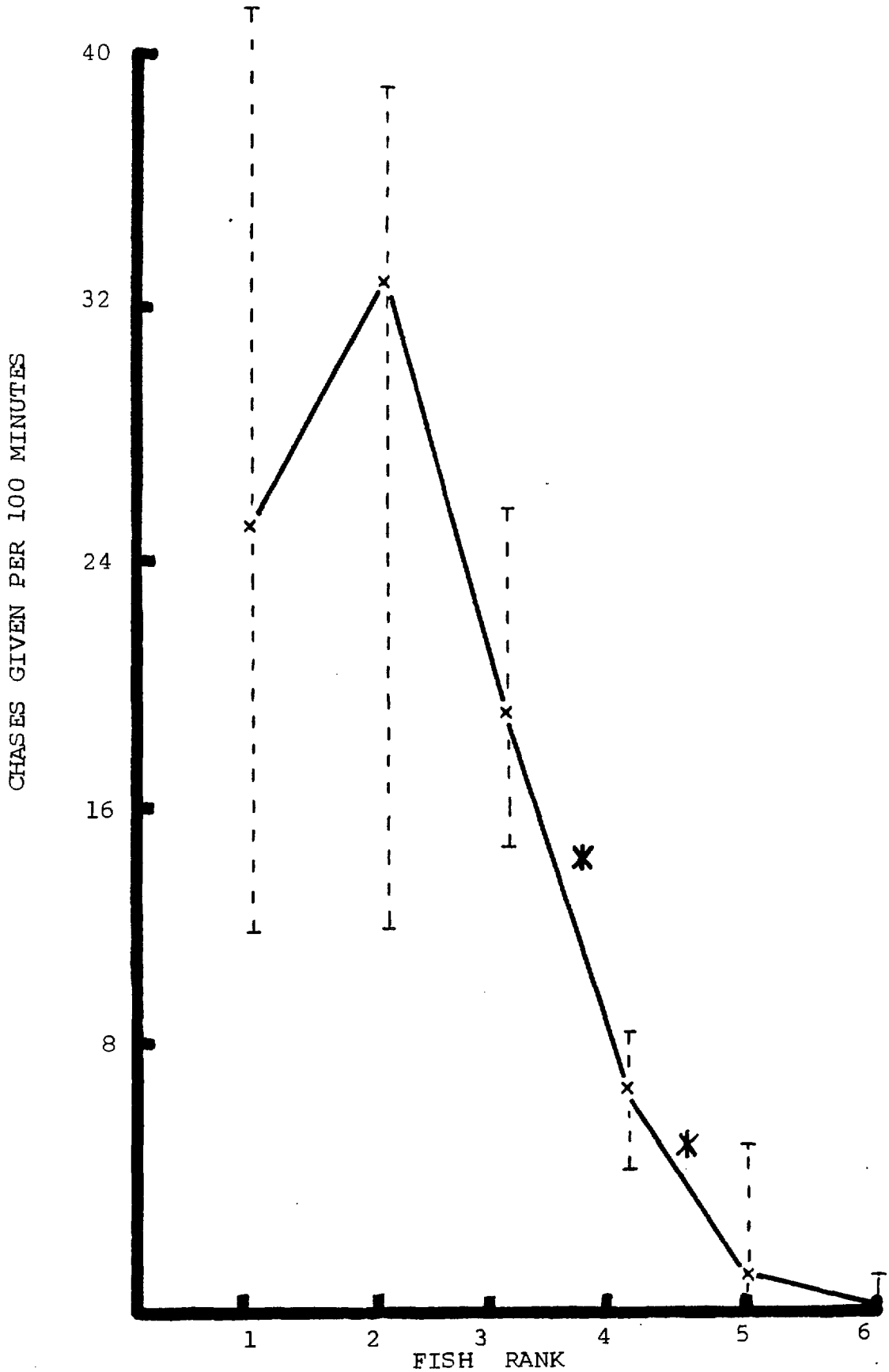

Figure 2.--Chases given by each rank plotted as medians and interquartile ranges. The asterisks denote significant differences between adjacent points ($p < 0.05$); e.g., rank 4 gives fewer chases than rank 3.

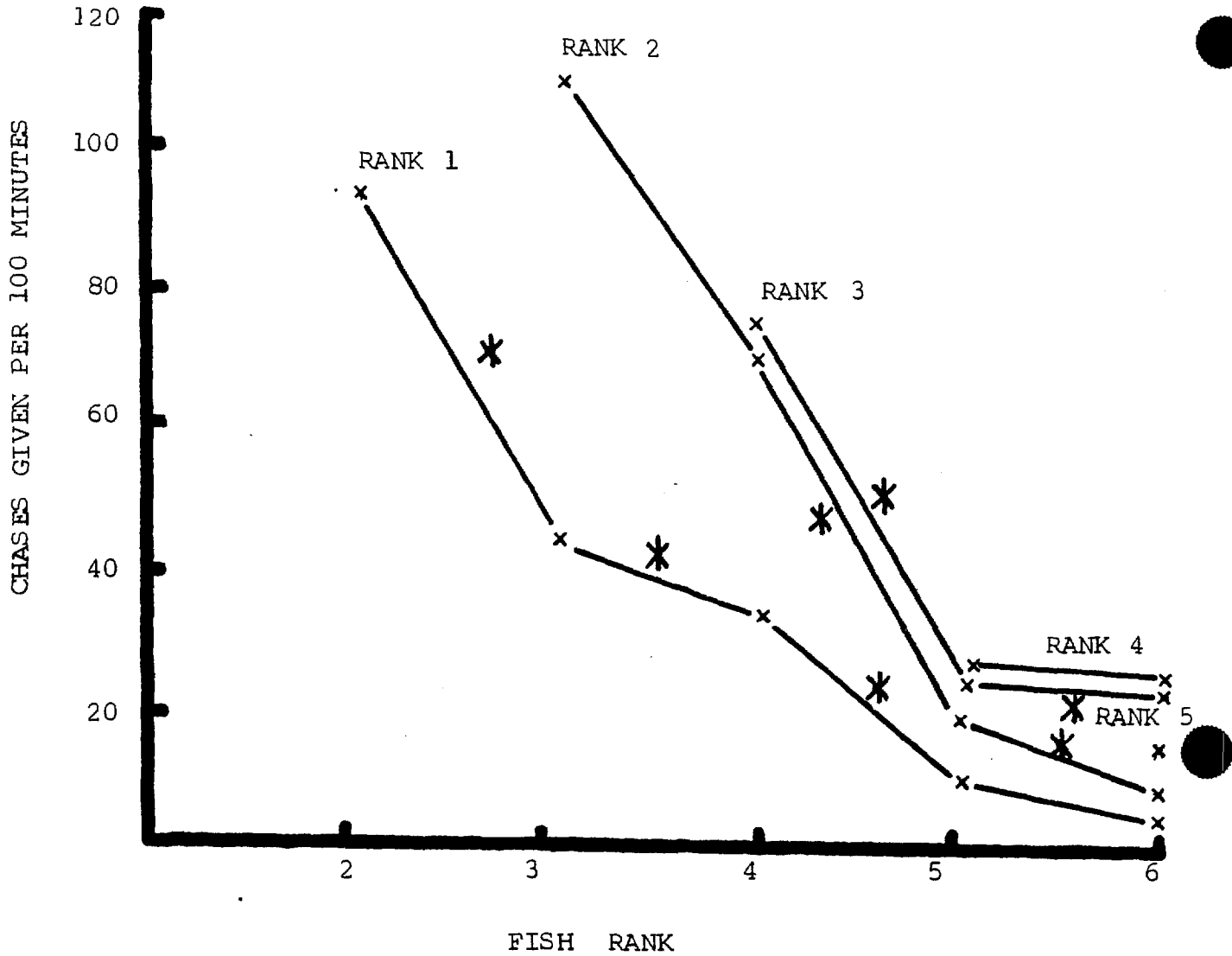

Figure 3.--Chases given by each rank to each rank below it. Data from all seven groups are summed. Each line represents the chases given by a particular rank to all ranks below it; e.g., rank 1 chased rank 2 a total of 96 times. The asterisks denote significant differences ($p < 0.05$) between adjacent points; e.g., rank 1 chased rank 2 significantly more than it did rank 3.

(d) ranks 2, 3, and 4 receive most chases and ranks 1, 5, and 6, the least.

It is clear that in the bicolor damselfish, size plays an important role in intraspecific aggression. As in many other species, dominance relations are strongly correlated with body size (beetles, Beebe, 1947; lobsters, Fielder, 1965; voles and deermice, Grant, 1970). Aggression is most intense between individuals of similar size and least intense between individuals most dissimilar in size (Noble, 1939; Collias, 1944; Miller, 1964; Coates, 1977).

The importance of size in the dominance relations of damselfish may result from size-dependent competition for certain resources. Individuals of different

sizes may have different food or shelter requirements (Rasa, 1969; Emery, 1973). Several studies have reported that in pomacentrids, small individuals often share the territory of an adult conspecific (Clarke, 1970; Emery, 1973; Sale, et al., 1980), either because the adult tolerates them or because of "topological deception" (Sale, et al., 1980) whereby they can avoid the adult by using space in which they cannot be pursued. The low number of chases given and received by these small individuals implies that they are not attempting to compete aggressively with the larger fish for the space they share. Large size in male bicolors appears to be one of the factors associated with high reproductive success (Schmale, 1980). In order to establish the significance of size and how it relates to aggression in this species, detailed studies on the feeding, reproduction, and use of space and shelter are necessary. Account should be taken of fish size, stage of maturation (juvenile, adult; reproductive, nonreproductive), and sex.

The present study demonstrates both similarities and differences between field and laboratory results on the dominance relations of the bicolor damselfish. Previous work on this species (Myrberg, 1972a) focused on two distinct time periods: reproductive and nonreproductive. The distribution of aggression between colony members was found to differ markedly between these two periods in the laboratory phase of the study. The field phase of the study covered only the reproductive period and was much less detailed than the laboratory phase because of the inability of the underwater camera to record all aggressive interactions between colony members, especially those involving very small fish. The present study is considered equivalent to the nonreproductive period of the Myrberg study, since little courtship activity and no egg-guarding behavior by males were observed.

The present field analysis and Myrberg's laboratory results for the nonreproductive period show the following similarities: There is a strong size-dependent linear dominance hierarchy with a very low percentage of reversals; the highest ranking individuals did the most chasing and the lowest ranks the least; the middle ranks received the most chases and rank 1 and the lowest ranks the least.

However, there were two differences between the two studies. First, the rate of interactions was markedly higher in the laboratory study, in which a rate of 10 chases per individual per hour was recorded as opposed to the 1.5 chases per individual per hour in the present study. This is a common difference between field and laboratory studies and may be due to: (a) the inability of small individuals to escape those chasing them in an aquarium, (b) the lack of interspecific interactions in the laboratory, and/or (c) the lack of space available per individual in an aquarium, although both the present study and Myrberg's laboratory study had similar fish densities of 0.2 m^2 (Myrberg) and 0.1-0.2 m^2 (this study).

Second, the relative distribution of chases given by each rank to each other rank below it in the hierarchy differs between the two studies. In the laboratory (Myrberg, 1972a), the distribution of chases among individuals showed no clear pattern, except for one fish, YB, which directed successively fewer chases at individuals ranked progressively further away from itself. This 'YB' pattern of chasing was seen very clearly and consistently in all colony members of the present study.

It is of considerable interest that during the reproductive period of Myrberg's study, the pattern of intracolony aggression in the laboratory and possibly in the field differed from that recorded during the nonreproductive period, with more aggression being directed towards the lowest ranking individuals than towards those closest in rank. Field work similar to that of the present study needs to be conducted during the reproductive period to establish if this difference is significant and related to the phase of the reproductive cycle.

In conclusion, the dominance relations in the bicolor damselfish during the nonreproductive period show both similarities and differences when laboratory and field studies on colonies of similar size are compared. The nature of these differences implies that the laboratory may be used for detailed work impossible to carry out in the field, but that laboratory results must be interpreted with caution and should not be used as the sole source of information on the ecological significance of dominance relations. The importance of parallel field and laboratory studies is emphasized, since it is evident that many factors may influence intracolony aggression.

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A COMPARISON OF FORE AND BACK REEF POPULATIONS OF *DIADEMA ANTILLARUM* PHILIPPI AND *EUPOMACENTRUS PLANIFRONS* CUVIER AT ST. CROIX, U.S. VIRGIN ISLANDS[1]

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ABSTRACT

The community structure of populations of threespot damselfish (*Eupomacentrus planifrons*) and the black sea urchin (*Diadema antillarum*) in fore reef and back reef habitats of Teague Bay reef off the West Indies Laboratory, St. Croix, U.S. Virgin Islands, was examined during July and August 1981. All populations studied occupied patches of *Acropora palmata* at depths of 3-5 m and were observed with SCUBA.

Field observations indicated that populations of *Diadema* within back and fore reef habitats differed in the following ways: 1) mean urchin test diameter was significantly larger on the back reef ($\bar{X}$ = 74.48 mm) than on the fore reef ($\bar{X}$ = 47.94 mm), 2) mean urchin density, sampled during daylight hours was lower on the back reef ($\bar{X}$ = 2.3 urchins m^{-3}) than on the fore reef ($\bar{X}$ = 5.04 urchins m^{-3}), and 3) on the back reef 60.8% of the urchins were found on coral branches more than 60 cm above the substrate, whereas on the fore reef 74.5% of the urchins were found below that level. Damselfish densities were significantly lower on the back reef ($\bar{X}$ = 0.18 m^{-3} vs. 0.31 m^{-3}) and algal lawns were significantly smaller ($\bar{X}$ = 146.1 cm^2 vs. 349.1 cm^2) than on the fore reef. Back reef damselfish were more aggressive ($\bar{X}$ bites min^{-1} = 27.6) than those on the fore reef ($\bar{X}$ bites min^{-1} = 6.6).

These differences in community structure may indicate differing levels of competitive interaction between threespot damselfish and *Diadema*. The higher energy environment of the shallow fore reef may effectively reduce the size of *Diadema* by reducing urchin grazing. Thus, competitive interactions between threespots and *Diadema* may be lower on the fore reef than on the back reef.

INTRODUCTION

The community structure and competitive interactions between threespot damselfish (*Eupomacentrus planifrons* Cuvier) and the herbivorous sea urchin (*Diadema antillarum* Philippi) have been documented in the East Back Reef of

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Discovery Bay, Jamaica, West Indies (Williams, 1978, 1979, 1980, 1981). The damselfish maintains algal lawn territories on dead branches of staghorn coral (Acropora cervicornis Lamarck) and actively excludes herbivores, such as Diadema, from these territories (Myrberg and Thresher, 1974; Williams, 1979). Through these competitive interactions, habitat partitioning occurs which affects the distribution and abundance of Diadema on the reef (Williams, 1979, 1981). Because of its influence on the distribution of grazing sea urchins, the damselfish is considered to be a keystone species (Williams, 1980). Sammarco and Williams (1982) also have suggested that E. planifrons indirectly affects shallow reef coral community structure by influencing the differential success of coral recruitment and algal growth both within and outside damselfish territories.

This preliminary study examines the structure of two similar communities and the interactions of these species on the reefs of St. Croix, U.S. Virgin Islands, to determine whether or not damselfish occupy a similar role in reef communities other than Jamaica. Both fore and back reef communities were examined for comparison with each other and with previous observations from Jamaica.

MATERIALS AND METHODS

Field studies were conducted on the bank barrier reef (Adey, 1978) located north of West Indies Laboratory on the northeast coast of St. Croix, U.S.V.I. (17°45.5'N, 64°35.5'W). The reef studied was representative of the area, with the back reef composed of elkhorn coral (Acropora palmata) in the shallower areas and various head corals (Montastrea annularis, Diploria spp., etc.) found in deeper water. Millepora complanata and A. palmata were found in the high energy areas of the crest, while A. palmata, A. cervicornis, and several species of head corals prevailed on the fore reef (Ogden, 1974). A study site was established west of the WIL pier at the site of solar panels on both fore and back reefs in comparable water depths. This area was chosen because of accessibility of the fore reef through a swim cut in the reef crest. All observations and experiments were carried out between 1030 and 1545 hr using SCUBA.

Study of the interactions between threespot damselfish and Diadema was restricted to those which took place among branches of A. palmata, an apparent preferential substrate for threespots in the absence of A. cervicornis (Williams, pers. obs.; Itzkowitz, 1974). Individual stands of A. palmata were selected for observation by the following criteria: at least two threespot damselfish per coral stand; coral stand boundaries easily discernible; and coral stands located in -3 to -5 m of water. Aluminum tags were used to identify the A. palmata stands. Length, width, and height of each stand were recorded and used in calculating densities of damselfish and urchins (number of individuals m^{-3}). Wilcoxon rank sum tests were used to compare densities and coral stand measurements between fore and back reefs. Correlation analysis (Sokal and Rohlf, 1969) was utilized to examine relationships between the species' densities.

Vertical distributions of urchins within coral stands were recorded by suspending a leaded line, calibrated in centimeters, among the branches of

coral and counting individuals located within 5 cm intervals above the substrate. A G-test of independence (Sokal and Rohlf, 1969) was used to compare distributions of urchins above and below 60 cm coral height on both sides of the reef.

A comparison of urchin populations located in the two habitats was made by examining the size class structure of Diadema. Haphazard samples of individuals from each population were collected by hand from several areas east and west of the study sites. Greatest test diameter was measured (to the closest 0.01 cm) across the ventral surface using vernier calipers for 106 individuals from both fore and back reefs. Mean test diameters were compared using a Student's t-test, and size class structures were determined by the method of Harding (1949).

A measure of the relative aggression of threespots toward Diadema in both habitats was recorded. These data were obtained by placing an urchin representative of the mean size in the algal lawn of a haphazardly chosen damselfish and counting the number of bites on urchin spines made by the damselfish in 1 min or until the urchin was outside the algal lawn. Relative levels of aggression were compared using a Student's t test. All statistical computations were completed by using the Statistical Analysis System (SAS).

RESULTS

Stands of elkhorn coral were significantly smaller in total volume on the fore reef than on the back reef due to significantly smaller width dimensions (table 1). Densities of Eupomacentrus planifrons associated with the fore reef stands were significantly higher than those of the back reef. Algal lawns were significantly larger on the fore reef than on the back reef (table 1). Although more coral substratum apparently was available in the back reef, fewer fish maintained smaller territories in this region.

The density of Diadema was higher on the fore reef than on the back reef (table 1). Additionally, mean test diameter was significantly smaller ($t = 18.64$; $df = 191$; $p < 0.0001$) on the fore reef ($\bar{X} = 47.94$ mm) than on the back reef ($\bar{X} = 74.48$ mm). Population size class structure exhibited no apparent differences between habitats (fig. 1). When all urchins from both habitats are considered, a probable negative relationship may exist between the size and density of Diadema. However, because of the limited data available on mean test diameter and mean density of Diadema in each habitat ($N = 2$), correlation analysis could not be completed.

Although significance was not testable due to small sample sizes ($N = 3$), an apparent negative correlation was demonstrated between the density of Diadema and the density of E. planifrons on the back reef, but this was not the case on the fore reef (fig. 2). Thus, in the back reef habitat where densities of E. planifrons were low and algal lawns were small, small numbers of large Diadema were found.

Relative aggression levels of E. planifrons toward Diadema were found to be much higher ($t = 5.25$, $df = 13$, $p < 0.0002$) on the back reef ($\bar{X}$ bites $min^{-1} = 27.6$) than those exhibited by threespots on the fore reef ($\bar{X}$ bites $min^{-1} = 6.6$) (fig. 3). Thus, intensity of the behavioral interaction between

Table 1.--Comparison of communities on fore and back reefs at St. Croix, U.S.V.I. Data are means (± SE) and were tested with Wilcoxon rank sum tests (Z statistic) for all tests except for algal lawn, where a t test was used.

	Fore Reef	Back Reef	Test Statistic	P
A. palmata (m^3)				
Volume	9.5(1.3)	16.79(2.52)	Z = 1.75	0.04
N	3	3		
A. palmata (m)				
Height	1.42(.03)	1.5(.05)	Z = 1.03	n.s.
N	3	3		
A. palmata (m)				
Width	1.87(.19)	2.63(.28)	Z = 1.75	0.04
N	3	3		
Threespot Density				
No. ind. m^{-3}	0.31(.04)	0.18(.01)	Z = 1.75	0.04
N	3	3		
Diadema Density				
No. ind. m^{-3}	5.04(1.86)	2.30(.47)	Z = -1.75	0.04
N	3	3		
Algal lawn				
(cm^2)	349.11(44.57)	146.11(12.89)	t = -4.38	< 0.002
N	9	9		

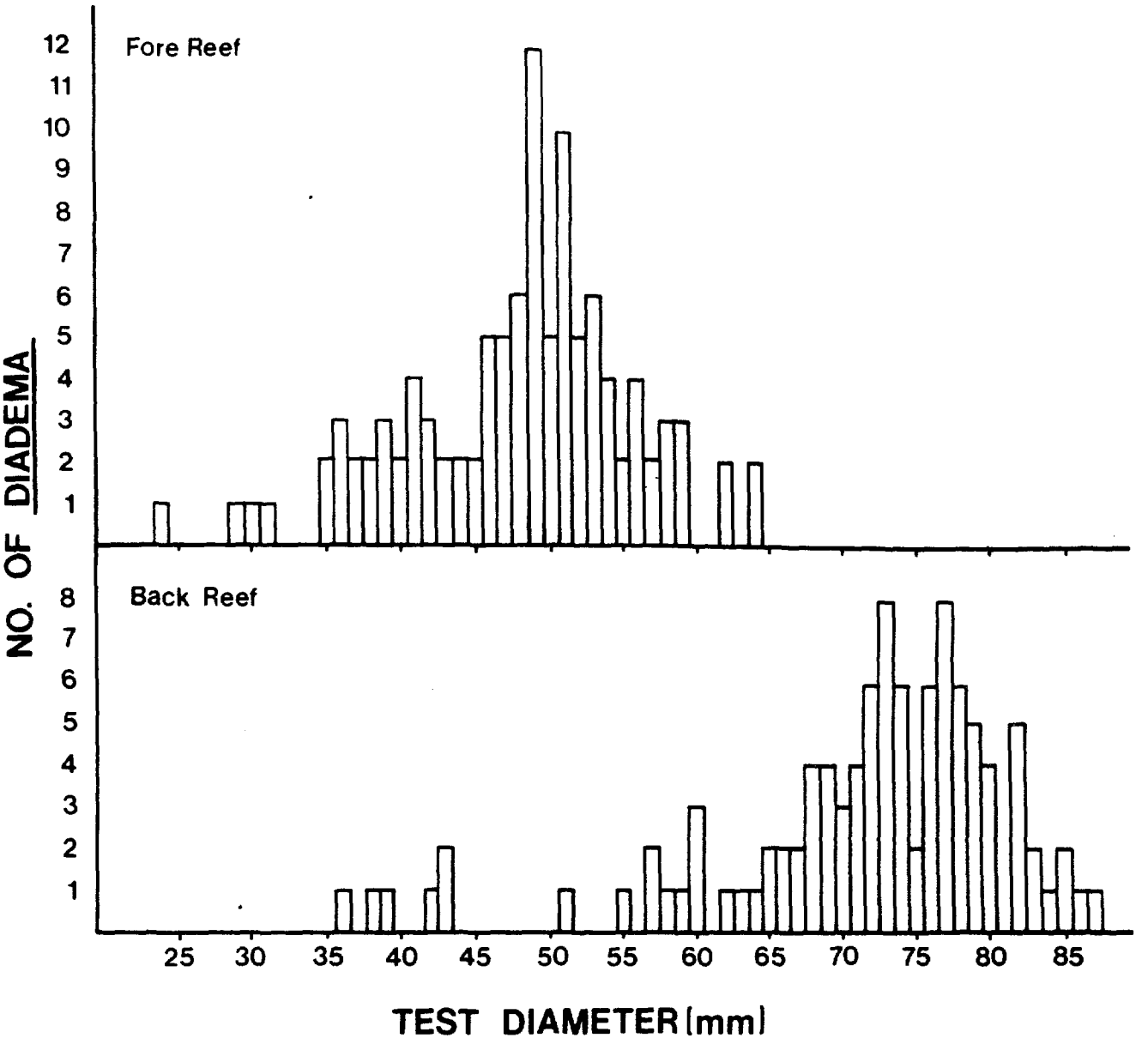

Figure 1.--Frequency distribution of size classes (mm) for Diadema occurring on the fore reef (top) and back reef (bottom) of St. Croix; N = 106 for each site.

threespots and Diadema was strongest, and Diadema density varied inversely with damselfish density on the back reef.

Although the volume of A. palmata per stand differed in the two habitats, the heights of A. palmata stands were not significantly different (table 1). However, within A. palmata stands on the fore and back reefs, the vertical distribution of Diadema was found to differ significantly (table 2). A large

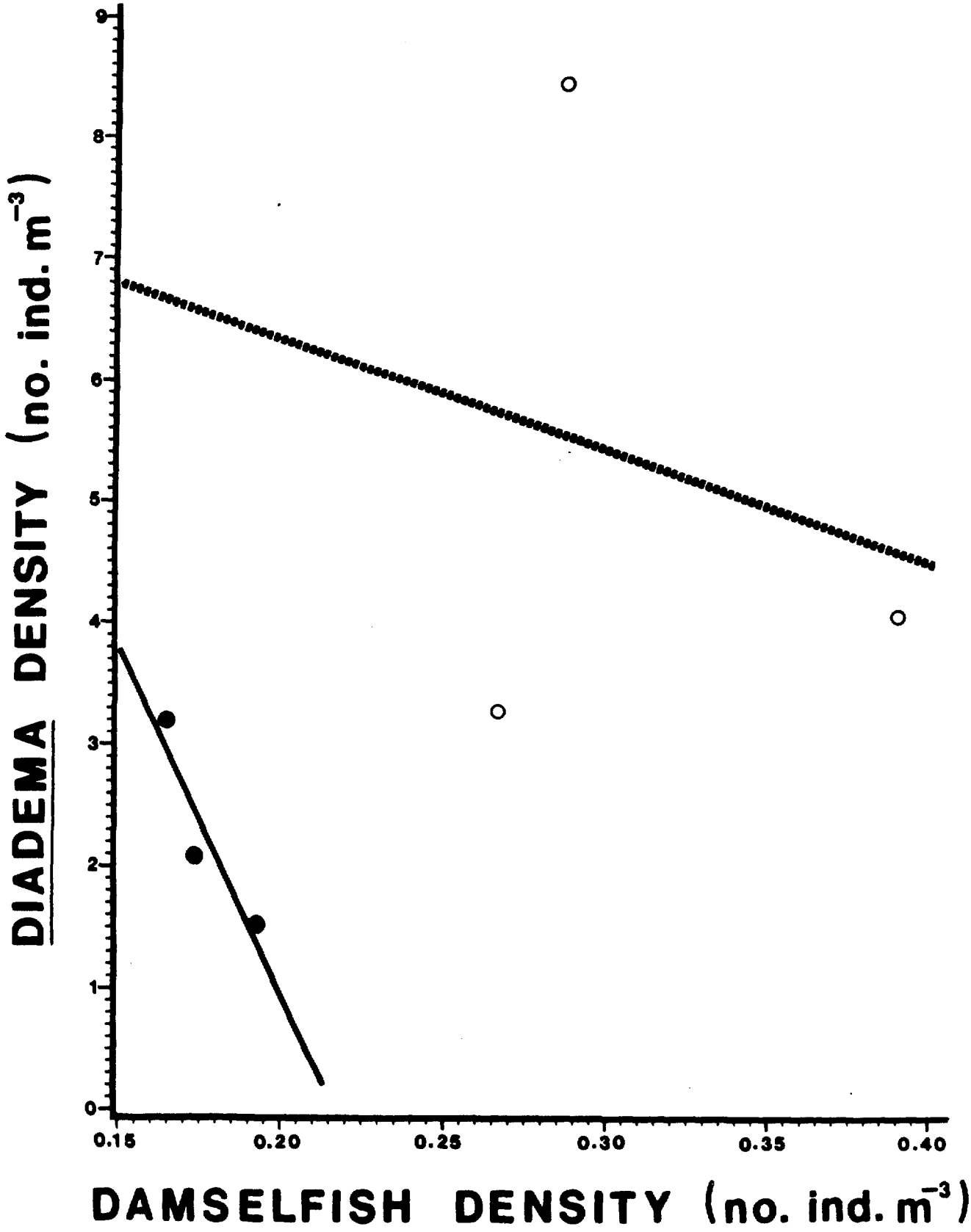

Figure 2.--Relationship between density of Diadema (no. inds. m^{-3}) and threespot damselfish (no. inds. m^{-3}). Closed circles = back reef populations; open circles = fore reef populations.

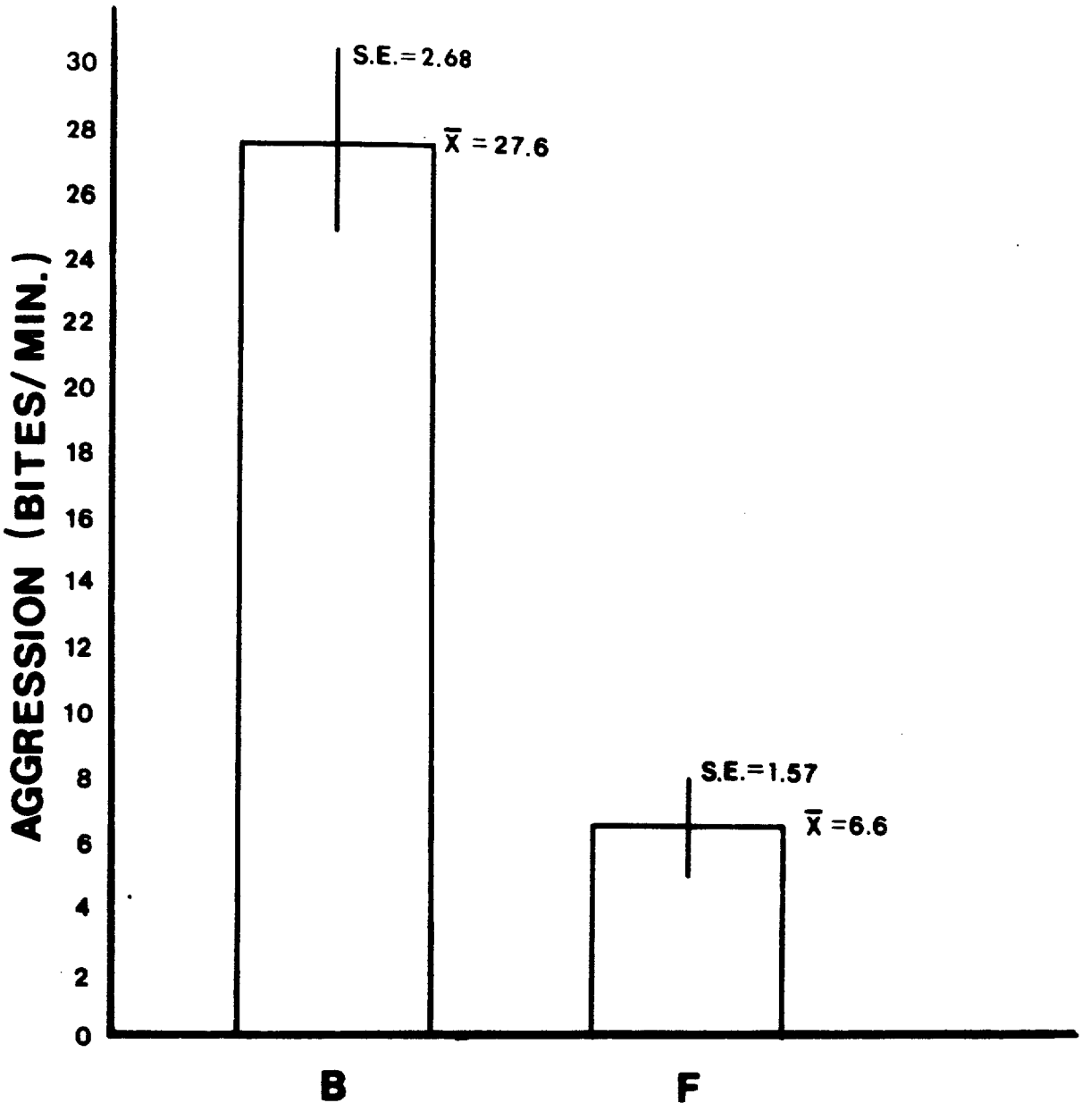

Figure 3.--Mean relative aggression level (bites min^{-1}) of threespot damselfish toward urchins on the fore reef (F) and back reef (B) of St. Croix. Fore reef N = 5, back reef N = 10.

proportion of the Diadema (60.8%) tended to occupy the upper branches of coral (> 65 cm in height) on the back reef, while 74.5% of the urchins on the fore reef were located on coral branches less than 60 cm above the substrate. Differences in sampling times cannot account for these differences, since all observations but one were made between 1545 and 1830 hr. One back reef

Table 2.--Comparison of proportional (%) vertical distributions of Diadema within stands of A. palmata on fore and back reefs. A G-test compared individuals found at heights of < 60 cm or > 65 cm ($G = 10.76$, $p < 0.005$, $df = 1$).

Ht. (cm)	Fore Reef	Back Reef
15-30	13.9	19.6
35-60	50.6	19.6
65-90	21.5	12.2
95-135	13.9	48.6
N	79	107

observation was made at 1030 hr; however, it did not differ from samples taken later in the same area. Thus, differences in vertical distribution must have been due to differing urchin behavior.

DISCUSSION

Although the damselfish-Diadema assemblages in the fore and back reef environments at St. Croix appear similar in population composition, the structures of these two assemblages differ in population abundances, distributions, and mean size. These differences may be the result of differing physical factors and/or biological interactions.

Colonies of Acropora palmata were similar in height but significantly smaller in volume on the fore reef (table 1). The difference in volume was attributable to differences in width of coral stands. This structural difference in the corals may be related to the higher wave energy on the fore reef. Waves can cause considerable damage to fore reef corals, as evidenced by abundant coral rubble found on the fore reef substratum (Robinson, pers. obs.; Van den Hoek, et al., 1978). Rogers, et al. (1982) documented that storm damage on the reefs of St. Croix was due to fractures of the distal ends of A. palmata branches.

Mean test diameters of Diadema from the fore reef are smaller and those from the back reef are larger in the present study than those reported by Ogden,

et al. (1973) on patch reefs at St. Croix ($\bar{X}$ = 59 mm). They also are slightly larger than mean diameters measured by Bauer (1980) on the back reef at St. Croix ($\bar{X}$ = 52.3 mm). Such differences may indicate differences in the availability of food, mortality, or adaptations to energy levels in the three different habitats.

The differences between fore and back reef observed in this study also may reflect differences in the availability of food, mortality, and/or adaptations to differing wave energy levels. Preliminary data indicate that smaller urchins, such as those found on the fore reef, may feed at a faster rate than the larger urchins of the back reef (Robinson, unpub. data). However, the larger algal lawns also found on the fore reef indicate a reduced grazing pressure by urchins (table 1). Van den Hoek, et al. (1975, 1978) attributed a higher biomass of algal turf to lower grazing pressure from Diadema in similar high energy regimes. Thus, the smaller body size of urchin populations found on the fore reef may be due to food limitation (Carpenter, 1981) even though abundant food is present (i.e., larger damselfish lawns, table 1). High wave energy may force urchins to remain lower in the coral matrix, preventing them from reaching this potential food source (table 2). High energy regimes either may select for individuals with smaller test diameters (i.e., smaller surface area for exposure to wave energy) or may result in smaller urchins by reducing their effective feeding periods. Lissner (1980) reported an inverse relationship between turbulence and activity of the urchin Centrostephanus coronatus.

Williams (1981) demonstrated that Diadema and threespot damselfish in Jamaica were actively involved in competition for either food or space in the back reef. This competition affected the amount of algae accumulating outside of algal lawns. The relative level of competition in differing environmental conditions was not measured in that study. We believe that the lower levels of aggression in damselfish (fig. 3) and their larger lawns on the fore reef provide evidence of reduced competitive interactions in this environment as compared to the back reef. Additionally, larger lawns and a greater food supply may be necessary for damselfish to maintain themselves in this high energy regime. Reduced competition may be the result of environmental mediation, whereby high wave energy reduces urchin grazing and thus increases the size of damselfish territories.

Sammarco, et al. (1974) and Sammarco (1980) indicated that, at high densities of Diadema, successful settlement of corals was inhibited; in contrast, maximum diversity of successfully settled coral spat was achieved at lower densities of Diadema. Sammarco and Williams (1982) also indicated that settlement success varied within and outside of damselfish algal lawns due to alterations in urchin grazing levels. Similar factors affecting the settlement success of corals will vary between fore and back reef habitats at St. Croix and may account for differences in adult coral diversities in these two environments.

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CARBONATE SEDIMENT PRODUCTION BY THE ROCK-BORING URCHIN ECHINOMETRA LUCUNTER AND ASSOCIATED ENDOLITHIC INFAUNA AT BLACK ROCK, LITTLE BAHAMA BANK

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ABSTRACT

Bioerosion studies were conducted during four cruises in 1982-83 to Black Rock, a 405 m long island of carbonate eolianite on Little Bahama Bank. The urchin population ($\bar{X}$ = 37 adults m^{-2}, 92 x 10^3 total) bores in a 6 m wide zone at depths of 0.5-3 m. SCUBA divers using chisels collected rocks with urchins in their bore holes and similarly sized rocks without urchins and placed them separately in 20 l buckets with 0.0625 mm screen-walls for 2 days (13 usable measurements). Urchins produced spherical to elliptical pellets 1-2 mm in diameter. Disaggregated pellets contained no particles > 1.00 mm. The pellets were 46% (wt) unimodal sand, with a modal grain size between 0.125-0.177 mm, and 54% mud. Urchins produced an average of 242 mg sediment $urchin^{-1}$ day^{-1} (dry wt), which is equivalent to 8.9 g m^{-2} day^{-1}, or 9 tons yr^{-1} for the entire population. Volume of individual urchin bore holes averaged 72 cm^3. Calculating from boring rates, the bore holes were excavated in an average of 2.9 years.

Rocks without urchins (controls) produced an average of 0.5 mg organic-free sediment cm^{-2} day^{-1} (dry wt). These particles were produced by bioerosion of the infauna, which included eunicid and sipunculid worms, sponges, Lithotrya barnacles, pelecypods, and microborers. Inorganic sediment weight was correlated ($r = 0.968$, $p < 0.05$) with surface area of the control rocks. Infauna from control rocks produced 5.0 g m^{-2} day^{-1}, equivalent to 6.5 tons yr^{-1}, for Black Rock.

INTRODUCTION

Bioerosion has a two-fold role in coral reefs; hard substrate is removed, creating cavities, and some of the former substrate becomes sedimentary particles that may be transported to new environments (Hopley, 1982). We have been studying the area surrounding Black Rock, a small Pleistocene eolianite island on the southwestern Little Bahama Bank, in order to identify and measure sources of sediment, to follow dispersal pathways, and to measure the rate at which the sediments accumulate.

Bioerosion by the urchin Echinometra lucunter (Linnaeus) has been studied previously in Barbados (McLean, 1967), Bermuda (Hunt, 1969), and the Virgin Islands (Ogden, 1977). Another species, E. mathaei, has been studied in Persian Gulf reefs by Shinn (p. 39, in Hughes Clarke and Keij, 1973) and Enewetak (Russo, 1980). The purposes of this study are to determine the rate of sediment production and cavity formation by E. lucunter using a new method, to characterize

A
B
100μ
C
D
200μ
E
F
20μ

the size distribution of the particles produced, and to compare these data with the rate of production and size of particles produced by the rock-boring infauna closely associated with the urchin bore holes.

METHODS

Urchin Population

The distribution and abundance of E. lucunter adults (about 3 cm test diameter) was determined by SCUBA divers off western Black Rock. Most of the eastern side is sand, without urchins. Using a 0.25 m^2 PVC frame, the divers counted the adult urchins within each frame (total of 35 frames) on three separate transects that were continuous from the intertidal zone seaward until no more urchins were found. The number of adult urchins was calculated for each linear meter in a seaward direction. These numbers were extrapolated for the lateral extent of the island to yield the total number of urchins.

Sediment Yield

Using chisels, SCUBA divers collected rocks, each containing one urchin in its intact bore hole, from 2-3 m depths off western Black Rock. Similarly sized rocks without urchins were collected for controls. Each rock was brushed underwater to remove loose particles. The rocks were placed separately, without exposure to air, in 20 l plastic buckets. Each rock was placed on a styrofoam pad and secured to the bottom of the bucket by criss-crossed rubber bands latched onto plastic hooks attached inside the buckets. The buckets were ventilated with 1150 cm^2 of 0.0625 mm nylon screen on the side and 72 cm^2 of 0.5 mm nylon screen at the top. Using an oxygen electrode, measurements made at the start and end of an experimental run showed only a small decrease (maximum decrease of 0.4 mg l^{-1}) in dissolved oxygen within the bucket. Buckets were secured to the seafloor at the collection site in various ways, all designed to minimize movement of the rock within the bucket, which otherwise might have produced sediment particles by abrasion (fig. 1A). Buckets were deployed for 43-50 hr during four separate cruises. Five control and eight experimental buckets yielded thirteen usable measurements out of the twenty-four buckets deployed. Some buckets were lost in squalls and others had rips in the nylon mesh and therefore were not included.

Figure 1 (opposite page).--(A) Buckets (20 l) in situ at 2.5 m depth used for urchin study; (B) SEM of limestone (eolianite) wall in Echinometra lucunter bore hole. Upper right - encrusted with lithothamnoid algae. Lower left - algae-free area eroded by urchin and showing spherical grains in the limestone; (C) Fecal pellets from alimentary tract of E. lucunter. Bar = 0.5 mm; (D) Broken and partially regrown spine of E. lucunter; (E) Abraded end of tooth from Aristotle's lantern of E. lucunter; (F) SEM close-up of fig. 1E (arrow), showing laminated microstructure of tooth tip visible from abrasion. Tip pointing to right.

The particles produced were recovered by gently washing the rock (and urchin) while inside the bucket, siphoning off the water, and then washing the particles into polyethylene bags. Particles, rocks, and urchins were labelled and then preserved in 70% ETOH. Particles were washed free of salt, oven dried at 95°C, and weighed to 0.01 mg. Twelve free-living urchins were collected and their alimentary tracts removed by dissection, measured, and the length of tract containing sediment estimated. The gut contents were removed, washed, dried, and weighed. The organic content of sediment from the urchin alimentary tracts, experimental buckets, and control buckets was determined by weight loss following H_2O_2 digestion. Subsequently, inorganic sediment from each sample was wet sieved (0.0625 mm stainless steel screen) to separate mud. Gravel and sand size particles (> 0.0625 mm) were oven dried at 95°C and dry sieved at 0.5 Phi intervals for 5 min using agitation by Vibrapad. Weight of each sieve fraction was recorded to 0.01 mg. Particle size distributions were generated by the Cal-Comp plotter from these weights.

Attached organisms (mostly algae) were removed from each rock, washed, dried, and weighed. Each rock was then oven dried, and the exposed surface area was measured by the aluminum foil method (Reed, et al., 1982). The volume of each urchin bore hole was measured by determining the volume of water contained in a latex sheath placed inside the bore hole. Each rock was dissolved in acid ($HCl + HNO_3$) to recover the infauna, which was washed, dried, and weighed. Urchins were dried and weighed, and test dimensions and volume were determined.

RESULTS

Urchin Population

The total urchin population at Black Rock was 92.4×10^3 adults within an area of 2521 m^2. Average urchin density was 37 adults m^{-2} (maximum was 100 m^{-2}). Urchins were present between the intertidal zone and 7 m depth. Urchins never were observed to leave their bore holes; during the day they remained stationary at the bottom of the hole, but at night they moved within their individual bore holes. The urchins fed upon both endolithic algae and pieces of algae that apparently drifted into the bore holes.

Sediment Yield

For control rocks (without urchins), a significant correlation ($r = 0.968$, $p < 0.05$) was found between the total inorganic weight of sediment recovered from buckets and the total surface area of the rocks. Linear regression gave the formula for this relationship:

$$Y = 1.133X - 119.71,$$

where Y = inorganic sediment weight and X = total rock surface area. The average organic content of sedimentary particles recovered was 23.74% (range = 14.99 - 41.98%). The mean weight of attached macro-organisms on control rocks

was 4.6 g dry weight (range = 1.3 - 13.9). The average yield of inorganic particles produced by infauna of the control rocks was 0.50 ± 0.07 mg cm^{-2} day^{-1} ($\bar{X}$ + 1 SD; table 1). This rate of sediment production was equivalent to 5.0 g m^{-2} day^{-1}, and for the area of 2521 m^2 in which these rocks occurred, the yield was 12.6 kg day^{-1}. The average dry weight of infauna recovered by acid dissolution of each control rock was 8.6 g (range = 4.5 - 13.8).. Dominant infauna included eunicid polychaetes, sipunculids, boring sponges, Lithotrya barnacles, pelecypods, and other microborers.

For experimental buckets (rock + urchin), the sediment recovered was a mixture of particles produced by the rock infauna and by the urchin inside its bore hole. We assumed that the amount of sediment passing through the mesh from outside sources was the same for control and experimental buckets. Because our underwater observations showed that visibility was 12-18 m, we further assumed that the possibility of mud contaminating the buckets was insignificant. The average organic content of particles recovered was 15.83% (range = 11.75 - 20.30%). The average weight of attached macro-organisms was 6.7 g dry weight (range = 1.0 - 13.1). To calculate the weight of sediment produced solely by the urchin, we used the regression formula (above) and subtracted the weight of sediment made by the infauna of the experimental rock from the total inorganic weight of sediment recovered. The calculation for each experimental bucket was made as follows:

$$\text{mg urchin}^{-1}\ \text{day}^{-1} = \frac{[\text{total organic-free wt}] - [1.133 \times \text{area of experimental rock} - 119.71]}{\text{duration of experiment in hours}} \times 24.$$

These calculations indicated that the average weight of inorganic sediment produced by adult urchins was 242.2 ± 146.0 mg $urchin^{-1}$ day^{-1} ($\bar{X}$ ± 1 SD, table 1). The total urchin population produced 22.4 kg day^{-1} or an average of 8.9 g m^{-2} day^{-1} within the 2521 m^2 area containing urchins. Urchin bioerosion was 64% of the total 13.9 g m^{-2} day^{-1} measured by our bucket experiments. In nature, physical processes of abrasion and other bioeroders (fish) would contribute additional particles.

Particle size analysis showed that the percentages of sand (2.00 - 0.0625 mm) and mud (< 0.0625 mm) were similar for sediment from alimentary tracts of uncaged urchins and from control and experimental rocks. The alimentary tracts of the urchins contained mostly pellets (fig. 1C) which readily disintegrated into sand and mud. No gravel (> 2.00 mm) was found in alimentary tracts of urchins. Sediment from control and experimental buckets contained 0 - 28.5% gravel. Sand fractions from alimentary tracts of uncaged urchins contained particles most abundantly between 0.125 - 0.177 mm (fig. 2, top) and particles of this size were also the most abundant in sediment recovered from experimental buckets which contained eolianite and a living urchin (fig. 2, middle). As determined with a low-power microscope, the grain size of sand particles in the eolianite is the same as the modal grain size of sand from urchin alimentary tracts (0.125 - 0.177 mm). However, sediment from urchin alimentary tracts was 50% mud, which greatly exceeds the mud content of the eolianite. These observations suggest that urchins cause erosion at Black Rock by breaking individual eolianite grains away from the substrate, yielding sand, and also by

Table 1.--Comparison of sediment production rates of infauna (control rocks) and urchins (experimental rocks)

Date and Duration	Total Organic-free Sediment Recovered (dry wt, mg)	Rock Surface Area (cm^2)	Sediment Production Rate by Infauna ($mg\ cm^{-2}\ day^{-1}$)
Control (rock, no urchin)			
25-27 August 1982 43.5 hr	442.13	428.1	0.57
	286.63	396.5	0.40
	500.19	591.6	0.47
13-15 April 1983 45.5 hr	689.78	722.6	0.50
	814.86	802.4	0.54
			$\bar{X} = 0.50 \pm 0.07$
Experimental (rock + urchin)			
25-27 August 1982 43.5 hr	1507.63	640.2	497.65
	1031.92	774.5	169.99
	1044.32	621.0	254.03
13-15 April 1983 45.5 hr	1146.83	902.4	128.77
21-23 June 1983 49.5 hr	1278.27	1119.5	62.83
	1270.90	795.5	237.24
	1588.92	756.0	413.13
	1355.85	985.9	173.84
			$\bar{X} = 242.2 \pm 146.0$

abrading more tightly cemented eolianite grains, yielding mud (fig. 1B). Infaunal bioeroders produced a much broader spectrum of particle sizes (fig. 2, bottom), perhaps due to the many species of bioeroders active within these rocks.

Evacuation of Bore Holes

Inspection of eolianite at the bottom of urchin bore holes by low-power microscope and SEM revealed no scratches on the substrate (fig. 1B). Individual

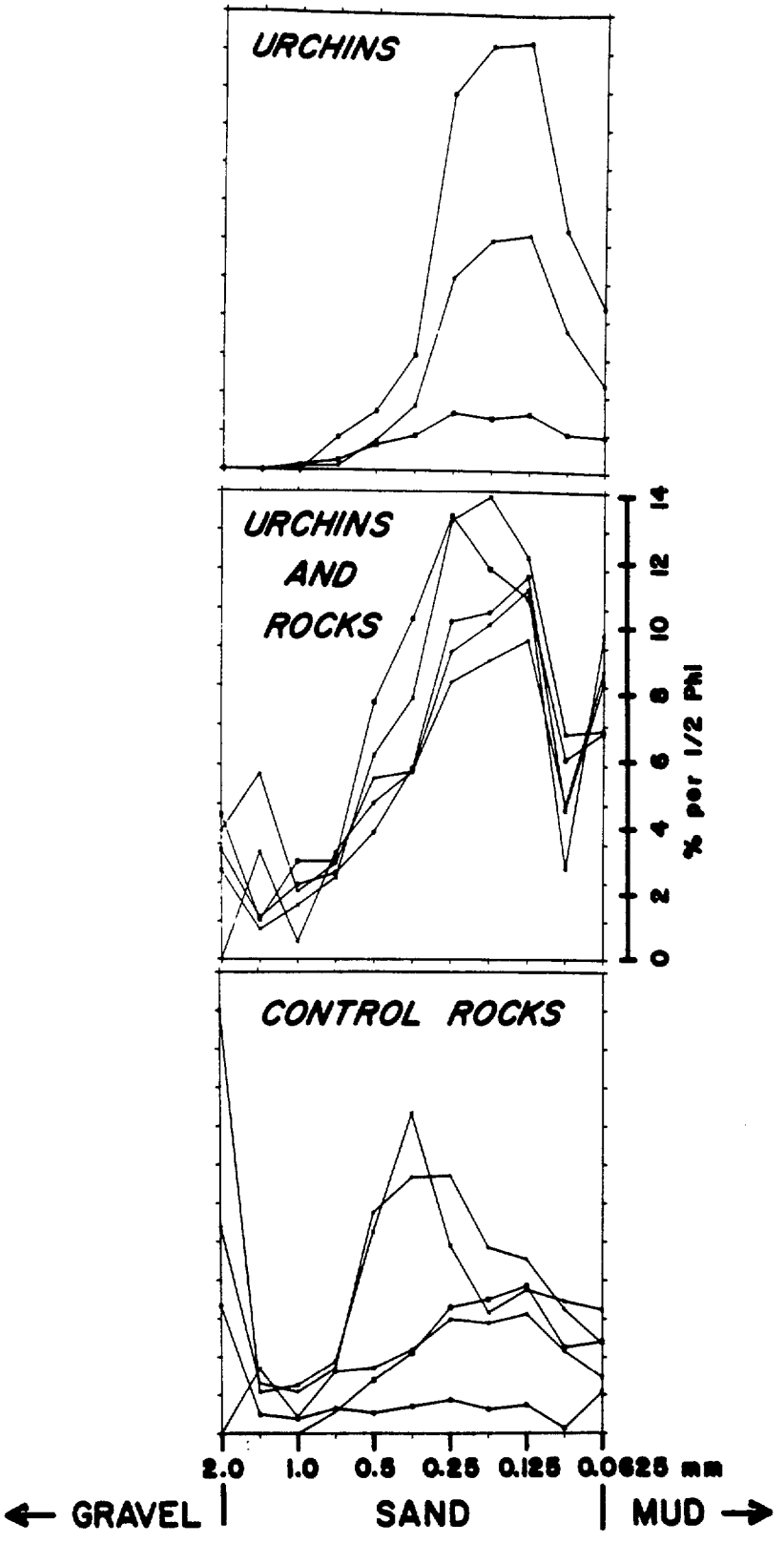

Figure 2.--Size-frequency curves for the sand fraction of sediment from alimentary tracts of uncaged urchins (upper), from urchins and rocks in bucket enclosures (middle), and from rocks without urchins in bucket enclosures (bottom). Data for the gravel and mud fractions are not given; scale of the y-axis is identical for all sediments.

Table 2.--Bioerosion by Echinometra lucunter.

Method	Substrate	Rate of Erosion (g urchin^{-1} yr^{-1})	Author
Gut contents	Beachrock	18.6	McLean, 1967
Gut contents	Algal ridge on coral reef	44.0	Ogden, 1977
Gut contents	Eolianite	128.0	Hunt, 1969
Bucket enclosure	Eolianite	88.0	This paper

teeth from the Aristotle's lantern of the urchin had abraded tips; most spines were sharply pointed, but a few had broken and re-grown tips (fig. 1D, E, F). It is possible that E. lucunter may use its spines in addition to teeth in substrate erosion (McLean, 1967; Hunt, 1969). The rate of spine re-growth may be so rapid, averaging 0.3 mm day^{-1} at 20°C (Davies, et al., 1972, fig. 1, p. 874), that damage to spine tips is not ordinarily observable.

Volume of bore holes for individual urchins averaged 72 cm^3 (range = 17 - 126). Using a measured density of 2.13 g cm^{-3} for the eolianite and the average rate of substrate erosion by the urchins, we estimated that an average of 2.9 yr was required to excavate a bore hole (range = 0.7 - 10.3 y).

DISCUSSION

Previous studies (McLean, 1967; Hunt, 1969; Ogden, 1977) measured only the amount of sediment within urchin alimentary tracts and assumed that frequency of gut turnover was once each day. Disadvantages of the gut contents method are that 1) gut turnover frequency is not verified, 2) the material in the gut is not necessarily produced by urchin activity and may have been ingested after transport to the urchin bore hole from an allochthonous source, and 3) not all particles produced by urchin tooth and spine movements may be ingested.

The advantages of the bucket enclosure method are that 1) all sediment produced by the urchin is captured, 2) rates of infaunal sediment production and the grain size of their product can be determined, and 3) contamination by sediment from outside sources is minimized. There is, however, the possibility of loss of some mud-sized particles through screen windows in the buckets, the exclusion of drifting algal bits, and reduced water flow inside the buckets.

Measurements of bioerosion by E. lucunter from various places are summarized in table 2; there are too many variables to resolve the different rates reported. To place our measurements in perspective, a comparison with other erosion

Table 3.--Comparison of erosion agents and rates for Black Rock (unpublished data of C. M. Hoskin, D. H. Mook, and J. K. Reed)

Process	Agent	Average Rate of Substrate Erosion (mg cm^{-2} yr^{-1})
Bioerosion	*E. lucunter* (bucket enclosures)	667
	Rock infauna (bucket enclosures)	183
	Intertidal microborers (tethered limestone blocks)	26
Physical abrasion	Waves and currents (tethered limestone blocks)	5.5
Chemical solution	Intertidal seawater (filter-protected, suspended limestone blocks)	0-2

processes at Black Rock (table 3) indicates that biological activities are more significant than physical and chemical processes in the degradation of reef substrates.

In terms of paleoecological significance, we suggest that the most preservable part of the bioerosive activity of *E. lucunter* at Black Rock will be the band of bore holes. However, with SEM we searched for and did not find appropriately sized scratch marks on the bottoms of bore holes which might be expected from urchin teeth. The sediment produced by *E. lucunter* is initially pelleted, but the pellets quickly disintegrate. Sand from the pellets is most abundant at sizes between 0.125 - 0.177 mm, but other processes may produce sand of the same size. Approximately half (by weight) of the disintegrated pellets is mud with no distinctive properties. Although the urchin population density was as high as 100 adults m^{-2}, the total amount of echinoderm skeletal fragments in the sand fraction of nearby shallow water sediment was < 1%; Hine, *et al.* (1981, table 1, p. 288) did not include echinoderm skeletons in their listing of carbonate constituents.

Hine, *et al.* (1981, fig. 17-B, p. 278) have shown by seismic reflection profiling that the southwest margin of the Little Bahama Bank in the vicinity of Black Rock is a rocky surface, barren of sediment. Our seismic reflection profiling confirms the seismic findings of Hine, *et al.* (1981), but from the JOHNSON-SEA-LINK submersibles we have seen sediments a few centimeters thick overlying hardgrounds on the western bank margin. Using the geometry of sand bodies 3-12 km northeast of the bank margin as an indicator, Hine, *et al.* (1981, fig. 14, p. 275, and table 1, p. 268) suggested that sand is transported onto the Little Bahama Bank. Sediment produced by *E. lucunter* and the associated

roc infauna is predominantly fine sand and mud. The amounts of this sediment are considerable: 9 tons yr^{-1} for the urchins plus 6.5 tons yr^{-1} for the infauna at Black Rock. This sediment probably does not accumulate in the shallow bank margin environment because currents are strong (Hine, et al., 1981, fig. 24, p. 287).

From the JOHNSON-SEA-LINK submersibles we observed sediment-containing grooves passing through the bank-edge reefs and have counted 70 grooves in a 400 m long segment of bank edge west of Black Rock. Hubbard, et al. (1981, fig. 17, p. 26) have illustrated similar sediment-containing grooves off Lucaya, Grand Bahama Island. We made sediment trap measurements in the grooves (32 m depth) west of Black Rock and found an average of 5.4 kg m^{-1} yr^{-1} of carbonate sediment moving westward. We suggest that this sediment, in part, represents the products of urchin and rock infauna bioerosion being transported over the bank edge and into deeper waters of the Northwest Providence Channel.

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HIGHLY PRODUCTIVE EASTERN CARIBBEAN REEFS: SYNERGISTIC EFFECTS OF BIOLOGICAL, CHEMICAL, PHYSICAL, AND GEOLOGICAL FACTORS

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ABSTRACT

Studies of reef productivity and community structure were conducted on three bank barrier reefs along the south shore of St. Croix, U.S. Virgin Islands. Primary productivity (rate of organic carbon fixation) was measured using upstream/downstream flow respirometry techniques. Mean annual gross primary productivity of the St. Croix reef ranged between 17-33 g $C/m^2/d$. These are among the highest values reported for reefs or for any biological community.

Reef productivity corresponds with the distribution and abundance of turf algae. These algae are minute filamentous forms which are highly diverse, productive, and abundant. Algal turf productivity is limited primarily by available solar energy and is influenced by wave surge and water flow (which enhance metabolite exchange). Turf cover is limited by the total surface area of standing dead coral. Nitrogen availability is increased by in situ nitrogen fixing blue-green algae, as evidenced by increased concentrations of inorganic nitrogen in water flowing over the most productive reef zones. Phosphorus availability is enhanced by wave surge and maintained by inflowing water from the open ocean.

Over geological time, reefs grow toward sea level. The three reefs we studied represent three stages in reef development. Younger reefs to the east are deeper, with considerable live branching coral (Acropora palmata) and with a low abundance of turf algae. The reverse is true for the older reefs to the west, where live coral is minimal but the dominant algal turfs occupy a rather smooth pavement of limited surface area. Intermediate between these two types of reefs, the abundance of live coral is low but biomass of algal turf is very high due to the large surface area left by the dead branching coral. The greatest reef productivity was measured under the latter conditions because of the synergistic effects of large surface area with abundant algal turf cover in shallow, strongly lighted, and turbulent water. It is clear that, given optimum conditions, coral reef algal turfs can develop primary productivities that reach and perhaps exceed the accepted theoretical maximum for primary production in the sea.

INTRODUCTION

Coral reefs have attracted interest over the last 30 yr in part because they are among the most productive biological communities in the world. Early studies of reef productivity (Sargent and Austin, 1949; Odum and Odum, 1955) focused on determining the productivity of individual reefs. There is little agreement in these and subsequent studies as to how productive reefs can be, and there is even less agreement concerning why high levels of production are attained or why reefs differ from each other so much (Lewis, 1977; Sournia, 1977; Mann, 1982). Smith (1981) considered some of these problems in an examination of the Houtman Abrolhos Islands off western Australia. We address these questions in some detail in our study of the reefs of St. Croix.

In an examination of the "Potential Productivity of the Sea," Ryther (1959) concluded that (net) "primary productivity of organic matter of some 10-20 g (dry)/m^2/d may be expected," with a maximum of 25 g (dry)/m^2/d under ideal conditions of maximum radiation and no nutrient limitation. Expected gross primary production (GPP) levels of up to 23-38 g (dry)/m^2/d (50-80% higher than the net values) also were cited. Ryther suggested that, while planktonic open ocean production (particularly in tropical/subtropical areas) is limited by nutrients, such limitation in benthic communities is not likely because nutrients "are continually being replenished as the water moves over the plants [and] probably prevents their ever being [nutrient] limited."

Recent reviews of coral reef primary productivity by Lewis (1977) and Sournia (1977), integrating 30 yr of research, reveal a range in GPP of nearly an order of magnitude (3.4 - 20 g C/m^2/d). The mean of these cited reef values is about 10 g C/m^2/d, but only a few points are above 13 g C/m^2/d. The mode is 7 g C/m^2/d, which, using a typical conversion ratio, would convert to a net biomass production of about 15 g (dry)/m^2/d. Overall, these values are much less than the theoretical maximum suggested by Ryther (1959). Significantly, all but one of the 17 coral reefs cited by these authors were located in the Indo-Pacific.

Despite Ryther's (1959) suggestion to the contrary, nutrient limitation of reef productivity has been the focus of numerous studies. Many of these have focused on explanations of how highly productive reef ecosystems can thrive in nutrient deserts (Odum and Odum, 1955; Stoddart, 1969; Johannes, et al., 1972; D'Elia, et al., 1981; Andrews and Muller, 1983). Recently, the role of major nutrients was questioned due to the finding that benthic algae have lower nutrient requirements than once thought (Atkinson and Smith, 1983). Also, some reefs are known to have a surplus of nitrogen (Webb, et al., 1975; Wiebe, et al., 1975) due to the in situ nitrogen fixation by cyanobacteria (blue-green algae) (Mague and Holm-Hansen, 1975; Capone, et al., 1977; Hatcher and Hatcher, 1981; Wilkinson and Sammarco, 1983). The benthic algal turf of reef communities usually is dominated by cyanobacteria (Sammarco, 1983; Van den Hoek, et al., 1975).

Phosphorus concentrations over reefs generally have been thought to change little (Pilson and Betzer, 1973), and some authors have suggested that a "tight recycling" or retention of phosphorus occurs (Pomeroy, et al., 1974; Pomeroy and Kuenzler, 1969). Atkinson (1982), on the other hand, has shown reactive phosphate depletion over broad reef flats.

Our study examines the productivity of three reef environments in tropical, oligotrophic seas. Large-scale temporal and spatial variations in their primary productivity with respect to potentially important biological, chemical, physical, and geological differences between the reefs are explored.

MATERIALS, METHODS, AND STUDY SITES

Our study was conducted on the southeastern bank barrier reef of St. Croix from October 1977 to November 1978. It extends 35 km along most of the windward shore of the island and is the most extensive reef system on the Puerto Rican-Virgin Island shelf. St. Croix is a small island which is unaffected by neighboring islands. Temperature, salinity, and wind direction and intensity are all remarkably constant. The south shore is relatively unpopulated, and it has no natural rivers affecting salinity or ambient nutrients. The south shore of St. Croix is ideal for examining the factors that affect reef productivity. The two major factors that change from east to west are water motion (decreasing) and geological reef development (increasing).

The western reefs of St. Croix lie on a shallower limestone basement than do the eastern reefs; they were the first to grow to sea level (Adey, 1975; 1978a), and they developed broader, more continuous reef flats. Several of these reefs have become so shallow that the abundance of live coral is reduced due to the negative effects of intense sunlight (including ultraviolet), temperature fluctuations, and desiccation during periods of extraordinarily low tides.

We studied three reefs on the south shore of St. Croix intensely and several others to a lesser extent (fig. 1). The following is a description of the morphology of the reefs from east to west. Isaac Bay Reef is a "young" reef with a high coral cover, rapid reef growth rates, and a crest that is just reaching sea level today. Mean depths are 6.3 m for the fore reef and 0.9 m for the back reef. The reef structure is open (many channels and breaks in the reef crest), and there is no continuous reef flat. Robin Bay Reef is more mature, with a nearly continuous crest and a moderately deep and broad reef flat. Mean depths are 5.1 m for the fore reef and 0.7 m for the back reef. Halfpenny Bay Reef is mature, with a continuous, broad, and shallow reef flat. Mean depths are 5.1 m for the fore reef and 0.3 m for the back reef. We selected these reefs because they fall along a gradient of reef maturity and because they are particularly well suited for the upstream/downstream method. All of these reefs have a continuous unidirection water flow inward across the reef to the lagoon.

A profile of Robin Reef along a permanent transect line established at the beginning of our study is shown in figure 2. Comparisons with Isaacs and Halfpenny Reefs are given in the accompanying table. The transects were parallel to the predominant current flow and were established using drogues to indicate the exact current flow. We omitted breaker zones due to logistic and scientific problems created by the turbulence (accelerated diffusion). The outer (seaward) limit to the fore reef was defined by the first appearance of the dominant reef-building coral, Acropora palmata. The inner fore reef and outer back reef zone were adjacent to the breaker zone. The inner (landward) limit of the back reef was defined by the abrupt transition between the reef and sandy lagoon. Our fore and back reef zones are consistent with other published studies (Adey, 1975; Adey and Burke, 1976).

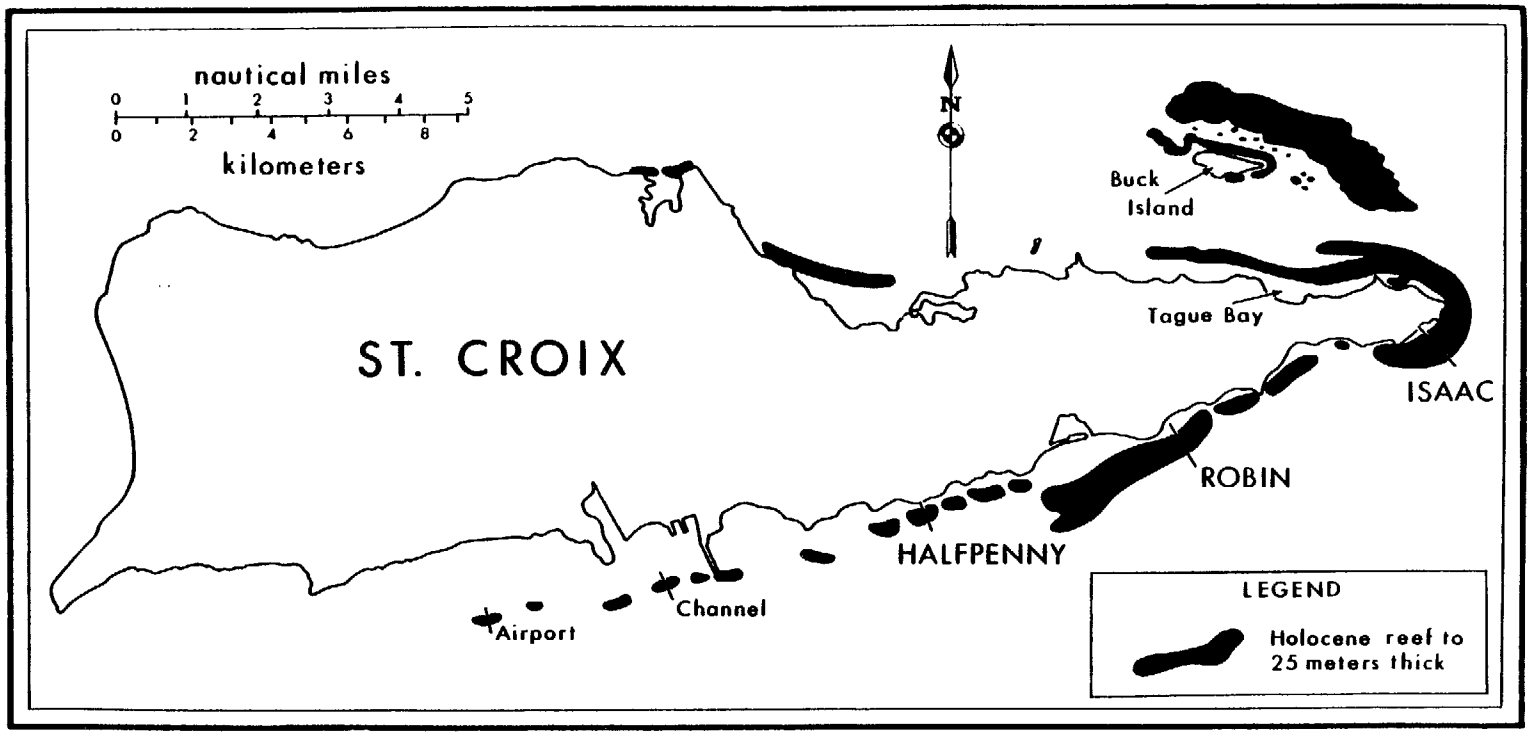

Figure 1.--Locations of transects across bank barrier reefs studied on the south shore of St. Croix, U.S. Virgin Islands, northeastern Caribbean.

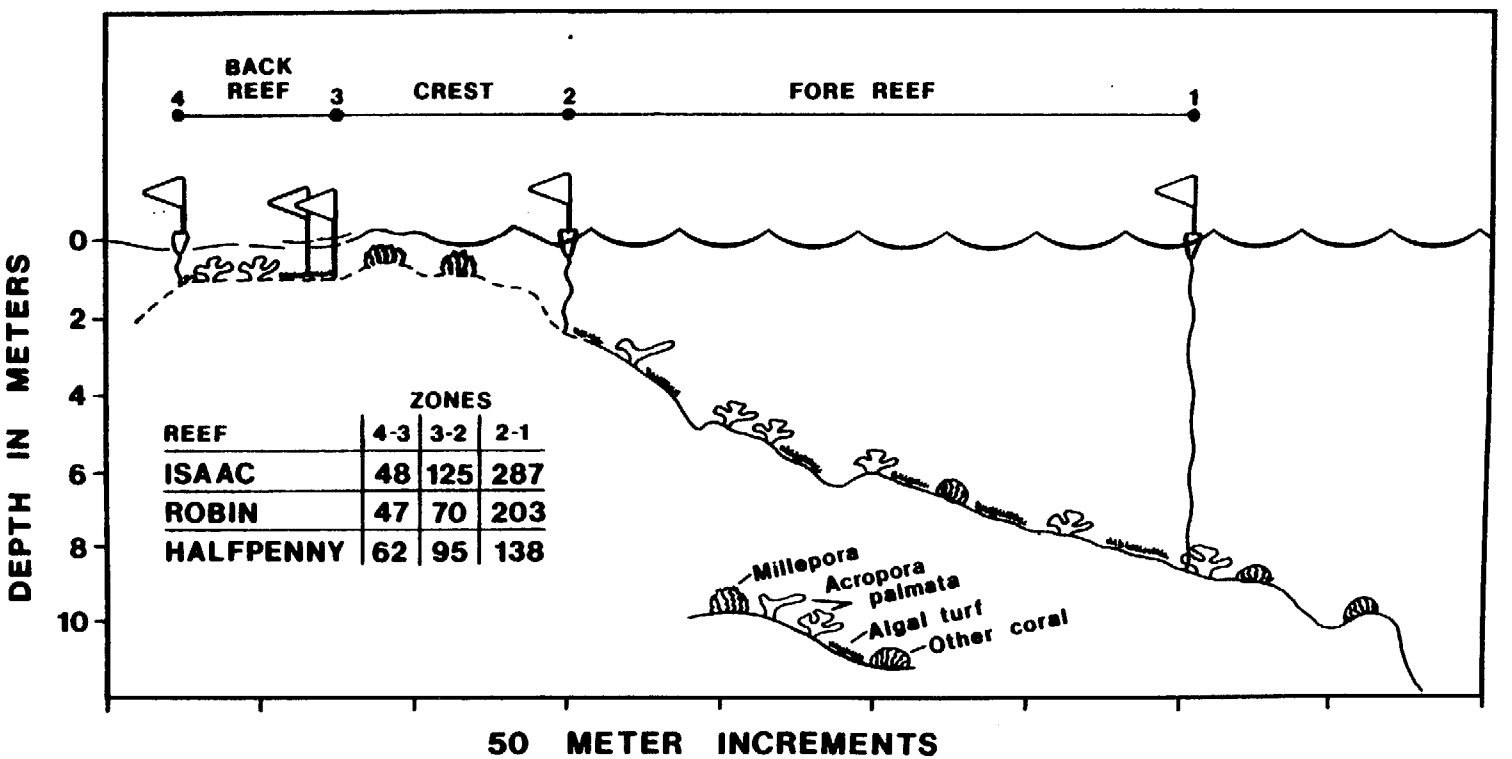

Figure 2.--Typical reef transects (Robin Reef).

Diurnal measurements of changes in oxygen concentration and water flow were taken in all seasons of the year and were used to derive rates of community oxygen production (which reflect net or apparent productivity) and consumption (respiration). Accurate measurements of discharge rates (rate of water volume flow) are crucial to this upstream/downstream method. For this, we used a Marsh-McBirney model 527 electromagnetic, x-y current meter. Water samples were taken at each transect every 2 hr over a 2- to 3-day period during each season. Particular care was taken to maximize the level of precision at every step of analysis (see Adey, et al., 1981). A plot of a typical diurnal cycle of oxygen concentration at the Robin Bay site is shown in figure 3. Standard methods of calculating production in upstream-downstream methods were employed (Marsh and Smith, 1978). Computer plotting and integration of the area under the curve above the zero oxygen production level provided net daytime primary productivity values. The area below the zero line provided respiration values.

The biotic composition (percent cover) and surface area of these reefs were determined with chain transects (methods detailed in Rogers, et al., 1982). We measured all surfaces along each transect that we could reach, except for truly cryptic habitats (nearly devoid of light). This method also gave a measure of surface area per projected square meter of bottom [m^2/m^2, called a surface area ratio (SAR)].

To examine community structure of algal covered surfaces, random Acropora palmata substrate samples were collected from both fore and back reef zones. Algal cover and distribution on the surface were mapped using grids with 1 cm squares placed over the top and bottom surfaces. Algal turfs were subsampled by scraping from 3-12 visually representative, but distinct, 1 cm^2 microquadrats. Each sample included the upper millimeter of calcium carbonate in order to sample endolithic, crustose, and tightly adherent algae. Solutions of 5% HCl and 5% formalin were used to decalcify and fix the samples. A representative subsample of the scraped algal turf samples was spread in a monolayer over a microscope slide. Species composition of algal turf communities was quantified using a "point count" technique. This involved counting the number of times identifiable algae crossed points of intersection on an ocular grid placed within a compound microscope.

At each of the reef study sites, water samples were collected and analyzed for nutrients at the beginning and end of each field session, between 1000 and 1400 hr. Standard precision handling techniques were employed at every stage, and analyses for nitrate, nitrite, phosphate, and total dissolved phosphorus were accomplished with a Beckman DU spectrophotometer. Extensive descriptions of methods and data taken during the course of this study appear in Adey, et al. (1981).

RESULTS AND DISCUSSION

Reef Productivity

The reefs studied were highly productive. Community metabolism, as shown by mean diel oxygen production at each station, and seasonal metabolism at all stations is given in figures 4 and 5. Gross primary productivity (GPP), net

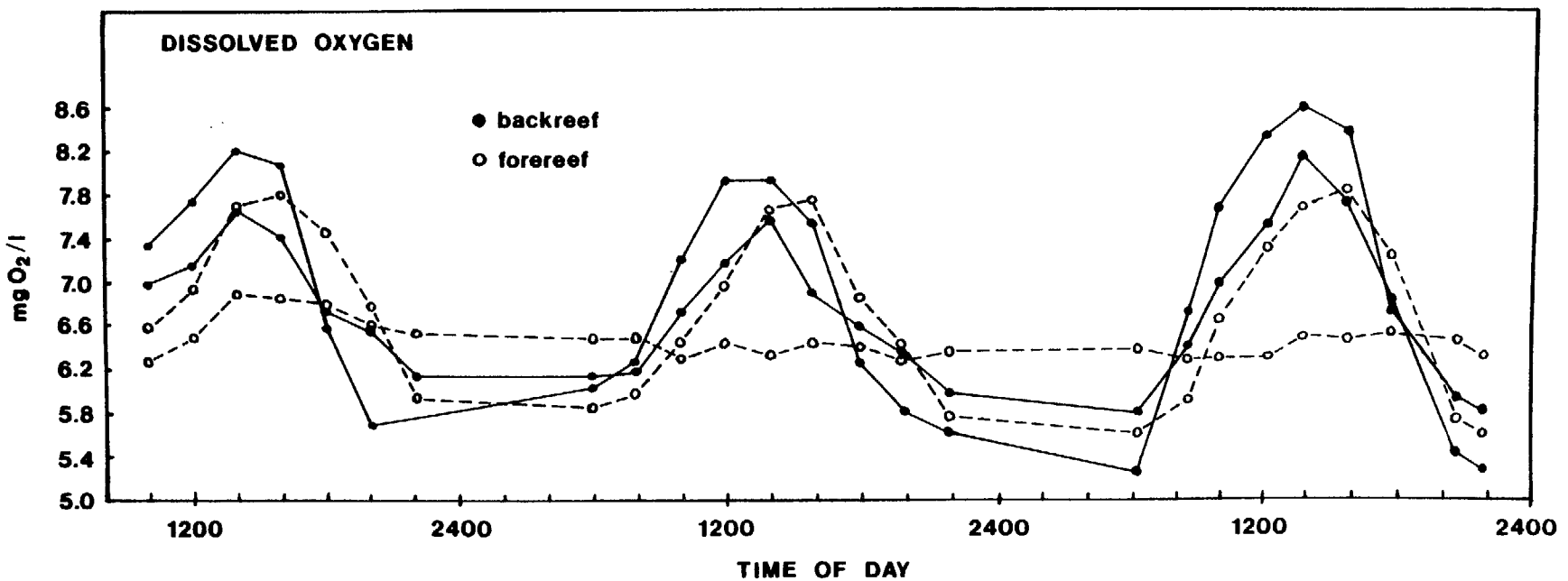

Figure 3.--Dissolved oxygen concentration across Robin Reef from 1/21/78 to 1/23/78. Numbers on individual plots refer to standard reef sites.

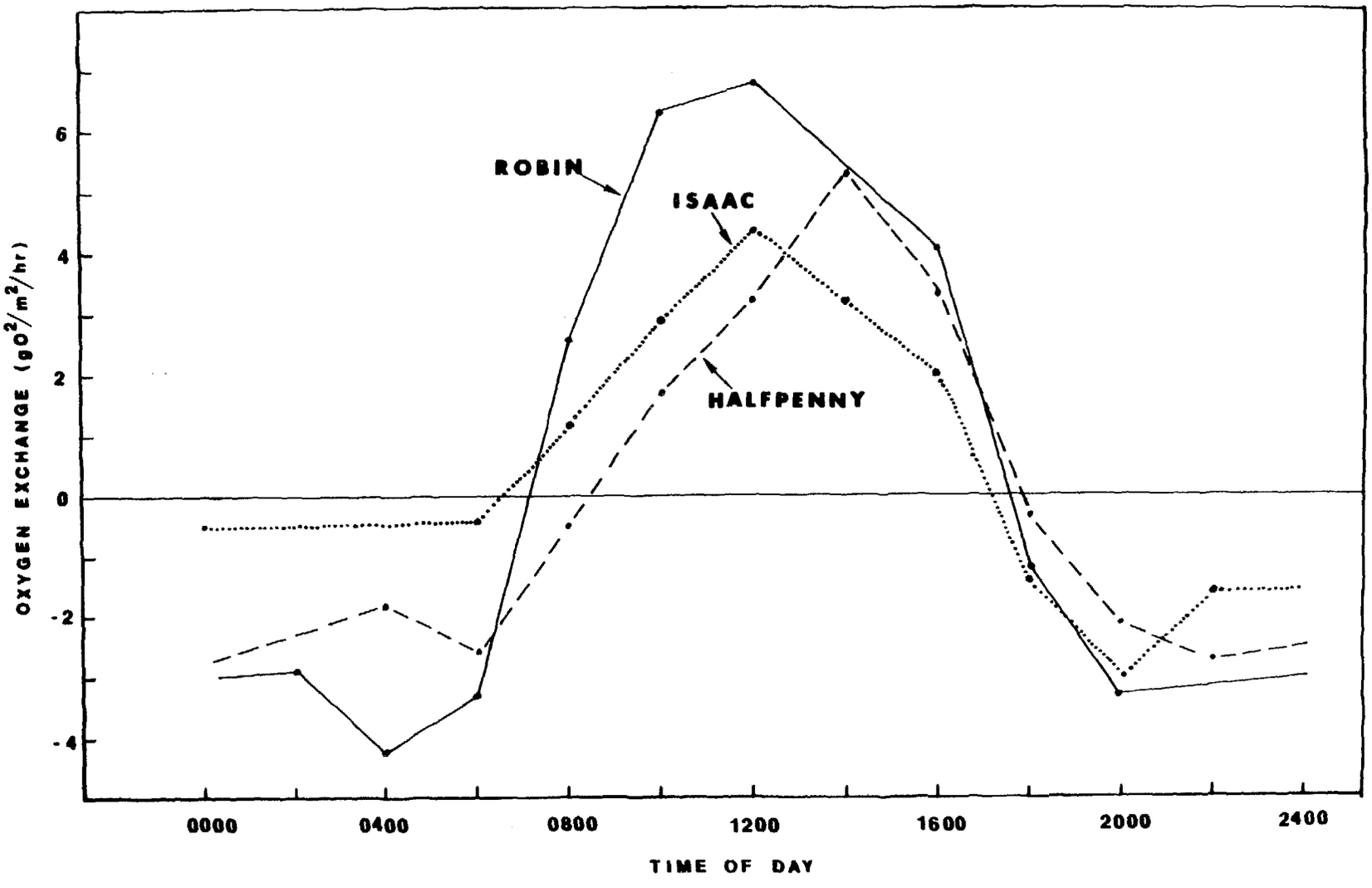

Figure 4.--Mean yearly diurnal oxygen exchange for the reef transects.

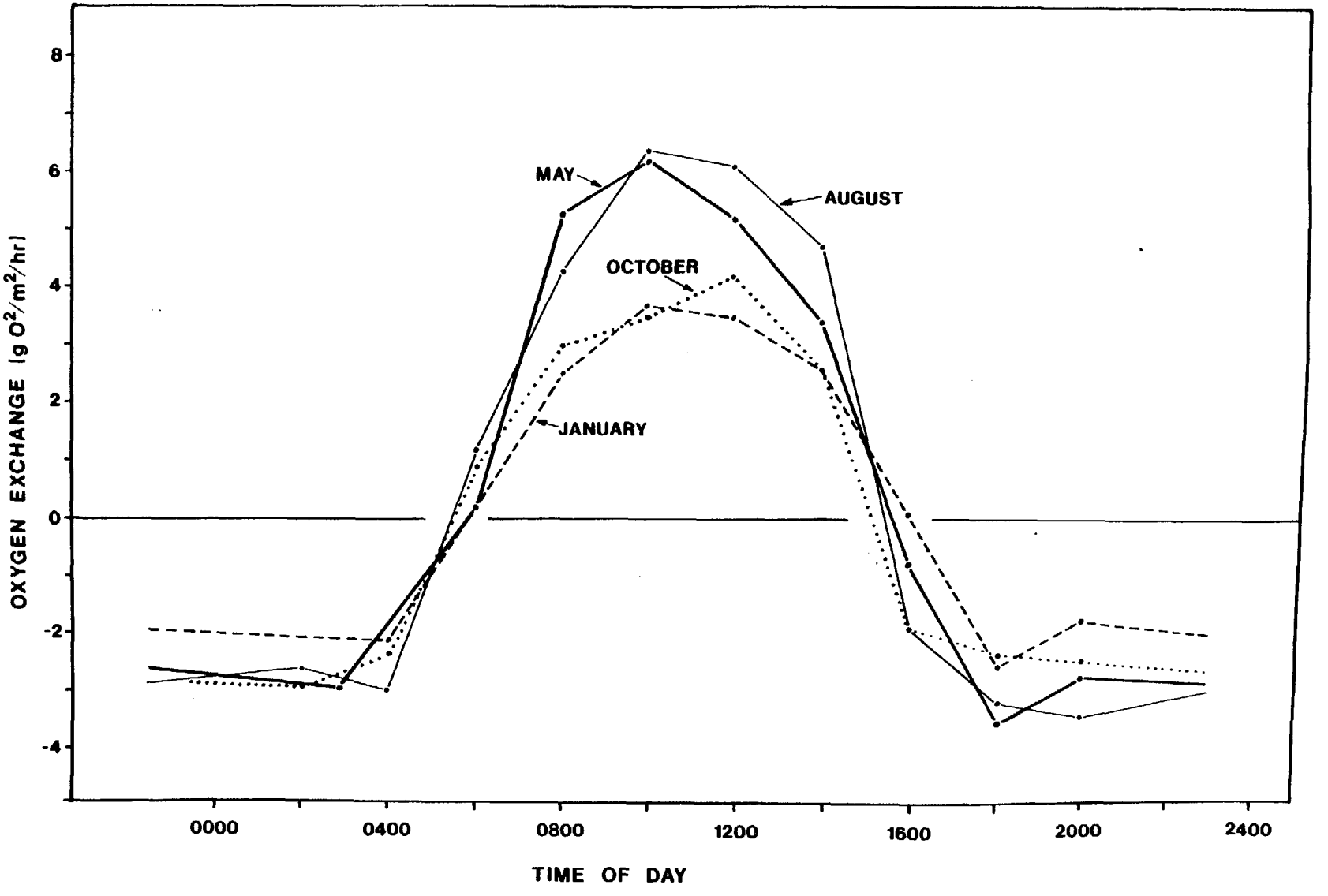

Figure 5.--Mean seasonal diurnal oxygen exchange: summary of all transects.

Table 1.--Summaries of daily metabolism.

		Gross Primary Productivity ($gO_2/m^2/day$)			Net Community Primary Productivity ($gO_2/m^2/day$)				Respiration (-) ($gO_2/m^2/hr$)	
		Fore	Back	Means	Fore	Means	Back	Means	Fore	Back
Isaacs	Jan.	10.02	36.5		6.1		23.0		0.4	1.4
	May	17.4	48.9	46.7	9.3	8.4	32.7	27.5	0.8	1.6
	Aug.	12.4	57.6		6.6		29.1		0.6	2.8
	Oct.	13.8	43.7		11.5		25.2		0.2	1.8
Robin	Jan.	14.3	56.2		9.2		28.7		0.5	2.8
	May	15.2	109.0	88.4	10.6	10.5	72.4	55.7	0.5	3.7
	Aug.	18.3	115.3		15.0		78.9		0.3	3.6
	Oct.	14.6	72.9		7.2		41.0		0.7	3.2
Halfpenny	Jan.	17.3	40.2		10.9		22.0		0.6	1.8
	May	20.4	59.8	50.9	8.1	7.9	32.0	26.3	1.2	2.8
	Aug.	17.6	64.7		3.6		32.7		1.4	3.2
	Oct.	17.5	38.8		9.2		18.5		0.8	2.02

daytime primary productivity (NPP), and respiration (R) for each reef at each season appear in table 1. Back reefs are more productive than fore reefs. A mean annual GPP of about 17.5 g $C/m^2/d$ is recorded at Isaac Reef, 19 g $C/m^2/d$ at Halfpenny Reef, and 33 g $C/m^2/d$ at Robin Reef (with a mean maximum value of 43.2 g $C/m^2/d$ recorded in August and a mean all-reef productivity of 8500 g $C/m^2/yr$). These values are based on a conversion ratio of 0.375 g C/gO_2 with a metabolic quotient for reefs of 1.1 (Marsh and Smith, 1978) applied to the means in table

1. They are derived from the molecular weight difference and the ratio of oxygen to carbon dioxide exchange (the metabolic quotient) for reefs (Marsh and Smith, 1978). Higher GPP have been reported (Helfrich and Townsley, 1963; Connor and Adey, 1977), but such high levels of productivity have been subject to question. Because of this, great care was taken in data collection, and every potentially error-producing factor has been carefuly considered (see Adey, et al., 1981). The patterns we observed are not surprising once the processes affecting reef productivity are examined.

Processes Affecting Reef Productivity

Rates of carbon fixation on reefs reflect a complex interaction of environmental factors. Slight variations in some of these factors (water depth, biotic composition, substrate availability, or solar radiation) will affect these values. In the remaining sections of this paper, we will describe the results of our studies of biological, chemical, physical, and geological factors as they affect overall reef productivity.

Biological Components: The Role of Algal Turfs

Benthic algae, as both free-living forms and endosymbionts in coral and other invertebrates, are the primary producers on reefs. The focus of our study was on free-living benthic algae because it was the most abundant biological component of the reefs we studied (see table 2). Large-scale and small-scale data were integrated to determine community structure. Large-scale cover was based on chain transects and is presented as a measure of reef complexity (SAR) for the fore and back reef of each transect in table 2. Small-scale cover is based on point counts of prepared microscope slides (table 3).

To test the hypothesis that algal turfs are the most important primary producers of the St. Croix reefs, we compared rates of turf biomass production with rates of flow respiratory production. To make such a comparison, several conversions are necessary to obtain common units of measure. All conversions involve values from either table 1 or 2, or from published literature for a similar environment. Values for each back reef will be reported in east to west order (i.e., Isaac, Robin, and Halfpenny Reefs, respectively). Algal NPP was calculated from community GPP values (table 1) by multiplying by 0.24, which is the mean NPP/GPP ratio derived from chamber studies of algae by Wanders and Wanders-Faber (1974) and Rogers and Salesky (1981). The resulting algal NPP values for back reefs are 11.2, 21.2, and 12.2 g $O_2/m^2/d$. To equate our projected m^2 of a complex reef to a surface rather than a projected area, we divided by the SAR (table 2). This gave values of 4.1, 7.1, and 9.9 g O_2/(surface)/m^2/d. Assuming that all productivity was from algal turfs, we divided the surface production values by the proportion of turf in the back reef (table 2) (values of 15.8, 19.7, and 18.5 g O_2/(planar) m^2/d. Oxygen production was converted to carbon production by multiplying by the difference in molecular weight (0.375) and dividing by the photosynthetic quotient for reefs (1.1) (Smith and Marsh, 1978), giving values of 5.4, 6.7, and 6.3 g C/(surface) m^2/d. The conversion of carbon to organic matter involves the ratio of 2.2 dry wt/g C (Westlake, 1963, and confirmed by our carbon analysis of

Table 2.--Mean depth, major benthic components (% cover), and surface area ratio on chain transects.

	Mean Depth	*Acropora palmata*	Other Corals	*Millepora*	Corallines	Algal Turf	Macro-Algae	Sand	# (m)	Surface Area Ratio
Fore Reefs										
Isaacs	6.3	18.9	7.2	5.1	8.4	40.1	10.1	8.2	16	1.87
Robin	5.1	16.2	1.5	0	8.2	65.1	0	0	13	2.36
Halfpenny	4.5	10.3	9.2	11.2	16.2	9.9	8.6	35.0	14	2.51
Back Reefs										
Isaacs	0.9	65.9	0.8	0	1.9	25.9	5.7	0	6	2.70
Robin	0.7	19.7	0	0.6	6.5	36.1	10.1	26.7	10	2.98
Halfpenny	0.3	0	8.2	0	0	53.5	8.4	29.9	25	1.23

St. Croix turfs). This means that the rates of organic matter production of 10.0, 14.7, and 13.9 g (dry)/m^2/d on actual reef surfaces (rather than projected area) are necessary to produce the rate of oxygen production we observed in the water flowing over reefs.

Tests of these theoretical rates of biomass production were supported in a recent study in similar lagoon and back reef environments of Mayaguana in the Bahamas (Adey and Goertemiller, in ms.). By harvesting algal turfs grown on screens, actual biomass production was found to be 6-18 g (dry)/m^2/d. A mean rate of 12 g (dry)/m^2/d, under a nutrient regime of 0.10-0.13 microgram-at N/l (NO_2 + NO_3) (D'Elia, in prep.), was achieved. A similar and more recent study at Grand Turk, Turk, and Caicos Islands (Peyton, *et al.*, in prep.) gave rates of algal turf production of up to 31.8 g (dry)/m^2/d at nutrient concentrations (as measured by NO_2 + NO_3 nitrogen) of less than 0.2 microgram-at N/l. Steneck and Porter (in prep.) used a similar harvest technique for turfs growing on slabs of coral substrata at a depth of 10 m and found a production rate of 6.0 g (dry)/m^2/d. These harvest production rates are minimal since they do not include losses to micro-herbivores, abrasion, leaking of dissolved organics, or the release of reproductive structures. Thus, the values we obtained using upstream/downstream flow respirometry correspond well with measured rates of biomass produced by this "functional group" of algae (*sensu* Steneck and Watling, 1982) in the Caribbean. This also supports the pattern of high rates of production (per unit biomass) for turf algae that have a high surface area to volume ratio (Odum, *et al.*, 1958; Littler, *et al.*, 1983) and, perhaps equally important, live in a strong wave surge environment.

Table 3.--Dominant algal turf genera and abundance as determined by point counts (% mean abundance top and bottom of samples). Data were generated at the species level and are in Adey, et al. (1981).

		Mean	Isaac	Robin	Halfpenny
Fore Reef	Non-Heterocysted Blue Greens	10.7	9.5	12.7	10.1
	Heterocysted Blue Greens	7.3	14.6	5.1	2.2
	Sphacelaria spp.	7.2	7.3	11.8	2.7
	Endolithic algae	7.1	7.1	5.1	9.1
	Polysiphonia spp.	3.9	2.6	3.1	6.0
	Taenioma sp.	3.8	0.7	2.1	1.0
	Herposiphonia spp.	4.4	2.1	3.6	7.7
	Lobophora sp.	2.7	3.7	4.4	0
	Jania spp.	2.5	2.4	4.2	1.0
Back Reef	Non-Heterocysted Blue Greens	18.9	18.0	20.0	18.5
	Jania spp.	10.8	8.0	18.7	5.8
	Amphiroa spp.	10.3	13.4	14.5	3.2
	Endolithic algae	3.7	2.7	0	8.5
	Gelidiopsis sp.	2.1	3.8	2.0	0.4
	Asparagopsis (Falkenbergia stage)	1.6	0.6	3.9	0.2
	Heterocysted Blue Greens	1.5	3.7	0.3	0.5
	Sphacelaria spp.	0.8	2.2	0.4	0

We found over 100 species of algae (mostly in turfs) in the course of this study. Of these, only 30-50 species were common throughout the year, and fewer than 10 were common at any site in a given season (table 3). The most consistent elements on (and in) the upper surfaces of dead coral substrata were cyanobacteria, boring algae, and filamentous red and brown algae. A high

diversity of algae in low abundance was recorded on virtually every specimen regardless of season, reef, or zone.

Cyanobacteria of 6-8 species formed a large part of the turf biomass on both fore and back reefs. Heterocysted species (particularly Calothrix spp.) are far more abundant in fore reefs than back reefs, but nonheterocysted species (e.g., Oscillatoria) were most abundant overall. Of eukaryotic filamentous algae, the brown (Sphacelaria spp.) and red (Polysiphonia spp., Herposiphonia spp., and Taenioma macrourum) species dominate fore reef substrates. Boring filaments (usually green algae, e.g., Ostreobium) were also ubiquitous. The predominant macroalgae are calcareous, articulated red algae (e.g., Jania capillacea and Amphiroa fragilissima) which are found on bottom surfaces in the fore reef and on both top and bottom surfaces in back reefs. Crustose corallines (Porolithon pachydermum and Neogoniolithon megacarpum) were most abundant in the shallow fore reefs, particularly where grazing is intense. Of the fleshy macroalgae, Lobophora variegata and Acanthophora spicifera were found but they were not abundant compared to the turf community. Minute macrophytes such as Gelidiella trinitatensis and Gelidium pusillum commonly were found in the turfs of the back reef.

As shown in table 3, the differences between fore reef and back reef turf community structure along the St. Croix reef track are rather consistent. These numbers and the community structure of the turf species we found agree with that found on a reef in Curacao by Van den Hoek, et al. (1975). With the exception of Lobophora variegata (which does not appear in Van den Hoek, et al., 1975, for Curacao) and Dictyota dichotoma (which was common in Curacao but not in St. Croix), the floras for Curacao and St. Croix are quite similar. There are also floristic similarities for the same reef zones between the Caribbean and Indo-Pacific at the genus level (Hatcher and Larkum, 1983; Sammarco, 1983).

It is beyond the scope of this study to examine the myriad of factors maintaining turf algal community structure. Most studies indicate that intensive herbivory in productive environments is important for maintaining a turf community (Borowitzka, 1981; Carpenter, 1981; Littler, et al., 1983; Sammarco, 1983; Hatcher and Larkum, 1983).

Primary Production: Not Nutrient Limited

High primary productivity on reefs growing in nutrient poor water has received considerable scientific attention (reviewed by Mann, 1982). The resulting research has focused on the role of cyanobacteria as in situ nitrogen fixing organisms (Mague and Holm-Hansen, 1975; Capone, et al., 1977). Recently, Sammarco (1983) demonstrated that fish grazing on the Great Barrier Reef can cause a shift in the community structure of turf algae from filamentous reds (e.g., Polysiphonia) to minute filamentous cyanobacteria. Other studies have demonstrated that, as a result of this change in community structure, nitrogen fixation is significantly enhanced (Wilkinson and Sammarco, 1983). Our results support their conclusions.

Heterocysted (nostocacean) and nonheterocysted (hormogonalean) cyanobacteria are abundant in turfs growing on the upper surfaces of all reefs that we

Table 4.--Nutrient levels. Each value is a mean of two replicates taken on different days over approximately a 10-day period.

Nitrate + Nitrite (ug-at/l - N as $NO_3 = NO_2$)

		Jan	May	Aug	Oct	Yearly Mean
Isaac	Fore	0.386	X	0.345	X	0.366
	Back	0.980	0.302	0.391	.772	0.611
Robin	Fore	0.294	0.175	0.549	.075	0.273
	Back	1.016	0.328	0.589	.220	0.538
Halfpenny	Fore	0.340	X	0.823	.107	0.423
	Back	0.650	0.629	0.816	.099	0.549
Channel	Fore			0.457	.150	
	Back			0.686	.130	
Airport	Fore	0.223	0.228	X	.050	0.167
	Back	0.466	0.350	X	.130	0.315
						Grand Mean
Means	Fore	0.311	0.134	.572	0.096	0.283
	Back	0.778	0.401	.599	0.270	0.512

Phosphate (ug-at/l - P)

Isaacs	Fore	0.024		0.118	0.032	0.058
	Back	0.046		0.020	0.038	0.035
Robin	Fore	0.010		0.055	0.187	0.084
	Back	0.037		X	0.047	0.042
Halfpenny	Fore	0.010		0.275	0.049	0.111
	Back	0.034		0.392	0.161	0.196
Channel	Fore				0.080	
	Back				0.030	
Airport	Fore	0.010		0.145	0.052	0.138
	Back	0.017		0.165	0.143	0.108
Means	Fore	0.013		0.148	0.080	
	Back	0.033		0.192	0.084	

studied, but particularly on fore reef and sand substratum habitats of Isaac Reef. Results of nutrient analyses for nitrate plus nitrite and phosphate are listed in table 4. The nitrite and nitrate concentration strongly increases in the water as it flows over the three reefs studied. Ten of the twelve sets of measurements showed a highly significant yearly increase of 0.35-0.57 microgram-at/l across the reef. With a mean yearly flow rate of 6.83 m^3/min/m for all three transects (discussed below), this translates to a net "fertilization rate" of 0.82 kg N/hectare/d (or 0.08 g N/m^2/d). While this is roughly half the rate estimated by Wieb, et al. (1975) for Eniwetak, the maximum rates we encountered on the south shore reef of St. Croix were three times the mean.

We assume that this fertilization is due to nitrogen fixation by cyanobacteria (Wilkinson and Sammarco, 1983), but other possibilities exist. Regeneration of nutrients from the internal cavity of a reef was demonstrated by Andrews and Muller (1983). However, this is unlikely to occur on St. Croix reefs, since the coral of these reefs grows on a pavement, below which the reef structure is remarkably tight, with cavities usually sand filled (Adey, 1975; Adey and Burke, 1976). Empty cavities for nutrient regeneration are rare in St. Croix, which is arid, devoid of rivers, and lacking in upwelling aquifers. Thus, nutrient enrichment from ground water, such as that described in Jamaica (D'Elia, et al., 1981) is unlikely. Nitrogen fixing algae may achieve a competitive advantage in more oligotrophic waters, and thus nutrient availability probably has some significance in determining community structure. Nevertheless, the fact that this "excess" nitrogen escapes from the reef and flows over the highly productive back reef suggests that primary production on the reef proper is not nitrogen limited.

Phosphorus is more problematic, since an atmospheric source is not possible. Reactive phosphorus as phosphate can be difficult to measure and, as briefly discussed above, older work did not generally show any consistent pattern of change in reef environments. A recent paper by Atkinson (1982) does show significant upstream-downstream depletion of phosphate across 1000 m of reef flat in Hawaii. However, in our St. Croix situation, with a mean incoming concentration of 0.084 microgram-at/l and a mean current flow of 6.83 m^3/min/m, phosphorus as phosphate is delivered to a meter width transect of reef at a rate of about 25 g/d. Even if all net primary productivity were to be exported from these reefs, using a C/P of 430 (from Atkinson and Smith, 1983, for turfs), only about 6.4 g P/d/meter width would be removed. Thus, phosphorus is present in large quantities, though at low concentrations, from the constantly inflowing waters of the North Equatorial Current as it impinges on St. Croix.

Epibenthic Water Flow and Discharge Rates

Nutrient availability, gas exchange, and metabolite release for aquatic primary producers is facilitated by water flow past algal thalli. Water flow over reef substrata (epibenthic water flow) is dependent upon the discharge rate (movement rate per volume of water), water depth, and on the wave surge or oscillation rate of the overflowing water. In St. Croix, water movement over the reefs results primarily from wind-driven wave energy. Thus, measured rates of epibenthic water flow have geologic (depth) and geographic (wind) components.

Epibenthic flow rates over reefs are variable in space and time. These variations can affect both the productivity of the reef and the measurements of

it. For these reasons, great care was taken in determining water flow and discharge rates (this information is provided in detail by Adey, et al., 1981). Our measurements of water motion demonstrate that water flowing over the reefs oscillates but has a net shoreward flow. Typically, we recorded a landward surge of 6-8 s duration (reaching speeds of about 0.3-0.6 m/s) and a reverse surge lasting 2-4 s (reaching 0.05-0.3 m/s). Net epibenthic water flow was determined from chart recordings of mean maximum currents in both directions (i.e., the peaks of spikes) integrated over 1 hr intervals from Marsh-McBirney current meter data. Reversing wave surges and accompanying turbulence produced by waves breaking over irregular reef surfaces mix the water flowing over the reef, particularly for back reef habitats where measured rates of production are the greatest. The turbulent effect of wave surges also significantly increases metabolite exchange and resulting photosynthesis and growth (Hackney, et al., in ms.).

Epibenthic flow rates increase dramatically from fore to back reef. Means for all reef transects were 1.2 $\pm$ 0.066 m/min for fore reefs and 11.0 $\pm$ 3.5 m/min for back reefs. This increased flow rate results from the progressive shallowing from fore reef (overall mean depth of 5.3 m) to back reef (overall mean depth of 0.6 m). With a constant discharge rate, flow rate varies with depth. Since depth changes daily with tidal changes, we recorded tidal heights during each sampling period.

Discharge rates are not constant because wind-induced water movements change geographically along the south shore of St. Croix due to the island's effect of diminishing the strength of easterly trade winds. Specifically, in the fore reef environments, Isaacs Reef to the east has the highest discharge rate (mean 8.1 m^3/min/m, range 2.5-12.1 m^3/min/m, N = 65 1 hr intervals). Robin Reef is intermediate (mean 6.2 m^3/min/m, range 2.8-9.8 m^3/min/m, N = 86 1 hr intervals), and Halfpenny Reef is the lowest (mean 5.3 m^3/min/m, range 1.4-9.8 m^3/min/m, N = 79 1 hr intervals). These discharge rates created mean back reef epibenthic flow rates of 9.2, 8.8, and 15 m/min/m, respectively. Although a geological pattern in exposure from east (most exposed) to west (least exposed) results in a similar pattern of decreased discharge rates, the magnitude is much less than the difference observed between back reef and fore reef at any one location.

There is little support for the hypothesis that reef productivity is controlled by water motion even though differences in flow rates between fore and back reefs roughly correspond with differences in rates of production. If reef productivity was primarily dependent upon water flow, diurnal reef productivity curves (figs. 4 and 5) would level off at the point where light saturation occurred rather than corresponding closely with variations in light intensity (discussed below). Also, for any given reef, productivity would correspond with data on water currents, which we did not observe. Water motion is an important factor, but the south shore of St. Croix is characterized by consistently high wind-induced wave energy year round (see Adey, 1978b); thus, water motion does not appear to limit productivity. Note that there is no relationship between reef productivity (table 1) and epibenthic flow rates.

Light

Primary production on the reefs we studied is most likely controlled by light. Evidence for this comes from the correspondence between diurnal and seasonal cycles in light intensity (fig. 6) and measured rates of primary

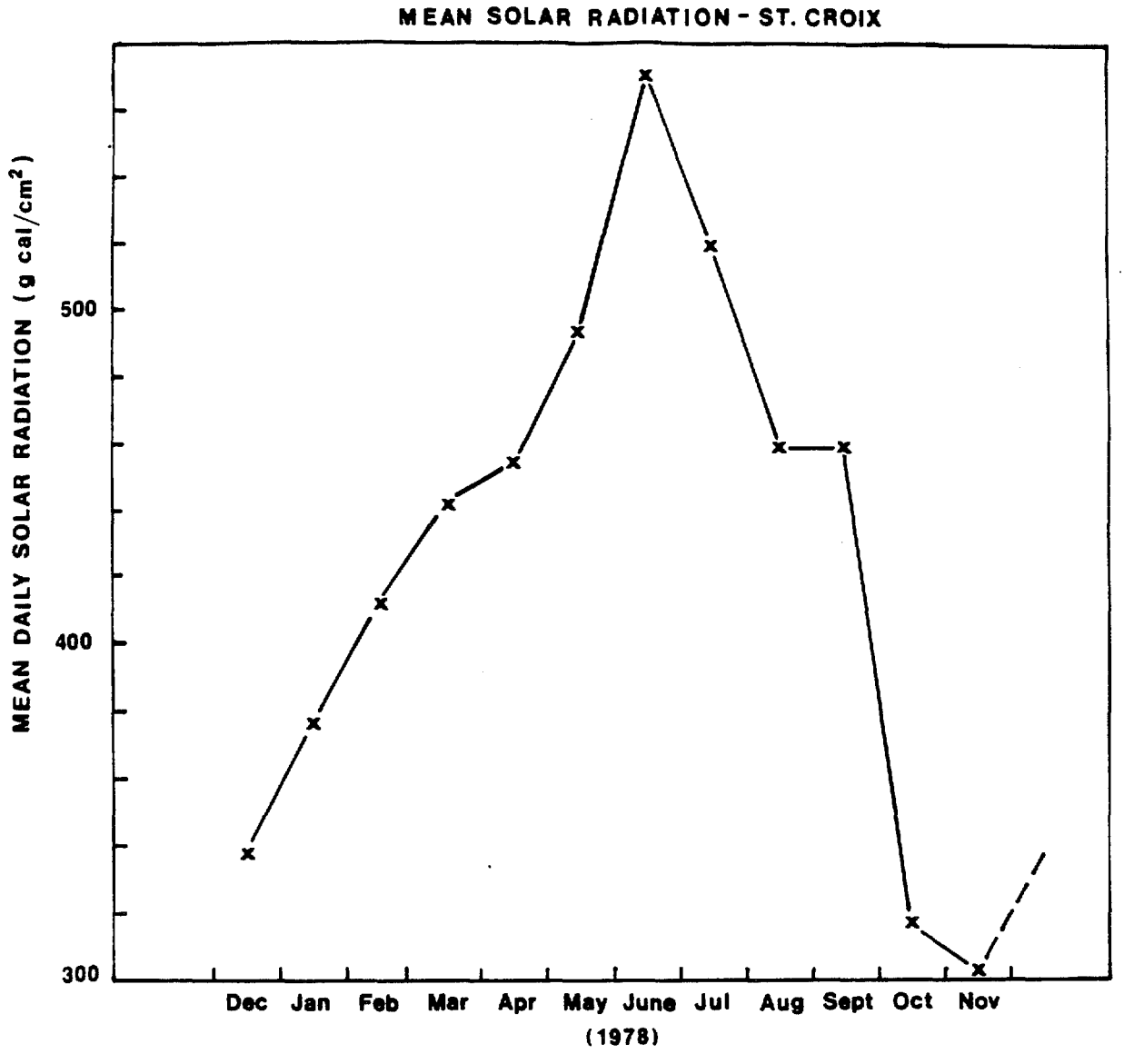

Figure 6.--Monthly means of daily solar radiation.

production (figs. 3, 4, and 5). If any other environmental factor was limiting, the rate of oxygen production would level off, indicating light saturation. In contrast to our field measurements, most studies using enclosures, even with stirring, commonly report light saturation. This is likely an artifact of insufficient water motion. In more recent work with chambers (e.g., Carpenter, in ms.), where efforts have been made to simulate surge motion, this lack of light saturation for algal turfs is repeatedly demonstrated.

In this investigation, daily solar radiation levels were recorded with a pyroheliometer (see fig. 6 for monthly mean values). During our study we sampled two periods of high light intensity (May and August) and two periods of lower light intensity (January and October). Averaging hourly production rates

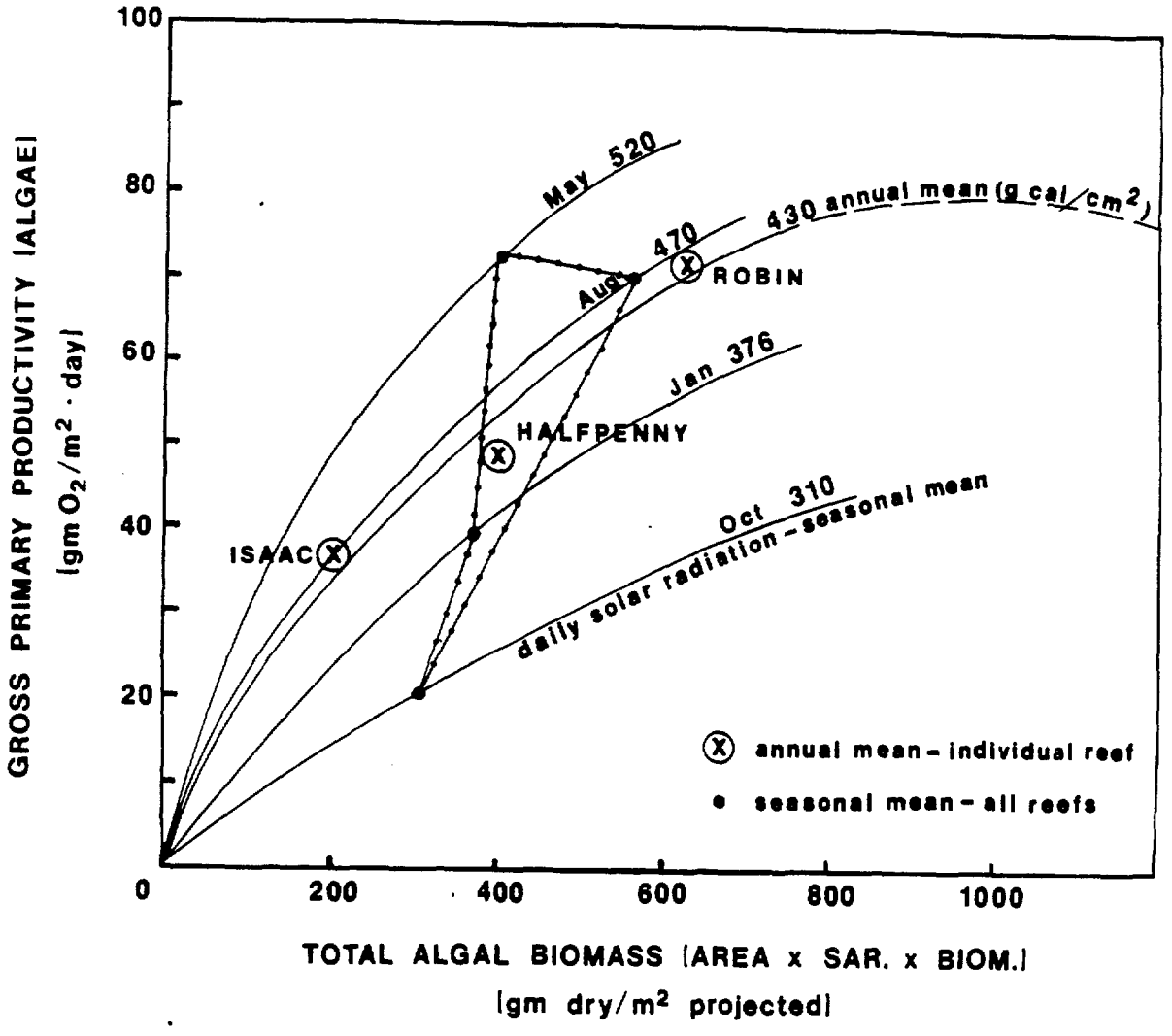

Figure 7.--Back reef: Gross primary productivity as a function of total algal biomass and monthly solar radiation

for all reefs reveals a strong seasonal pattern in productivity corresponding to these seasonal differences in light intensity (fig. 5). Although the seasonal decrease in primary productivity roughly corresponds to a 40% reduction in light during that period, the relationship is not exact, since the GPP in October is reduced to only 30% of that value in May. A better correspondence exists between the seasonality of primary production and the combination of algal biomass and solar radiation. Loss of light in autumn is exacerbated on St. Croix by a higher frequency of rainfall and cloudiness. Thus, incoming light in October and November is considerably below that of December and January (fig. 6).

The GPP data, when plotted directly against total algal biomass (per projected m^2, fig. 7), suggests that a weak relationship between productivity and total biomass exists on these reefs (note that this is not surface biomass alone, but includes the effects of SAR and percent cover of algae). Also, the

plot of biomass as a function of seasonal productivity (line with closed circles, fig. 7) indicates a cyclic pattern. The sharp reduction in algal biomass recorded in the fall of 1978 (45% of that recorded in May) cannot be attributed to wave action, since that is generally a quiet season and no unusual conditions were experienced during the period of study. Data for nutrients (table 4) and suspended matter (Adey, et al., 1981) suggest very minimal effects of runoff on the reefs. We observed, but did not quantify, changes in the abundance of micrograzers (amphipods and worms). It is possible that during the spring and summer algal biomass and the resident micrograzers increase with higher levels of solar radiation. As light levels fall in autumn, grazing by the resident micrograzers exceeds rates of algal growth. Such overgrazing could result in a "crash" in both algal biomass and productivity.

Geological Control of Reef Productivity: Synergy of Multiple Factors

It is to be expected that those reefs which are less complex (lower SAR), deeper, with lower epibenthic water currents, and have a larger percentage of living stony coral (relative to algae) will be less productive than the shallow, complex, algae-dominated reefs of the south shore of St. Croix. All of these factors, however, are ultimately the result of the reef's geological history, and thus the relationship between reef morphogenesis and primary production should be considered.

The south shore bank barrier reef system of St. Croix "matured" (i.e., reached sea level) from west to east (see Adey, 1975; Adey and Burke, 1976, for a summary of the geological history of the reefs of St. Croix). Isaac Reef is relatively young and is just reaching sea level today. Its live Acropora palmata cover is high (table 2), but its reef flats are narrow and the crest is broken (forming numerous channels). Robin Reef is more mature, as evidenced by its nearly continuous crest and wide, relatively shallow back reef. While living Acropora palmata is still an important constituent, the percent cover of A. palmata on Robin back reef is less than a third of that found on Isaac back reef (table 2). Halfpenny Reef is older and has a continuous crest and a very shallow reef flat with very few living acroporids. The age difference between Isaacs and Halfpenny Reefs is about 500-1,000 yr.

Productivity on the young Isaac Reef is low, even though its SAR is quite high. This is because coral is less productive than algae per unit of surface area (Rogers and Salesky, 1981). At the other extreme, coral cover is low at Halfpenny Reef, and this shallow reef flat is dominated by turf algae. However, this reef is nearly planar (the SAR is half that of the other reefs), and thus the surface area available for turf photosynthesis is proportionately reduced.

Because carnivorous predators are so abundant on reefs, herbivores do not stray far from their refuge in the spaces within the reef (e.g., Ogden, et al., 1973; Talbot and Goldman, 1972). Thus, reefs with a high SAR are more heavily grazed because they have more habitat space for reef-dwelling herbivores. In this way, geological events that contribute to a high SAR on reefs also maintain herbivore populations that intensely graze the dead coral substrate, thereby maintaining the turf communities.

Light levels, depth, current velocity, and abundance of live Acropora palmata all increase with geological time as a reef grows toward sea level. As it reaches the surface, several of these trends reverse (i.e., coral dies and water flow decreases). Aspects of this complex relationship between reef morphogenesis and primary productivity can be seen along the south shore of St. Croix. For example, productivity was greatest for the mature Robin Reef and lower on the younger Isaacs and older Halfpenny Reefs (fig. 7). On Robin Reef, the SAR of primarily dead Acropora palmata is very high and algal cover is about 80% greater than that of Halfpenny. Thus, peak productivity probably occurs soon after the transition from a live, coral-dominated reef to one of equal surface area but dominated by algae. With time, productivity declines as destructive forces (e.g., bioeroding sea urchins or severe storms) reduce the standing dead coral to a pavement-like algal-dominated flat. This pattern of reef succession is characteristic of many reef systems. Adey, et al. (1977) described a similar history for the now largely planar algal dominated pavement in eastern Martinique. Over the past 500 yr the open Acropora palmata reef matured and lost its structure, possibly due to a catastrophic event such as a hurricane. It has remained an algal pavement, devoid of coral, ever since. In the case of Martinique, excess sediment and nutrient runoff from the island following the introduction of intense sugar cane farming in the 17th century undoubtedly was a major factor in transforming these reefs into macroalgal pavements. After the completion of this study in 1978, a similar event occurred at the south shore of St. Croix when a hurricane passed off the coast in 1979. Rogers, et al. (1982) documented the event and showed a significant reduction in SAR and live coral following the hurricane.

Differences in reef morphogenesis may be responsible for some of the reported differences in reef productivity. Holocene sea level characteristics for the Indo-Pacific differs from that of the Caribbean. Sea level rise stopped over 5,000 yr ago in the Indo-Pacific (reviewed by Adey, 1978a), resulting in the characteristic old reefs of the region having emergent, broad reef flats (many km wide), often with no epibenthic water flow during low tide and with a low SAR. This extreme "old age" condition of Indo-Pacific reef flats, developed under stable or dropping sea levels, contrasts with conditions in the Caribbean, where sea level has been slowly rising until the past several centuries (e.g., Adey, et al., 1978a). This geological characteristic of reefs could be responsible for the lower levels of primary production reported for the Indo-Pacific compared to results presented here for the St. Croix reefs.

CONCLUSIONS

Fundamentally, reef productivity is controlled by its geology (reef growth and morphogenesis). Coral reefs grow slowly towards sea level over time, thereby changing their physical, chemical, and biological environment. Primary productivity is maximal at the time when the reef surface is becoming too shallow to support a large cover of live coral but still deep enough for continuous water flow. Dead branching coral (Acropora palmata) in standing position provides a complex and convoluted substratum on which minute algal turfs can grow and herbivores can take refuge. The structurally complex reefs maintain a high biomass per projected area of reef, thereby increasing the total turf

biomass. The intense grazing maintains the algal community at the turf stage, wherein the productivity per unit biomass is very high.

Facilitating this high productivity are nitrogen fixing cyanobacteria that fix more nitrogen than is required by even the most productive reef zones. Other nutrient requirements, particularly phosphorus, are met by the combination of continuous and strongly flowing equatorial currents as well as by constant wave-driven currents. This, with the lower phosphorus requirements of algal turfs, results in a highly productive community that is not limited by nutrient availability.

Thus, synergy is attained by the interaction of factors that optimize reef productivity. If any factor is removed from this system (i.e., water depth, SAR, wave oscillation, water flow, or algal community structure), the primary productivity would be less than we found.

The back reefs we studied are among the most productive biological communities in the world. Using standard conversions, our measurements of a mean annual gross production of about 23 g $C/m^2/d$ and a net production of about 14 g $C/m^2/d$ exceed the theoretical maximum gross productivity hypothesized by Ryther (1959) of 17 g $C/m^2/d$ and the net productivity of 12.3 g $C/m^2/d$. On the other hand, this is not unreasonable, since maximum experimental rates of net production of 22-31 g (dry)$/m^2/d$ (approximately 9-12 g $C/m^2/d$) have now been found in both laboratory and field environments. Limitations to primary production due to desiccation, nutrient availability or gas exchange (Lieth and Whittaker, 1975) are nonexistent or of reduced importance on the reefs of St. Croix. Thus, productivity of these reefs seems to be limited by the ultimate limiting source: incoming solar radiation.

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STUDIES ON THE BIO-OPTICS OF CORAL REEFS

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ABSTRACT

This paper examines the possibility of using underwater light measurements to study the primary productivity of coral reefs. This is a new technique that may have wide ranging uses as man begins to use remote sensing to study the processes taking place on the surface of the Earth.

INTRODUCTION

Sunlight is the primary source of energy for the coral reef ecosystem. Photosynthetic reef organisms utilize light to liberate oxygen from water, fix carbon, and enhance the rate of calcification. This paper will examine the concept of using bio-optical techniques (Smith and Baker, 1978a; Gordon, et al., 1980) to measure the input of light energy to coral reef ecosystems. The simplicity of the technique, combined with nondestructive sampling, may enable reef ecologists to study the productivity and flow of energy into coral reefs at a higher level of ecosystem organization than is presently possible. In addition, it is of interest to understand the entrance of energy into these benthic ecosystems since many reef organisms may be termed polytrophic (Muscatine and Porter, 1977), and because the structure and dynamics of the primary production trophic level may have an influence on the structure and/or organization of subsequent higher trophic levels. Understanding the optics of coral reefs also holds the promise of one day being able to study these complex and remote ecosystems from orbiting spacecraft and other remote sensing platforms.

Investigators have long sought a technique that would quantify the primary productivity of coral reefs. For the most part, estimates have been made using respirometry and/or radiotracer experiments which have been extrapolated to the areal extent of the reef (see part III in Stoddart and Johannes, 1978, for review). While these techniques usually are precise, they are subject to errors in scale which arise from extrapolating data from an experimental specimen to the reef community. Another way to estimate primary production is to measure the input of light energy to the system over a relatively large area of substrate. Then, using known and theoretical estimates of the quantum efficiency for photosynthesis, it should be possible to estimate primary production on a scale commensurate with the scale of the reef ecosystem.

The initial step in primary production is the harvesting of light by the photosynthetic pigments of the primary producers (Rabinowich and Govingee, 1969). This process is a function of the available light, both spectral quality and intensity, and the absorption characteristics of the algae. The absorption and reflectance of light by phytoplankton also can be influenced by the nutritional state and age of the alga (Kiefer, 1973; Kiefer, et al., 1979;

Wilson and Kiefer, 1979). Present models that describe the light-limited growth rate of cultured phytoplankton have been formulated using the estimated quantum efficiency of photosynthesis and the cellular cross sectional area for light absorption (Laws and Bannister, 1980; Kiefer and Mitchell, 1983). The formulation of similar models for coral reefs might provide estimates of primary production that would be applicable to different reef systems, habitats, or zones on a scale that is commensurate with the scale of these ecosystems. Formulation of such models requires the ability to make reliable estimates of light reflectance and absorption for the reef community.

Morel (1978) defined a measure of light absorption termed Photosynthetically Useable Radiation (PUR). PUR defines the fraction of Photosynthetically Available Radiation (PAR) that a photosynthetic organism can absorb and have available for chemical work. PUR is the integrated product of normalized cellular spectral absorption and the spectral irradiance available to the organism (Morel, 1978). Measures of PUR are relative measures, though, and cannot be related to an absolute measure of the quantity of light being absorbed. However, much can be learned by comparing the relative light absorption of photosynthetic organisms from different light environments.

Calculations of PUR for isolated zooxanthellae from the reef-building coral Montastrea annularis (Ellis and Solander) have shown that the fraction of light absorbed varies at different depths, suggesting that the capture of light energy by these zooxanthellae varies as a function of the available light field (fig. 1; and Dustan, 1982).

METHODS

Optical oceanographers have developed precise terminology that describes the behavior and measurement of light in the underwater environment. Spectral irradiance is defined as the spectral components of the light field that impinge on a flat-plate, or cosine collector. Across each horizontal plane in the hydrosol are upward and downward flowing flux defined as upwelling and downwelling (Tyler and Preisendorfer, 1962; Gordon, et al., 1980). The ratio of upwelling to downwelling is termed spectral reflectance and is the basis for the measurement of remotely sensed optical signals (Gordon, et al., 1982; Smith and Baker, 1978b). The difference between upwelling and downwelling at the surface of a substrate is the amount of light that is absorbed by the substrate. It is presently impossible to directly measure the upwelling irradiance close to the substrate because the shadow of the instrument alters the light field. However, the upwelling and downwelling irradiance at the reef substrate can be estimated by taking sets of upwelling and downwelling measurements above the substrate. From these data, the diffuse attenuation coefficient for spectral irradiance is calculated, and this quantity is used to calculate the light intensities at the surface of the substrate (Smith and Baker, 1978b). These derived data will vary with water depth, species absorption properties, and the ambient light field. Thus, measurements must be taken throughout the daytime period and at systematically varying depths to use these measurements as an index of light energy absorption and a community-specific spectral absorption signature. At this time, we do not fully understand the relationship between this derived measure and the actual amount of light absorbed by photosynthetic reef organisms, but, as a first approximation, the measure represents a maximum value which includes

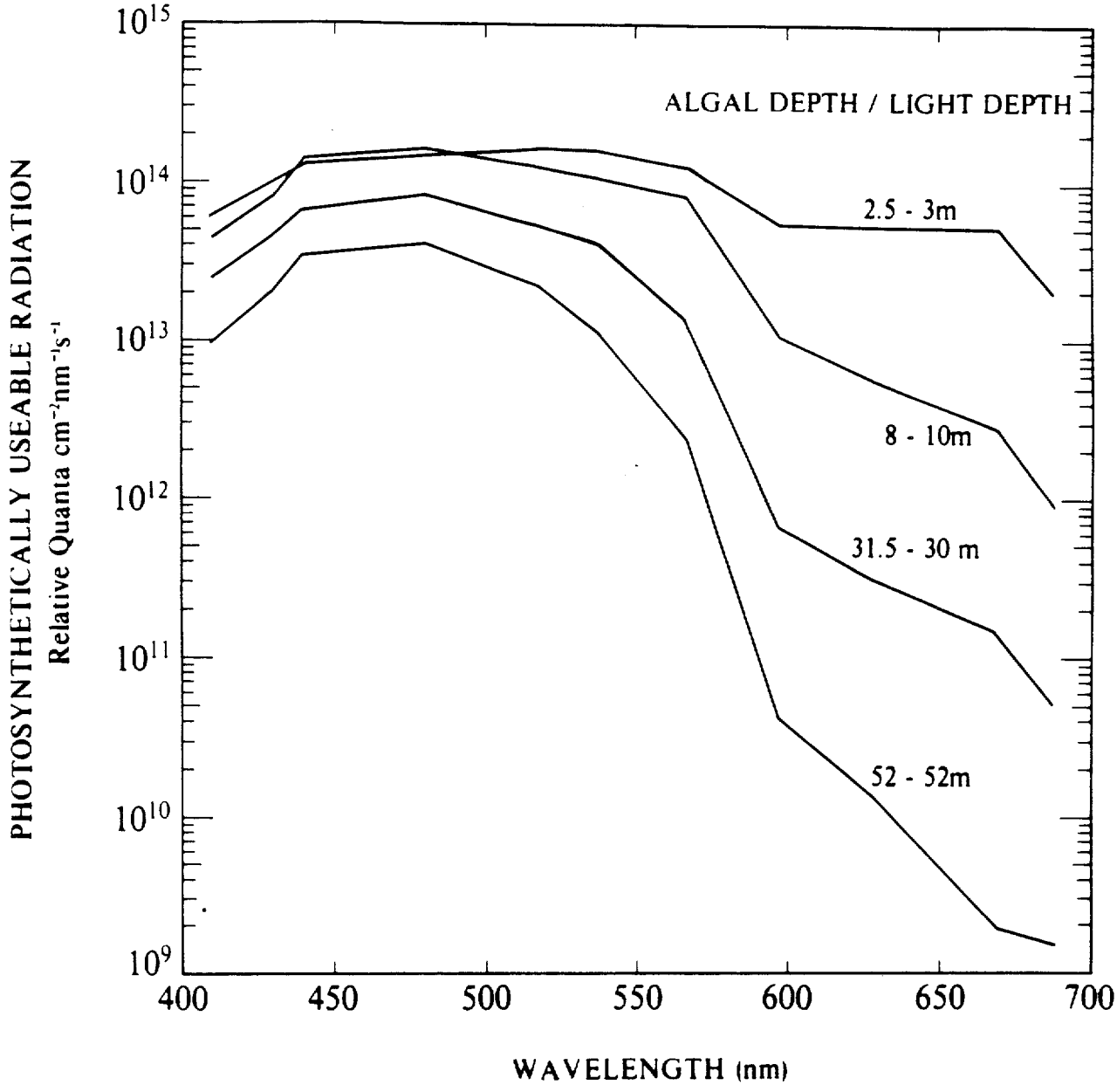

Figure 1.--Photosynthetically Useable Radiation of zooxanthellae isolated from Montastrea annularis, Discovery Bay, Jamaica. Relative whole cell absorbance was measured at low temperature with a modified Cary 14 spectrophotometer. Measurements of underwater spectral irradience were made with a prototype spectroradiometer. Note that the algae from different depths vary with respect to their absorbance of light energy and its spectral quality (see Dustan, 1982, for experimental details).

the absorption of light by both animals and plants. As such, the data will overestimate actual primary production until the measure is more fully understood and the model appropriately refined.

Table 1.--Preliminary calculations of light energy absorbed by a coral reef community. Surface PAR light levels averaged 1.47×10^{17} quanta/cm^2/s during the experiment. Measurements were carried out on Dancing Lady Reef, Discovery Bay, Jamaica, W.I.

Depth	Substrate	Calculated quanta Absorbed (q/cm^2/s) (400-700 nm)	Percent of Incident Downwelling PAR (400-700 nm)
10 m	sand	2.679×10^{16}	87.0
	coral	2.429×10^{16}	92.7
30 m	sand	7.42×10^{15}	68.0
	coral	1.08×10^{16}	95.7

FIELD STUDIES

In 1978 we developed a small submersible spectroradiometer to study the photobiology of zooxanthellae (Booth and Dustan, 1979). I used the instrument to characterize the light field on Dancing Lady Reef, Discovery Bay, Jamaica, with special emphasis on the photobiology of Montastrea annularis, one of the principal reef-building corals on both the deep and shallow reefs of the region (Dustan, 1982). As part of this study, I made systematic measurements of upwelling and downwelling irradiance and reasoned that it might be possible to measure the amount of light energy that the reef community "absorbs." In this experiment measurements were taken over sand, which was reasoned to be an almost perfect reflective surface, and over areas covered with living coral (see table 1).

The calculations suggest that corals resemble black bodies in their absorption properties in both shallow and deep water environments. Reef sand is not a very good reflective surface, as I had first thought, but does absorb a smaller fraction of the incident light than corals. The difference in absorption between coral and sand is greater in deep than shallow water, possibly suggesting photoadaptive or geometric change in the members of the coral community. The percentage of incident light absorbed by both substrates seems high, but since a reference of known standard reflectance was not used to "calibrate" the methodology, the degree to which light scattering and other possible nonlinear effects may distort the data is unknown. In addition, the sandy environment of coral reefs contains a variety of photosynthetic organisms, each with its own particular light absorption characteristics.

A second set of spectroradiometer measurements was made in August 1982 on the Molasses Reef in the Key Largo National Marine Sanctuary, Florida. Spectral measurements were taken with a 15 channel spectroradiometer (Biospherical Instruments Mer-1015) during a research expedition in support of remote sensing of coral reefs (P. Dustan, C. R. Booth, and A. R. Hibbs, unpub. data). Data from a sandy zone on Molasses Reef gave a net absorbance of 1×10^{14} quanta/cm^2/s which was 51% of the downwelling irradiance at the substrate surface (fig. 2).

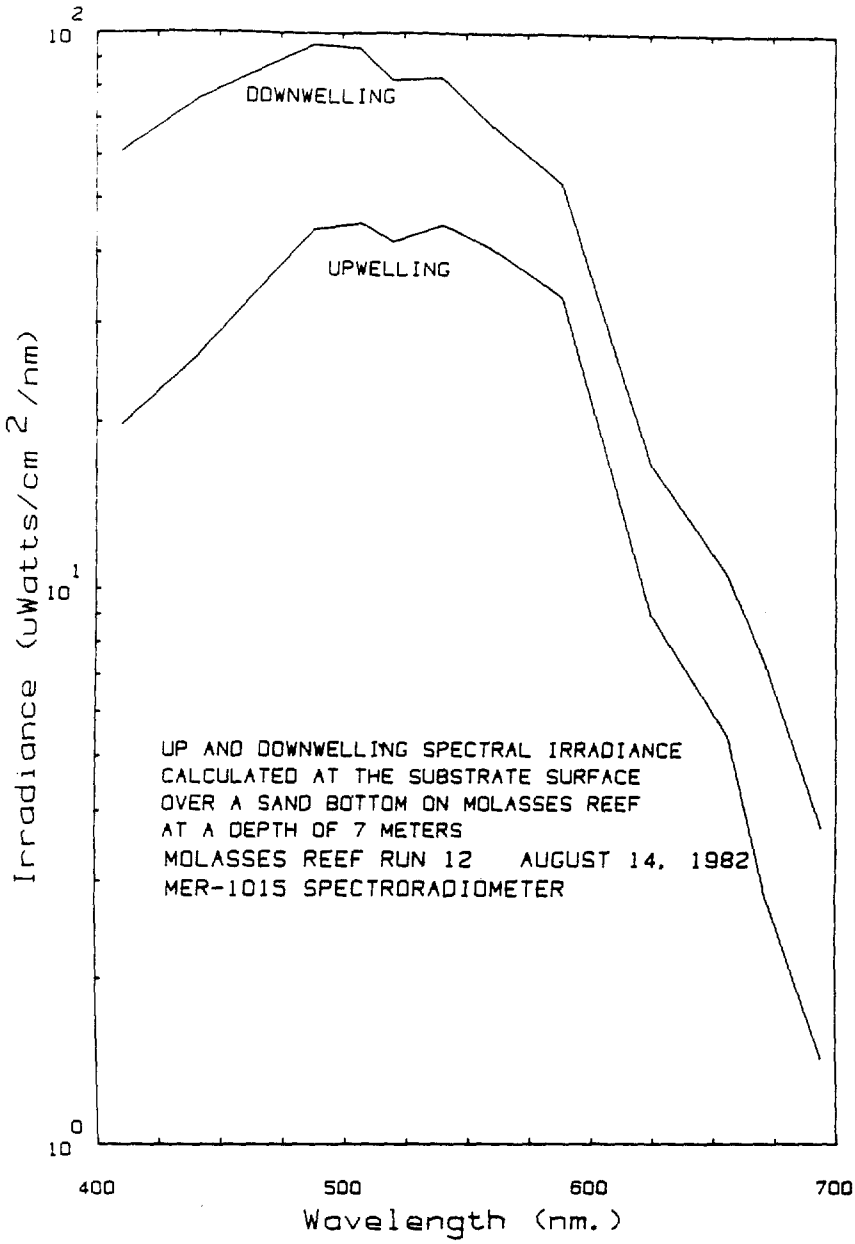

Figure 2.--Calculated upwelling and downwelling spectral irradiance at the substrate surface of a sandy area 7 m deep on Molasses Reef, Key Largo. The difference between upwelling and downwelling irradiance equals the light absorbed by the substrate (1×10^{14} q/cm^2/s). Scans were calculated from sets of spectral irradiance data as described in the text.

This fraction is somewhat higher than the earlier data from Jamaica but is within a range that could be considered acceptable, since the technique is in an early stage of development.

Similar measurements made over a nearby grove of living coral on Molasses Reef revealed somewhat different and unexpected results. The values for

upwelling spectral irradiance did not follow the expected pattern of exponential decrease with depth. As the instrument approached the coral, the spectral distribution of the upwelling irradiance showed a decrease in the blue and green regions of the spectrum but an increase at wavelengths greater than 589 nm. Particularly striking was an increase in the far red at 694 nm (fig. 3). The total integrated quanta in each scan follows the rule for conservation of energy and decreases with depth. The increase in the signal between 589 and 671 nm results from reflectance of the yellow brown coral, which begins to "dominate" the spectral irradiance signature. The far red signal may be interpreted as an emission of red light due to algal fluorescence, as has been seen in oceanographic measurements of spectral irradiance (R. C. Smith, C. R. Booth, and P. Dustan, unpub. obs.). The intensity of the signal increases as the instrument approaches the coral (depth approx. 4.4 m), suggesting that the fluorescence may emanate from the zooxanthellae in the tissues of the coral. These findings complicate the calculation of an energy absorption budget for the coral, since the organism is simultaneously absorbing and emitting light and each process is functioning with its own wavelength dependency. However, the results suggest that we may have uncovered a measurable parameter that may one day be used to probe the photophysiology of corals and the bio-optics of coral reef ecosystems.

Researchers are beginning to realize that the fluorescence signature of an alga contains information about the plant's photosynthetic apparatus, including information on its potential for primary productivity (Kiefer, 1973; Vincent, 1979; Harris, 1980; Abbott, et al., 1982). The data on corals are particularly exciting, since they suggest that the spectral signals may contain information on the physiological state of corals and their zooanthellae in addition to possible estimates of primary production. This suggests that there is much to learn about the optics of corals and their associated zooxanthellae using the passive techniques of bio-optics.

REMOTE SENSING

Coral reefs cover areas of the ocean that are remote and difficult to work in for extended periods of time. They are also vast in their coverage of the world's tropical oceans and may play a significant role in the carbonate balance of the seas. If the optical signal emanating from the reef can be understood sufficiently to provide interpretation from an orbiting spacecraft, estimates of coral reef primary productivity and possibly calcification could be made on a global scale. The importance of this cannot be underestimated when one considers man's impact on the coral reef ecosystems that are presently in close proximity to centers of human habitation.

Our research expedition to Florida in 1982 gathered data to test the hypothesis that coral reefs may be resolvable in spacecraft imagery (Landsat) (P. Dustan, C. R. Booth, and A. R. Hibbs, unpub. data). We obtained measurements of upwelling spectral irradiance from a variety of habitats in the shallow coral reef ecosystem of John Pennekamp Coral Reef State Park, including grass flats, coral colonies, and sand. We then simulated the spectral sensitivity of the Multispectral Scanner (MSS) onboard Landsat 3 so that the optical signal we recorded could be compared to the signal recorded by a Landsat MSS sensor. The equation for the simulation then "converts" the spectroradiometer signal into

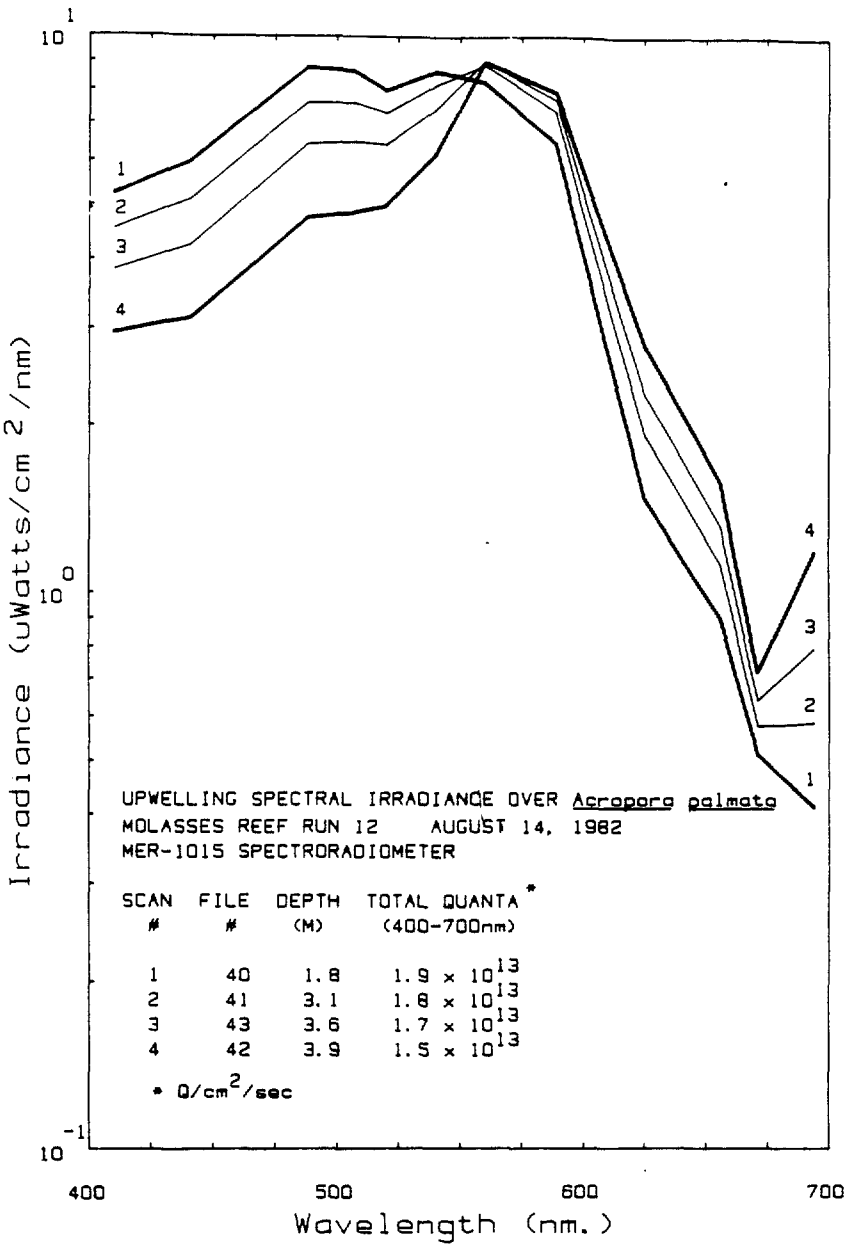

Figure 3.--Upwelling spectral irradiance scans taken over a grove of elkhorn coral, Acropora palmata, at 4.4 m depth on Molasses Reef, Key Largo. Note that 589 nm is a relatively invariant wavelength. The increase in far red at 694 nm is interpreted as in situ fluorescence by the symbiotic zooxanthellae of the coral.

the bandwidths of the Landsat MSS sensor:

Band 1 (green) = (.091x488nm + .76x507nm + .913x520nm + .98x540nm
+ .97x570nm + .75x589nm + .05x625nm) / 4.514

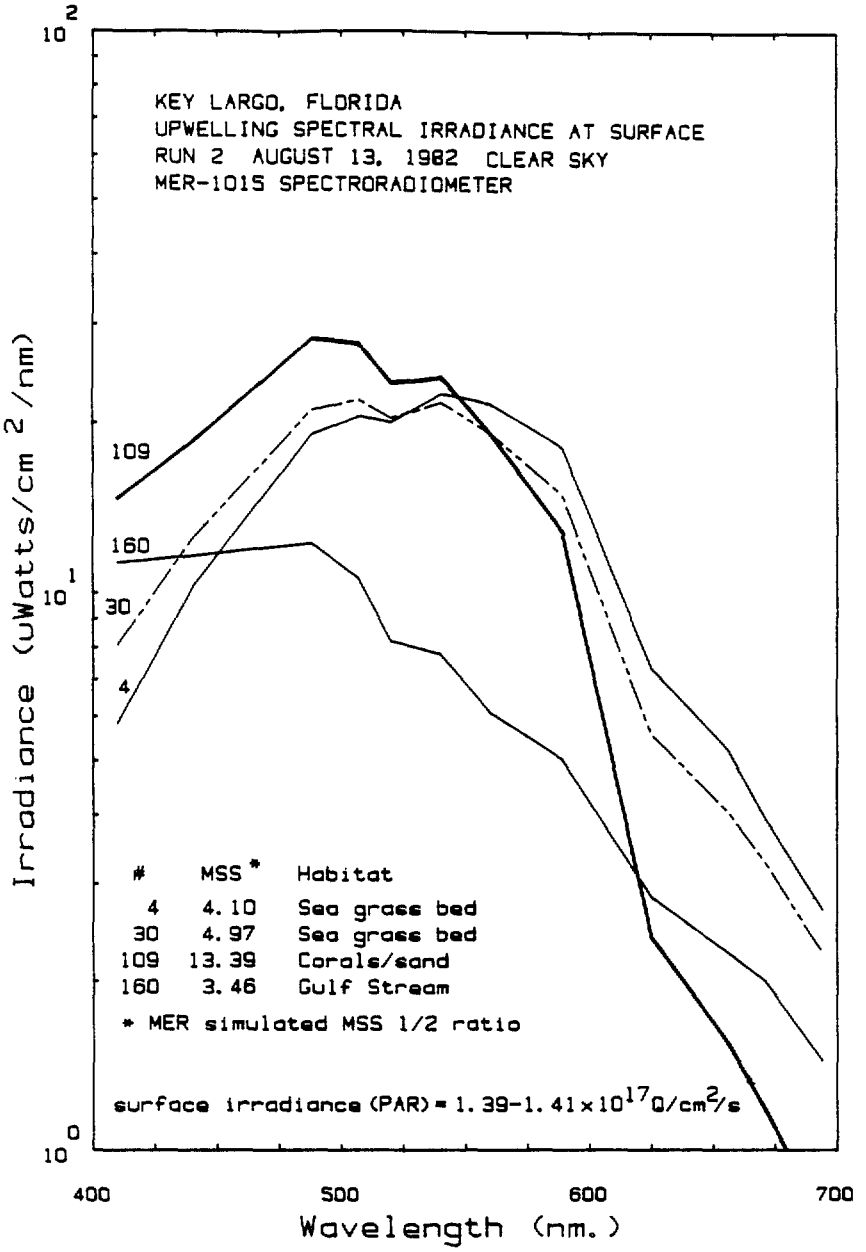

Figure 4.--Upwelling spectral irradiances taken just beneath the sea surface over a variety of coral reef environments and the western edge of the Gulf Stream. The Mer simulated MSS ratio is the ratio of Band 1/Band 2 of Landsat, calculated from measurements taken with the Mer-1015 Biospherical Instruments spectroradiometer and wavelength weighting functions as described in the text.

Band 2 (red) = (.036x589nm + .927x625nm + .960x656nm + .90x671nm
+ .810x694nm) / 3.633

We then calculated the ratio of the bands (Band 1/Band 2) to allow for differences in absolute intensity between the ground and spacecraft signals.

Figure 4 shows the spectral signals that upwell from different types of reef habitats in relation to the blue waters of the nearshore Gulf Stream. Different habitats are clearly distinguishable. The calculated MSS ratios for each habitat are also different, suggesting that reefs and their associated habitats may be distinguishable and quantitatively studied using multispectral spacecraft imagery.

CONCLUSIONS

While our work is by no means complete, we are beginning to show that an understanding of the bio-optics of the system can contribute to our understanding of the dynamics of coral reef ecosystems. The techniques that I have described suggest that optical measurements can be used to estimate the input of light energy into benthic ecosystems at various depths and habitats. Such data are necessary to understand and compare the energetics of coral reef communities and the degree to which the process of primary production varies and influences the organization of the ecosystem. The studies described in this communication are parallel to laboratory and field investigations on marine phytoplankton. The techniques are nondestructive, which means that the same environment can be repeatedly sampled. The measurements can be made over a variety of temporal and spatial scales, providing the potential to investigate large areas of coral reef ecosystems. The results are encouraging and suggest that with more research into the optics of coral reefs we may be able to use the techniques of remote sensing to routinely delineate, monitor, and, perhaps, manage these coral reef ecosystems.

ACKNOWLEDGMENTS

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PRELIMINARY STUDIES OF DENITRIFICATION ON A CORAL REEF

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ABSTRACT

This preliminary study presents evidence that coral reefs may be the sites of potentially high rates of denitrification. Qualitative evidence for the existence of denitrification in dead coral heads and in sediments from a sea grass community were obtained using the acetylene blockage technique and by measuring the rate of nitrate reduction occurring in sediment slurries incubated under anaerobic conditions. The degree to which this denitrification offsets nitrogen fixation is unknown and awaits quantification with better techniques, but from rough approximation it appears to be considerable.

INTRODUCTION

Many studies on coral reefs have shown that while standing stocks for N species are low, rates of transformations of N species are rapid (Szmant Froelich, 1983). Coral reefs typically exhibit high rates of nitrogen fixation (Wiebe, et al., 1975; Mague and Holm-Hansen, 1975; Bunt, et al., 1970; Capone and Taylor, 1977), the process by which atmospheric N_2 gas is chemically transformed into "combined" nitrogen forms (e.g., ammonia) that can be utilized as nutrients by autotrophs. Indeed, some of the highest rates of N_2 fixation for any ecosystem have been reported for coral reef areas. However, denitrification, the process by which combined nitrogen is chemically transformed back to atmospheric N_2 gas, has received much less attention in reef environments. Denitrification represents a potential removal mechanism for combined N both on the reef and in lagoons behind reefs. Recent reports of substantial rates of nitrification (ammonia oxidation to NO_2^- and NO_3^-) on coral reefs (Webb and Wiebe, 1975; LIMER Expedition, 1977) indicate that a potential exists for denitrification to occur.

This paper presents preliminary measurements of denitrification on a coral reef in Abrahams Bay, Mayaguana, Bahamas, and from sediments behind the reef in a lagoon with Thalassia beds. We used techniques suitable for qualitative determination of denitrification under field conditions. This work was carried out on the R/V MARSYS RESOLUTE with the cooperation and support of Dr. Walter Adey of the Marine Systems Laboratory of the Smithsonian Institution. Additional support also was provided by the Ruth Patrick Foundation at the Academy of Natural Sciences of Philadelphia.

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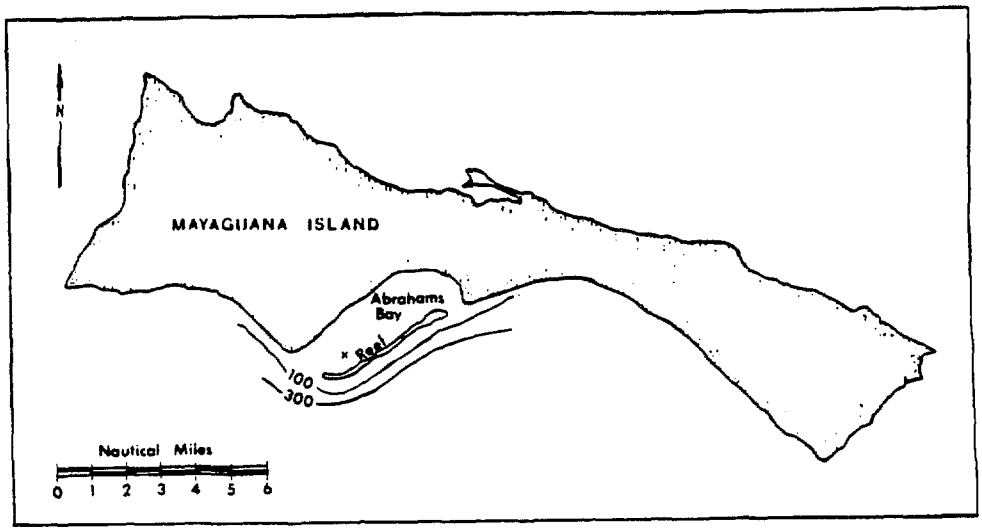

Figure 1.--Mayaguana (Abrahams Bay) Coral Reef and Lagoon. Depths in fathoms; x indicates the study area.

MATERIALS AND METHODS

This study was conducted during May 1983 in Abrahams Bay, Mayaguana, located in the southern Bahamas (fig. 1).

Dead coral heads, each with a displacement volume of about 250-300 cm^3, were collected by SCUBA divers from several areas behind the reef crest. The heads which were covered with algae and organic matter were brought back to the ship's laboratory and placed in gas tight glass incubation chambers (Seitzinger, et al., 1980) which were then filled to within 1 cm of the top with reef water (500 ml). Denitrification rates were measured using acetylene to inhibit N_2O reduction to N_2 (Balderston, et al., 1976). The gas phase (60 ml) was flushed with acetylene, and the water in the chambers was stirred with floating magnetic stir bars to equilibrate the gas and water phases. Samples (30 ml) of seawater were then withdrawn at time intervals into stoppered 50 ml serum bottles and 1 ml of saturated KOH solution added to each. After 3 hr a concentrated NO_3^- solution was added to two of the chambers to make the seawater concentration 40 µM NO_3^-. Time-series samples for N_2O continued to be taken at 7, 9, and 17 hr. The N_2O concentration in the gas phase of the serum bottles was measured by ECD gas chromatography within 1 week (Seitzinger, et al., 1980). The total amount of N_2O in the samples was calculated using Weiss and Price's (1980) N_2O solubility equation for the appropriate temperature and salinity. The production of N_2O in the presence of acetylene by the coral heads then was calculated based on the change in concentration between sequential samples and equated to the denitrification rate.

The potential for denitrification in the sediments from the reef lagoon was examined using measurements of pore water NO_2^- and NO_3^- concentrations, NO_3^- reduction rate measurements, and measurements of N_2O production in the presence and absence of acetylene. Sediment cores (47 cm^2 x 25 cm deep) were collected

Table 1.--Rate of denitrification by dead coral heads as measured by N_2O production (nmol N_2O h^{-1} coral $head^{-1}$) in the presence of acetylene, but without added NO_3^-, except as indicated. Acetylene was added at time = 0 hr. * = after 3 hr a concentrated NO_3^- solution was added to make seawater 40 µM NO_3^-.

Dead Coral Head	Incubation Period	Rate of N_2O Production nmol N_2O h^{-1}
1	2.5 - 5.5 hr	1.3
2	2 - 5 hr	2.1
3	0 - 3 hr	1.6
	*3 - 7 hr	57
	7 - 9 hr	38
	9 - 17 hr	16
4	0 - 3 hr	0.8
	*3 - 7 hr	51
	7 - 9 hr	16
	9 - 17 hr	6

by SCUBA divers from the Thalassia beds in the reef lagoon. One core was sectioned at 2.5 cm intervals and the pore water NO_2^- and NO_3^- concentrations determined using a Technicon AutoAnalyzer.

NO_3^- reduction rates were measured in a second core sectioned at intervals of 0-5 cm, 10-15 cm, and 20-25 cm. Sediment slurries from these depths were placed in serum bottles with 20 µM NO_3^- seawater solution and the change in NO_2^- + NO_3^- concentration with time measured. The incubations were done in the dark at 29°C.

Denitrification rates in the lagoon sediments were measured, again using acetylene inhibition of N_2O reduction. Sediments from three cores were sectioned at intervals of 0-5 cm, 10-15 cm, and 20-25 cm. Sediment slurries (14 cm^3) from those depths were incubated aerobically in serum bottles with 15 ml of 20 µM NO_3^- seawater solution and 0.3 atmospheres of acetylene. N_2O production rates in the presence of acetylene then were measured at each depth after intervals up to 15.5 hr by injecting 2 ml of a saturated KOH solution into the serum bottles after approximately 0, 6, and 15.5 hr. The production of N_2O in

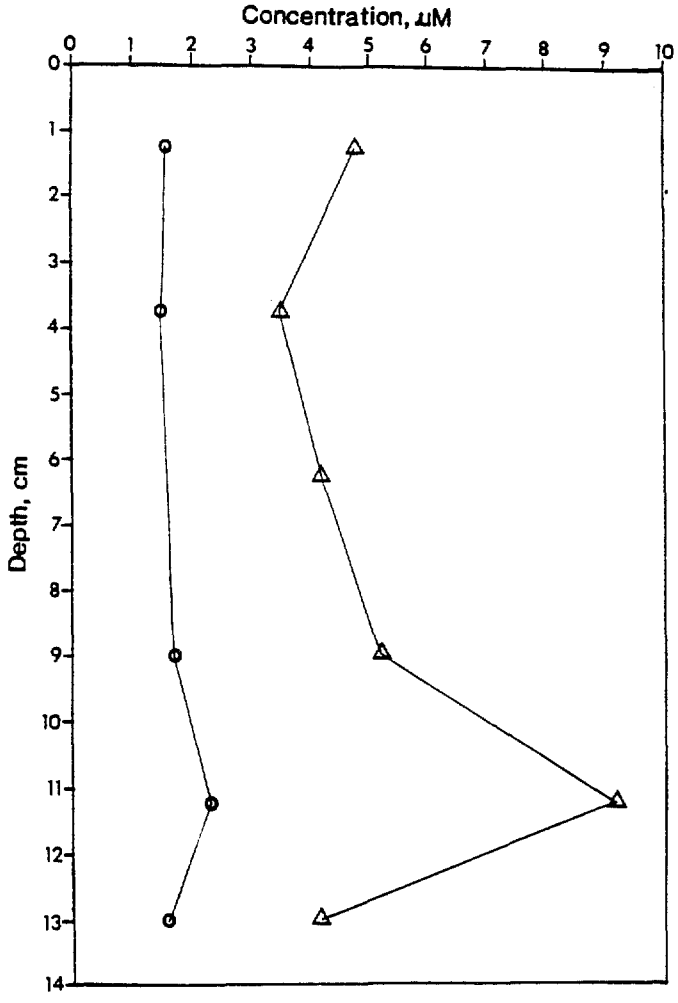

Figure 2.--Depth profile of pore water nitrite (circles) and NO_2^- + NO_3^- (triangles) in sediments of lagoon.

the absence of acetylene was measured in a parallel set of samples incubated with 20 µM NO_3^- but without acetylene. The reduction of NO_3^- also was measured in another parallel set of samples with acetylene and 20 µM NO_3^-. NO_2^- + NO_3^- concentrations were measured immediately after approximately 0, 6, and 15.5 hr (KOH was not added).

RESULTS

When coral heads were incubated in seawater that was not enriched with nitrate, the rate of denitrification (N_2O production in the presence of acetylene) was approximately 1-2 nmol N_2O per coral head per hour (table 1). When the NO_3^- concentration in the surrounding seawater was increased to 40 µM, the rate of N_2O production increased to approximately 50 nmol per hour per coral head and then decreased during the subsequent 14 hr.

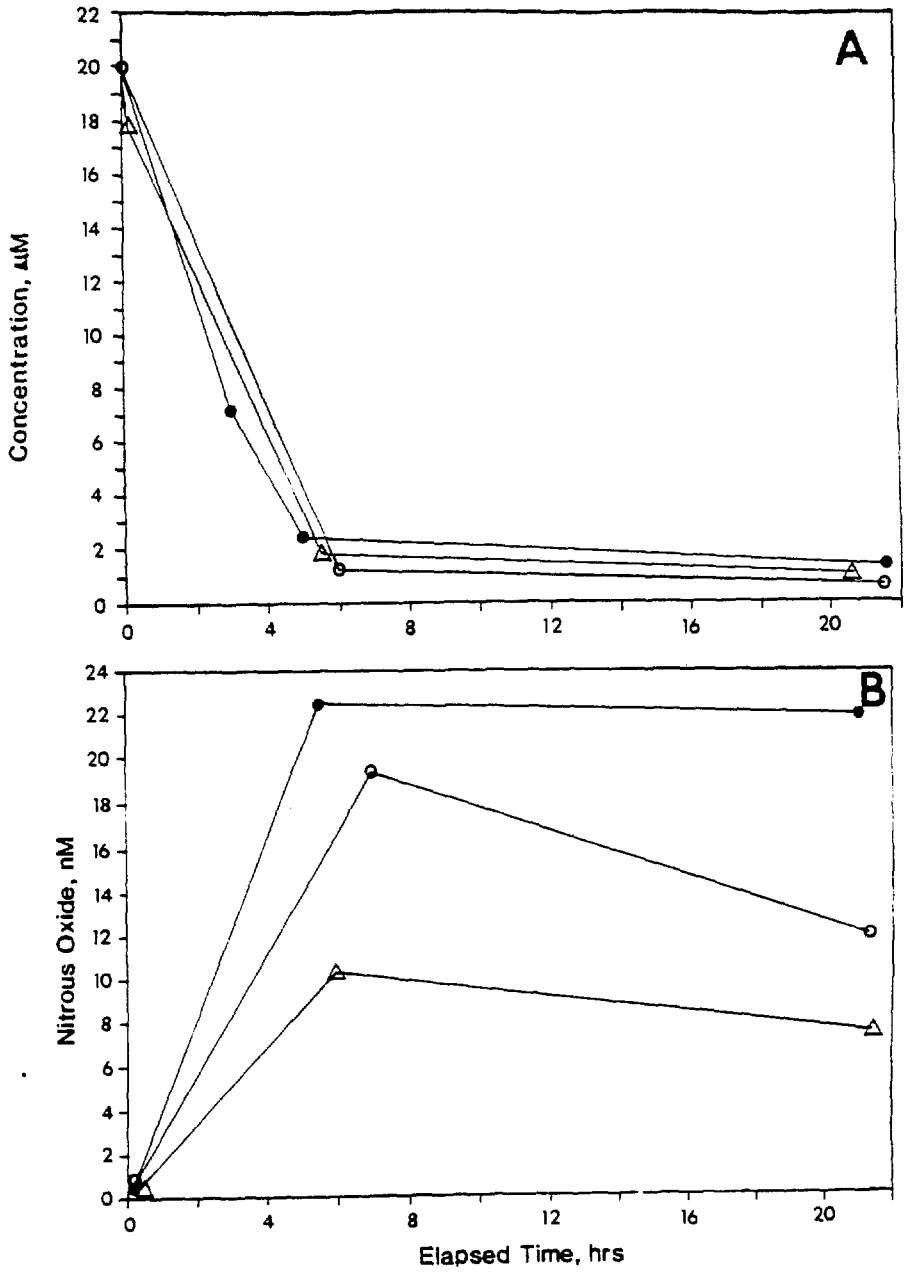

Figure 3.--(A) NO_3^- depletion in lagoon sediments spiked to 20 µM NO_3^-; (B) N_2O production by lagoon sediments incubated with a 20 µM NO_3^- solution and in the presence of acetylene. Open circles = 0-5 cm depth; triangles = 10-15 cm depth; and closed circles = 20-25 cm depth.

The concentrations of NO_2^- + NO_3^- in the sediments of the Thalassia bed were higher than the overlying seawater (0.5 µM NO_2^- + NO_3^-), ranging from 3.5 to 9 µM with a peak concentration at about 11 cm depth (fig. 2).

When sediments were incubated in seawater enriched to a concentration of 20 µM NO_3^-, NO_3^- concentrations decreased rapidly in sediments from all depths to below concentrations found in the pore waters (fig. 3A). Since this experiment

Table 2.--Rate of denitrification as measured by N_2O production in lagoon sediments incubated with 0.3 atm acetylene and 20 μM NO_3^-. Rates are expressed per cm^3 of sediment per hour.

Depth Interval (cm)	Time Interval (hr)	N_2O Production (nmol N_2O cm^{-3} h^{-1})
0 - 5	0 - 7	$1.9 \times 10^{-}$
	7 - 15.5	-0.3×10^{-1}
10 - 15	0 - 6	1.2×10^{-1}
	6 - 15.5	-0.1×10^{-1}
20 - 25	0 - 5.5	2.8×10^{-1}
	5.5 - 15.5	-0.02×10^{-1}

was performed in the presence of acetylene, no new nitrification was occurring, inasmuch as acetylene also blocks nitrification (Bremner and Blackmer, 1979). During that same period of rapid decrease in NO_3^- concentration (0-6 hr), there was a rapid increase in N_2O concentration in samples incubated with acetylene (fig. 3B). The highest rates of N_2O production during the first 6 hr was seen in the 20-25 cm depth interval (table 2). The concentration of N_2O tended to decrease during the next 16 hr interval. The rate of NO_3^- reduction increased with increasing concentration of substrate (fig. 4).

Concentrations of N_2O in sediments incubated with NO_3^- but without acetylene were negligible and tended to decrease slightly with time (not shown). Changes were small compared to changes measured in the presence of acetylene.

DISCUSSION

The preliminary measurements of denitrification reported here indicate that coral reefs and associated lagoon sediments are potentially active sites for denitrification. Nitrate concentrations inside dead coral heads have been reported by Webb and Wiebe (1975) and Risk and Muller (1983) to be higher than the surrounding seawater; this undoubtedly indicates that nitrification is occurring in dead coral heads. Low oxygen concentrations occur as organic matter decays in coral heads, thus providing the proper conditions for denitrification (Risk and Muller, 1983). Although nitrification and denitrification require different concentrations of oxygen to proceed, both can occur simultaneously in coral heads due to microdistributional variations in oxygen concentration that certainly must occur (Risk and Muller, 1983).

Sediments in the lagoon behind the reef also appear to be active areas for denitrification as well. This was demonstrated by both the N_2O production

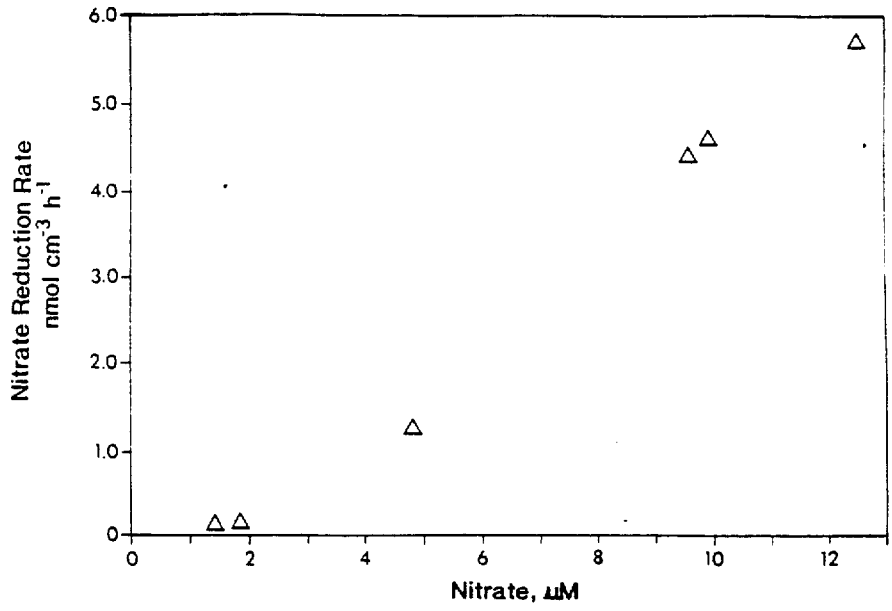

Figure 4.--Rate of NO_3^- reduction (nmol NO_3^- cm^{-3} h^{-1}) vs. concentration of NO_3^- (µM) in sediment experiment.

rates measured in the presence of acetylene and the NO_3^- reduction rates. The source of NO_3^- for denitrification must come from nitrification in the sediments as opposed to diffusion of NO_3^- from the overlying water, since the NO_3^- concentrations in the pore waters were much greater than in the overlying water. The NO_3^- concentrations we measured in the pore waters must be maintained by relatively high rates of nitrification. Two lines of evidence support this: (1) NO_3^- concentrations were shown to decrease rapidly below concentrations measured in the pore waters when nitrification was inhibited by acetylene, and (2) denitrification rates were indicated to be high in the sediments and thus, to maintain NO_3^- concentrations in the pore waters with active denitrification occurring, nitrification must also be rapid.

The rates of decrease of NO_3^- we observed in lagoon sediments were much greater than the rates of N_2O production. One would expect them to be equal if all of the NO_3^- decrease was due to denitrification (see Taylor, 1983, for a review of the problems associated with these measurements). We can presently only speculate as to why the discrepancies occurred (figs. 3A and 3B). For example, acetylene blockage may not be complete or may not yield stoichiometric quantities of N_2O. Alternatively, NO_3^- could be reduced assimilatively, e.g., by foraminiferans (Webb and Wiebe, 1978).

We emphasize that the results presented here are preliminary for several reasons. First, we did only a limited number of experimental measurements and feel that a more detailed study is needed. Second, the techniques we used to measure denitrification are adequate for a preliminary survey in the field like this one but should be supplemented by the preferred, direct measurement of denitrification (Seitzinger, et al., 1980). We consider the use of sediment

slurries that are enriched with nitrate and incubated under anaerobic conditions (Billen, 1978; Koike and Hattori, 1978, 1979; Oren and Blackburn, 1979; Iizumi, et al., 1980) to be good qualitative but not necessarily good quantitative tools--such experimental conditions destroy sediment microenvironmental structure (e.g., nitrate, oxygen, and organic matter concentrations) that cannot be simulated exactly in the laboratory. This is particularly problematic in the Thalassia bed sediments with their complex root structure. The use of the acetylene blockage technique also incurs problems. For example, acetylene blockage of N_2O reduction may be inhibited by the presence of sulfide (Tam and Knowles, 1979), and acetylene itself may be oxidized anaerobically (Culbertson, et al., 1981) or may inhibit nitrification (Bremner and Blackmer, 1979; Blackmer, et al., 1980), methanogenesis (Oremland and Taylor, 1975), methane oxidation (deBont and Mulder, 1976), and the growth of sulfate-respiring bacteria (Payne and Grant, 1982). Considering these limitations, it is likely that the denitrification rates reported here are underestimates of the field rates.

The amount of fixed N being lost through denitrification in the lagoon behind the coral reef conceivably could be as high as that fixed by N_2 fixation on the reef itself. No measurements of N_2 fixation are available for Mayaguana. However, measurements of N_2 fixation have been made on a number of other coral reefs. Maximum rates found at Enewetak, for example, were 600 μmol N_2 m^{-2} h^{-1} during daylight (Wiebe, et al., 1975; Webb, et al., 1975). For an average rate over 24 hr, this rate should be decreased by approximately 50% to 300 μmol m^{-2} h^{-1}, since such high rates only occur during daylight. The above methodological limitations aside, we can make a rough approximation of denitrification in the lagoon. The results from the acetylene inhibition experiments indicated that denitrification rates were approximately 0.2 nmol cm^{-3} h^{-1} throughout the top 25 cm of lagoon sediment. The integrated value for the top 25 cm is then 50 μmol m^{-2} h^{-1}. The area of the lagoon is estimated to be 10 times the area of the reef. Therefore, in the reef-lagoon ecosystem, denitrification in the lagoon would more than balance the N_2 fixation on the reef. While these measurements and calculations are only preliminary, they do point to the probable importance of denitrification in reef ecosystems and to the need for further measurements.

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